

Studies of Ephydrinae
(Diptera: Ephydriidae), VI:
Review of the Tribe Dagini

WAYNE N. MATHIS

SMITHSONIAN CONTRIBUTIONS TO ZOOLOGY • NUMBER 345

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ABSTRACT

Mathis, Wayne N. Studies of Ephydrinae (Diptera: Ephydridae), VI: Review of the Tribe Dagini. *Smithsonian Contributions to Zoology*, number 345, 30 pages, 89 figures, 1982.—Dagini, new tribe, comprising the genera *Diedrops* Mathis and Wirth, *Physemops* Cresson, *Dagus* Cresson, and *Psilephydra* Hendel, is reviewed. The systematics and classification of these genera have been confused, with their placement varying from the subfamily Parydrinae to Ephydrinae. Here they are placed in Ephydrinae and are recognized as a separate tribe. The basis for this arrangement and the monophyly of the tribe are discussed. A cladogram of the tribe is proposed that elaborates relationships between genera. The phylogeny, as now conceived, is an unresolved trichotomy, with the following lineages: *Diedrops*, *Psilephydra*, and the stem lineage that gave rise to *Dagus* and *Physemops*. The latter two taxa are suggested to be sister genera. Species of the included genera are systematically reviewed, and for the genus *Physemops* a hypothetical phylogeny is suggested that has the genus divided into two species groups: the *nemorosus* group and the *panops* group. Character evidence for these conclusions are given. Keys to genera, species groups, and species and appropriate illustrations are provided.

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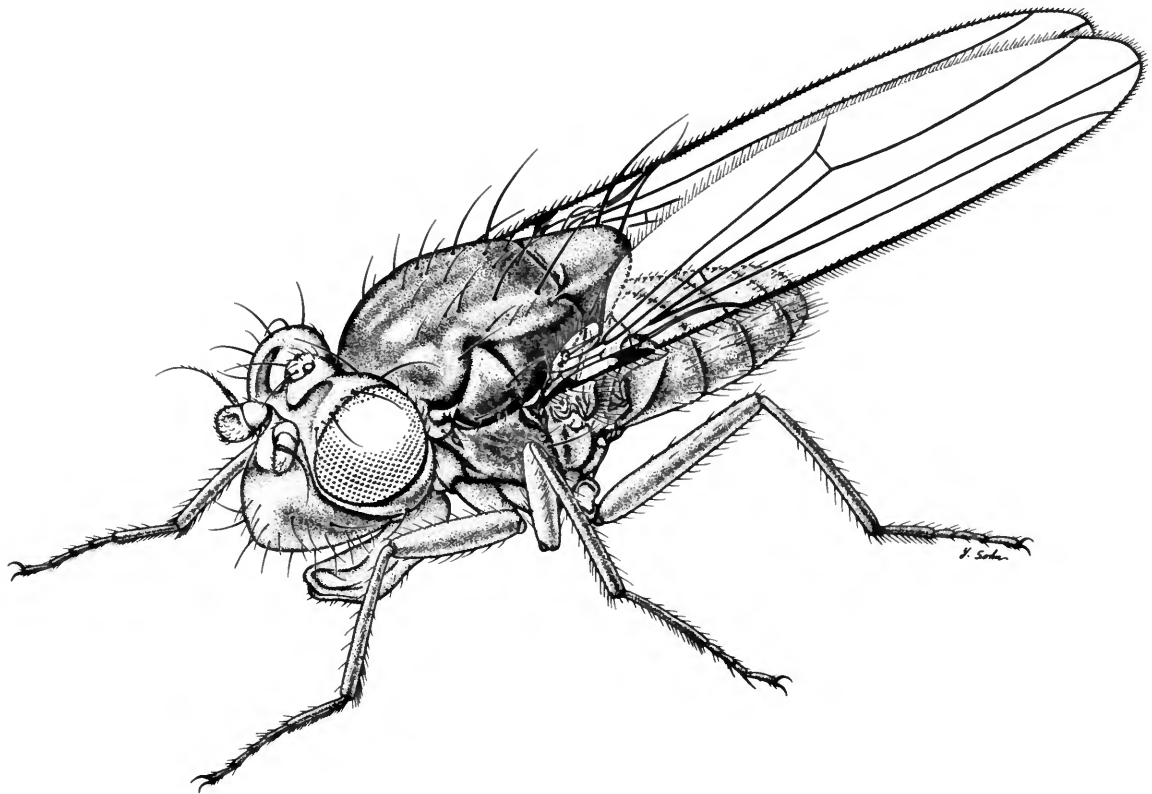


FIGURE 1.—Habitus of *Dagus rostratus*, female.

