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# A Revision of the Neotropical Genus *Dagus* Cresson (Diptera: Ephydridae)

JULIAN STARK[1]

## ABSTRACT

Three new species in the genus *Dagus* (*D. grimaldii*, *hermani*, and *mathisi*) endemic to the Dominican Republic are described. A revised diagnosis of the genus and a key to all the species are provided, as is an account of the feeding and mating behavior of *Dagus mathisi* and its possible sympatry with several other *Dagus* species. A phylogenetic analysis using the Hennig86 program is discussed, and a phylogeny and character transformation scheme are proposed. Biogeographic patterns are discussed with relation to other Caribbean groups and plate tectonic hypotheses.

## INTRODUCTION

This revision is a continuation of the study of *Dagus* and the Dagini that began with the description of *Ephydra pygmaea* by Williston (1896). *Dagus* is an ephydrine generally feeding upon algal mats in the splash areas of small to medium-size streams. The cephalopharyngeal skeleton of the third instar larvae and the puparium have been described only for *Dagus dominicanus* (Mathis and Zatwarnicki, 1988), and for one other dagine, *Diedrops roldanorum* (Mathis and Hogue, 1986). The lack of described larvae in the tribe precluded the use of larval characters in this study. The puparia and presumably the larvae are flattened ventrally with setulose lateral welts, these likely used in locomotion. Their dorsum is convex, with some degree of sclerotization and ornamentation. They have been found (although not as yet by the author) affixed to rocks in the same habitat as the adults (Mathis and Hogue, 1986; Mathis and Zatwarnicki, 1988; Willis Wirth, personal

[1] Scientific Assistant, Department of Entomology, American Museum of Natural History.

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commun.). *Dagus*, so far as it has been collected, shows high endemicity and is thus of interest biogeographically. Of the eight known species, six are single-island endemics, one is known from Cuba and the Dominican Republic, and one is circum-Caribbean. There is also some evidence to suggest a sister-group relationship between *Dagus* and the east Asian dagine *Psilephydra* (Mathis and Zatwarnicki, 1988, and this manuscript), further enhancing biogeographic interest. A historical review of *Dagus* and Dagini in general is given in the review of the tribe by Mathis (1982). A subsequent revision of *Dagus* by Mathis (1983) added the species *trichocerus* and *wirthi* to the formerly monotypic species *rostratus*. Mathis and Zatwarnicki (1988) described two further species, *dominicanus* and *spanglerorum*, as well as four new *Psilephydra*. The head and wing ratios outlined in Mathis (1983) are included here for consistency; the ratios have become less characteristic with the addition of new taxa, and I have removed them from the diagnosis of the genus. Unfortunately, wing characters were not closely examined in this study. Mathis and Zatwarnicki, however, made no note of characters other than the vein ratios (Mathis, 1983; Mathis and Zatwarnicki, 1988) within *Dagus*. Within Dagini, apomorphic states of wing characters are seen only in *Diedrops* and the *nemorosus* group of *Physemops* (Mathis, 1982). A possible character state uniting *Dagus dominicanus* and *D. spanglerorum*, namely a preapical ventral tuft of long setae on the foretibia, was determined to be autapomorphic for *spanglerorum*. This is reflected in a modified diagnosis for the two species given here.

## Acknowledgments

I am indebted to Wayne Mathis, of the Smithsonian Institution (USNM), for presenting me with a specimen that was to become *Dagus mathisi* and thus with the beginning of this manuscript. He also provided the ingroup and outgroup specimens without which I would not have been able to perform this analysis, and reviewed the manuscript. David Grimaldi, of this institution, has been of invaluable aid in offering advice, comments, and time on my behalf. Materials and the travel expenses have been paid for by his NSF Grant BSR 34504720. Jim Carpenter, Lee Herman, Bruce Lieberman, Jim Miller, Norman Platnick, Willis Wirth, and David Yeates made useful comments; Wirth also reviewed the manuscript. Peling Fong prepared the SEM photographs. Edward Bridges and Linda Krause mounted some of the specimens. Margaret Landry gave advice on the Latin, and Marilyn Stark advice on illustration techniques. Norman Platnick was another careful reviewer. Finally, I wish to thank Steven Arnone for giving me the information that led to my reentry into Entomology.

## TAXONOMY

### TRIBE DAGINI MATHIS, 1982
### GENUS *DAGUS*

*Dagus* Cresson, 1935: 345. Type: *Ephydra rostrata* Cresson, 1918, by original designation and monotypy. Wirth, 1968: 24 [neotropical catalog]. Mathis 1982: 20–23 [review]; 1983: 717–726 [revision].

DIAGNOSIS: The addition of three new species to the genus necessitates modification of the diagnosis given by Mathis (1983).

Ocellar bristles well developed, but very weak in *mathisi*. Three lateroclinate frontoorbital bristles, the anterior subequal to the two posterior. First flagellomere nearly twice the length of second antennal segment and greater than combined length of first 2 segments. Ventral portion of face ½ to ⅔ protrudent, uniformly arched vertically, pointedly arched transversally, with dark brown sparse microtomentum and metallic reflections on dorsum of protrusion in all species except *mathisi*, where the protrusion is completely covered with a lighter brown microtomentum. Facial setae sparse except along oral margin and from facial carina to posteroventral angle of face; longest bristles porrect and anaclinate at lateral extreme of face. Genal bristle present, but relatively small compared to the larger setae on head.

Prescutellar acrostichal setae variable. Anterior scutellar setae up to ½ length of posterior setae, generally less. Dorsocentral bristles stronger posteriorly, variably present presuturally. Posterior notopleural bristle variably positioned even with or above in-

sertion of anterior. Propleuron bare of setulae, humeral callus with one or two small setulae. Katepisternal bristle subequal to anepisternal, very weak in *mathisi*. Apex of $R_{2+3}$ well separated from $R_{4+5}$, the distance between these veins equal to the distance between $R_{4+5}$and M. Pulvilli lacking or greatly reduced, tarsal claws comparatively long, straight, oriented anteriorly, frequently held together through their length.

Epandrium in posterior view abbreviated dorsally, not forming cercal cavity including cerci; ventral portion variously broadly notched or tapered and cleft. Cerci at dorsum of epandrium. Aedeagal apodeme about 2× as long as wide, articulating variously with aedeagus. Aedeagus variable in shape and length, subequal to or exceeding length of epandrium.

## Described Species

*Dagus dominicanus* Mathis, 1988: 116.

Diagnosis: This species can be distinguished from others in the genus by the insertion of the posterior notopleural bristle at the same level as that of the anterior, and the lack of a clearly preapical ventral pencil of long, fine setae on the foretibia.

Type Locality: Dominican Republic: **La Vega**: 12 km S Constanza.

Distribution: Dominican Republic.

*Dagus rostratus* Cresson, 1918: 66 (*Ephydra*); 1935: 346 [combination, designated as type species of *Dagus*]. – Wirth, 1968: 28 [neotropical catalog]. – Mathis, 1982: 21–23 [review, lectotype designation]; 1983: 720–722 [revision].

*pygmaea* Williston, 1896: 402 (Ephydra) [preoccupied, Haliday 1833].

Diagnosis: This species can be distinguished from the others in the genus by its smaller size, well-developed chaetotaxy, and bare arista less than 3× the length of of the first flagellomere.

Type Locality: West Indies: St. Vincent: Perseverance Valley.

Distribution: West Indies (Cuba, Dominica, Jamaica, St. Vincent); Mexico south through Guatemala and Costa Rica to Venezuela and Brazil.

*Dagus spanglerorum* Mathis, 1988: 114.

Diagnosis: This species can be distinguished from its congeners and from *Dagus dominicanus*, which it closely resembles, by the insertion of the posterior notopleural bristle above that of the anterior, combined with the presence of a well developed, clearly preapical ventral pencil of long fine setae on the foretibia.

Type Locality: Dominican Republic: **La Vega**: 3.5 km S Constanza.

Distribution: Dominican Republic.

*Dagus trichocerus* Mathis, 1983: 724–725.

Diagnosis: This species is easily recognized by its aristal length, 3.5× the length of the first flagellomere, and the length of the longest aristal rays, which exceed the diameter of the arista at its base.

Type Locality: Cuba: **Pinar del Rio**: Soroa.

Distribution: Cuba, Dominican Republic.

*Dagus wirthi* Mathis, 1983: 722–724.

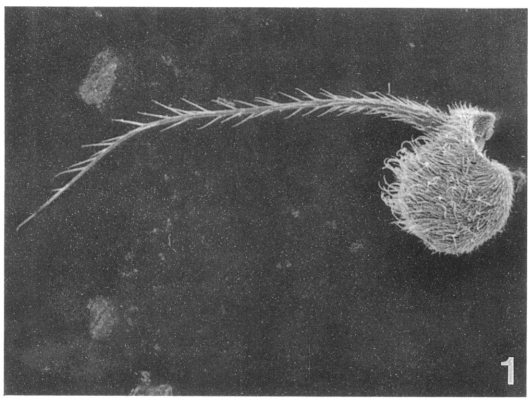
Diagnosis: This species can be recognized by the presence of 1–2 setulae on the hindcoxal strap.

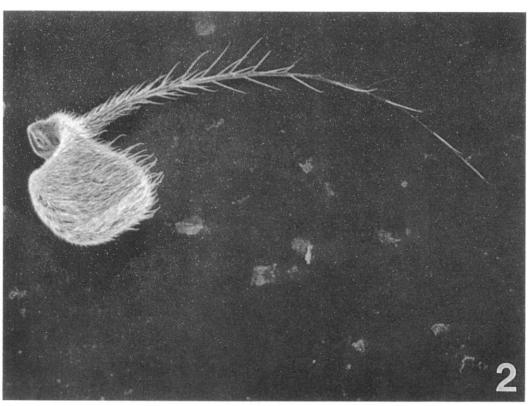
Type Locality: Jamaica: Port Parish.

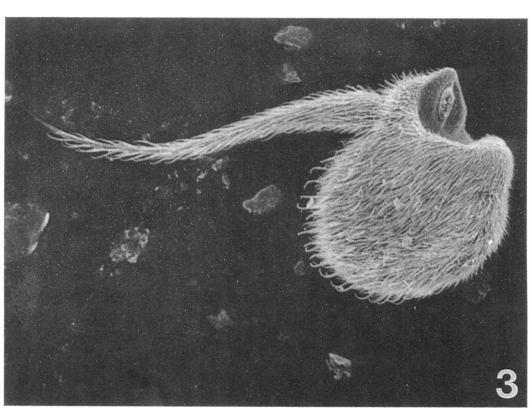
Distribution: Jamaica.

