A REVISION OF THE SHORE-FLY GENUS DIPHUIA CRESSON
(DIPTERA: EPHYDRIDAE)

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Abstract.—Diphuia Cresson, a New World genus of shore flies, is revised and found to be close phylogenetically (the sister group) to the lineage giving rise to Allotrichoma Becker, including Pseudohecamede Hendel. Although four species (D. anomalal Cresson, D. nasalis Wirth, D. nitida Sturtevant and Wheeler, and D. zatwarnickii, new species (Jamaica) are recognized, the second and third are very similar and may prove to be conspecific when adequate material of D. nitida is available. Characters of the male postabdomen and terminalia are described and illustrated.

Key Words: Ephydridae, shore flies, Diphuia, revision, systematics

While conducting field work on several cays within the Stann Creek District of Belize, I found a tiny, black-colored shore fly that is associated with mangrove peat. The peat, which is exposed at low tide, is shaded during most of the day beneath the dense canopy of well-developed fringe red mangrove (Rhizophora mangle L.). The specimens did not occur on peat that is the substrate for scrub or dwarf red mangrove and where little or no shade is provided. Determining the identity of this species, which is less than two mm in length, has led to this revision of Diphuia Cresson, the genus to which the species has been assigned. In addition to determining the identity of the specimens from Belize, the other specific purposes of this revision are to provide the first illustrations of the male terminalia and to determine the phylogenetic position of Diphuia, which Cresson (1944) suggested was related to Allotrichoma Becker in the tribe Atissini.

Shore flies of the genus Diphuia are anomalies among atissines in being mostly black, lacking dense vestiture of gray to brown micromotementum, and having a distinctively marked face that is black with silvery white, micromotentose lines. The facial markings of micromotementum are similar to specimens of Discocerina nitida Cresson (tribe Discocerinini) and several genera of the tribe Gymnomyzini. The superficial resemblance of this genus to discocerines or gymnomyzines prompted Cresson to formulate the generic name Diphuia, which is a Latin transliteration of Greek words meaning double nature. Although similar to genera in other tribes, the genus is related most closely to Allotrichoma, as Cresson concluded in the original description, and the similarities noted are apparently the result of convergences.

When Cresson (1944) originally proposed Diphuia he included only the type species, D. anomalal Cresson, which was described in the same paper. Two years later, Cresson again treated Diphuia and its type species in his synopsis of Neotropical Psilopinae (= Gymnomyzinae). The genus then remained unstudied for nearly a decade, which is not surprising in view of their diminutive size,
restricted distribution, and rarity in collections. Sturtevant and Wheeler (1954) wrote the concluding part for Cresson's synopses of Nearctic shore flies, following the latter's death, and described *D. nitida* from a single specimen that was collected near New York City. Two years afterwards, Wirth (1956) reviewed the shore flies of the Bahamas and described a third species, *D. nasalis*. Aside from catalogs of the Nearctic and Neotropical Regions (Wirth 1965, 1968, respectively), no further work has been published on *Diphuia*. Nothing is known of the immature stages, no key is available, and the structures of the male terminalia have not been investigated, described, or illustrated.

Methods.—The terminology and methods used in this study were explained previously (Mathis 1986a, b). Because of the small size of specimens, study and illustration of the male terminalia required the use of a compound microscope. To better assure effective communication about structures of the male terminalia, I have adopted the terminology of other workers in Ephydridae (see references in Mathis 1986b). Usage of these terms, however, should not be taken as an endorsement of them from a theoretical or morphological view over alternatives that have been proposed (Griffiths 1972, McAlpine 1981). Rather, I am deferring to tradition until the morphological issues are better resolved.

Two venational ratios are used commonly in the descriptions and are defined here for the convenience of the user (ratios are averages of three specimens).

1. Costal vein ratio: the straight line distance between the apices of *R*<sub>2+3</sub> and *R*<sub>4+5</sub>/distance between the apices of *R*<sub>1</sub> and *R*<sub>2+3</sub>.

