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Redescription of *Drosophila endobranchia* (Diptera, Drosophilidae), an aberrant member of the *canalinea* species group

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The Cayman crab fly *Drosophila endobranchia* Carson & Wheeler, 1968 is redescribed based on 11 adult specimens (8 males, 3 females) recently collected in Grand Cayman. Line drawings, in addition to black and white photomicrographs, of male and female terminalia are included.

Keywords. aedeagus, epandrium, hypandrium, female tergite 8, oviscapt valve, spermathecae.

INTRODUCTION

According to Ratcov & Vilela (2007), the Neotropical and ecologically poorly known *Drosophila canalinea* group consists of 13 described species. For many years, based on the drawings of the general design of male genital sclerites (Carson & Wheeler, 1968: 677, figs 6–11), one of us (CRV) had suspected that there was a close relationship between *Drosophila endobranchia* Carson & Wheeler, 1968, known as the Cayman crab fly, and the species of the *canalinea* group. As the number of described species of the *canalinea* group increased (Vilela & Bächli 1990, Ratcov & Vilela 2007) the putative relationship became more evident.

Meanwhile, a molecular analysis of the nucleotide sequences of one mitochondrial and four nuclear genes of specimens of *D. endobranchia* collected in early 2007 by one of us (MCS) in the Grand Cayman Island (Stensmyr *et al.* 2008), had also coincidentally suggested a close relationship with the species of the *canalinea* group. Thus, *D. endobranchia* was recently included in the group, as an aberrant member and sole representative of its own subgroup, by Stensmyr *et al.* (2008), who based their decision mostly on molecular data.

To get additional data in order to confront the morphological similarity with results of the molecular analyses we here present a redescription of *D. endobranchia*, as previously stated by Stensmyr *et al.* (2008: 4), based on some of those recently sampled specimens cited above.

MATERIAL AND METHODS

Eleven imagines (8 ♂♂, 3 ♀♀) of *D. endobranchia* aspirated by one of us (MCS) from the carapaces and legs of black crabs, *Gecarcinus ruricola* (Linnaeus, 1758), in January 2007 on Grand Cayman, British West Indies (for further details

refer to Stensmyr *et al.* 2008) were used to prepare the present redescription. The 11 specimens, originally preserved in 100 % ethanol, were dehydrated and glued to points according to the method of treatment with liquids (alternative b of Bächli *et al.* 2004: 3). Before being dehydrated, three (2 ♂♂, 1 ♀) of them were dissected in order to analyze their terminalia.

Label data attached to each specimen are cited in full with a backslash indicating a label change. Our own notes or interpretations are included in brackets (also in other items throughout the text).

We followed Wheeler & Kambysellis (1966) and Kaneshiro (1969) in preparing the microscope slides. The disarticulated sclerites are preserved in microvials filled with glycerin and attached by the stopper to the pin of the respective specimen. For further details refer to Bächli *et al.* (2004).

Male and female terminalia were drawn using a camera lucida (1.4x or 1.8x) attachment on a compound microscope under a 20x or 25x objective. They were photographed with a photomicroscope under a 6.3x objective.

Photomicrographs were taken of the following structures: aedeagus connected to hypandrium, and also isolated, in dorsal or ventral and left lateral view, female tergite 8, epiproct, hypoproct, and spermathecal capsules in lateral view. Whenever in the same plate, all figures were drawn to the same scale and all photomicrographs were taken and enlarged to the same magnification, except where otherwise indicated. All the illustrations were scanned and improved with Adobe® Photoshop®.

For measurements and indices see Vilela & Bächli (1990), for morphological terminology see Vilela & Bächli (2000) and Bächli *et al.* (2004).

The specimens analyzed in the present redescription were donated by the collector and junior author (MCS) of this paper to the Museu de Zoologia da Universidade de São Paulo (MZSP; 2 ♂♂, 2 ♀♀) and to the Zoologisches Museum der Universität Zürich, Zürich (ZMUZ; 6 ♂♂, 1 ♀ [dissected: 2 ♂♂, 1 ♀]), where they will be deposited.

Genus *Drosophila*

Drosophila canalinea species group Wheeler, 1957

Drosophila canalinea species group Wheeler 1957: 90 [diagnosis, species included]; Wasserman 1960: 843 [phylogeny], 1963: 344 [phylogeny], 1982: 68 [phylogeny]; Throckmorton 1962a: 252 [phylogeny], 1962b: 469 [phylogeny], 1975: 441 [phylogeny], 1982: 43 [phylogeny]; Johnson & Bealle 1968: 3 [phylogeny]; Starmer 1981: 49 [phylogeny]; Val *et al.* 1981: 142 [species included]; Batterham *et al.* 1984: 650 [phylogeny]; Vilela & Bächli 1990: 54 [diagnosis, species included]; Durando *et al.* 2000: 300 [phylogeny]; Tatarenkov & Ayala 2001: 329 [phylogeny]; Markow & O'Grady 2006: 132 [key]; Ratcov & Vilela 2007: 336 [diagnosis, species included].