### Key to the Species of *Dagus*

1. Antennal insertions separated by a distance less than length of first flagellomere ..... 2 (*rostratus* species group)
1a. Antennal insertions separated by a distance equal to or greater than length of first flagellomere ..... 5
2. Posterior notopleural seta inserted clearly above level of anterior ..... 3
2a. Posterior notopleural seta inserted at level of anterior; face with central vertical crease ..... *hermani*, n. sp.
3. Arista less than 3× length of first flagellomere and bearing minute hairs shorter than width of arista at base ..... *rostratus*
3a. Arista longer than 3× length of first flagellomere and bearing rays at least as long as width of arista at base ..... 4
4. Longest aristal rays equal to width of arista at base (fig. 1); no dark stripe or unicolorous region posterior to genal suture ..... *grimaldii*, n. sp.
4a. Longest aristal rays exceeding width of arista at base (fig. 2); dark stripe present posterior to genal suture ..... *trichocerus*




Figs. 1–3. *Dagus* antennae. **1**. *D. grimaldii*. **2**. *D. trichocerus*. **3**. *D. mathisi*. (Figures not to same scale.)

5. Antennal insertions separated by a distance equal to length of first flagellomere ..... ..... 6(clade 2)

5a. Antennal insertions separated by a distance greater than length of first flagellomere .. ..... 7(clade 1)

6. Posterior notopleural seta inserted above level of anterior; hind coxal strap bearing 1–2 small setulae ..... *wirthi*

6a. Posterior notopleural seta inserted at level of anterior; hind coxal strap with tufts of microtomentum, but no setulae ..... ..... *dominicanus*

7. Ocellar setae very weakly developed; foretibia without preapical tuft of long setae ventrally ..... *mathisi*, n. sp.

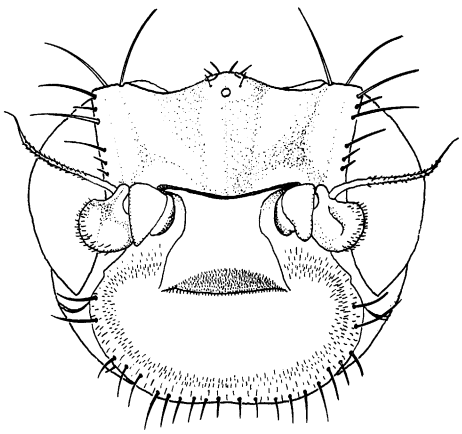
7a. Ocellar setae well developed; foretibia with preapical tuft of long setae ventrally ..... ..... *spanglerorum*

### ***Dagus mathisi,*** new species
Figures 3–5, 8, 10, 11, 21

DIAGNOSIS: This species resembles the other described species in the genus, but is unique in having ocellar bristles and the facial setae along the oral margin much more weakly developed.

DESCRIPTION: Small to medium-size shore flies, 2–4 mm. Entire frons densely microtomentose, appearing velvety; anteriorly dark brown with M-shaped pattern when viewed face-on, grading to lighter brown. Postvertically with two silvery-white fields inclined toward occipital foramen, their opposite ends opposing apices of the M-shaped pattern. Arista less than three times the length of first flagellomere, bearing minute hairs. Face protruded in lateral view, with anterodorsal surface less acutely angulate to oral margin than in the *rostratus* group; with brown microtomentum, bordered by silvery-white except at ptilinum, including the antennal insertions. Dorsal third of face prominent between antennal insertions. Gena moderately short, eye-to-cheek ratio 0.49 (defined: Mathis, 1983). Eye-width-to-face length ratio 0.70.

Chaetotaxy evident but less developed, both in strength and number of bristles, than in other species. Three equally and strongly developed dorsocentral setae, including laterally displaced posterior pair. Anteriormost postsutural fourth pair of dorsocentral setae less than ½ length of succeeding pair. Other dorsal thoracic setae weak, except for pair of well-developed supra-alar setae and two pairs of scutellar setae, the basal pair less than ½



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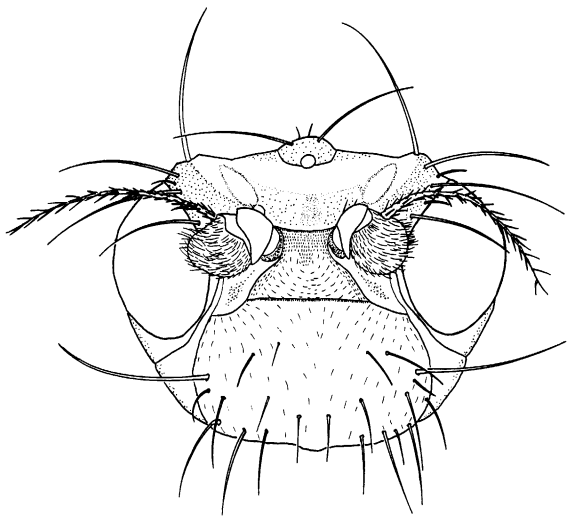

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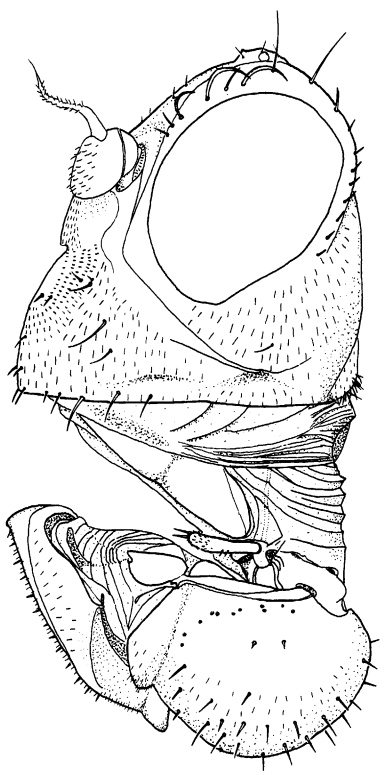

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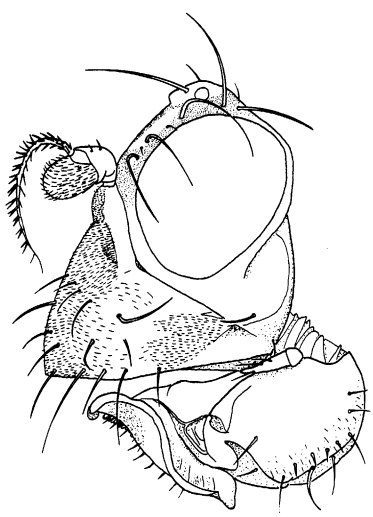

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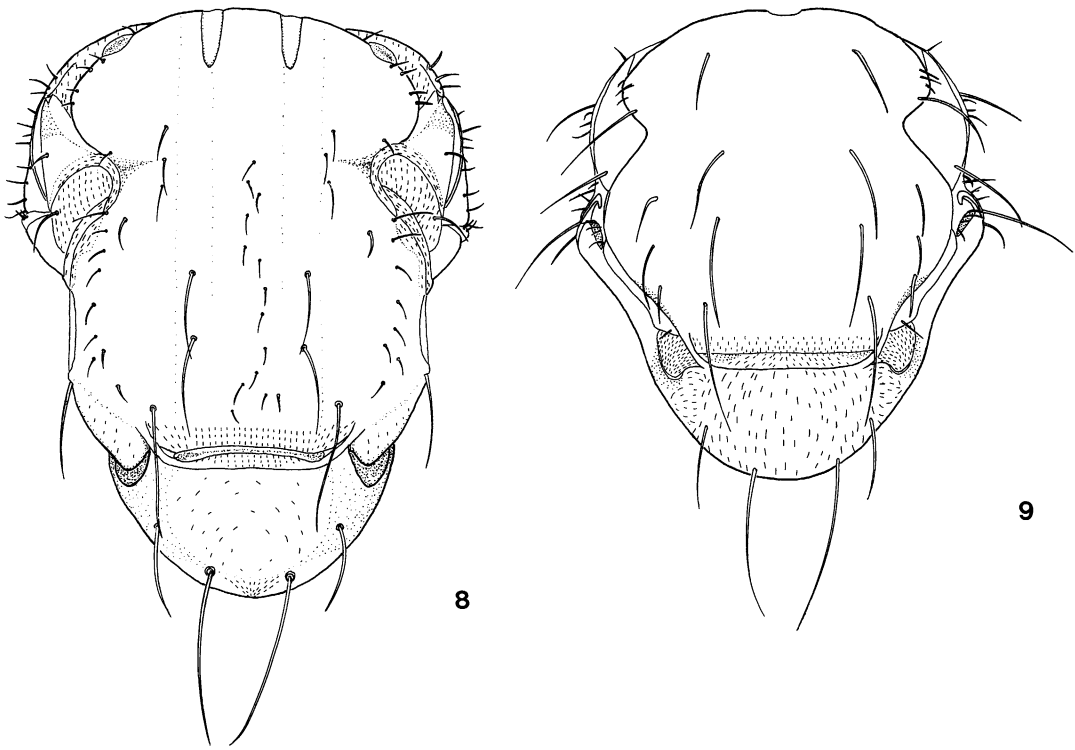
Figs. 4–7. *Dagus* heads. **4**. *D. mathisi*, frontal. **5**. *D. mathisi*, lateral. **6**. *D. grimaldii*, frontal. **7**. *D. grimaldii*,lateral. (Figures not to same scale.)

length of apical pair. Other smaller setulae present including one presutural and two postsutural dorsocentrals and ten intra-alars. Acrostichal setulae present postsuturally, irregularly arranged. Posterior notopleural seta stronger than and inserted above level of anterior. One small dorsally curved postpronotal seta. Anepisternum with small scattered setulae and one strong seta directed posteriad. Katepisternum with one weak porrect




Figs. 8, 9. *Dagus* thoraces. **8**. *D. mathisi*, dorsal. **9**. *D. grimaldii*, dorsal. (Figures not to same scale.)

seta. Pleuron otherwise bare, with grayish-white microtomentum. Hindcoxal strap bare of setae or setulae, but variously with tufts of microtomentum. Costal vein ratio 0.14 (Mathis, 1983); M-vein ratio 1.12.