2. M vein ratio: the straight line distance along *M* between crossveins (dm-cu and r-m)/distance apicad of crossvein dm-cu.

Most of the specimens used in this study, a total of 225, are housed in the National Museum of Natural History (USNM), Smithsonian Institution. Prior to my tenure at the Smithsonian, W. W. Wirth had accumulated several specimens of what appeared to be the same tiny fly. His collections from Jamaica and Dominica are especially noteworthy in that regard. I also examined collections of the Academy of Natural Sciences of Philadelphia (ANSP), the American Museum of Natural History (AMNH), and the University of Texas (UTA).

**Diphuia Cresson**


Diagnosis.—Mostly black, subshiny to shiny, microtomentum usually sparse; small shore flies, length 1.35 to 1.80 mm.

**Head:** Wider than high; face width-to-head width ratio 0.28; frons black, mostly unicolorous, lacking distinctively colored ocellar triangle; frons wider than long, frontal length-to-width ratio 0.58; frontal vestiture variable; ocellar seta well developed, inserted slightly in front of alignment of anterior ocellus and at about the same distance apart as between posterior ocelli; pseudo-postocellar setae usually well developed, length subequal to ocellar setae, proclinate, slightly divergent; 1 reclinate and 1 proclinate fronto-orbital seta present, reclinate seta inserted slightly anteromediad of proclinate seta; both inner and outer vertical setae present; ocelli arranged to form isosceles triangle, with distance between posterior ocelli larger than between anterior ocellus and either posterior ocellus. Antenna exerted; pedicel with well-developed, proclinate, dorsal seta; aristal length subequal to antennal length and bearing 4–5 dorsal rays, with basal 3 rays longer than apical 1–2, the latter subequal. Eye apparently bare of microsetulae (using a stereomicroscope). Face black in both sexes and with silvery white, microtomentum antennal grooves and with
2 lines, sometimes irregular, paralleling parafacials, these and similarly invested and colored ventral margin (microtomentum sometimes interrupted at middle) form a facial triangle that has a small microtomentose area below facial prominence; face not carinate between antennal bases but slightly, conically protrudent at middle (best seen in lateral view); ventral facial margin shallowly emarginate; face bearing 2 facial setae, the dorsal seta very slightly larger, both inserted near parafacials; parafacials densely microtomentose, silvery white; clypeus very sparsely microtomentose, black; palpus blackish brown to black; mouthparts not geniculate, labella shorter than mediopro-boscis.

Thorax: Generally black, vestiture of microtomentum variable with species, although generally sparse; pleural areas lacking stripes of distinctly colored microtomentum. Chaetotaxy with mesonotal setae poorly developed except for those at posterior margin; mesonotal setulae numerous and not arranged in well-defined setal tracks; prescutellar acrostichal setae much larger than other acrostichal setulae and more widely set apart; only 1 dorsocentral seta, inserted posteriad; intra-alar setulae irregularly seriated; presutural seta well developed, length subequal to notopleurale setae; 2 scutellar setae and scutellar disc with sparse, scattered setulae; postpronotal seta 1; postalar seta 1; notopleurale setae 2, insertion of posterior seta elevated dorsally above anterior one; anepisternal setae 2, inserted along posterior margin; katepisternal seta well developed, conspicuous. Wing: membrane mostly hyaline to very slightly milky white; veins behind costa pale, usually yellowish to yellowish brown; vein R$_{2+3}$ extended well beyond level of crossvein dm-cu. 2nd costal section at least 1½ times longer than 3rd section; alular marginal setulae short, less than ½ alular height. Legs: femora black; tibiae dark basally, concolorous with femora, apices yellowish.