Studies of Ephydrinae (Diptera: Ephydridae), VI: Review of the Tribe Dagini

Wayne N. Mathis

Introduction

While conducting studies on the subfamily Ephydrinae, I encountered several problematic genera that were not easily accommodated within existing classifications, particularly at the tribal level. In the past, with my own research, I have either dealt with these genera by simply noting their existence and that they were probably members of the subfamily Ephydrinae (Mathis, 1979b) or I have not treated them at all, as they did not belong to any existing tribe, as then characterized, and the studies were limited to those tribes (Mathis, 1980).

The problem does not lie solely with the problematic genera but is also a reflection of the inadequate classifications. The tribe Scatellini, for example, is obviously paraphyletic, as noted previously (Mathis, 1979b, 1980), which indicates the need for further resolution at the suprageneric level.

To remedy these conditions, I am reviewing the problematic genera, here recognized as the tribe Dagini, with the immediate objective of providing perspective for the group within the subfamilial classification. In many respects the results to be presented are preliminary, and other adjustments will undoubtedly be necessary as

further data are discovered that relate to questions of relationship within the subfamily. For the present, however, I am bringing existing information forward and presenting an overview of the group, somewhat in synoptic form, but also with new data and a reinterpretation.

It is hoped that this study will prompt further research on the group, particularly the natural history of the included species. To date, neither the immature stages nor the natural history of any of the species is known.

HISTORICAL REVIEW.—The history of the genera and species now included in Dagini is relatively recent, with the first reference dating to Williston (1896), who described *Ephydra pygmaea*. Unfortunately, the name Williston chose was preoccupied (Haliday, 1833), and the species is not a member of the genus *Ephydra* Fallén, as noted and changed by Cresson (1918, *Ephydra rostrata* Cresson, new name; 1935, species assigned to *Dagus*). In 1914, Hendel and Cresson published on additional species now included in Dagini: Hendel described *Psilephydra cyanoprosopa* from Taiwan, as a new genus and species, and Cresson described a second species in that genus, *P. nemorosa*, from Costa Rica. Some years later, Cresson (1934) proposed the genus *Physemops*, with *Psilephydra nemorosa* as type-species, and a year afterward (1935) he erected the genus *Dagus*, with *Ephydra rostrata* as type-species. After a 35-year

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hiatus of work on the included genera and species, Wirth (1970) revised the genus *Physemops*, adding five more species: *P. azul*, *P. fairchildi*, *P. maldonadoi*, *P. panops*, and *P. wheeleri*. More recently, Mathis and Wirth (1976) described the genus *Diedrops*, which included two new species: *D. aenigma*, as type-species, and *D. hitchcocki*.

In previous studies dealing with various taxa now comprising Dagini, considerable divergence of opinion was expressed concerning the affinities of the included genera. Cresson (1914, 1934) was of the opinion that the genera *Psilephydra* and *Physemops* were allied with the subfamily Parydrinae and enumerated several apparent similarities between these two genera and several genera of Parydrinae (genera of Parydrinae used in his comparison included *Hydrina* of Robineau-Desvoidy (= *Hyadina* Haliday), *Axysta* Haliday, *Gastrops* Williston, *Lytogaster* Becker, and *Parydra* Stenhammar). Later, when Cresson described the genus *Dagus* (1935), he allied that genus with the tribe Ephydrini, subfamily Ephydrinae. Character evidence for this alliance was as follows (Cresson, 1935:345): "The laterally curved frontorbitals, the prominent setulose medi-facies, the long rather straight claws and rudimentary pulvelli [sic], place this genus in the tribe Ephydrini."

In a recent revision of the genus *Physemops*, Wirth (1970:170) stated that

some of the most striking characteristics of *P. nemorosus* [the type-species of *Physemops*] are of a specific nature. The presence in some of these species of distinct series of dorsocentral and acrostichal bristles, and of a pair of enlarged bristles on the medifacies suggests that *Physemops* belongs in the subfamily Ephydrinae. Examination of the Oriental *Psilephydra cyanoprosopa* Hendel reveals that it is related to *Physemops* on one hand and to the Polynesian genus *Apulvillus* Malloch on the other.

The disposition of *Apulvillus*, as a subgenus of *Scatella* Robineau-Desvoidy, was dealt with in an earlier study (Mathis, 1980).