Epandrium in ventral view rectangular, with small median cleft and two rounded, tapered, densely setulose lateral projections. Epandrium in lateral view somewhat bullet-shaped, ventrally rounded, with stronger arc transversely; tapered to apical point. Ventral surface of epandrium mainly flat. Gonite less than twice length of aedeagus, bearing two paired and one more posteriorly situated seta in ventral view. Apex of gonite sharply tapered, directed dorsad. Gonite fused medially with aedeagal apodeme. Aedeagus thin, gradually tapered, protrudent under apex of epandrium, and curved, hoodlike, behind cerci.

HOLOTYPE: Dominican Republic: **Peravia**: 18 km N San José de Ocoa, 830 m, July 24, 1986, D. A. Grimaldi, male (AMNH).

PARATYPES: Same data as holotype (AMNH), female (allotype), 1 male and 3 females.

OTHER MATERIAL: **Peravia**: 19 mi N San José de Ocoa, 3000 ft, July 30, 1991, near stream, Grimaldi and Stark, 83 males, 71 females (AMNH); same information, 10 specimens (deposited in USNM).

ETYMOLOGY: It is a pleasure to name this species after Wayne N. Mathis, Smithsonian Institution, who indicated its new species status to me.

### ***Dagus grimaldii,*** new species

Figures 1, 6, 7, 9, 12, 13, 27

DIAGNOSIS: This species resembles the other described species in the genus but may be distinguished from them by its gray color, as in *mathisi*, combined with its long, haired arista.

DESCRIPTION: Small to medium-size shore flies, 1.5–2.2 mm. Entire frons densely and

finely microtomentose, appearing velvety. Postvertically with two silvery-white fields inclined toward occipital foramen, their dorsal origin lying between dorsalmost orbital and outer vertical setae. Arista less than four times length of first flagellomere, with prominent hairs, the largest equal in length to the width of the arista at its base. Face protruded in lateral view, with anterodorsal surface bare and intermediately angulate to oral margin between the *rostratus* and *wirthi* groups. Prominence between antennal insertions less than ¼ depth of face, with glabrous lower area of face extended to corners of prominence. Gena with silver-white microtomentum and of moderate depth, eye-to-cheek ratio 0.48. Eye-width-to-face length ratio 0.61.

Chaetotaxy typical for genus: four well-developed dorsocentral setae, one pair presutural, bases of penultimate pair slightly displaced medially. Posterior dorsocentrals one-half again as long as preceding pairs. Four pairs of intra-alar setae, first pair subequal to longest dorsocentrals, the other three pairs about one-half length of dorsocentrals. One weakly developed postalar seta. Acrostichal setae absent. Two pairs of scutellar setae, basal pair ⅓ length of apical pair. Notopleural setae equally developed, posterior seta inserted well above the level of the anterior. Single postpronotal seta well developed and directed posteriad. Row of small setulae running dorsoventrally on anepisternum, followed by row of four setae directed posteriad at mid-height on border with anepimeron; penultimate ventral seta more than twice length of other three. Katepisternum with well-developed porrect seta. Scutum covered with brown microtomentum, but less densely than on head. Microtomentum grayish on pleuron and sides of legs, brown on dorsal surfaces of legs. Hindcoxal strap bare. Costal vein ratio 0.17; M-vein ratio 1.1.

Epandrium in ventral view roughly quadrate, but not nearly as quadrate as in *wirthi* (Mathis, 1983) and lacking median cleft; anterior corners setulose, but more sparsely than in *mathisi* or *dominicanus*. Lateral view of epandrium bullet-shaped, ventrally rounded, of about even curvature longitudinally and transversely, not tapered to a point; ventral surface flat. Gonite about one-half length of aedeagus, with four setae apically and one basoventrally. Base of gonite conical, tapered to clublike apex. Gonites articulated with dorsum of epandrium and joining aedeagal apodeme and each other at medial point. Aedeagus somewhat stout, similar to that in *dominicanus*, protrudent under apex of epandrium and with hoodlike curve behind cerci.

HOLOTYPE: Dominican Republic: **Peravia**: 18 km N San José de Ocoa, 830 m, July 24, 1986 D. A. Grimaldi, male (AMNH).

PARATYPES: Same data as holotype (AMNH), female (allotype), 1 male and 2 females.

OTHER MATERIAL: Dominican Republic: **Peravia**: 19 mi N San José de Ocoa, 3000 ft, July 30, 1991, near stream, Grimaldi and Stark, 3 females; **La Vega**: 12 mi W Bonao, 3100 ft, August 3, 1991, Grimaldi and Stark, 1 female.

ETYMOLOGY: This species is named after David A. Grimaldi, AMNH, who introduced me to the uniqueness of the Diptera.

### ***Dagus hermani,*** new species
Figure 14

DIAGNOSIS: This species resembles the other described species in the genus but may be distinguished from them by its smaller size, and from the remaining species by the insertion of the posterior notopleural bristle at the same level as the anterior.

DESCRIPTION: Small to medium-size shore flies, 1.7–2.1 mm. Entire frons densely and finely microtomentose, appearing velvety, as in the other two species. Arista less than four times length of first flagellomere, with minute hairs basally as in *grimaldii*. Longest aristal rays equal in length to diameter of aristal base. Face protruded in lateral view with anterodorsal surface almost glabrous, having only widely spaced minute hairs; intermediately angulate to oral margin between extremes of *trichocerus* and larger Dominican species, and uniquely bearing a depression or crease medially from frons to oral margin. Prominence between antennal insertions about ⅓ depth of face, and with carinalike ridge running dorsoventrally. Gena of microtomentum silver-white, eye-to-cheek ratio 0.43. Eye-width-to-face length ratio 0.53.

Typical chaetotaxy: Four well-developed dorsocentral setae, one pair presutural, bases

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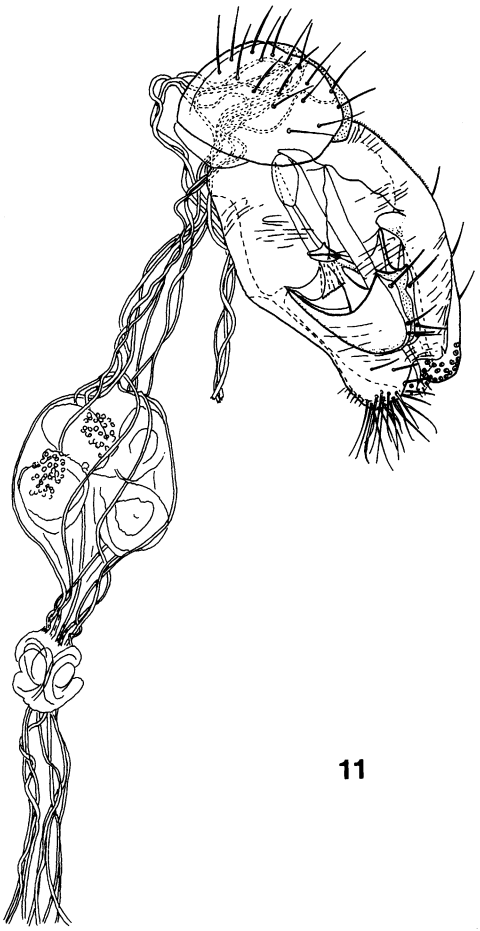

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Figs. 10–13. *Dagus* male genitalia. **10**. *D. mathisi*, ventrolateral. **11**. *D. mathisi*, lateroventral. **12**. *D. grimaldii*, ventrolateral. **13**. *D. grimaldii*, lateroventral. (Figures not to same scale.)

of the penultimate pair slightly displaced medially. Dorsocentrals graduated in size proceeding posteriorly. Four pairs of intra-alar setae, first pair subequal to the longest dorsocentrals, the other three pairs about ½ length of dorsocentrals. One weakly developed postalar seta. Two pairs of acrostichal setae present, one presutural, the second prescutellar. Two pairs of scutellar setae, the basal pair ½ length of apical pair. Notopleural setae equally developed, posterior seta inserted at or slightly above level of anterior one. Single weakly developed postpronotal seta directed posteriad. Row of small setulae running dorsoventrally on anepisternum, at mid-height extending posteriorly to row of three setae directed posteriad on border with anepimeron; dorsal seta more than twice length of other two. Katepisternum with well-developed dorsally curved seta, and much smaller anterodorsal setula. Scutum covered with brown microtomentum, but less densely than on head. Microtomentum grayish on pleuron and sides of legs, brown on dorsal surfaces of legs. Hindcoxal strap bare. Costal vein ratio 0.213; M-vein ratio: 1.326.

Epandrium in ventral view rectangular, with prominent and wide median cleft. Anterior corners more densely setulose than in *grimaldii*, but more sparsely than in *mathisi* or *dominicanus*. Lateral view of epandrium bullet-shaped, ventrally rounded, of about even curvature longitudinally and transversely, not tapered to a point; ventral surface

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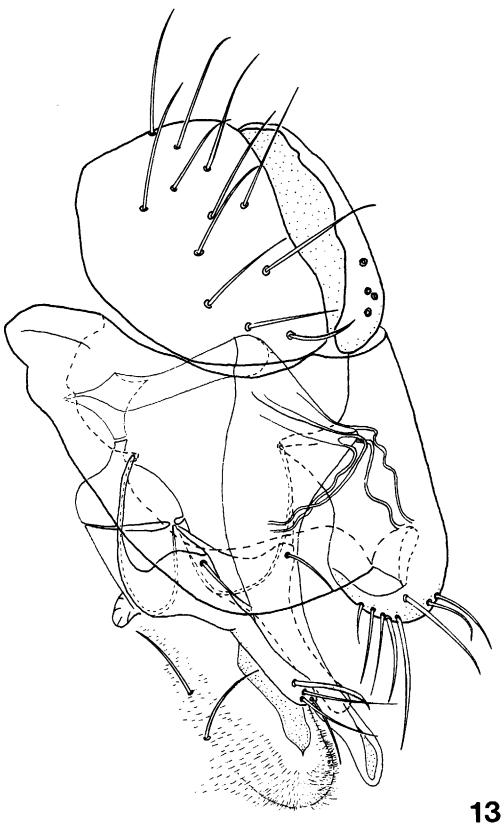

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of epandrium flat. Gonite less than one-half length of aedeagus, with apparently seven ventrally directed setae in apical one-third. Base of gonite conical, with indentations on inner margin, tapering to dorsally bent apex. Gonites articulated with lateral margins of epandrium and aedeagal apodeme. Aedeagus strongly and uniquely bent ventrally, articulated with aedeagal apodeme dorsally and ventrally by a process extending from inner surface of epandrium. Membranous extension of aedeagal apodeme extended posteriorly to cerci.