Abdomen: Fifth segment of male well sclerotized, elongate, not normally visible from a dorsal view, usually retracted within 4th segment; 5th tergum and sternum of male united anteriorly to form a complete annulus. Male terminalia as follows: cercus rod shaped, bearing 2–3 conspicuously longer setae at ventral margin; surstylus well developed, well sclerotized, and conspicuous, length as long as cercus.

Distribution.—New World. Temperate to tropical zones, in North America along the east coast (New York south to Florida) and the Caribbean to Colombia and Ecuador in South America.

Phylogenetic relationships.—Diphuia is related to a group of taxa (Allotrichoma Becker, Eremotrichoma Soika, Pseudohecamede Hendel, and Hecamede Haliday) within the tribe Atissini that is characterized by having very sparse or lacking microsetulae on the compound eyes; a conically prominent face (degree of development varies) that is emarginate ventrally and with the clypeus exposed in the emargination; oral opening and clypeus narrow; area surrounding crossvein dm-cu not infuscate; the apex of the wing broadly rounded, not pointed at the apex of vein R$_{4+5}$; fifth tergum of male retracted within the enlarged fourth, usually not visible; and cerci with elongate setulae at ventral margin. Diphuia appears to be the sister group to the lineage giving rise to taxa closely related to Allotrichoma sensu lato, including Pseudohecamede. This relationship is evidenced by the characters noted previously, especially the retracted fifth tergum of the male, which is moderately elongate, almost tubular. Although related and similar to this group, Diphuia may be distinguished as follows (characters indicated by an asterisk are autapomorphies that corroborate the monophyly of Diphuia): *coloration very dark, usually black; *microtomentum of head and thorax generally sparse, giving a subshiny to faintly dull appearance; facial coloration of male and females similar, lacking sexual dimorphism; face, although slightly pro-
trident medially (best seen in profile), not acutely pointed in lateral view; *face with silvery microtomentum markings, antennal grooves, 2 vertical lines, ventral margin, an area below the facial prominence, and parafacials; presutural and prescutellar setae well developed; *pleural region lacking a stripe or stripes; 5th segment of male well sclerotized and its tergum moderately elongate; *5th tergum and sternum of male united anteriorly to form a complete annulus; and male genitalia with distinct, well-sclerotized, elongate surstyli. The placement of Diphuia as the sister group to the lineage of Allotrichoma sensu latu follows Cresson's original assessment. The evidence supporting this relationship is not strong, however, and Diphuia could be related to Hecamede.

Two species groups are evident within Diphuia, each comprising two species: D. anomala Cresson and D. zatwarnickii, a new species that is described below; and D. nitida and D. nasalis. For species in the former group, I have found that characters of the male terminalia only are adequate to distinguish between the species. In the second group, the degree of microtomentum on the frons may be a distinguishing character, although that character is questionable (see "Remarks" under D. nitida).

Discussion.—Two shore-fly species (Discocerina quadripunctinata (Becker) and Allotrichoma argenticinctum Lamb) that are now or perhaps should be assigned to Allotrichoma and related genera and that are dark colored are not closely related to Diphuia (Zatwarnicki, in litt.).

Nothing is known about the immature stages or natural history of any of the species included in Diphuia.

**Key to Species of Diphuia**

1. Mesofrons bare of microtomentum, shiny (New York) ................ D. nitida Sturtevant and Wheeler

2. Mesofrons thinly invested with microtomentum, subshiny; anepisternum with anteroventral ½-½ bare, shiny black, otherwise with thin investment of whitish gray microtomentum

   - Mesonotum moderately densely microtomentose, golden brown; anepisternum almost entirely invested with whitish gray microtomentum .................. 3

3. Surstyli long and narrow, length subequal to that of cercus (Fig. 3); gonite with pointed posteroventrally; aedeagus only moderately curved apically .................. D. anomala Cresson

   - Surstyli moderately short and robust (Fig. 18), length shorter than cercus; gonite with posteroventral portion broadly bifurcate; aedeagus more curved apically, point oriented anteriorly .................. C. zatwarnickii, new species

**Diphuia anomala** Cresson

Figs. 1–7


Description.—Small shore flies, length 1.60 to 1.80 mm.