When Mathis and Wirth (1976) described *Diedrops*, they noted several similarities between it and *Psilephydra*. In their summary of generic relationships (p. 128), they mentioned that "*Diedrops* is probably most closely allied with the subfamily

Parydrinae, but it shares many characters with the Ephydrinae and perhaps is an annectant genus."

In 1977, Mathis published a key to the Neotropical genera of the subfamily Parydrinae and commented on several of the genera. His key included *Physemops* and *Diedrops* largely because previous authors had associated both genera with Parydrinae. Mathis noted several possible relationships with taxa in the subfamilies Parydrinae and Ephydrinae but also noted (1977:556) that "it is obvious that the relationships of the *Physemops*-group with other ephydrid taxa are poorly known. An evaluation of pertinent characters, to determine their relative derived versus primitive states will be necessary before the sequence of lineages can be better clarified."

Finally, in a preliminary study of the subfamily Ephydrinae, Mathis (1979b) stated that *Dagus* and related genera (*Diedrops*, *Physemops*, and *Psilephydra*) should be included in Ephydrinae as a distinct sublineage. No clarification, however, as to the relationships of this sublineage with other lineages of Ephydrinae was then elaborated, and in his tentative classification of Ephydrinae, this sublineage, with its included genera, was listed as "Group VII."

METHODS.—The general methods used in this study were explained in previous parts of this series (Mathis and Shewell, 1978; Mathis, 1979a, 1980; Mathis and Simpson, 1981). Three aspects, however, are newly incorporated in this study.

One of the major objectives of this study is to bring published but scattered taxonomic data together that relates directly to Dagini. In consequence of this goal, I have purposely written descriptions more in the style of diagnoses, with some additional elaboration. Moreover, the section on the genus *Physemops* is to a large extent a synthesis of Wirth's (1970) previous revision. In view of this level of descriptive treatment, the headings to the appropriate sections are labeled "Diagnostic Description," and these sections take the place of having separate diagnosis and description sections.

In previous parts of this series, wing ratios were

expressed as components, e.g., costal vein ratio 1:0.25. Here I have simply carried out the appropriate division, and the ratios are given as a single number, i.e., costal vein ratio 4.

In previous publications, I have either separated the combining adjectives "fore-" and "mid-" from the nouns they modified or have used noncombining, anglicized counterparts, such as front or middle. Here I am using the combining form of these adjectives. Their proper use requires the formation of a single word, the combining adjective plus the noun being modified, e.g., foreleg, midtarsi, etc.

ACKNOWLEDGMENTS.—Most specimens I examined are housed in the National Museum of Natural History, Smithsonian Institution, although material was also borrowed from other institutions. To the curators of these collections and their respective institutions, I express my grateful thanks for their cooperation. Designations of all collections, as cited in the text, are as follows.

ANSP	Academy of Natural Sciences of Philadelphia, Pennsylvania (Drs. Daniel Otte and Curtis Dunn)
BMNH	British Museum (Natural History), London, England (Mr. Brian H. Cogan)
CAS	California Academy of Sciences, San Francisco, California (Dr. Paul H. Arnaud, Jr.)
NMW	Naturhistorisches Museum, Vienna, Austria (Dr. Ruth Contreras-Lichtenberg)
USNM	former United States National Museum, collections in the National Museum of Natural History, Smithsonian Institution, Washington, D.C.

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Subfamily EPHYDRINAE Zetterstedt

DIAGNOSIS.—Members of this subfamily closely resemble those of Parydrinae but may be distinguished from them and those of other subfamilies by the following combination of characters: fronto-orbital bristles present, laterocline, usually 2, although number variable; face generally transversely arched; clypeus concealed; midfacies bearing setulae or setae, facial series of setae frequently convergent dorsally; oral opening usually large and cavernous, oral margin often ciliate with setae, these sometimes long; mesopleuron with a single large bristle inserted along the posterior margin at about midheight, frequently with smaller bristles dorsally and ventrally; vein R_{2+3} usually long, terminating much closer to vein R_{4+5} than to R_1 ; larvae generally in mud, secondarily in algal mats and excrement.

DISCUSSION.—As characterized here, the subfamily Ephydrinae agrees with the concept of most authors of this century (Cresson, 1930:112, 1931:104; Sturtevant and Wheeler, 1954:154–161; Wirth and Stone, 1956:463; Dahl, 1959:105; Wirth, 1965:753, 1968:22; Hennig, 1973:62; Cogan and Wirth, 1977:338; Miyagi, 1977:81; Cogan, 1980:668). The concept and characterization were developed primarily by Cresson (1930), with most subsequent authors following his precedent.