HOLOTYPE: Dominican Republic: **La Vega**: 12 mi W Bonao, 3100 ft, August 3, 1991, Grimaldi and Stark, male (AMNH).

PARATYPES: Same data as holotype (AMNH), female (allotype), 2 males and 3 females.

ETYMOLOGY: This species is named after Staphylinologist Lee Herman, AMNH, who was both a resource and an inspiration on the collecting trip.

## OBSERVATIONS OF FEEDING AND MATING BEHAVIOR, AND A NOTE ON POSSIBLE SYMPATRY

*Dagus mathisi* individuals were observed on a 6-m high vertical seepage along an outcropping in Peravia, 19 mi north of San José de Ocoa in the Dominican Republic, at an elevation of 3000 ft (fig. 15). The seepage is characterized by spray onto rocks intermingled with moss and low ground cover. Brown algal scum covered the rock. The specimens of *Dagus* were creeping slowly over the rocks and feeding with very rapid labellar extensions several times per second. Individuals disturbed by droplets responded with short hopping flights backward or forward. The *Dagus* were seemingly indifferent to much larger dolichopodids that walked among them.

An interesting mating formation was noted with the flies aligned vertically, resting on an outcropping inclined approximately 110° (fig.

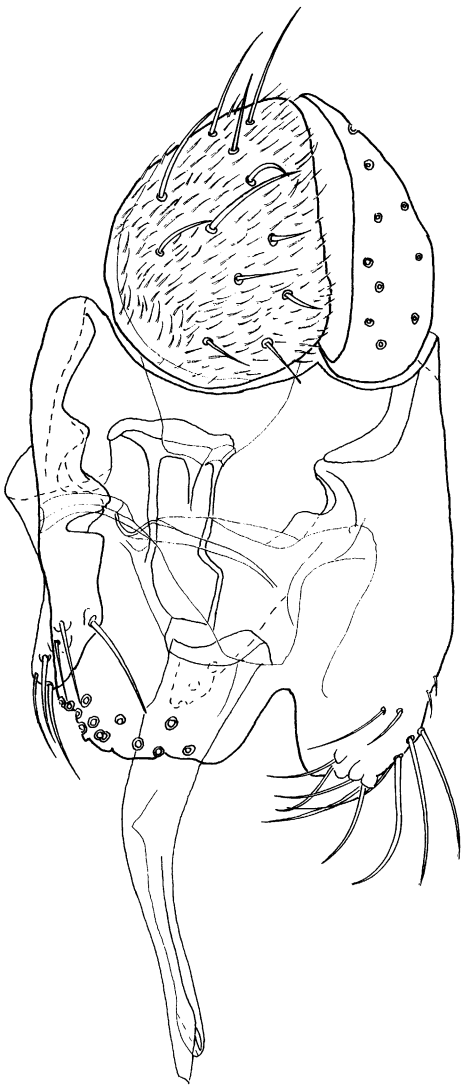


Fig. 14. Male genitalia of *Dagus hermani*, ventrolateral.

16). This group of about 20 flies was at least twice as large as any of the randomly arranged feeding groups (fig. 17). A sample of the group was taken, and it was later revealed to contain only males. Such an arrangement might constitute a lek. No feeding was observed in the group. Lekking males would copulate with a female if she approached. Isolated males also copulated in random feeding groups. Copulation proceeded with the males moving mostly downward, abdomen first, but sometimes upward to the side of the female (mainly the left side) then hopping onto the female, pushing her wings to either side, copulating for a few seconds, then hopping off to the rear. Males would mount several females in succession, and the females continued to feed, seemingly undisturbed.

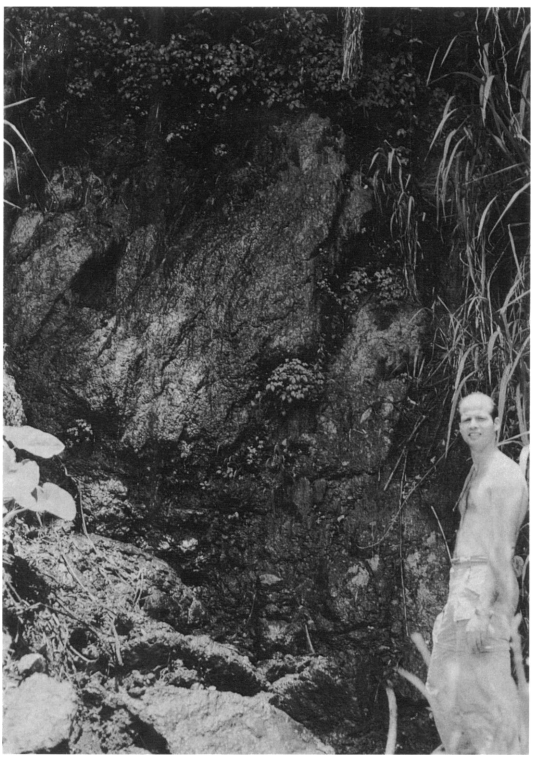


Fig. 15. Collecting locality: Peravia, 19 mi N San José de Ocoa.

It is worth mentioning that all the species of *Dagus*, with the exception of *rostratus* and *wirthi*, were collected at this locality. This may be attributable to exceptional and natural sympatry of the species, or, more likely, to "desperation" as the species crowd into the very little and probably marginal (*D. grimaldii* was relatively uncommon) habitat which remains in the face of almost total deforestation.

## CHARACTERS USED IN THE CLADISTIC ANALYSIS

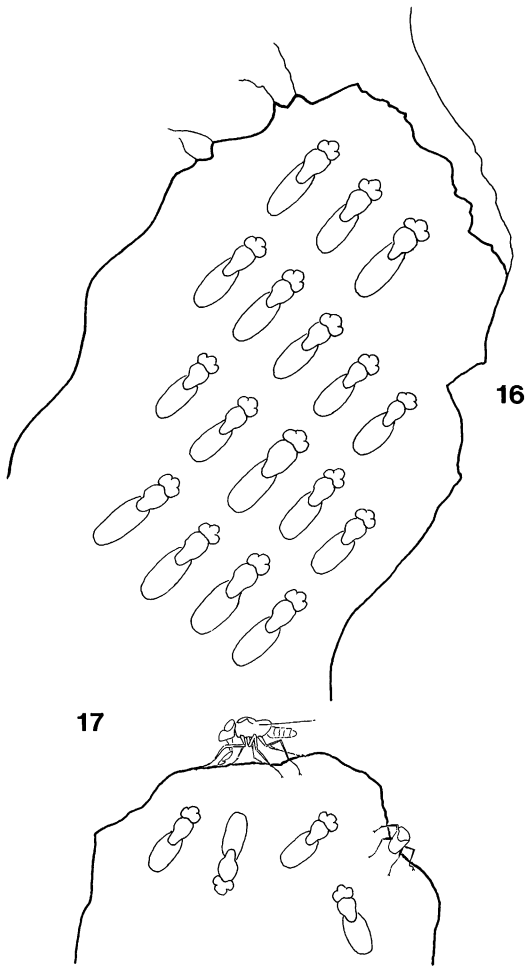
This is a list of the characters and states entered into the Hennig86 matrix that follows this section. The matrix corresponds to

the listing, i.e., the leftmost character is the first. "A" or "P" (or "0") represents apomorphic or plesiomorphic polarity evaluations I have made. Initial polarity decisions were reevaluated after the program was run. The outgroup taxa are from the other three genera in the tribe Dagini (Mathis, 1982). A fifth genus, *Brachydeutera* Loew, which has been only tentatively placed in the tribe (Mathis, 1990; personal commun.), possesses several characters rather divergent from the other four, and was not included in the analysis. An attempt was made to include outgroup species that among them displayed the total character variation for the given genus. This is why three species of *Physemops* Cresson and two of *Diedrops* Mathis and Wirth were included. Both species groups of *Physemops* (Mathis, 1982) are represented, and a new species near *wheeleri* (henceforth referred to as nr. *wheeleri*), of which several individuals were available, was dissected for examination of the ventral receptacle. Unfortunately, a specimen of the *fluvialis* group of *Psilephydra* was not available. *Psilephydra fluvialis* was coded as possible from Mathis (1982) and Mathis and Zatwarnicki (1988).

## Head

**1.** The shape of the face is generally shield-like in the Dagini (0), and slightly protrudent in the *fluvialis* group of *Psilephydra* (1). In *Dagus*, it becomes either shallowly protrudent and rectangular (*mathisi*, *spanglerorum*) (2), more protrudent and ovate (*dominicanus*, *wirthi*) (3), or markedly protrudent (*grimaldii*, *hermani*, *rostratus*, *trichocerus*) (4).