**Head:** Frons moderately invested with brownish microtomentum, microtomentum sparse or lacking on 2 small areas lateral of posterior ocelli and 2 spots along the anterior margin.

**Thorax:** Mesonotum densely invested with brownish to golden brown microtomentum, especially medially, along posterior portion of scutum and scutellum; anepisternum with fine investment of whitish microtomentum. Wing with costal vein ratio 0.50; M vein ratio 0.41.

**Abdomen:** 5th tergum (Figs. 1, 2) almost as high as long, anterior margin in dorsal view with deep, broadly V-shaped emargination (Fig. 2), posterior margin with sparse setae; 5th sternum clearly divided into 2 broad sternites that are connected only anteroventrally (Fig. 1). Male terminalia (Figs. 3–7) as follows: epandrium bulbous, shiny, in lateral view almost as wide as high (Fig. 3); surstylus long, narrow, parallel sided, width and length subequal to that of cercus, apex angulate, pointed anteriorly, and bear-
ing a few setulæ (Fig. 3); gonite broad basally, with posteriorly extended process sheathing aedeagus, posterior apex of gonite curved anteroventrally (Figs. 4, 5); aedeagal apodeme triangular in lateral view (Figs. 5, 7), narrowly produced dorsally; aedeagus in lateral view broad, thumblike, produced posterovertrad to a ventral point, in dorsal view becoming wider apically, apex broadly rounded (Figs. 5, 7); hypandrium in ventral view longer than wide, anterior margin with a small, anterior process (Figs. 5, 6).

Type material.—The holotype male is labeled “Monte Lirio[,] PANAMA[,] RCShannon[,] IV.6.23 [6 Apr 1923]/δ/ TYPE DIPHUIA ANOMALA δ E.T. Cresson, Jr. [red, species name and δ handwritten]; TypeNo 70450 USNM [red, number handwritten].” The holotype is point mounted, is in good condition (the right first flagellomere is missing), and is deposited in the USNM. The allotype and several paratypes are also deposited in the USNM.


Distribution.—Colombia, Ecuador, El Salvador, and Panama.

Remarks.—This is the type species of Diphuia. It is very similar externally to D. zatwarnickii and can be distinguished only by reference to structures of the male terminalia (see “Remarks” under D. zatwarnickii and couplet 3 of the key). From D. nasalis and D. nitida it may be distinguished by the following characters: frons and mesonotum invested moderately densely with brownish to golden brown microtomentum; anepisternum invested with fine, grayish to whitish microtomentum, anteroventral portion not bare, shiny; second costal section long, costal vein ratio 0.50; and several characters of the male terminalia (see description and figures).

**Diphuia nasalis** Wirth

Figs. 8–15

Diphuia nasalis Wirth, 1956: 3; 1968: 5 [Neotropical catalog].

Description.—Small shore flies, length 1.35 to 1.75 mm.

**Head:** Frons sparsely invested with fine brownish microtomentum, microtomentum becoming sparser or lacking on 2 small areas laterad of posterior ocelli, 2 spots along the anterior margin, and sometimes a small spot in front of the anterior ocellus.

**Thorax:** Mesonotum sparsely invested with fine brownish to golden brown microtomentum, mostly subshiny to shiny; anepisternum with anteroventral ¼ to ½ bare of microtomentum, shiny, posterodorsal portion invested with fine, grayish microtomentum. Wing with costal vein ratio 0.58; M vein ratio 0.40.