Diagnosis. Refer to Vilela & Bächli 1990: 54 and Ratcov & Vilela 2007: 336.

Taxa included (14). *Drosophila albomarginata* Duda, 1927; *D. annularis* Sturtevant, 1916; *D. annulosa* Vilela and Bächli, 1990; *D. canalinea* Patterson & Mainland, 1944; *D. canalinoides* Wheeler, 1957; *D. davidgrimaldii* Vilela and Bächli, 1990; *D. endobranchia* Carson and Wheeler, 1968; *D. hendeli* Vilela and Bächli, 1990; *D. melanoptera* Duda, 1927; *D. panamensis* Malloch, 1926; *D. paracanalinea* Wheeler, 1957; *D. parannularis* Vilela and Bächli, 1990; *D. piratininga* Ratcov and Vilela, 2007, and *D. sampa* Ratcov and Vilela, 2007.

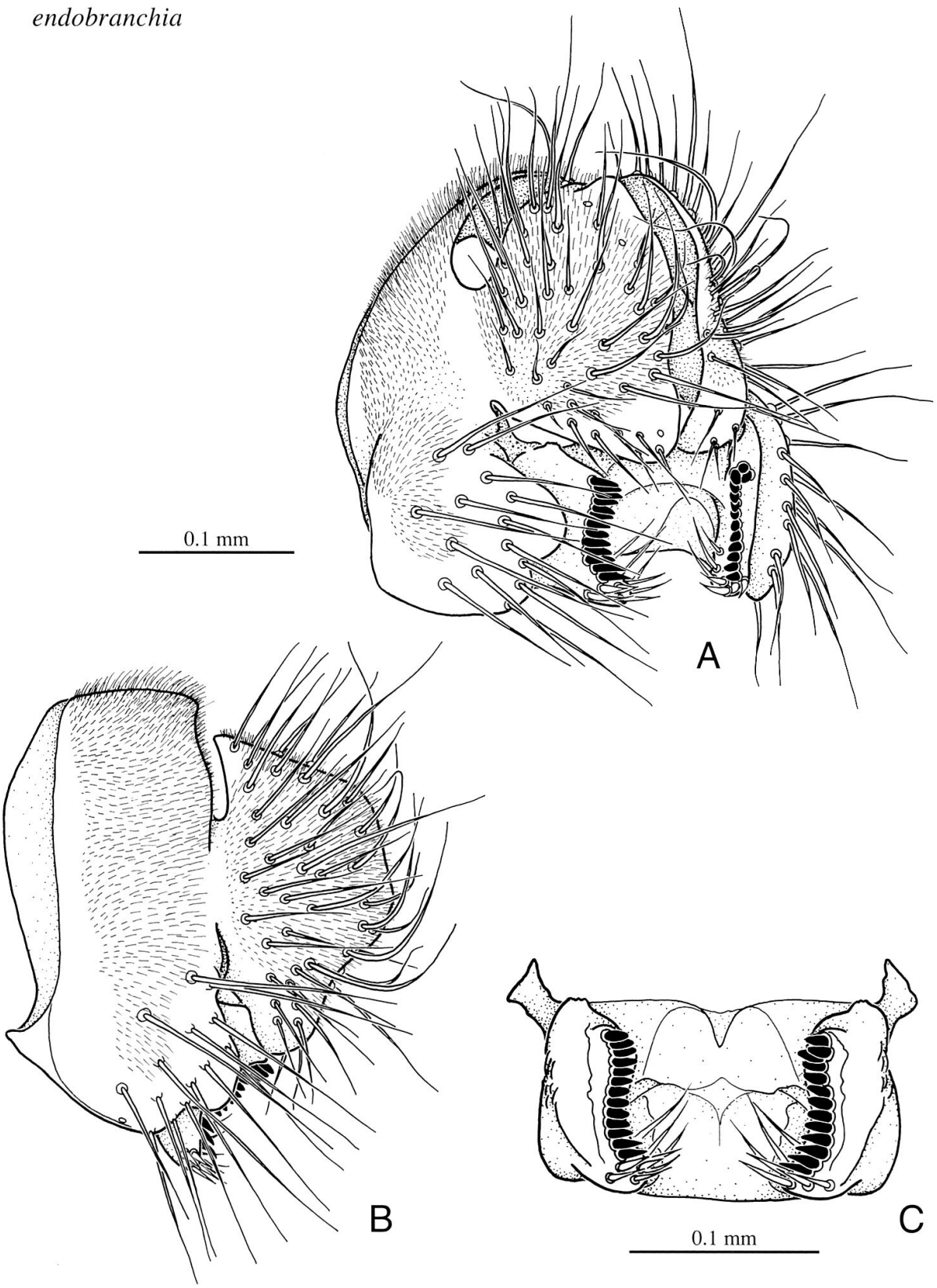

Fig. 1. *Drosophila endobranchia* Carson & Wheeler, from Beach Bay, Grand Cayman Island, BWI, external male terminalia. A, epandrium, cerci, surstyli, and decasternum, oblique posterior view. B, epandrium, cercus and surstylus, left lateral view. C, surstyli and decasternum, posterior view.