The subfamily is doubtlessly monophyletic, as established by the character evidence (see "Diagnosis" above). Its sister group, however, has not been identified, although I suggest that it will be found to be either the subfamily Parydrinae as a whole or an included taxon of that subfamily. Parydrinae may be paraphyletic, and perhaps the classifications of Dahl (1959) and Miyagi (1977), which further divide Parydrinae into other subfamilies, will have merit. The cladistic relationships of Parydrinae and its included taxa need clarification.

DAGINI, new tribe

DIAGNOSIS.—Specimens of Dagini are similar to those of Scatellini and Ephydrini but are dis-

tinguished by the following combination of characters: face shieldlike, uniformly and shallowly protrudent, lacking distinctly protrudent dorsal facial prominence in lateral view (*Dagus* has a ventral prominence); frons uniformly dark colored, brownish black and usually contrasting with lighter colored face, lighter facial coloration usually due to whitish to silvery white tomentum, especially on ventral portion; lacking cruciate intrafrontal bristles inserted near anterior margin of face; dorsocentral and acrostichal series lacking large presutural bristles but usually with 1-3 large postsutural dorsocentral bristles, rarely with a prescutellar pair of acrostichal bristles; anterior notopleural bristle and sternopleural bristles frequently weak, especially as compared with posterior notopleural bristle and mesopleural bristle respectively; lacking a supra-alar bristle; prosternum bare of setulae; hind coxal strap bare of setulae; pulvilli generally present (except for *Dagus*); tarsal claws conspicuously curved and short; propleuron bare of setulae (except for *Diedrops*); coloration generally dull to subshiny brown dorsally, contrastingly gray below with a rather sharp demarcation between the coloration change (except for *Physemops*).

PHYLOGENETIC CONSIDERATIONS.—Following an earlier arrangement (Mathis, 1979b), I have tentatively placed Dagini as a third lineage of a trichotomy within Ephydrinae. The other two lineages of the trichotomy are Ephydrini and Scatellini. The tribal relationships of the subfamily Ephydrinae need further resolution.

In the diagnosis of Dagini, several exceptions are noted. I consider them to be secondary developments to the basic ground plan of the tribe, and, for the most part, they represent autapotypies of their respective taxa. In the presentation of character evidence to follow, the numbers accompanying the discussion of a particular character correspond with those used on the cladogram.

Dagini is apparently a monophyletic group, although the character evidence is not overwhelming.

1. *Sternopleural bristle*: Generally in Ephydrinae the sternopleural bristle is as well developed as the mesopleural

bristle, but in most lineages of Dagini, the sternopleural is conspicuously weaker than the latter.

2. *Conformation of face*: In several genera of Parydrinae and nearly all genera of Ephydrinae, the face is transversely arched, the oral opening is large, sometimes gaping, and there are usually distinct antennal foveae. The genera of Dagini also have the face vertically arched, usually lacking distinct antennal foveae, and the face extends ventrally, giving the appearance of a shield.

The four genera now included in Dagini are schematically arranged as outlined in Figure 2. The basic branching sequence is an unresolved trichotomy, with each lineage comprising the trichotomy having its probable monophyly estab-

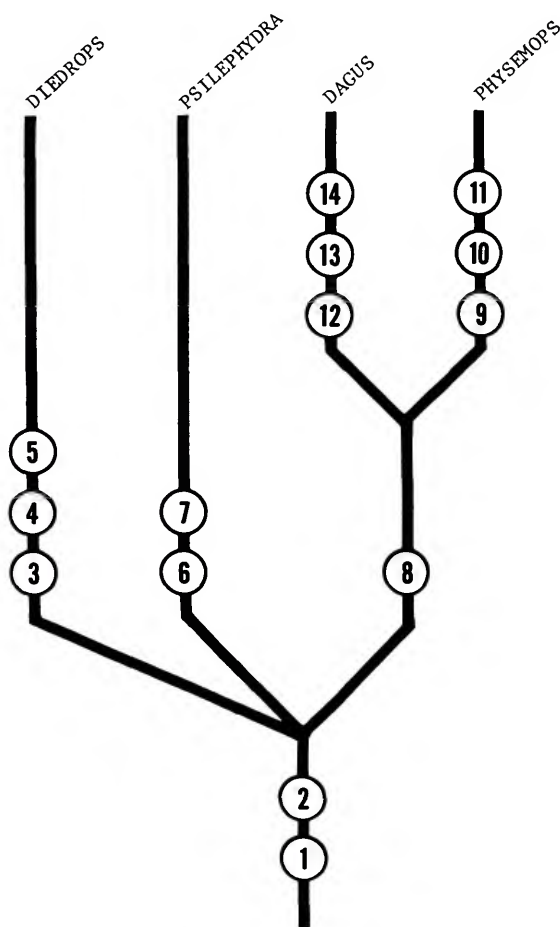


FIGURE 2.—Hypothetical phylogeny for tribe Dagini (based on character evidence in text).

lished by character evidence without clarification as to the relationships between them.

