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A remarkable species of drosophilid fly (Diptera) with “mandibles”

DAVID A. GRIMALDI¹

ABSTRACT

A distinctive species in the family Drosophilidae, *Drosophila ancora* Okada, 1968, is re-described from specimens from Vietnam, and transferred to the genus *Dichaetophora* Duda sensu lato. It is exceptional among Diptera for its labellar sclerites that in males have grown into a pair of heavily sclerotized, pointed lobes at the tip of the labellum, producing what appear to be chewing mandibles. This is analogous to the condition in the dolichopodid *Melanderia* Aldrich, but there it is not sexually dimorphic. The structures are doubtfully used in male-male aggression or in postcopulatory mate guarding. Based on their shapes and fit, it is proposed that the “mandibles” are used by males to grasp the tip of the female oviscapt during courtship or for the male to grasp the female wing edge while mounted.

INTRODUCTION

While examining specimens of Drosophilidae from Vietnam, two males and a female of a dark-brown species were found with an extraordinary feature: the labellum of males has a small pair of heavily sclerotized, pointed “mandibles,” like those found on chewing insects, such as beetles (fig. 1). Some flies do possess mandibles, but not for chewing. In various nematoceran and tabanomorph flies that feed on blood, the female mandibles are sharp, knife- or needle-like stylets that slice into skin (McAlpine, 1981). True mandibles seem to be lost in higher flies, the Muscomorpha. To my knowledge the only other fly in which labellar sclerites are developed into what appear as chewing “mandibles” is *Melanderia* Aldrich (Dolichopodidae), whose species live in the intertidal zone in the Pacific Northwest of North America. The similarities and

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differences between the drosophilid and dolichopodid “mandibles” are discussed at the end of this paper, along with possible functions.

The taxonomic position of the drosophilid was at first ambiguous. On the one hand, it possesses the distinctive oviscapt typical of *Dichaetophora* Duda, a genus of African and Asian drosophilids that is growing through comprehensive revisionary work (Hu and Toda, 2002, 2005; Katoh et al., 2018, 2021; Yang et al., 2017). Nevertheless, the new species lacks many features that have classically defined *Dichaetophora* in addition to possessing several unusual ones besides the “mandibles.” These are discussed below as well.

The specimens were point mounted; dissections of terminalia and mouthparts were made with gentle maceration in warm 10% KOH, followed by rinsing and slide-mounting in glycerine-jelly to observe structures at 200X. Photomicrographs used a Nikon SMZ1500 stereoscope with Nikon Elements© software; drawings were made using a drawing tube on a Wild compound scope before inking. The labella of several representative drosophilids were compared to identify homologs of the *Dichaetophora* “mandibles.” Abbreviations for ratios in the description follow the standard measurements and ratios given in Baechli et al. (2004); values given are means.

TAXONOMY

Dichaetophora ancora (Okada), **new combination**

Drosophila (*Psilodorha*) *ancora* Okada, 1968: 334.

Drosophila (*Drosophila*) *ancora* Okada: Yassin 2013 (synonymy of s.g. *Psilodorha* with s.g. *Drosophila*)

DIAGNOSIS: Distinguished from other species in the genus by frons and face broad, frons very short; facial carina well developed but short; prescutellar setae present; genal setae stout, sizes nearly equal to vibrissa; anterior reclinate orbital seta lateral to proclinate (figs. 1; 3A, B); wing with heavy costal spinules extended to tip of vein R_{4+5} ; tip of male wing more pointed than in female (cf., fig. 2D, E); aedeagus with two hornlike, preapical lateral spines pointed posteriad and one dorsomedial spine retrorse to axis of aedeagus (fig. 3F, H); male with labellar sclerites heavily sclerotized, dorsal portion extended into apically pointed lobes that form pair of “mandibles” (figs. 1; 3A; 4A, B).