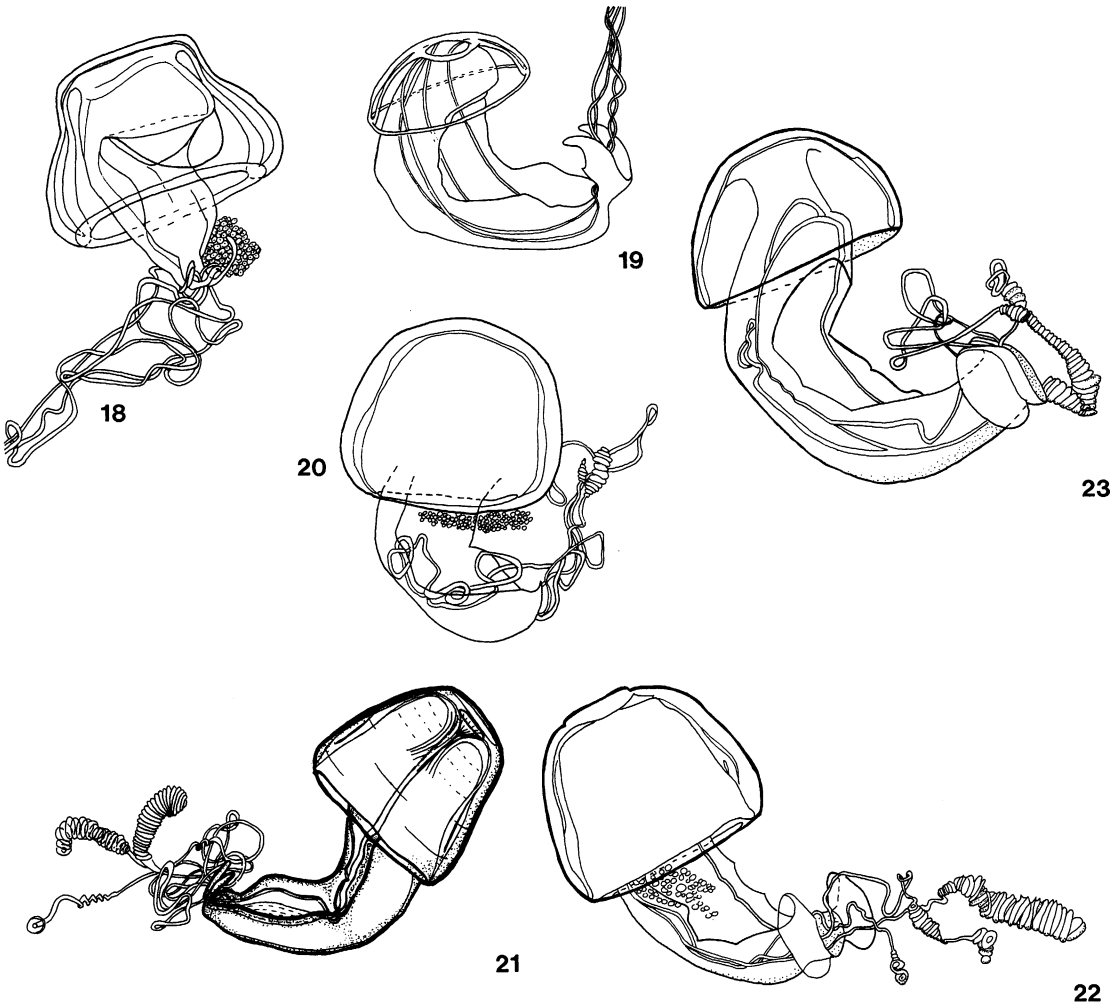
**2.** The distance between the bases of the antennae is a three-state character in the Dagini. In *Diedrops*, *Physemops azul*, *fairchildi*, *maldonadoi*, and *panops*, *Psilephydra*, and *Dagus grimaldii*, *hermani*, *rostratus*, and *trichocerus*, the antennae lie closer together than the length of the first flagellomere (0). In *Physemops nemorosus* and in *Dagus dominicanus* and *wirthi*, the antennae are separated by about the length of the first flagellomere (1). In *Physemops* nr. *wheeleri*, *Dagus mathisi*, and *D. spanglerorum*, the antennae are separated by more than the length of the first flagellomere (2).




Figs. 16, 17. Observed aggregations of *Dagus mathisi*. **16.** "Lek" of *Dagus mathisi*. **17.** Random feeding group of *Dagus mathisi*.

**3.** Aristal length in the Dagini can be distilled to a two-state character. An aristal length less than three times the length of the first flagellomere is the widespread case in the tribe, occurring in all four genera (P). In *Dagus*, *Physemops*, and *Psilephydra*, however, several of the species (*Dagus*: *trichocerus*, *grimaldii*, *hermani*; *Physemops*: *nemorosus* group; *Psilephydra*: all except *fluvialis*) have aristae exceeding three times the length of the first flagellomere (A).

**4.** In Dagini, there are three states of development of aristal rays. In *Diedrops* and *Psilephydra*, the "rays" are less in length than the diameter of the arista at its base (0). In




Figs. 18–23. Ventral receptacles of *Physemops*, *Diedrops*, and *Dagus*. **18**. *Physemops*, nr. *wheeleri*. **19**. *Diedrops steineri*. **20**. *Dagus spanglerorum*. **21**. *Dagus mathisi*. **22**. *Dagus dominicanus*. **23**. *Dagus wirthi*. (Figures not to same scale.)

*Dagus* and *Physemops*, three states are present: the aforementioned (*Dagus*: *dominicanus*, *mathisi*, *rostratus*, *spanglerorum* , *wirthi*; *Physemops*: *azul*, *fairchildi*); a second in which the longest rays equal the diameter (*Dagus*: *grimaldii*, *hermani*; *Physemops: nemorosus*, nr. *wheeleri*) (1); and the third in which the rays markedly exceed the diameter (*Dagus*: *trichocerus*; *Physemops*: *maldonadoi*, *panops*, *wheeleri*) (2).

**5**. Development of the genal bristle occurs in three states in Dagini. It is strongly developed in *Dagus dominicanus*, *rostratus*, *trichocerus* and *wirthi*, *Diedrops aenigma*, *hitchcocki* and *steineri*, and the *Psilephydra fluvialis* group (0). It is weakly developed in *Dagus grimaldii*, *hermani*, *mathisi* and *spanglerorum*, *Diedrops roldanorum*, *Physemops maldonadoi*, *nemorosus*, *panops* and *wheeleri*, and the *Psilephydra cyanoprosopa* group (1). It is absent in *Physemops azul* and *fairchildi* (2).

**6**. The development of the ocellar setae may also be summarized in three states. They are well developed in all *Dagus* except *mathisi*, where they are weak (1), the *panops* group of *Physemops*, and in *Psilephydra* (2). They are absent in *Diedrops* and the *nemorosus* group of *Physemops* (0).

7. A darker coloration either in the form of a stripe or a unicolorous region to the posterior of the head occurs at the parafacial posterior to the genal suture in all the genera except *Psilephydra* (P). Exceptions are *Diedrops roldanorum* and *Dagus grimaldii*, *hermani*, and *mathisi* (A).

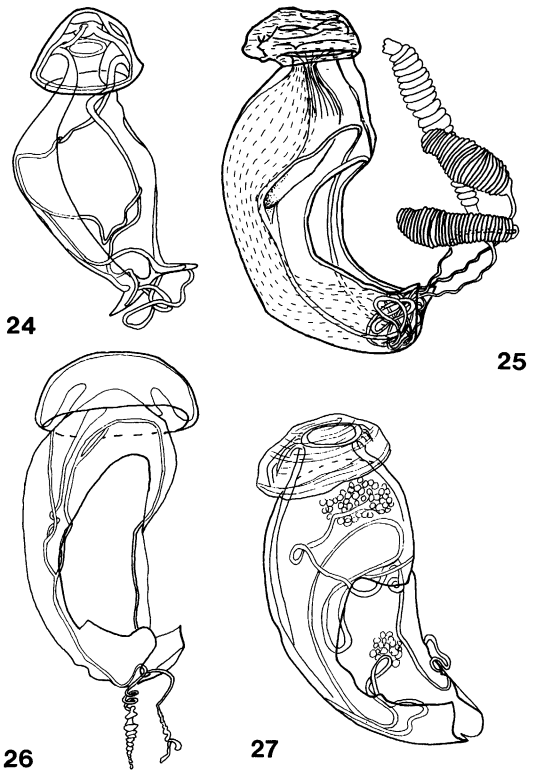
8. The presence of strongly developed lateral mid-facial setae is unique to *Dagus*, and absent in the other three genera (0). Within *Dagus*, there is a grade from weakly developed setae (*mathisi*, *spanglerorum*) (1), to two to three well-developed setae (*rostratus*, *trichocerus*, *wirthi*) (2), to one well-developed seta (*dominicanus*, *grimaldii*, *hermani*) (3).

## Thorax

9. The hindcoxal strap in Dagini has variable vestiture at its posteromedial extremity. It is bare in *Diedrops steineri*, *Psilephydra cyanoprosopa*, *Physemops* except for *fairchildi* and *nemorosus*, and *Dagus grimaldii*, *hermani*, *rostratus*, and *trichocerus* (0). In *Physemops fairchildi* and *nemorosus*, as well as *Dagus dominicanus*, *mathisi*, and *spanglerorum*, there are tufts of microtomentum (1). In *Dagus wirthi* there are one or two setulae, in *Psilephydra kaskiensis* there is variable setation, and in *nepalensis*, one setula (2).

10. Presutural dorsocentral setae are either weakly (P) or strongly (A) developed. The dorsocentrals are weakly developed in *Physemops*, *Psilephydra*, *Diedrops roldanorum*, and *Dagus mathisi*, *rostratus*, *spanglerorum*, and *trichocerus*. They are strongly developed in *Diedrops steineri*, and in *Dagus dominicanus*, *grimaldii*, *hermani*, and *wirthi*.

11. The insertion of the posterior notopleural setae relative to the anterior is an important character in the Dagini. In *Dagus dominicanus* and *hermani*, *Diedrops roldanorum*, and the *cyanoprosopa* group of *Psilephydra*, the posterior notopleural seta is inserted at or only slightly above the level of the anterior notopleural seta (0). In *Dagus mathisi*, *spanglerorum*, and *wirthi*, *Diedrops steineri*, and all *Physemops*, the insertion is clearly above that of the anterior seta, but by less than one-half the length of the posterior notopleural seta (1). In *Dagus grimaldii*, *rostratus*, and *trichocerus*, the posterior seta is inserted above the level of the anterior by one-half or more of its length (2).




Figs. 24–27. Ventral receptacles of the *rostratus* group. **24**. *Dagus rostratus*. **25**. *D. trichocerus*. **26**. *D. hermani*. **27**. *D. grimaldii*. (Figures not to same scale.)

## Male Genitalia

12. Due to modifications sufficiently far from the morphology in *Dagus*, epandrial shape appears difficult to characterize relative to the ingroup. Within *Dagus*, three states are apparent. In *rostratus*, *spanglerorum*, and *trichocerus*, the epandrium tapers sharply anteriorly and is cleft at the anterior end (0). In *hermani* and *mathisi*, it is rectangular (1). In *dominicanus*, *grimaldii*, and *wirthi*, it is quadrate (most obvious in *wirthi*) (2).

## Ventral Receptacle (figs. 18–27)

13. The cap of the ventral receptacle is either narrower or wider than the base to which it attaches. Unfortunately, only the outgroup

specimens *Diedrops steineri* and *Physemops* nr. *wheeleri*, from dissections, and *Diedrops aenigma*, figured in Mathis and Wirth, 1976, were available for examination. In these three, as well as in *Dagus dominicanus*, *hermani*, *mathisi*, *spanglerorum*, and *wirthi*, the cap is wider (P). In *Dagus grimaldii*, *rostratus*, and *trichocerus*, it is narrower (A).

**14**. The terminus of the base of the ventral receptacle is variably lobed. In *Diedrops steineri* and *Dagus dominicanus* and *wirthi*, the terminus is broadly lobed (0). In *Physemops* nr. *wheeleri* and *Dagus mathisi* and *rostratus*, there are thin, fingerlike lobes (1). In *Dagus grimaldii*, *hermani*, *spanglerorum*, and *trichocerus*, lobes are absent (2).