Diedrops is monotypic. Its monophyly is established as follows:

3. *Vestiture of propleuron*: With few exceptions (Ephydrini and *Teichomyza* Macquart) the propleuron is bare of setae or setulae in Ephydrinae. The setulose propleuron in species of *Diedrops* is a synapotypic condition.
4. *Ocellar bristles*: Ocellar bristles are generally present throughout the family Ephydridae. Their absence in species of *Diedrops* is likewise a synapotypy.
5. *Apical position of vein R₂₊₃*: Vein R₂₊₃ is usually relatively long in Ephydrinae, terminating about as far from vein R₄₊₅ as the latter is from vein M. In species of *Diedrops*, however, vein R₂₊₃ ends much closer to vein R₄₊₅, at about half the distance between R₄₊₅ and vein M. This character is unique to *Diedrops*.

Psilephydra is probably monophyletic, with evidence as follows:

6. *Shape of gonite*: The shape of the gonite in the two known species of *Psilephydra* appears to be unique within the tribe and not only characterizes the genus but is evidence to establish its monophyly. See generic and species treatments for descriptions of the shape and illustrations (page 24).
7. *Shape of the aedeagal apodeme*: In both known species of this genus, the aedeagal apodeme is very slender, apparently a condition unique to *Psilephydra*.

I have tentatively allied *Dagus* with *Physemops* as sister groups. This relationship and the monophyly of their joint stem lineage are established as follows:

8. *Position of posterior notopleural bristle*: Generally the posterior notopleural bristle is inserted at about the same level as the anterior bristle. In species of *Dagus* and

Physemops, the posterior bristle is inserted at a level distinctly higher than that of the anterior bristle, and this I interpret to be a synapotypy.

The monophyly of the genus *Physemops* is established as follows:

9. *Number and orientation of fronto-orbital bristles*: The generalized ground plan of Ephydrinae is for two laterocline fronto-orbital bristles. In species of *Physemops* the anterior fronto-orbital bristle is lost, and the posterior bristle is oriented posterolaterally.
10. *Genal bristle*: The species of *Physemops* lack a genal bristle. With the exception of *Psilephydra cyanoprosopa*, this condition is unique within Dagini, and I interpret it to be synapotypic and to have arisen independently in both *Physemops* and *Psilephydra*.
11. *Upper facial setae*: A character of Ephydrinae is the presence of facial setae, and frequently there is an outstanding row of larger setae extending from the midfacial height to the posteroventral corner. In species of *Physemops*, the distinct row, as described, is lacking, but there is a conspicuous pair of porrect, divergent setae at the midfacial height that is unique to the genus.

The monophyly of the genus *Dagus* is established as follows:

12. *Vestiture of humeral callus*: In most genera of Ephydrinae, the humeral callus is either bare of setulae or bears conspicuous setae that are large, bristle-like. In species of *Dagus*, the humeral callus is mostly bare except for one or two small setulae that are sometimes difficult to see except in profile.
13. *Pulvilli*: *Dagus* is the only genus of the tribe where the pulvilli are lacking, and I interpret this condition to be autapotypic.
14. *Shape of the face*: In most species of Dagini, the face is shieldlike and shallowly protrudent. In the only known species of *Dagus*, however, the lower one-half to two-thirds of the face is distinctly protrudent and is evenly arched both horizontally and vertically.

Key to Genera of Dagini

1. Ventral one-half to two-thirds of face distinctly protrudent anteriorly, arched transversely and vertically (best seen in profile); pulvilli lacking; 3 fronto-orbital bristles, anterior bristle smaller, about one-half length of posterior bristles; humeral callus with 1 small seta *Dagus* Cresson, 1935
 Face shieldlike, broadly but more shallowly protrudent over most of height; pulvilli present; usually 1-2 fronto-orbital bristles [a third bristle sometimes present in *Psilephydra fluvialis* (Miyagi)]; humeral callus bare ... 2