REDESCRIPTION: Coloration (figs. 1, 2): Head unicolorous dull, light brown; carina, flagellomere 1, oral margins slightly lighter; gena dark yellow; palps brown; eyes pale red; male labellar sclerites dark, shiny brown; all setae black. Notum dull brown, with pair of faint, incomplete, paramedian lighter stripes; notopleural area, anepisternum and katapisternum slightly darker than surrounding areas; halter knob cream colored; femora light brown, remaining leg segments yellowish; wing clear, no infuscation even around crossveins. Abdomen lighter than rest of body, dark yellowish, grading posteriorly to light brown.

HEAD (fig. 3A, B): Carina well developed, short, height carina/face 0.55; edge flattened but narrow; oral margin of face slightly swollen; frontal W-index 2.42. Frons short, FL/LFW 0.53, UFW/LFW 1.29; frontal triangle reaching ptilinal suture; frontal vittae narrow, dull, finely stri-



FIG. 1. *Dichaetophora ancora* (Okada) A–D: Male, from Vietnam (Quang Nam) A. Lateral habitus. B. Head, lateral. C. Head, frontal. D. Male mouthparts, frontal view. E. Female mouthparts, frontal view.

ate; fronto-orbital plates and frontal triangle slightly shiny. All setae robust, thick, black; anterior reclinate fronto-orbital seta relatively large, OR_2/OR_1 0.77, lateral to proclinate, posterior reclinate is longest fronto-orbital, OR_1/OR_3 0.62. Ocellar setae large, OC/POC 1.38, sockets within ocellar triangle; postocellars cruciate for $\sim 0.25\times$ their length. Verticals and postgenal setae robust, VT index 1.12. Antenna: pedicel and flagellomere 1 aligned $\sim 30^\circ$ outward from vertical; pedicel with five stout setae, several smaller ones, longest seta on ventromedial corner (length equal to flagellomere 1); microtrichia on flagellomere 1 short; arista with 6 or 7 dorsal,



FIG. 2. *Di. ancora*. A–D: Male (same specimen as in fig. 1). A. Thorax, dorsal. B. Abdomen, dorsal. C. Right hind tarsus, mesal view. D. Wing. E. Female wing tip. F. Oviscapt, ventral.

2 or 3 ventral branches (exclusive of terminal fork). Vibrissa stout and long; genal setae on ventral margin of head are stout, sizes approximately equal to vibrissa, vibrissa index GS1/VL 1.10. Cheek very shallow, cheek/eye depth 0.07, gena deep, setose. Eye with dense ommatrichia, ED/EW 1.32; posteroventral margin flattened.

MOUThPARTS (fig. 4A, B, D): Clypeus shallow, narrow. Cibarium very constricted closest to proximal end (shaped like a bowling pin); hypopharynx flared at proximal end (array of very fine muscle scars developed, broad and flat for most of distal end; dorsal keel present but barely sclerotized; long row of 23 or 24 short sensilla trichodea lateral to hypopharynx in middle, lateral to these a finely granular area; cibarium distally with row of 7 longer sensilla trichodea. Palp dorsoventrally asymmetrical but broad, with 2 large apical setae and 2 smaller ventral setae. Lacinia with distal arm very slender; proximal arms opposing each other 180°, one about twice the width of other. Prementum with ventral swelling. Labellum with each lobe having five pseudotracheae of equal diameters, proximally these converge in a pair of dark sclerites (“pseudotracheal sclerites”) at base of the labellum. Slender lateral labellar sclerite articulating with, apparently not fused to, the apical labellar sclerite; apical sclerites with broad ventral portion, in males there is a pair of dorsal, heavily sclerotized