**15**. The shape of the ventral receptacle's cap is quite variable in Dagini. In *Diedrops steineri* and *Dagus hermani* and *wirthi*, it is hemispherical (0). In *Physemops* nr. *wheeleri*, it is umbate: conical tapering to a more cylindrical shape (1). In *Diedrops aenigma* and *Dagus dominicanus*, *mathisi*, and *spanglerorum*, it is truncate-conical (2). In *Dagus rostratus*, it is a small conus (3). In *Dagus grimaldii* and *trichocerus*, it appears compressed and wrinkled (4).

**16**. Cap weakly (0), somewhat (1), or heavily (2) sclerotized. The sclerotization of the ventral receptacle's cap occurs in three states in the Dagini. In *Diedrops steineri*, and *Dagus grimaldii* and *trichocerus*, it is weakly sclerotized (0). In *Physemops* nr. *wheeleri*, and *Dagus hermani*, *rostratus*, and *wirthi*, it is somewhat more sclerotized (1). In *Dagus dominicanus*, *mathisi*, and *spanglerorum*, it is heavily sclerotized (2).

## RESULTING TOPOLOGIES FROM HENNIG86 PROGRAM: DISCUSSION

After several phases of character coding and selection and the use of differing outgroup taxa, the final characters, states, and taxa were coded into a 19 taxon by 16 character matrix (table 1). Characters 3, 9, 10, and 13 are binary. 2, 4, 5, 6, 7, 11, 12, 14, and 15 are three-state; 8 is four-state; and 1 and 16 are five-state. The Hennig86 program, run with the ie algorithm and all multistates additive, found four trees (figs. 28–31) of 79 steps, with a consistency index (ci) of 0.41 and a retention index (ri) of 0.64. There is no difference in ingroup topology in these trees. Outgroup differences involve the relative placement of four taxa, *Diedrops rolandorum* and *steineri*, and *Psilephydra fluvialis* and *nepalensis*. In trees 1 to 3 (figs. 29–31), *Diedrops steineri* is placed in the basal polytomy, while in tree 0 (fig. 28), *Diedrops rolandorum* is in the basal polytomy. The other topological differences regard the relationships of *Dagus* as a monophyletic group to various arrangements of *Psilephydra fluvialis* and *nepalensis*. In trees 0 and 1 (figs. 28 and 29) *Dagus* is sister to a clade containing *fluvialis* and *nepalensis*. In tree 2 (fig. 30) there is a nested (*fluvialis* (*nepalensis* (*Dagus*)) topology. In tree 3 there is an unresolved *fluvialis* / *nepalensis* /*Dagus* trichotomy.

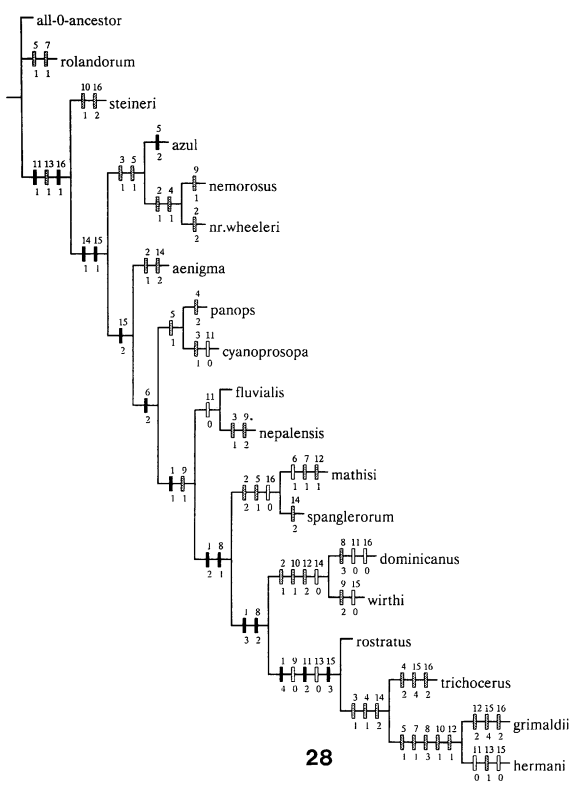
Running the matrix using successive weighting resulted in three trees (figs. 32–34) of 156 steps, a ci of 0.62, and a ri of 0.88. Topologies of these trees are identical with trees 1–3 of the unweighted data set, the tree with *Diedrops rolandorum* in the basal polytomy not appearing. Character optimization differences of these trees, as well as those of the unweighted trees, are summarized in table 2.

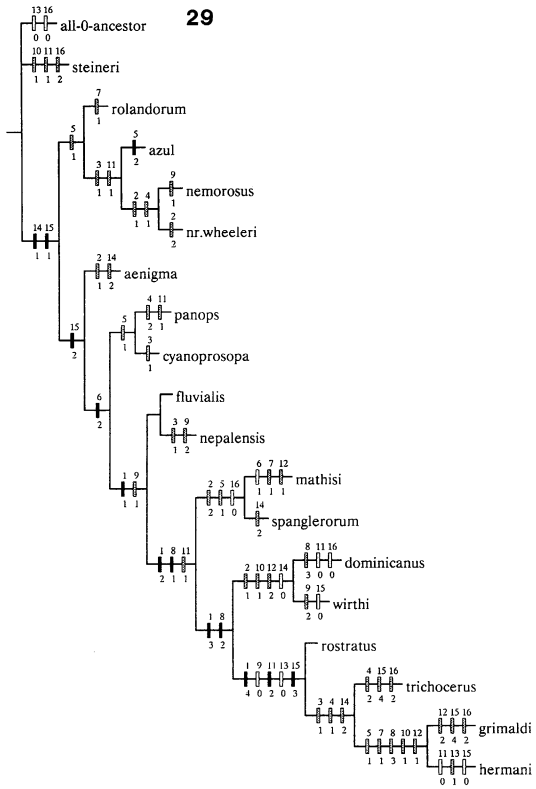
Although the proposition of the phylogeny of the tribe as a whole is outside the scope of this paper, the inclusion of *Dagus* within a clade containing members of *Psilephydra*, specifically the *fluvialis* group, *fluvialis* and *nepalensis*, is in agreement with the last-stated position of Mathis and Zatwarnicki (1988), of a possible sister-group relationship between the two genera. Common support is found in state 1 of character 1, a slightly protrudent face, and state 1 of character 9, a tomentose hind coxal strap. This may merely be a result of ambiguous character information in the outgroup, however, as there are several questionable groupings there that undoubtedly arise from missing data.

## CHARACTER TRANSFORMATION

From the mutually corroborating ingroup topology found in both the weighted and unweighted data sets, the character transformations within *Dagus* may be summarized and six clades proposed:

1. A shallowly protrudent and rectangular




Figs. 28, 29. CLADOS output of Hennig86 derived unweighted trees (refer to text). Shading of hashmark indicates homoplasy of state: solid = non-homoplasious forward; intermediate = homoplasious forward; light = Homoplasious reverse. **28**. Tree-1. **29**. Tree-2.

face is a synapomorphy for *Dagus*. *D. mathisi* and *D. spanglerorum* (clade 1) retain this characteristic. In their sister clade (2) containing (*D. dominicanus* / *D.wirthi*)(*rostratus* group), the plesiomorphic condition has become a more protrudent and ovate face, exhibited by *D. dominicanus* and *D. wirthi* (clade 3). The most derived, markedly protrudent face is seen in the *rostratus* group (clade 4).

2. The distance between the antennal insertions shows no clear transformation in *Dagus*. Distance greater that the length of the first flagellomere is a synapomorphy for clade 1. Clade 3 is supported by the antennae being inserted at a distance equal to the length of the first flagellomere.

3. Antennae less than three times the length of the first flagellomere represent a pleisiomorphic state in *Dagus*. Length greater than three times the length of the first flagellomere is a synapomorphy for the (*D. trichocerus*)(*D. grimaldii* / *D. hermani*) clade (clade 5).

4. Having the longest aristal rays less in length than the diameter of the arista at its base is plesiomorphic in *Dagus*. In clade 5, they are synapomorphically equal in length to the basal aristal diameter, and autapomorphically modified in *D. trichocerus* to being greater in length than the diameter of the arista.

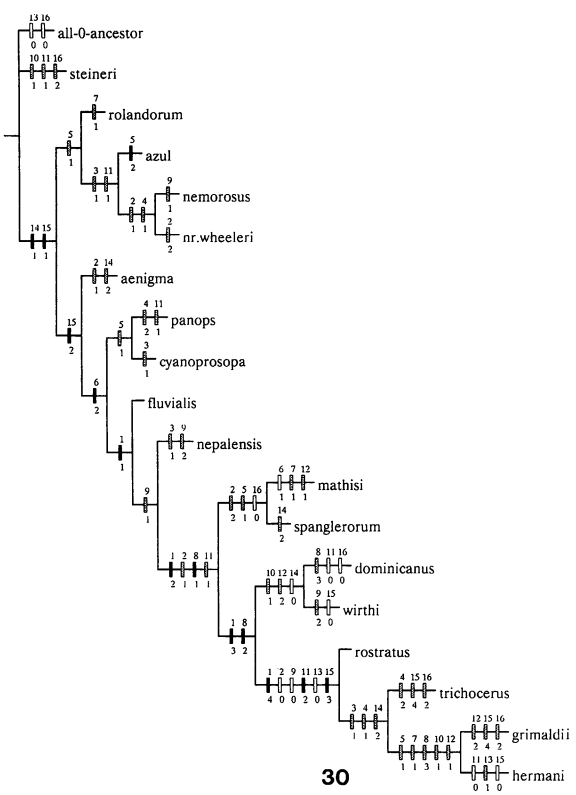
5. The genal bristle is plesiomorphically strong in *Dagus*. Weak development of the genal bristle is independently synapomorphic for both clade 1 and in (*D. grimaldii* / *D. hermani*) (clade 6).