Distribution. Refer to Stensmyr *et al*. 2008 (fig. S6) for a map with the known records of the 14 species of *Drosophila* included in the *canalinea* group.

Comments. *Drosophila endobranchia* is considered an aberrant member of the *canalinea* group based on what follows:

It shares the following characters with the remaining species in the *canalinea* group:

— The overall design of male and female terminalia. The spotted pattern of thorax and banded patterns of abdominal tergites, in addition to the imago habitus.

It differs from the remaining species in the *canalinea* group by the following characters:

— Thorax with 3 pairs of dorsocentral setae (two pairs in the remaining species);
— Asymmetry of the following male sclerites: aedeagus, paraphyses, hypandrium, and gonopods (symmetric in the remaining species);
— Aedeagal apodeme bearing a posterior ventral rod nearly as long as the ventral margin of paraphyses (absence of ventral rod in the remaining species);
— Female tergite 8 devoid of paragenital fringe (present in the remaining species);
— Eggs bearing only two anterior filaments (four anterior filaments in those species for which this character is known).

Drosophila endobranchia Carson and Wheeler, 1968

(Figs 1–4)

Drosophila endobranchia Carson and Wheeler, 1968: 675 [description, biology, karyotype, egg, puparium, terminalia drawings]; Wheeler 1970: 79.14 [distribution]; Carson 1971: 19 [biology]; Carson 1974: 3518 [biology, distribution]; Clayton & Wheeler 1975: 499 [metaphase chromosomes]; Ashburner 1981: 44 [biology]; Wheeler 1981: 40 [list]; Grimaldi 1988: 198 [phylogeny]; Stensmyr & Hansson 2007: 744 [distribution, host crab, and live imago photographs], 745 [host crab photograph]; Brake & Bächli 2008: 54 [world catalogue]; Stensmyr *et al*. 2008: 2 [behavior, distribution, live imagines, and holotype photographs], 5 [molecular phylogeny], 6 [imagines, male and female terminalia photographs].

Diagnosis. Body color yellowish, frons and thorax with complex pattern of brown and yellowish areas; three pairs of dorsocentral setae; mesonotal setae standing remarkably upright; abdominal tergites yellowish, distally with broad, black and medially interrupted marginal bands; hypandrium, aedeagus and their associate sclerites rather asymmetric.

Material examined (8 ♂♂, 3 ♀♀ [2 ♂♂, 1 ♀ dissected]), labelled: «British West Indies, Grand Cayman, Beach Bay, Beach Bay Road \ aspirated from *Gecarcinus ruricola*, M. Stensmyr & R. Stieber leg., 17.I.2007 \ ♂ or ♀ \ Drosophila endobranchia Carson & Wheeler, Bächli & Vilela det. 2007».

Type locality. Conch Point, Grand Cayman, Cayman Is., British West Indies.

Redescription. ♂.

Head. Frons flat, generally pale yellowish-brown, frontal vittae slightly darker brownish, frontal length 0.53 (0.47–0.58) mm; frontal index = 0.97 (0.89–1.10), top to bottom width ratio = 1.16 (1.13–1.19). Frontal triangle apically narrowed, about 74–83 % of frontal length; ocellar triangle somewhat elongated, flat, about