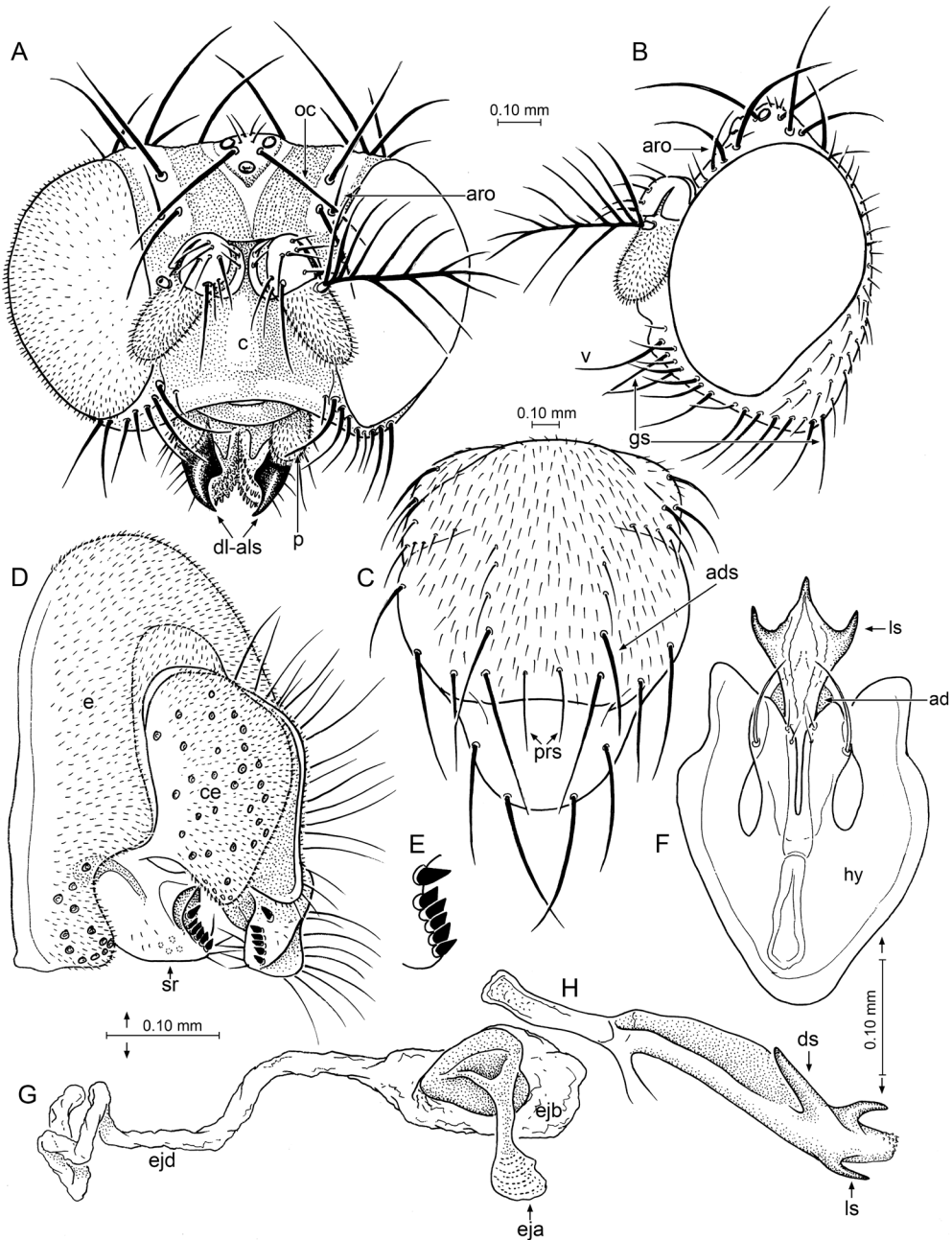


FIG. 3. Somatic and male genitalic structures of *Di. ancora*. **A.** Male head, frontal view. **B.** Male head, lateral view. **C.** Thorax, dorsal. **D.** Epandrium with cerci and surstyli. **E.** Detail of surstylus. **F.** Male genitalia, ventral view. **G.** Ejaculatory structures. **H.** Aedeagus, oblique lateral view. A and B; D and G; F and H to same scales. Abbreviations: **ad**, aedeagus; **ads**, anterior dorsocentral seta; **aro**, anterior reclinate orbital seta; **c**, carina; **ce**, cercus; **dl-als**, dorsal lobe of apical labellar sclerite ("mandibles"); **ds**, dorsal spine of aedeagus; **e**, epandrium; **eja**, ejaculatory apodeme; **ejb**, ejaculatory bulb; **ejd**, ejaculatory duct; **gs**, genal setae; **hy**, hypandrium; **ls**, lateral spine of aedeagus; **oc**, ocellar seta; **p**, palp; **prs**, prescutellar setae; **sr**, surstylus; **v**, vibrissa.