**Abdomen:** 5th tergum with anterior margin essentially straight, at most very shallowly arched anteriorly (Fig. 9); 5th sternum undivided, as a narrow band connected dorsonly with anteroventral portion of 5th tergum (Fig. 8). Male terminalia (Figs. 10–15) as follows: epandrium narrow in lateral view, much higher than wide (Fig. 10); surstylus as long as cercus but almost twice its width, broadly rounded apically (Fig. 10); gonite in lateral view parallelogram-shaped, posterior angles produced into pointed processes, posterovertral process sinuate (Figs. 11, 12); aedeagal apodeme rounded anter-
Figs. 1–7. *Diphuia anomalana*. 1, 5th tergum and sternum, lateral view. 2, 5th tergum, dorsal view. 3, Male terminalia (epandrium, cercus, surstyli), lateral view. 4, Gonite, lateral view. 5, Internal male terminalia (gonite, hypandrium, aedeagal apodeme, aedeagus), lateral view. 6, Hypandrium and aedeagal apodeme, ventral view. 7, Aedeagus and aedeagal apodeme, lateral view. Scale bar = 0.1 mm.

Oventrally (Figs. 12, 13); aedeagus acutely pointed apically, in dorsal or ventral view bifurcate apically (Figs. 12–14); hypandrium in ventral view wider than long, anterior margin shallowly arched anteriorly (Figs. 12, 14, 15).

Type material.—The holotype female is labeled “Long Island[,] Deadman’s Cay[,] March 11, 1953/Van Voast—A.M.N.H. Bahama Isl. Exped Coll. E. B. Hayden/♂/♂HOLOTYPE Diphuia nasalis W. W. Wirth [red, gender and species name handwritten].” The holotype is point mounted, is in good condition (tip of right wing folded back on itself), and is deposited in the AMNH. Although the holotype was listed as a male (Wirth 1956: 4) and the specimen is so marked, it is a female.

Other specimens examined.—BAHAMAS. Crooked Island. Landrail Point. 5 Mar 1953, E. B. Hayden, L. Giovannoli (1 ♀; AMNH); Exuma Cays, Staniard Bay, 13 Jan 1953, E. B. Hayden (1 ♀; AMNH); Long Island. Deadman’s Cay, 11 Mar 1953, E. B. Hayden (2 ♂; AMNH, USNM). BELIZE. Stann Creek District: Bread and Butter Cay,
Figs. 8–15. *Diphia nasalis*. 8, 5th tergum and sternum, lateral view. 9, 5th tergum, dorsal view. 10, Male terminalia (epandrium, cercus, surstyli), lateral view. 11, Gonite, lateral view. 12, Internal male terminalia (gonite, hypandrium, aedeagal apodeme, aedeagus), lateral view. 13, Aedeagus and aedeagal apodeme, lateral view. 14, Hypandrium, aedeagal apodeme, and aedeagus, ventral view. 15, Hypandrium, lateral view. Scale bar = 0.1 mm.

Figs. 16–22. *Diphiia zatwarnickii*. 16, 5th tergum and sternum, lateral view. 17, 5th tergum, dorsal view. 18, Male terminalia (epandrium, cercus, surstyli), lateral view. 19, Internal male terminalia (gonite, hypandrium, aedeagal apodeme, aedeagus), lateral view. 20, Gonite, lateral view. 21, Aedeagus and aedeagal apodeme, lateral view. 22, Hypandrium, ventral view. Scale bar = 0.1 mm.

Type Diphuia nitida Stvt & Whlr [pink]/
TYPE 6695 [dark pink; number handwritten].” The holotype is point mounted, is in poor condition (the antennae and several setae are missing and the left side of the body and wings are covered partially with glue), and is deposited in the ANSP (6695). Sturtevant and Wheeler stated that this specimen is a male, but is clearly a female.

Distribution.—USA. New York: Long Island, Douglasston (just within the city limits of New York City).