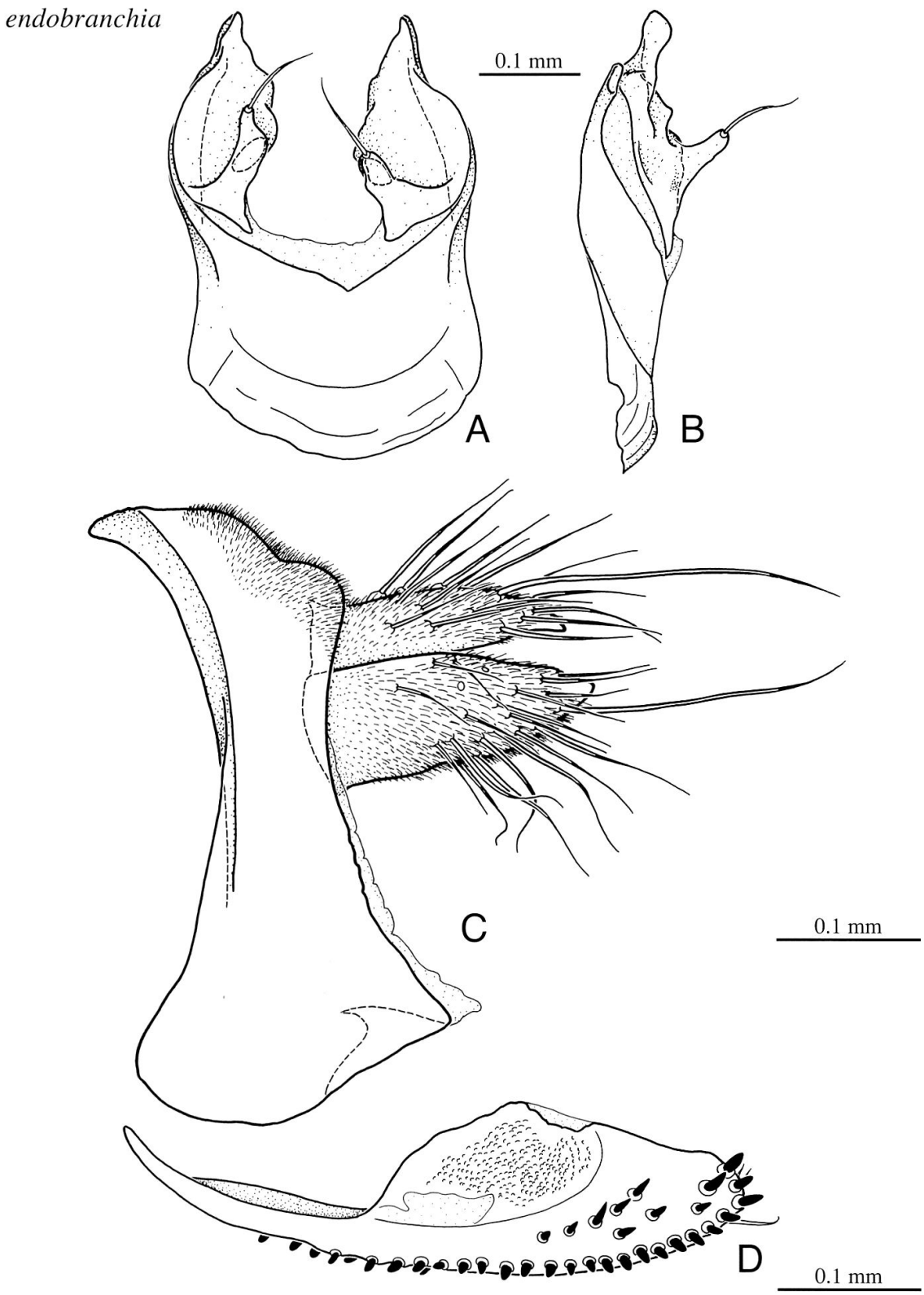

Fig. 2. *Drosophila endobranchia* Carson & Wheeler, male (A, B) and female (C, D) terminalia, specimens from Beach Bay, Grand Cayman Island, BWI. A, hypandrium and gonopods, ventral view. B, idem, left lateral view. C, tergite 8, epiproct and hypoproct, left lateral view. D, left oviscapt valve, left lateral view.