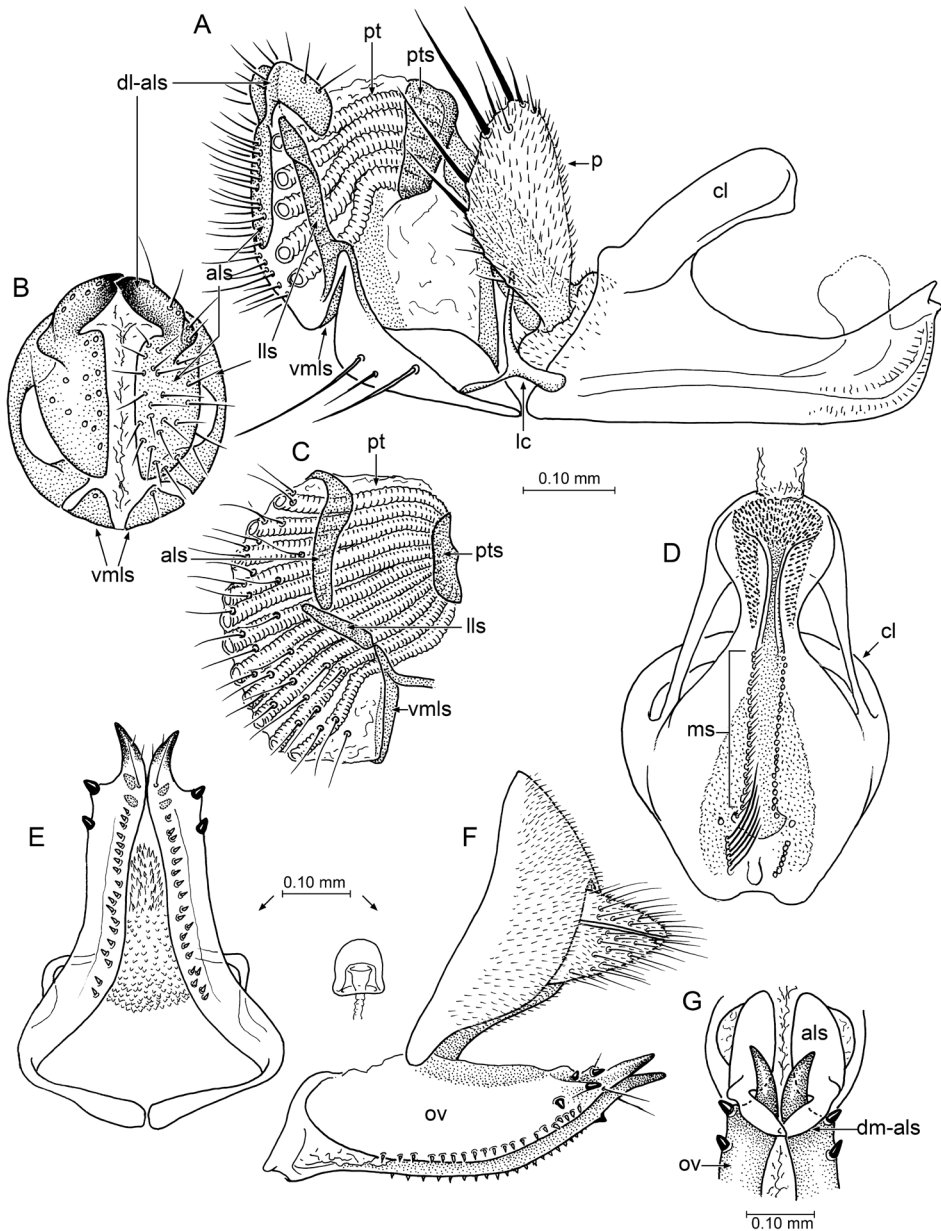


FIG. 4. Mouthparts and female terminalia of *Dichaetophora ancora* (A, B, D–G) and labellum of *Drosophila immigrans* (C). A. Male proboscis, lateral view. B. Male labellar sclerites, front view. C. Labellum of *Drosophila immigrans*, lateral view. D. Cibarium of *Di. ancora*, ventral view. E. Oviscapt, ventral. F. Oviscapt, tergite 7 and paraprocts, spermatheca, lateral view. G. Hypothesized function of male “mandibles,” in ventral view. Stippled portions are tip of female oviscapt. A–D: to same scale. Abbreviations: als, apical labellar sclerite; cl, clypeus; dl-als, dorsal lobe of apical labellar sclerite (“mandibles”); lc, lacinia; lls, lateral labellar sclerite; ms, medial sensilla of cibarium; ov, oviscapt; p, palp; pt, pseudotracheae; pts, pseudotracheal sclerite; vmls, V-shaped medial labellar sclerite.

lobes with pointed apices, which in frontal view resemble biting mandibles. Female lacks the “mandibles” (pointed lobes of apical labellar sclerite).

THORAX (figs. 1A, 2A, 3C): Mean length 1.28 mm; relatively broad and short in dorsal view, width $0.77\times$ its length (including scutellum). Postpronotal lobe with two setae of nearly equal size, h-index 1.19. Acrostichals not arranged in even rows, increasing in size from anterior to posterior; transverse row of three or four acrostichals anterior to transverse suture are slightly enlarged. Two large pairs of dorsoventrals present, DC-index 0.66, posterior pair slightly convergent, anterior pair slightly divergent; anterior to each are two smaller dorsoventrals; pair of prescutellar setae present, $0.45\times$ the length of posterior dorsocentral. Scutellum without setulae; anterior and posterior scutellar setae approximately equal in length, scut-index 0.90, posterior pair crossing for about $0.2\times$ their length. Scutum extended considerably ventrolaterally; notopleural suture near middle of depth of thorax. Anepisternum relatively large; katepisternum relatively small, with large anterior and posterior setae (nearly equal