2. Distance between apices of veins R_{2+3} and R_{4+5} narrow, less than half that between veins R_{4+5} and M; gena high, equal to or greater than eye height; genal bristle strong, conspicuous; 2 subequal fronto-orbital bristles; a distinct pair of prescutellar acrostichal bristles; propleuron setulose; fifth tarsomere with dorsoapical process extending beyond base of tarsal claws ***Diedrops*** Mathis and Wirth, 1976
- Distance between apices of veins R_{2+3} and R_{4+5} subequal to that between veins R_{4+5} and M; gena shorter, usually not more than half eye height; genal bristle, if present, small, inconspicuous; at most with 1 larger fronto-orbital bristle; prescutellar acrostichal bristles not evident; propleuron bare of setulae; fifth tarsomere not as above 3
3. Two or 3 large dorsocentral bristles, all postsutural; arista mostly bare, at most micropubescent along basal one-fourth ***Psilephydra*** Hendel, 1914
- One larger dorsocentral bristle inserted near scutellum; arista pectinate or macropubescent along at least basal two-thirds ***Physemops*** Cresson, 1914

Genus *Diedrops* Mathis and Wirth

Diedrops Mathis and Wirth, 1976:126 [type-species: *Diedrops aenigma* Mathis and Wirth, by original designation].—Mathis, 1977:555 [generic key].

DIAGNOSIS.—Specimens of *Diedrops* resemble those of *Psilephydra*, *Dagus*, and *Physemops* but may be distinguished by the following combination of characters: ocellar bristles lacking; laterocline fronto-orbital bristles 2, sometimes weakly developed; mesofrons in depression; arista moderately long, although not twice length of first 3 antennal segments, minute setulae on at least basal two-thirds, sometimes to apex; third antennal segment nearly twice length of second segment; face shieldlike, shallowly and evenly protrudent over entire height; facial setae uniformly sparse and subequal in size except those along oral margin, especially laterally, the latter setae longer, lacking facial series extending from midfacial height to posteroventral angles of face; genal bristle present, conspicuous; 1 pair of larger prescutellar acrostichal bristles; scutellar bristles variable as to comparative lengths; humeral callus bare of setulae; anterior notopleural bristle only slightly smaller than posterior one; posterior notopleural bristle inserted at about the same height as anterior bristle; propleuron with scattered setulae;

sternopleural bristle conspicuously weaker than mesopleural bristle; apex of vein R_{2+3} approximate to vein R_{4+5} , distance between these less than one-half that between veins R_{4+5} and M; capitellum of halter with some blackish gray, thinly tomentose areas; forefemur lacking row of spinelike setae.

MALE TERMINALIA.—Fifth sternum divided, each sternite with setulae more densely clustered toward posteromedian angle. Epandrium shieldlike, cerci and cercal cavity occupying dorsal one-half to one-third, ventral margin emarginate, setulose, and perhaps representing fused surstyli; gonite at least 3 times higher than wide, with gonial arch posterodorsally, latter with median, ventral projection; aedeagal apodeme comparatively large, J-shaped, ventral portion wider; aedeagus 2–3 times longer than wide in lateral view, variously shaped.

PHYLOGENETIC CONSIDERATIONS.—Although the monophyly of *Diedrops* is well established (see Figure 2, with accompanying character evidence), its relationship within the tribe remains unresolved. Externally the general habitus of the included species closely resembles that of *Psilephydra cyanoprosopa*, but character evidence to support this relationship is presently lacking.

GEOGRAPHIC DISTRIBUTION.—New World tropics: Mexico (Michoacan and Sinaloa) and Peru (Mariscal Nieto).

DISCUSSION.—Our knowledge of *Diedrops* is presently limited to minimal taxonomic data.

Since description of the genus, no other species have been discovered, no additional specimens from different localities have been collected, and nothing is known about the natural history of the included species.

Key to Species of *Diedrops*

- Pteropleuron bare of setulae; anterior scutellar setae nearly equal to length of posterior setae; wing apex rounded; vein R_{2+3} nearly parallel to vein R_{4+5} ; length of basitarsus equal to or shorter than combined length of remaining tarsomeres for each leg; larger species, length 4.13 to 4.53 mm (Mexico) 1. *D. aenigma* Mathis and Wirth, 1976
- Pteropleuron with 1 to several setulae near anterior margin; anterior scutellar setae distinctly smaller than posterior pair, usually less than one-half length; wing apex bluntly rounded; apex of vein R_{2+3} slightly sinuous; length of basitarsus larger than combined length of remaining tarsomeres for each leg; smaller species, length 2.78 to 3.52 mm (Peru) 2. *D. hitchcocki* Mathis and Wirth, 1976

1. *Diedrops aenigma* Mathis and Wirth

FIGURES 3-10

Diedrops aenigma Mathis and Wirth, 1976:129.