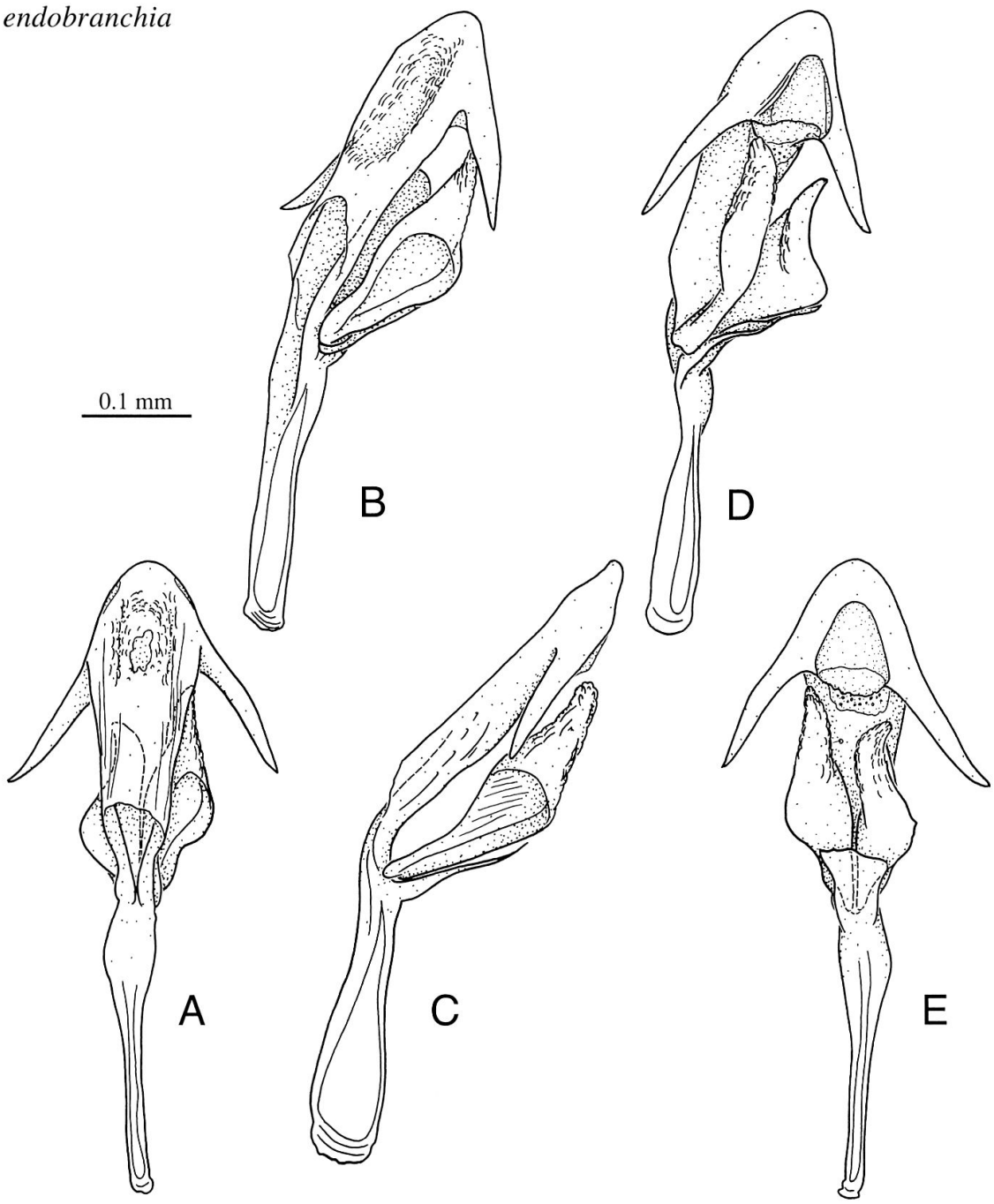

Fig. 3. *Drosophila endobranchia* Carson & Wheeler, from Beach Bay, Grand Cayman Island, BWI, male. A–E, aedeagus+aedeagal apodeme and paraphyses, several aspects from dorsal through ventral.

29–43 % of frontal length. Orbital plates in apical half distinctly diverging from eye margin, about 68–84 % of frontal length. Orbital setae black, or2 slightly closer to or1 and somewhat outside the connection line, distance of or3 to or1 = 67–87 % of or3 to vtm, or1 / or3 ratio = 0.94 (0.89–1.00), or2 / or1 ratio = 0.44 (0.40–0.47), postvertical setae converging but not crossed, 50 (47–54) %, ocellar setae = 0.62 (0.58–0.65) % of frontal length; vibrissae strongly bent inwards, vibrissal index = 0.43. Face brownish-yellow. Carina broad, bulbous but dorsally flat. Cheek medially dark brown, in particular along the lower margin, yellowish in hind third, index

about 3 (2–3). Eye index = 1.14 (1.12–1.18). Antennae brown, length to width ratio of flagellomere 1 = 1.69 (1.63–1.86). Arista with 6–8 long dorsal, 2–3 long ventral and about 8 small inner branches, plus terminal fork. Proboscis and clypeus pale yellowish. Palpus yellowish, slightly flattened.

Thorax length 1.30 (1.15–1.43) mm. Scutum yellowish, whitish along anterior margin and at postpronota, with a diffuse brownish median stripe and two diffuse brownish stripes along the dorsocentral lines, laterally with a pattern of brownish spots, 6 somewhat irregular rows of acrostichal setae. h index = 1.10 (0.94–1.30). Three pairs of dorsocentral setae (in some specimens 4 setae, irregularly placed), transverse distance of dorsocentral setae 114–154 % of longitudinal distance of the normal pair; dc index = 0.86 (0.76–0.93). Scutellum pale brownish, darker at base, distance between apical scutellar setae about 64–90 % of that between apical and basal one, basal setae divergent; scut index = 1.03 (1.00–1.08). Pleura with an irregular brownish pattern in the upper two thirds, yellowish below, sterno index = 0.53 (0.43–0.62), median katepisternal seta about 39–56 % of the anterior one. Halter yellow. Legs brownish-yellow, preapical setae on all tibiae, apical seta on mid tibia.

Wing hyaline, R_{4+5} and M distinctly converging, length 2.47 (2.27–2.66) mm, length to width ratio = 2.03 (2.00–2.12). Indices: C = 2.36 (2.22–2.50), ac = 2.77 (2.57–3.00), hb = 0.66 (0.61–0.72), 4C = 0.90 (0.86–1.00), 4v = 1.49 (1.38–1.56), 5x = 1.05 (1.00–1.13), M = 0.40 (0.35–0.43), prox. x = 0.57 (0.52–0.65).

Abdomen generally yellowish, on all tergites with black, broad marginal bands which are medially broadened and narrowly interrupted.