in size, S-index 0.89), small middle seta less than half the length of others, ~ 10 setulae on ventral portion of katepisternum. Hind leg: mesal surface of basitarsomere with row of nine combs of fine setulae, each comb with 5–7 setulae, the combs oblique to axis of tarsomere (2 or 3 smaller combs on adjacent tarsomeres); row or seam of ~ 30 cuneiform setulae along entire ventral margin of basitarsomere (fig. 2C).

WING (fig. 2D, E): Mean length 2.73 mm; clear, no markings; shape slightly dimorphic: tip of male wing pointed, that of female more rounded. C-index 1.77; costal spinules black, crowded, extend to tip of wing (R_{4+5}) (hb-index 1.0), vein C ends at apex of vein M_{1+2} . Sc break deeply incised. 4-V index 1.86; 5-X index 1.13.

Abdomen: Tergites mostly dark yellow, grading gradually to light brown posteriad.

MALE TERMINALIA (fig. 3D–H): Epandrium tall, narrow, fully covered with microtrichia; small cluster of ~ 10 setulae on short ventral lobe, setulae lacking on most of epandrium. Remnants of tergite 7 very small. Cercus relatively simple (no ventral lobes or spines), fully covered with microtrichia, without broad lateral connection to epandrium. Surstylus relatively broad, bare except a few sparse microtrichia, mesal row of six small, stout, pointed prensisetae; with narrow dorsal connections to cercus and bridge to other surstylus. Subepandrial sclerite broad, with pair of rounded lobes. Genitalia relatively simple; hypandrium without microtrichia, having pair of deeply incised postgonite lobes, each with large lateral setula and two small trichodea on mesal margin. Aedeagus nearly straight, apex with pair of lateral hornlike, sclerotized lobes/spines pointed apicad, plus median point having very fine papillae on dorsal surface; dorsally with a preapical, median, sclerotized spine pointing anteriad. Aedeagal apodeme short, straight, length $0.4\times$ that of aedeagus. Ejaculatory apodeme relatively large, lightly sclerotized; surface against ejaculatory bulb is concave. Ejaculatory bulb without diverticula.