Remarks.—This species is very similar to, and may be conspecific with, D. nasalis. Resolution of this question will depend on collection and study of additional material, especially males, from the type locality or a locality nearby. At present, the only known specimen of this “species” is the female holotype, which, as noted earlier, is in poor condition, making it impossible to ascertain its identity with certainty. I recognize the holotype as being different and possibly representing a separate species mostly because the few external features that are discernable, especially those of the head, are not within the variation among specimens of D. nasalis that I have studied. The shinier frons of the holotype appears to be unique. Furthermore, the distance between New York, which is the type locality of this species, and the nearest locality where D. nasalis is known to occur (North Carolina) is several hundreds of miles. As these populations are somewhat disjunct and are apparently different, I am provisionally recognizing them as representing separate species. If the populations prove to be conspecific, D. nitida is the senior synonym.

Diphuia zatwarnickii, New Species
Figs. 16–22

Description.—Small shore flies, length 1.40 to 1.90 mm.

Head: Frons moderately invested with brownish microomentum, microomentum sparse or lacking on 2 small areas la-
terad of posterior ocelli and 2 spots along the anterior margin.

Thorax: Mesonotum densely invested with brownish to golden brown microtomum, especially medially, along posterior portion of scutum and scutellum; anepisternum with fine investment of whitish microtomum. Wing with costal vein ratio 0.52; M vein ratio 0.42.

Abdomen: 5th tergum (Figs. 16, 17) about as high as long, anterior margin in dorsal view with deep, broadly V-shaped emargination (Fig. 17), posterior margin with sparse setae; 5th sternum clearly divided into 2 broad sternites that are connected only anteroventrally (Fig. 16). Male terminalia (Figs. 18-22) as follows: epandrium bulbous, shiny, in lateral view almost as wide as high (Fig. 18); cercus cylindrical; surstyli moderately long and narrow, parallel sided, width subequal to that of cercus but length shorter, apex angulate, pointed anteriorly, and bearing a few setulae (Fig. 18); gonite broad basally, with posteriorly extended process sheathing aedeagus, posterior apex of gonite bifurcate (Figs. 19, 20); aedeagal apodeme triangular in lateral view (Figs. 19, 21), narrowly produced dorsally; aedeagus in lateral view broad, thumblike, curved posteroventrad to an anteroventral point, in dorsal view becoming wider apically, apex broadly rounded (Figs. 19, 21); hypandrium in ventral view longer than wide, anterior margin with a small, anterior process (Fig. 22).

Type material.—The holotype male is labeled "JAMAICA 5mi.E.Negril 13March 1970 W. W. Wirth fresh marsh." The allotype female and three other paratypes (2 ♂, 1 ♀; USNM) bear the same label data as the holotype. Other paratypes are from: DOMINICA. Cabrit Swamp, 22-25 Mar 1965, W. W. Wirth (6 ♂, 2 ♀; USNM); Woodford Hill, 27 Feb 1965, W. W. Wirth (2 ♂; USNM). JAMAICA. Kingston, Fresh River, 24 Feb 1969, W. W. Wirth (8 ♂, 5 ♀; USNM); Milk River Bath, 11 Mar 1970, T. Farr, W. W. Wirth (7 ♂, 4 ♀; USNM); Rio Bueno, 21 Feb 1969, W. W. Wirth (1 ♂; USNM); Savanna La Mar, 13 Mar 1970, W. W. Wirth (2 ♂; USNM). The holotype is double mounted (minute nadel in poly porous block), is in excellent condition, and is deposited in the Smithsonian Institution (USNM).

Distribution.—West Indies: Dominica and Jamaica.

Etymology.—This species is named for Tadeusz Zatwarnicki, who first brought this species to my attention and who has contributed significantly to the study of shore flies.

Remarks.—This species is distinguished from D. nasalis and D. nitida by the sparsely microtomose mesofrons; the subshiny mesonotum that is very thinly invested with fine microtomum; the shiny anteroventral one-third to one-half of the anepisternum; and several characters of the male terminalia. This species is distinguished from D. anomala by characters of the male terminalia: especially the shorter, more robust surstyli; the gonite that is broadly bifurcate posteroventrally; and the more apically curved aedeagus (see description and figures).

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