♂ *terminalia* (Figs 1, 2A, B, 3, 4A–D). Epandrium dorsoposteriorly microtrichose, with ca. 14 lower, and no upper setae; ventral lobe roundish, not microtrichose, partially covering surstylus. Cerci anteriorly fused partially to epandrium, mostly microtrichose and devoid of ventral lobe (Figs 1A, B). Surstylus (Figs 1A–C) not microtrichose, bearing a slightly concave row of 13 peg-like prensisetae, ca. 5 thin inner and 2 outer setae. Decasternum as in Figs 1A, C. Hypandrium (Figs 2A, B, 4A, B) ca. 1.6x longer than epandrium, anterior margin convex and wide; posterior hypandrial process and dorsal arch absent; gonopod linked to paraphysis by membranous tissue, bearing one seta on the tip of a finger-shaped protuberance near the anterior inner margin; left protuberance positioned distally relative to right one (Figs 2A, 4B). Aedeagus (Figs 3A–E, 4A–D) fused to aedeagal apodeme, dorsoventrally flattened, subdistally with a shallow concavity mediodorsally, straight in profile, slightly bent dorsad at tip, ventrally bearing a pair of straight, asymmetric spurs projected anteriorly; left spur positioned distally relative to right one (Figs 3A, E, 4B, D). Aedeagal apodeme shorter than aedeagus, laterally flattened. Ventral rod dorsoventrally flattened, almost as long as paraphysis' ventral margin. Paraphysis bare, medially bent dorsad, surpassing tip of spur, and connected to distoventral margin of aedeagal apodeme by membranous tissue; left paraphysis positioned distally relative to right one (Fig 3E).

♀.

Measurements: Frontal length 0.61 (0.59–0.63) mm; frontal index = 1.01 (0.95–1.06), top to bottom width ratio = 1.25 (1.19–1.31). Frontal triangle about 80–81 % of frontal length; ocellar triangle about 43–46 % of frontal length. Orbital plates about 69–76 % of frontal length. Distance of or3 to or1 = 64–87 % of or3 to vtm, or1 / or3 ratio = 1.02 (1.00–1.06), or2 / or1 ratio = 0.41 (0,33–0.50), post-