FEMALE TERMINALIA (fig. 4E, F): Tergite 7 mostly covered in microtrichia, no setulae; posteroventral portion declivous. Epi- and hypoproct apically narrow; covered with microtrichia and setulae. Oviscapt well developed: in ventral view anterior end broad, posterior end narrow; posteriorly with apical pair of fanglike lobes that curve outward, base of each with fine setula; laterally with two small pegs, each on short tubercle; two additional small, preapical pegs dorsally. Ventrally with irregular row of 19 or 20 very small, spiculelike pegs near mesal margin of each valve.

Scales of oviprovectator membrane very fine. Spermathecal capsule small, dome shaped, with introvert extended about halfway into capsule.

SPECIMENS: VIETNAM: Quang Nam, 25 km SW Tam Ky, 15°11'39" N, 108°2'37" E, 940 m, 12–17/IV/1999, D. Grimaldi, coll. 1 male, in American Museum of Natural History (AMNH). Not dissected. Ninh Binh Prov. Cuc Phuong Nat. Park, 390 m, 20°21'103" N, 105°35'36" E [12-9], SD Gaimari, M Hauser, Pham HT, 24–28.III.2012, Malaise trap (terminalia and mouthparts dissected), 1 male, in Institute of Ecology and Biological Resources (IEBR), Hanaoi; Cao Bang Prov. Phia Oac Nat. Park, nr. Phia Den. 1000 m, 22°32'20" N, 105°51'57" E [12-01], SD Gaimari, M Hauser, Pham HT, 19.III.2012 (terminalia dissected), 1 female, in AMNH.

COMMENTS: *Dichaetophora ancora* is known from the Ryukyus, Japan (type locality: Iri-omote Island; also reported from Kume Island [Kondo and Kimura, 2008]); Taiwan and Hainan Island (Kai et al., 1993). Masanori Toda informs me that the specimen referred to as “sp. 8 Malaysia” in the preprint by Katoh et al. (2021) is *Di. ancora* or a very closely related species.

The two male Vietnam specimens may belong to a different species, since they show differences with the drawings of the type by Okada (1968: 335) and photomicrographs of specimens from the type locality sent to me by Toda (which are very consistent with each other). Definitive *ancora*, from Japan, have a male wing that is less pointed, and have the following differences in the male terminalia: longitudinally longer epandrium (i.e., not as broad in lateral view), cercus smaller, hypan-drium that is significantly broader; aedeagal apodeme with broad, fanlike apex (though not so broad in the illustration of the type); pair of lateral, preapical phallic horns that are smaller, protruding less; and the dorsal spine of the phallus projecting upright, perpendicular to the axis of the aedagus (rather than being reclined as in the Vietnam specimens).

Okada (1968) mentioned acrostichals in 10–12 rows, but which in the Vietnam specimens are not arranged in rows. Remarkably, the male “mandibles” were not mentioned in the original description, even though Okada was an excellent morphologist (Toda confirms their presence in the material from the type locality). Until the type male is dissected (presumably it is in the National Science Museum, Tokyo, where Okada typically deposited new types), it is best to regard the Vietnam specimens as *Dichaetophora ancora*.

The three Vietnamese specimens come from different areas, but there is no doubt in associating the female with the males, based on thorax- and abdomen-coloration patterns, distinctive proportions of the head, proportions of the various setal lengths and wing veins, carina shape, strong bristles on the oral margin, costal spinules running to the end of R_{4+5} , and various other features.

RELATIONSHIPS: Distinctive features of *Di. ancora* include the short frons, anterior reclinate lateral to the proclinate, stout setae on the pedicel, numerous large setae along the oral margin, numerous sensilla trichodea in the proximal group on the cibarium (23–24, vs. 4–~15 in *Drosophila*), and of course the male “mandibles.” Dissection of the female specimen revealed an egg with four fine, tapered filaments (their lengths slightly less than that of the egg), as occur in many drosophilines. Prescutellar setae occur in steganines and sporadically in drosophilines (many *Scaptodrosophila*, scattered *Drosophila*, etc.). Costal spinules that end at the wing tip is a very distinctive feature (usually they end approximately midway between the tips of R_{2+3} and R_{4+5}). Given such a unique array of features, it isn't surprising that Okada (1968) erected for it the *Drosophila* subgenus

Psilodorha. Also, at the time there was a much narrower concept of *Dichaetophora*. Clearly, however, *Di. ancora* does not belong in the subgenus *Drosophila*, as proposed by Yassin (2013), despite the diphyletic nature of the subgenus (Finet et al., 2021), nor can it even be accommodated in the genus *Drosophila*, based on the structure of epandrium, male genitalia, cibarium, and oviscapt.