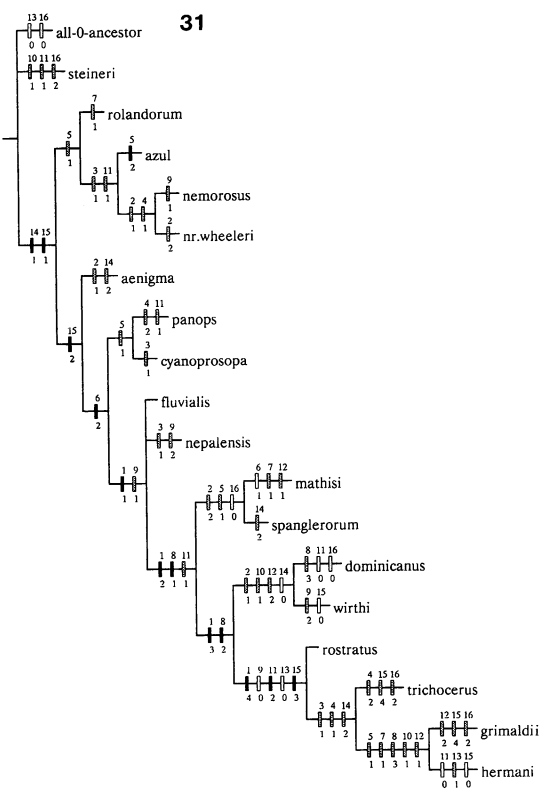
6. Well-developed ocellar setae are pleisomorphic in *Dagus*. Weak development of the ocellar setae is autapomorphic in *Dagus mathisi*.

7. A discontinous ventral head coloration

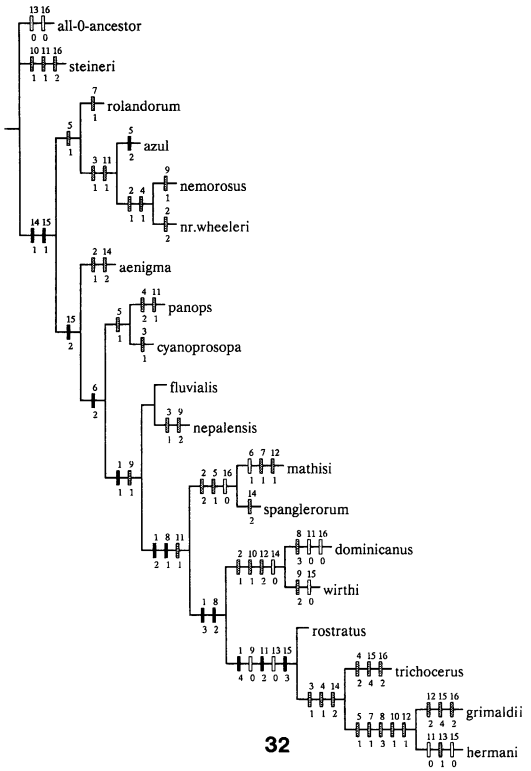
TABLE 1
**Data Matrix**

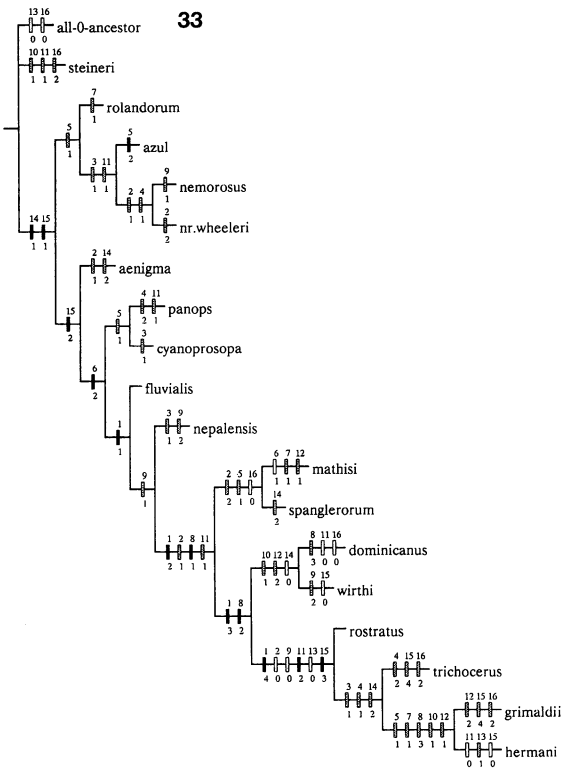
| | Head | Thorax | ♂ Genitalia | ♀ Receptacle |
|---|---|---|---|---|
| All-zero ancestor | 00000000 | 000 | 0 | 0000 |
| *Diedrops aenigma* | 0100000? | ?0? | ? | 122? |
| *Diedrops roldanorum* | 00001010 | 000 | ? | ???? |
| *Diedrops steineri* | 00000000 | 011 | ? | 1002 |
| *Physemops azul* | 00102000 | 001 | ? | ???? |
| *Physemops nemorosus* | 01111000 | 101 | ? | ???? |
| *Physemops panops* | 00021200 | 001 | ? | ???? |
| *Physemops* sp. nr. *wheeleri* | 02111000 | 001 | ? | 1111 |
| *Psilephydra cyanoprosopa* | 00101200 | 000 | ? | ???? |
| *Psilephydra fluvialis* | 100002?0 | ?00 | ? | ???? |
| *Psilephydra nepalensis* | 1?1002?0 | 2?0 | ? | ???? |
| *Dagus dominicanus* | 31000203 | 110 | 2 | 1020 |
| *Dagus grimaldii* | 40111213 | 012 | 2 | 0242 |
| *Dagus hermani* | 40111213 | 010 | 1 | 1201 |
| *Dagus mathisi* | 22001111 | 101 | 1 | 1120 |
| *Dagus rostratus* | 40000202 | 002 | 0 | 0131 |
| *Dagus spanglerorum* | 22001201 | 101 | 0 | 1220 |
| *Dagus trichocerus* | 40120202 | 002 | 0 | 0242 |
| *Dagus wirthi* | 31000202 | 211 | 2 | 1001 |




Figs. 30, 31. **30**. Tree-3. **31**. Tree-4.




Figs. 32, 33. CLADOS output of HENNIG86 derived successive-weighted trees (refer to text). **32.** Tree 1. **33.** Tree 2.

is pleisomorphic in *Dagus*. A continuous white tomentum extending from the parafacial posteriorly is independently synapomorphic for clade 6 and autapomorphic for *Dagus mathisi*.

8. Weakly developed lateral mid-facial setae are a synapomorphy for *Dagus*, a condition retained in clade 1. Strongly developed setae are a synapomorphy for clade 2, occurring as two to three well-developed setae in *D. wirthi*, *rostratus*, and *trichocerus*. Reduction to one well-developed seta has occurred synapomorphically in clade 6, and autapomorphically in *Dagus dominicanus*.

9. Microtomentose tufts on the hindcoxal strap are pleisomorphic in *Dagus*. *Dagus wirthi* has the autapomorphic development of one or two setulae on the hindcoxal strap. All vestiture is apparently lost in the *rostratus* group.

TABLE 2
**Ingroup Character Optimization Differences Among Trees**

| Tree | Node | Character | State | Transformation |
|---|---|---|---|---|
| 1. Unweighted | — | — | — | |
| 2. Unweighted | Base | 11 | 1 | →0, →2 |
| 3. Unweighted | Base | 2, 11 | 1, 1 | →2, →0; →0, →2 |
| 4. Unweighted | Same as 2 | Unweighted | | |
| 1. Weighted | Same as 2 | Unweighted | | |
| 2. Weighted | Same as 3 | Unweighted | | |
| 3. Weighted | Same as 2 | Unweighted | | |

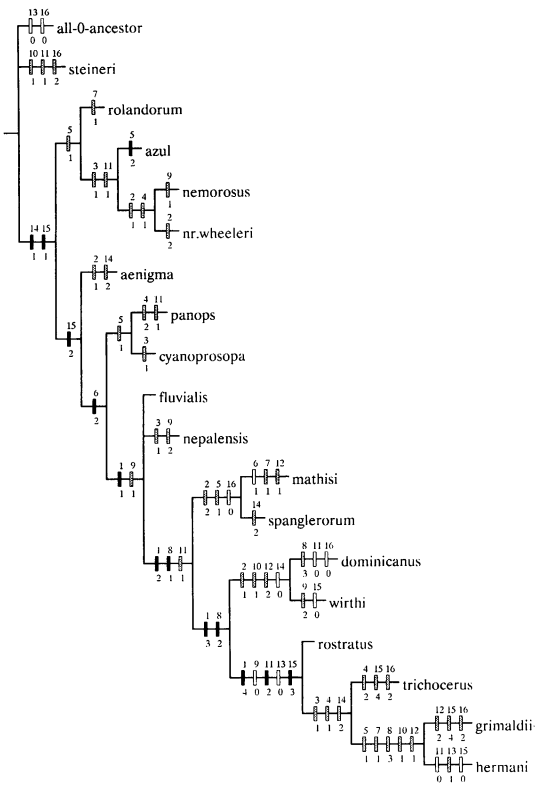



Fig. 34. Tree 3.

10. Absence of presutural dorsocentral setae is pleisomorphic in *Dagus*. The presence of presutural dorsocentral setae is independently synapomorphic for clades 3 and 6.

11. The insertion of the posterior notopleural bristle above that of the anterior, but by less than one-half its length, is plesiomorphic in *Dagus*. This condition is retained in clade 1, and in *Dagus wirthi*. Elevation of the posterior seta to a height one-half or more of its length higher than the insertion of the anterior seta is a synapomorphy for clade 2. In *Dagus dominicanus* and *hermani*, there is a reversal to the plesiomorphic state seen in the outgroup: the two setae are inserted at approximately the same level.

12. A rectangular epandrium is a synapomorphy for clade 6 and an autapomorphy for *Dagus mathisi*. Within clade 6, the state exists in *Dagus grimaldii* as an autapomorphic quadrate shape which is also a synapomorphy in clade 3.

13. The cap of the ventral receptacle being more narrow than its base is plesiomorphic in the *rostratus* group. It is autapomorphically wider in *Dagus hermani* within the *rostratus* group.

14. The end of the base of the ventral receptacle having thin, fingerlike lobes is plesiomorphic in *Dagus*. A reversal to a broadly lobed end of the base is a synapomorphy for clade 3. Synapomorphically in clade 5, and autapomorphically in *Dagus spanglerorum*, the lobes are absent.

15. A truncate-conical shape of the cap of the ventral receptacle is plesiomorphic in *Dagus*. This condition is retained in clade 1, and in *Dagus dominicanus*. It reverts to the hemispherical condition in *Dagus wirthi*. A small conus is a synapomorphy for the *rostratus* group. A compressed and wrinkled cap is independently autapomorphic in *D. trichocerus* and *D. grimaldii*. In *Dagus hermani*, the cap reverts to the hemispheric form.