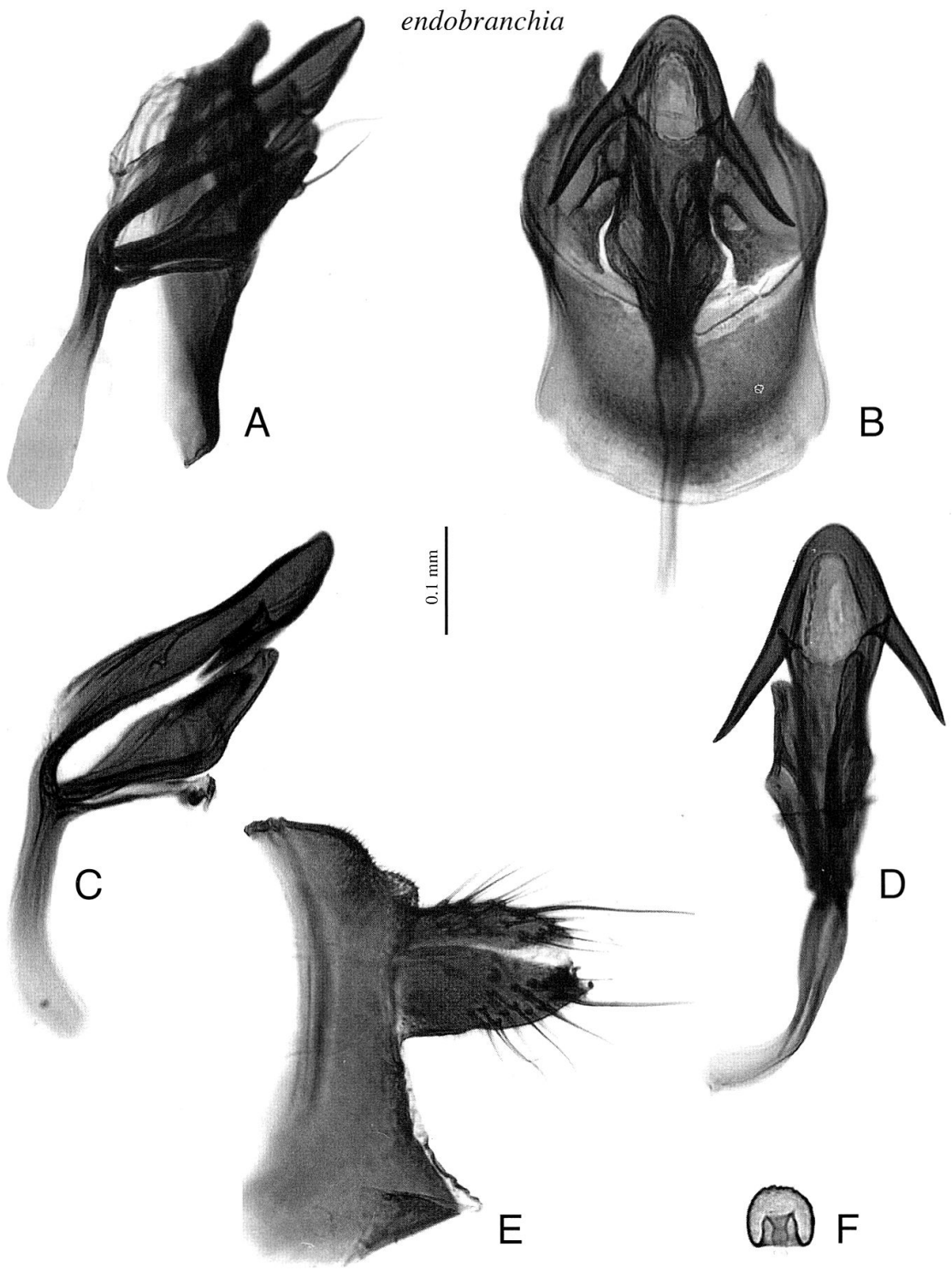

Fig. 4. Photomicrographs of male (A and B, same specimen; C and D, another specimen) and female terminalia (E and F) of *Drosophila endobranchia* Carson & Wheeler, from Beach Bay, Grand Cayman Island, BWI. A, internal male terminalia, left lateral view. B, idem, ventral view. C, aedeagus+aedeagal apodeme and paraphyses, left lateral view. D, idem, dorsal view. E, tergite 8, epiproct, and hypoproct, left lateral view. G, inner spermathecal capsule, lateral view.

vertical setae = 50 (49–51) %, ocellar setae = 59 (57–62) % of frontal length; vibrissal index = 0.65 (0.56–0.75). Cheek index about 3 (2–3). Eye index = 1.12 (1.12–1.13). Thorax length 1.49 (1.42–1.55) mm. h index = 1.09 (0.94–1.21). Transverse distance of dorsocentral setae 129–167 % of longitudinal distance; dc index = 0.99 (0.79–1.18). Distance between apical scutellar setae about 69–82 % of that of apical to basal one; scut index = 1.00 (0.94–1.07), sterno index = 0.53 (0.45–0.58), mid katepisternal seta about 44 % of anterior one. Wing length 2.82 (2.43–2.91) mm, length to width ratio = 2.03 (2.02–2.05). Indices: C = 2.59 (2.50–2.74), ac = 2.33 (2.22–2.38), hb = 0.62 (060–0.63), 4C = 0.92 (0.90–0.95), 4v = 1.67 (1.57–1.80), 5x = 1.08 (1.00–1.13), M = 0.44 (0.43–0.45), prox. x = 0.70 (0.68–0.71).

♀ *terminalia* (Figs 2C, D, 4E, F). Tergite 8 mediolaterally narrowed, mostly bare, slightly microtrichose dorsodistally; paragenital fringe absent; ventral margin remarkably wide. Epiproct and hypoproct microtrichose and remarkably long (Figs 2C, 4E). Oviscapt valve ventrally convex, apically blunt, with ca. 27 marginal and ca. 10 discal peg-like ovisensilla (Fig. 2D). Spermathecal capsule (Fig. 4F) small, warty, as long as wide, proximally flattened, distally roundish, weakly sclerotized; basal introvert around half the capsule length; apical introvert absent.

Distribution. Apparently endemic to three western Caribbean Islands: Grand and Little Cayman, and Cuba (as far as known only in Guantánamo Bay).

Biology. The larvae are found living in the nephric groves and particularly in the gill chambers of *Gecarcinus ruricola* (L.) and *G. lateralis* Fréminville. Resting adults can be aspirated from the aformentioned crab species. A recent review of the drosophilds and crabs associations was published by Stensmyr & Hansson (2007).

Comments. Internal characters and descriptions of eggs and pupae as well as data about the life cycle and the chromosome structure are provided by Carson & Wheeler (1968).

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REFERENCES

Ashburner, M. 1981. Entomophagous and other bizarre Drosophilidae. *In*: Ashburner, M., Carson, H.L. & Thompson, J.N. (eds), The Genetics and Biology of *Drosophila*, vol. 3a, pp. 395–429. — Academic Press, London.

Bächli, G., Vilela, C.R., Andersson Escher, S. & Saura, A. 2004. The Drosophilidae (Diptera) of Fennoscandia and Denmark. — Fauna Entomologica Scandinavica, vol. 39, 362 pp. Brill, Leiden.

Batterham, P., Chambers, G.K., Starmer, W.T. & Sullivan, D.T. 1984. Origin and expression of an alcohol dehydrogenase gene duplication in the genus *Drosophila*. — Evolution 38: 644–657.

Brake, I. & Bächli, G. 2008. Drosophilidae (Diptera). *In*: World Catalogue of Insects 9: 1–412. — Apollo Books, Stenstrup.

Carson, H.L. 1971. The ecology of *Drosophila* breeding sites. Harold Lyon Arboretum Lecture 2: 1–28.

Carson, H.L. 1974. Three flies and three islands: Parallel evolution in *Drosophila*. — Proceedings of the National Academy of Sciences of the USA 71: 3517–3521.

Carson, H.L. & Wheeler, M.R. 1968. *Drosophila endobranchia*, a new drosophilid associated with land crabs in the West Indies. — Annals of the Entomological Society of America 61: 675–678.

Clayton, F.E. & Wheeler, M.R. 1975. A catalog of *Drosophila* metaphase chromosome configurations. *In*: King, R.C. (ed.), Handbook of Genetics, vol. 3, Invertebrates of Genetic Interest, pp. 471–512. — Plenum Press, New York.