Oviscapt structure is the most obvious feature that places *Di. ancora* in *Dichaetophora* sensu lato (this includes *Nesiodrosophila*, some *Lordiphosa* [Hu and Toda, 2002], *Mulgravea* and the subgenus *Dudaica* of *Drosophila* [Katoh et al., 2018, 2021]). Other features that *Di. ancora* shares with *Dichaetophora* are on the cibarium: anterior end of hypopharynx expanded, anterolateral corners only slightly protruded (usually with a pair of hornlike lobes, the cornua), and the large number of sensilla trichodea. In the *sinensis* group there can be >40 medial cibarial sensilla per side (Hu and Toda, 2002, 2005), but the number is generally less (in *Dudaica* there are only about 12–15).

Also shared with some *Dichaetophora* are five pseudotracheae on each labellar lobe (e.g., *acutissima* group, in other groups there are four); and a surstylus bare of microtrichia (e.g., *tenuicauda* group) (Hu and Toda, 2005). A short, broad carina occurs in the *Dichaetophora trilobita* species group (Yang et al., 2017) and some others, as well as in *Dudaica*. Most other species in the genus (e.g., *agbo* group) have a face that is almost flat with a low carina. A small number (~4–7) of stout, small prensisetae with pointed tips is a common feature in *Dichaetophora*.

There are, however, features of *Di. ancora* that differ with *Dichaetophora*: ocellar setae not outside the triangle, costal spinules extended to the wing tip, a pair of strong prescutellar setae, and large genal setae on the oral margin. Based on the short frons, carina shape, eye shape, and male genitalia (with a distinctive pair of gonite lobes as in *Dudaica*), *D. ancora* may be in or near the clade consisting of the *acutissima* group and *Dudaica* (Katoh et al., 2018, 2021). The molecular phylogeny of Katoh et al. (2021) indicated two groups (parts “1” and “2”) with undescribed species, to which *Di. ancora* also might belong. The classification and taxonomy of genera now being included in an expanding *Dichaetophora* (*Mulgravea*, *D. [Dudaica]*) will need to be addressed, including the possibility that some of the earliest branches become separate genera.

In the collections from Vietnam are two females also from Cuc Phuong, but of a closely related species. These females have a darker thorax (scutellum slightly velvety), frons slightly pruinose blue, face light, abdominal tergites with dark bands (interrupted in middle), and the deep subcostal incision is slightly darkened on both sides of the break. Otherwise, this species shares the same distinctive features with the female of *Di. ancora*; it will be very interesting to eventually find the male of this other species and to examine the males of some other *Dichaetophora*.

DISCUSSION: MALE ‘MANDIBLES’

In *Melanderia* the labellar “mandibles” are not sexually dimorphic; they are probably used in prey capture since most or all adult dolichopodids are predatory, a function that is supported by the uniquely elaborate epipharyngeal armature in the genus (Snodgrass, 1922). The dolichopodid also has much larger “mandibles” than the drosophilid, with a gape greater than half the width of the head when they are fully opened. Both the drosophilid and dolichopodid “mandibles” are derived from labellar sclerites, but *Melanderia*’s labellar sclerite

wraps laterally and frontally and is surrounded by thick, dark membrane (labelled “a” and “c” in figs. 1 and 2 in Snodgrass, 1922). To my knowledge, these are the only brachyceran Diptera that possess labellar, chewing type “mandibles.” In the modified-mouthparts species group of Hawaiian *Drosophila* (also called *Idiomyia* and most closely related to *Scaptomyza*), setae on the labellum are enlarged into spine- and scalelike structures but are not mandiblelike.