16. The cap of the ventral receptacle is synapomorphically heavily sclerotized in clade 1, and autapomorphically so in *Dagus dominicanus*. It is independently autapomorphically weakly sclerotized in *Dagus trichocerus* and *grimaldii*.

## BIOGEOGRAPHY

Although faulty hypotheses may be formulated due to sampling error and vicariant patterns obscured by dispersal and extinction events, the distribution of the genus *Dagus* in the circum-Caribbean region appears to have a pattern which is corroborated by other taxa with differing habitats (fig. 35). The Brazilian locality for *rostratus* was given by Cresson and is nonspecific, as noted by Mathis (1983). The Cuban locality is reported by Mathis and Zatwarnicki (1988) but I have not seen the specimen and do not know the specific location. Figure 36 shows a concentration of six of the eight described species in Hispañola, or more specifically in the Dominican Republic, since there have been no specimens collected in Haiti. Outside of Hispañola there are only *Dagus wirthi* unique to Jamaica, *D. trichocerus*, which occurs on Hispañola and has been collected in Pinar del Rio, Western Cuba, and *D. rostratus*, the widespread species, found throughout the circum-Carribean region, but so far, not in the Dominican Republic (the lack of *rostratus* is

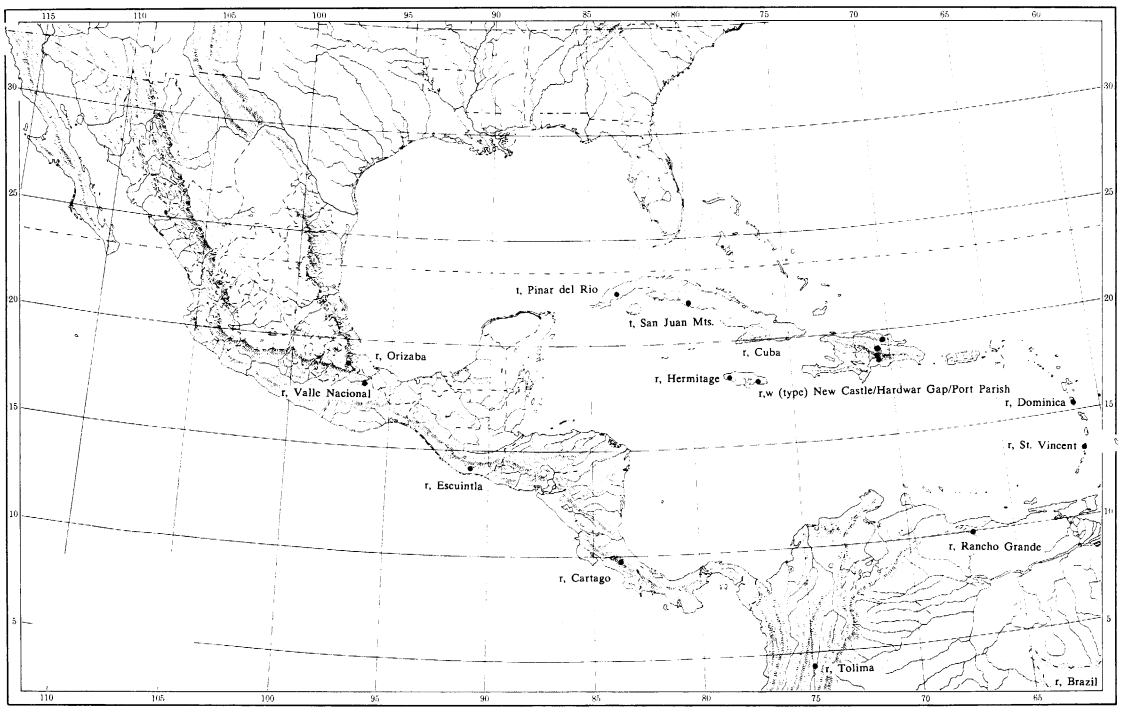



Fig. 35. Distribution map of *Dagus*. Lowercase letters correspond to first letter of specific name, (type) refers to type locality, Dominican localities unlabeled (see fig. 36).

interesting: is competition from the other species a factor?)

This distribution is paralleled by the poeciliid fish genus *Limia* (Carlos Rodriguez, personal commun.). Seventeen of the 20 described species are endemic to Hispañola. There is one species endemic to Cuba and one to Jamaica. Although *Limia* does not occur in Central or South America, its sister genus is widespread throughout the area. Several other authors have cited Hispañola by itself or in the context of the Greater Antilles as areas of surprising endemicity (Slater, 1988, Lygaeidae; Ramos, 1988, Auchenorrhyncous Homoptera). Hispañola has had a very active geologic past. The North American and Carribean plates move past each other in opposite directions at the location of the Cordilliera Septentrional. Additionally, a popular hypothesis suggests that a small land mass sutured onto the island at the southwest corner of the Dominican Republic, the Barahona peninsula (Liebherr, 1988; Pindell and Barrett, 1990; Morris, et al., 1990). The extensive uplifting of the Sierras Bahoruco and Neiba, as well as personal obervation of the unique terrain in this region lend support to this idea. No *Dagus* has yet been collected in this region, perhaps due to the lack of streams.

The concentration of diversity among the disparate groups discussed above, coupled with the highly active Hispañolan geology, provoke the idea that vicariance has played a major role in Hispañolan endemism. Recent finding in Dominican amber (ca. 25 myo) of a relatively recently derived ephydrid genus, *Beckeriella* (unpubl. data), lends credence to the hypothesis that the Caribbean ephydrids are old enough to have been affected by tectonics. *Beckeriella* will be the subject of another study. The distribution of the *rostratus* group accords well with mobilist concept of Rosen (1985), as outlined by Liebherr (1988). The close proximity of Jamaica, southern Hispañola, and western Cuba to northern Central America in the early Eocene would have allowed the dispersal of a widespread species to those areas. Such a species could have subsequently extended its range to the rest of Central America when it ap-

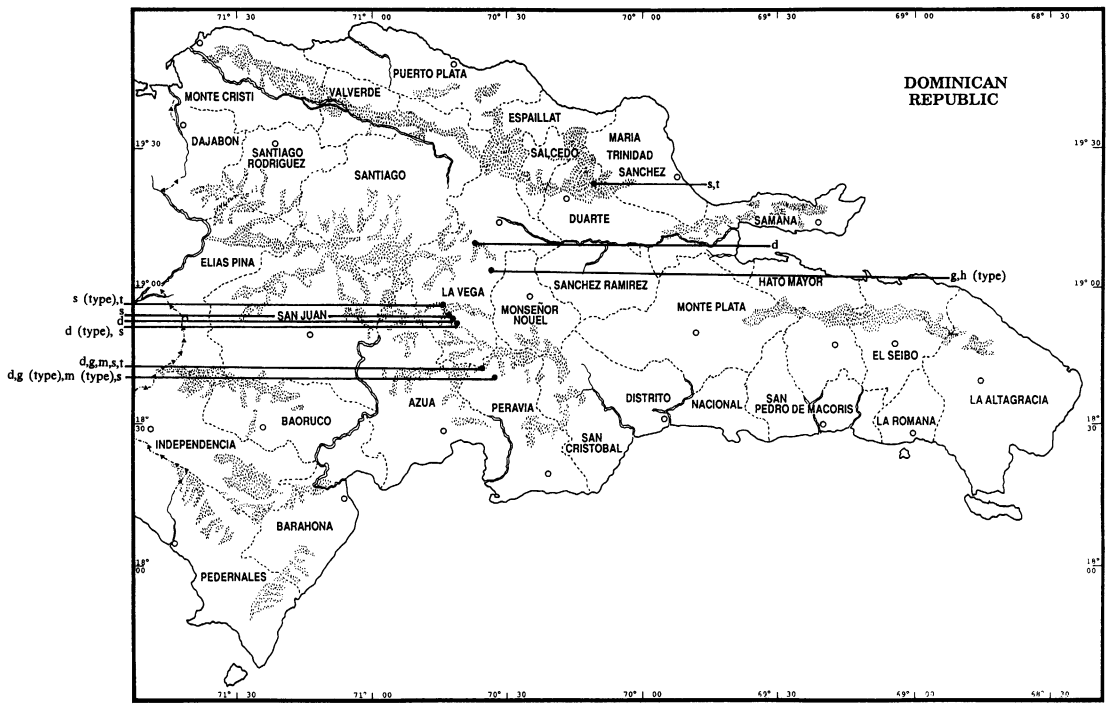



Fig. 36. Distribution map of *Dagus* in the Dominican Republic. Lowercase letters correspond to first letter of specific name, (type) refers to type locality. Localities of *grimaldii*, *mathisi*, and *hermani* are given with the species descriptions. Some of the other localities may be found in Mathis (1983) and Mathis and Zatwarnicki (1988).

proximated northern Central America in the late Eocene, and similarly to South America in the Oligomiocene. *D. rostratus* or a *rostratus*-like ancestor would fit the role of this species, as its distribution is conspicuously more widespread than any of the others. With the exception of *D. wirthi*, which would have had to escape the submergence of Jamaica during the late Eocene—mid-Miocene, the other endemics could have developed in isolation on the other Proto-Antillean fragments. *Dagus trichocerus* occurs in both western Cuba and in the Dominican Republic; western Cuba and southern Hispañola are similarly adjacent in the Rosen model during the early Eocene. If its absence in eastern Cuba is "confirmed," it might have possible corroborative value. One is reminded, however, of Slater's comment from the same volume, that "because of many such [geologic] hypotheses for the Caribbean, vicariance 'tests' will be, at most, possibilities." (Slater, 1988). Pindell and Barrett (1990) reviewed no fewer than 12 competing models of Caribbean paleogeography in formulating their own. In the same volume, Morris, et al. provided a very well-documented "surge tectonic" mechanism which differs fundamentally from the plate-tectonic mechanisms, although it finds little acceptance in the geologic community (Bruce Lieberman, personal commun.). New evidence of the K-T impact in the Yucatan Basin (Swisher, et al. 1992) could also have profound implications for Caribbean biogeography: it may well be a demarcation point between the biota present before and that which reinvaded afterwards (D. Grimaldi personal commun.). There is simply not enough geologic consensus at this time to constrain the discussion of the biogeography of this small genus to a primarily dispersalist, vicariant, or combined mode. The author suspects that such assertions for many other Caribbean groups are likely overly optimistic at this juncture: the cladistic patterns exist, but are insufficient to provide

anything but the most generalized conclusions about the land masses which may have been involved in their development. This is not meant to discourage the attempt, but merely to temper the discussion.

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