Durando, C.M., Baker, R.H., Etges, W.J., Heed, W.B., Wasserman, M. & DeSalle, R. 2000. Phylogenetic analysis of the *repleta* species group of the genus *Drosophila* using multiple sources of characters. — Molecular Phylogeny and Evolution 16: 296–307.

Grimaldi, D.A. 1988. Relicts in the Drosophilidae (Diptera). *In*: Liebherr, J.K. (ed.), Zoogeography of Caribbean Insects, pp. 183–213. — Cornell University Press, Ithaca.

Johnson, F.M. & Bealle, S. 1968. Isozyme variability in species of the genus *Drosophila*. V. Ejaculatory bulb esterases in *Drosophila* phylogeny. — Biochemical Genetics 2: 1–18.

Kaneshiro, K.Y. 1969. A Study of the Relationships of Hawaiian *Drosophila* Species Based on External Male Genitalia. — The University of Texas Publication 6918: 55–70.

Markow, T.A. & O'Grady, P.M. 2006. *Drosophila*. A guide to species identification and use. 259 pp. — Elsevier, Amsterdam.

Ratcov, V. & Vilela, C.R. 2007. Two new species of *Drosophila* belonging to the *canalinea* group (Diptera, Drosophilidae). — Iheringia, Serie Zoologia 97(3): 1–7.

Starmer, W.T. 1981. A comparison of *Drosophila* habitats according to the physiological attributes of the associated yeast communities. — Evolution 35: 38–52.

Sternsmyr, M.C. & Hansson, B.S. 2007. Flies's lives on a crab. — Current Biology 17: R743–R746.

Stensmyr, M.C., Stieber, R & Hansson, B.S. 2008. The Cayman crab fly revisited - Phylogeny and Biology of *Drosophila endobranchia*. — Public Library of Science ONE 3: 1–7.

Tatarenkov, A. & Ayala, F.J. 2001. Phylogenetic relationships among species groups of the *virilis-repleta* radiation of *Drosophila*. — Molecular Phylogeny and Evolution 21: 327–331.

Throckmorton, L.H. 1962a. The problem of phylogeny in the genus *Drosophila*. — The University of Texas Publication 6205: 207–343.

Throckmorton, L.H. 1962b. The use of biochemical characteristics for the study of problems of taxonomy and evolution in the genus *Drosophila*. — The University of Texas Publication 6205: 415–488.

Throckmorton, L.H. 1975. The phylogeny, ecology, and geography of *Drosophila*. *In*: King, R.C. (ed.), Handbook of Genetics, vol. 3, Invertebrates of Genetic Interest, pp. 421–469. — Plenum Press, New York.

Throckmorton, L.H. 1982. Pathways of evolution in the genus *Drosophila* and the founding of the repleta group. *In*: Barker, J.S.F. & Starmer, W.T. (eds), Ecological Genetics and Evolution, pp. 33–47. — Academic Press, New York.

Val, F.C., Vilela, C.R. & Marques, M.D. 1981. Drosophilidae of the Neotropical Region. *In*: Ashburner, M., Carson, H.L. & Thompson, J.N. (eds), The Genetics and Biology of *Drosophila*, vol. 3a, pp. 123–168. — Academic Press, London.

Vilela, C.R. & Bächli, G. 1990. Taxonomic studies on Neotropical species of seven genera of Drosophilidae. — Mitteilungen der Schweizerischen entomologischen Gesellschaft 63(Suppl.): 1–332.

Vilela, C.R. & Bächli, G. 2000. Morphological and ecological notes on the two species of *Drosophila* belonging to the subgenus *Siphlodora* Patterson & Mainland, 1944 (Diptera, Drosophilidae). — Mitteilungen der Schweizerischen entomologischen Gesellschaft 73(1–2): 23–47.

Wasserman, M. 1960. Cytological and phylogenetic relationships in the *repleta* group of the genus *Drosophila*. — Proceedings of the National Academy of Sciences of the USA 46: 842–859.

Wasserman, M. 1963. Cytology and phylogeny of *Drosophila*. — American Naturalist 97: 333–352.

Wasserman, M. 1982. Evolution of the *repleta* group. *In*: Ashburner, M., Carson, H.L. & Thompson, J.N. (eds), The Genetics and Biology of *Drosophila*, vol. 3b, pp. 61–139. — Academic Press, London.

Wheeler, M.R. 1957. Taxonomic and distributional studies on Nearctic and Neotropical Drosophilidae. — The University of Texas Publication 5721: 79–114.

Wheeler, M.R. 1970. Family Drosophilidae. *In*: A Catalogue of the Diptera of the Americas south of the United States, pp. 79.1–79.65. — Museu de Zoologia, Universidade de São Paulo.

Wheeler, M.R. 1981. The Drosophilidae: A taxonomic overview. *In*: Ashburner, M., Carson, H.L. & Thompson, J.N. (eds), The Genetics and Biology of *Drosophila*, vol. 3a, pp. 1–97. — Academic Press, London.

Wheeler, M.R. & Kambysellis, M.P. 1966. Notes on the Drosophilidae (Diptera) of Samoa. — The University of Texas Publication 6615: 533–565.

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