In figure 4A–C the labellar sclerites of *Di. ancora* and an exemplar species in *Drosophila*, *D. immigrans* Sturtevant are labeled as follows from ventral to dorsal: the V-shaped ventromedial labellar sclerite, the lateral labellar sclerite (slender, varying from long to short), and the dorsal labellar sclerite (which is typically slender and laterally positioned). In the drosophilines I have examined, the lateral and dorsal labellar sclerites are always slender. In *Di. ancora* the dorsal sclerite in males has two portions: a flat, broad apical portion and, attached dorsally to this, a heavily sclerotized lobe with a pointed tip (the “mandibles”). The “mandibles” are slightly flattened, which affects the shape depending on the view. In full frontal view of the labellum the “mandible” portion of the dorsal sclerite has a wider, blunt tip (fig. 4B); looking dorsally on these lobes (when viewing the fly head on), the mandibles are curved and the opposing apices very finely pointed (figs. 1C, D; 3A). The females of *Di. ancora* and the closely related species mentioned above, interestingly, also have broad dorsal labellar sclerites (fig. 1E), though lacking the mandiblelike lobes.

Opening and closing of the labellar “mandibles” is probably controlled by the same mechanisms as for the labellar lobes themselves. Labellum spreading and closing is known to be controlled by a pair of thin muscles whose origins are at the base of the theca/haustellum and the insertions at the base of the labellum (Pollack, 1977). The muscle is designated as no. “7” by McKellar (2016) and “z” in Graham-Smith (1930: fig. 11). Its insertion point is almost certainly the lateral labellar sclerite, possibly also the dorsal sclerite (fig. 4A).

How are male *Di. ancora* using these labellar “mandibles”? Available evidence suggests mating behavior. There has been intensive study of the mating behavior of a few species of *Drosophila*—from species-specific male wing-vibration “songs,” to pheromones, and genetics—but mating behavior in the family is largely based on the comparative studies of Spieth using primarily *Drosophila* (e.g., 1952, 1974) and *Idiomyia* (Spieth, 1974). Casual observations have been made in some genera other than *Drosophila*, but nothing is known about mating behavior in others, including *Dichaetophora* and *Mulgravea*. My inference therefore is based on *Drosophila*.

In many *Drosophila* and *Idiomyia* a male trailing a female extends his proboscis and palpates her terminalia with his labella. This seems to be the most likely functional context for the male “mandibles,” in which there presumably has been selection for males whose labellar sclerites protrude enough to grasp her oviscapt. Comparing a male and female specimen of *Di. ancora*, the oviscapt neck fits perfectly between the medial notches in the closed male “mandibles” (fig. 4G). If this interpretation is accurate, the male may be coercively forcing a female’s receptivity.

There are three alternative explanations for the labellar “mandibles,” the most plausible being number 2. The first is that the male bites onto the oviscapt as a postcopulatory mate-guarding device. However, I know of no behavioral context in drosophilids from which this could have evolved. In insects, males would typically stay mounted or coupled while mate-guarding (Alcock,

1994). Second, the male may be attaching itself to the female while mounted, by biting, for example, onto her wing edge.

Lastly, the “mandibles” could be used in male-male aggression. Male aggression is common in drosophilids, even among species of *Drosophila* (e.g., Spieth, 1952: table 2). In some drosophilid genera the males are territorial and pugnacious, engaging in ritualistic head butting (they don't make actual contact), which is why there has been repeated origin of hypercephalic (broad-headed) males in the family, in *Zygothrica* spp. (Burla, 1990; Grimaldi, 1987; Grimaldi and Fenster, 1989), *Idiomyia heteroneura*, *Chymomyza* spp. (Eberhard, 2002; Grimaldi, 1986; Tsacas, 1990; Watabe and Liang, 1990), the *Drosophila obscura* group (Gao et al., 2009), *Mulgravea asiatica* (Okada, 1965) and some undescribed species of *Cladochaeta* (D.G., unpubl.). This explanation also seems less convincing than the one involving courtship because the extent of the male secondary sexual characters in *Dichaetophora ancora* is limited almost entirely to the small “mandibles,” and combat using these structures would be difficult since the flies are hypognathous, not prognathous.

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