DIAGNOSTIC DESCRIPTION.—Resembling *D. hitchcocki* but differing from it as follows: larger species, length 4.13 to 4.53 mm.

Head: Frons width-to-length ratio 1 : 0.23; vestiture of frons uniformly tomentose, appearing dull, mesofrons not distinguished from parafrons; anterior surface of face nearly vertical, very slightly protrudent only at dorsal prominence; facial setae comparatively shorter and less conspicuous; eye width-to-face length ratio 1 : 0.43; anteroventral margin of eye rounded; eye-tocheek ratio 1 : 0.84.

Thorax (Figure 8): Setae of dorsocentral and acrostichal series generally less well developed, usually lacking a larger pair of prescutellar acrostichal setae; anteroventral scutellar bristle well developed, subequal in length to apical scutellar bristle; length of basitarsus equal to or shorter than combined length of remaining tarsomeres for each leg; capitellum of halter relatively lighter

in color, with considerable pale coloration. Wing (Figure 8): apex rounded; vein R_{2+3} more or less evenly and shallowly arched throughout its length, costal vein ratio 23; vein M ratio 1.35.

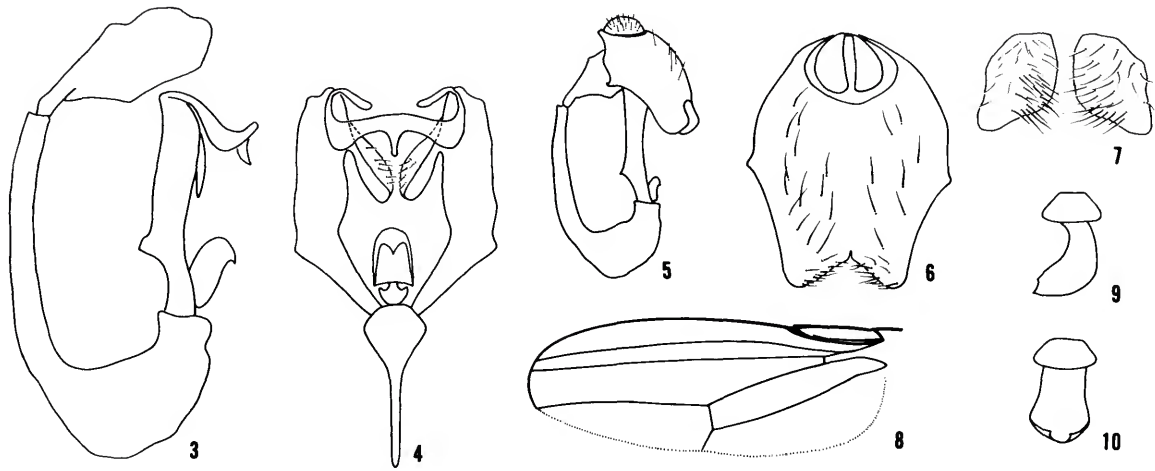
Abdomen (Figures 3-9): Dorsum concolorous with mesonotum; fifth tergum of male almost as long as wide; male terminalia as in Figures 3-7; female ventral receptacle as in Figures 8, 9.

TYPE-LOCALITY.—MEXICO. *Michoacan:* Puerto Morillos (a park workers' settlement in Atzimba National Park, located on Mexico Route 15, approximately 28 miles east of Morelia and about a mile west of the summit of Puerto Garnica, elevation 2825 m).

PRIMARY TYPE MATERIAL.—The holotype male is labeled "Puerto Morillos Mich[oacan]. MEXICO VIII-24-1959/L. A. Stange A. S. Menke Collectors/HOLOTYPE *Diedrops aenigma* Mathis & Wirth [red; handwritten]." The holotype is directly pinned, is in fairly good condition (slightly tattered, some setae missing), and is in the California Academy of Sciences, CAS 12426.

GEOGRAPHIC DISTRIBUTION.—Mexico (Michoacan and Sinaloa).

REMARKS.—In the small series of this species I



FIGURES 3-10.—*Diedrops aenigma*: 3, internal male genitalia, lateral aspect; 4, same, posterior aspect; 5, male terminalia, lateral aspect; 6, epandrium and cerci, posterior aspect; 7, fifth tergite, ventral aspect; 8, wing; 9, female ventral receptacle, lateral aspect; 10, same, anterior aspect.

examined, all that are apparently available, considerable variation exists with regard to number and size of setae, particularly those along major setal tracks, i.e., frontal-orbital bristles, dorsocentral bristles.

2. *Diedrops hitchcocki* Mathis and Wirth

FIGURES 11-26

Diedrops hitchcocki Mathis and Wirth, 1976:129.

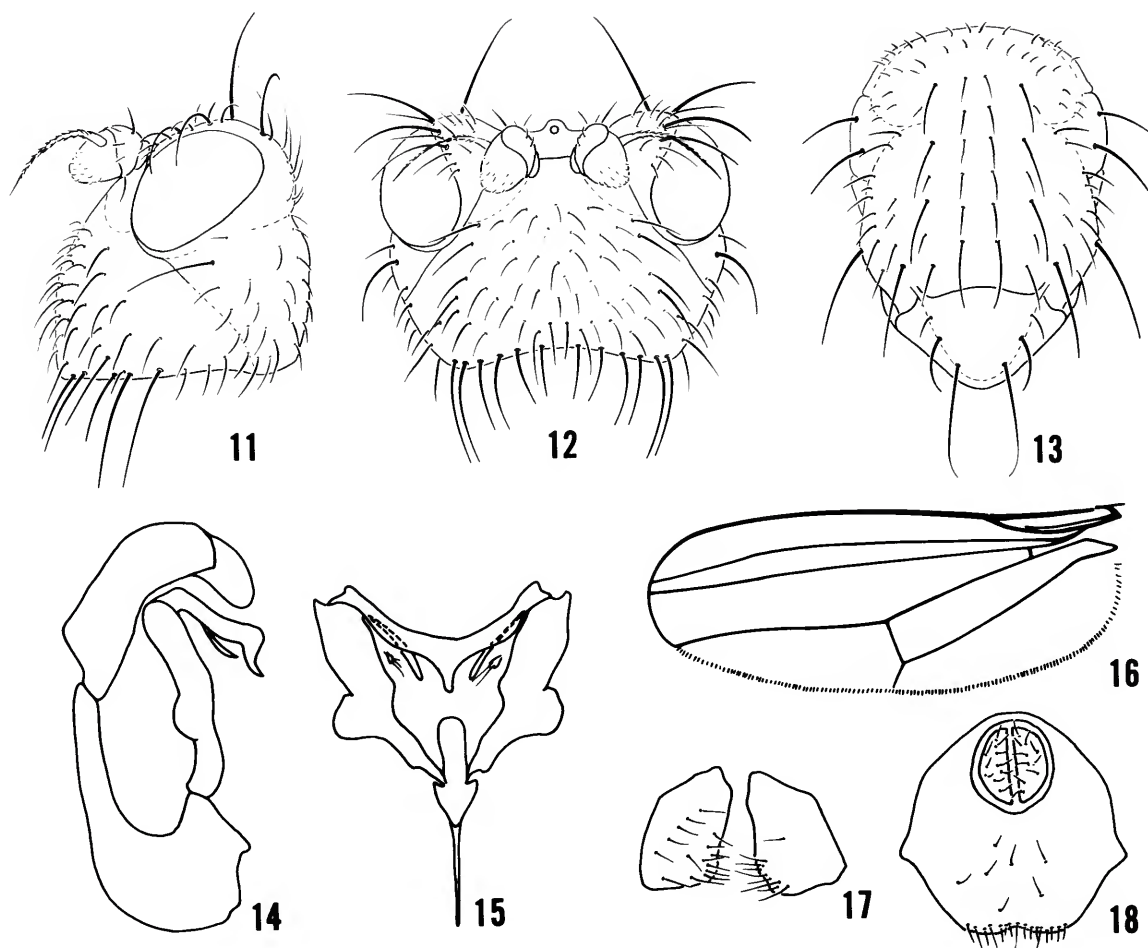
DIAGNOSTIC DESCRIPTION.—Resembling *D. aenigma* but differing from it as follows: smaller species, length 2.78 to 3.52 mm.

Head (Figures 11, 12, 19-22): Frons width-to-length ratio 1:0.29; vestiture of frons with mesofrons more thinly tomentose, subshiny, contrasting with dull appearing more densely tomentose parafrons and fronto-orbits; anterior surface of face in lateral view conspicuously longer at oral margin than at dorsal prominence, relatively more arched vertically; facial setae longer and more conspicuous; eye width-to-face length ratio 1:0.67; anteroventral margin of eye acutely rounded; eye-to-cheek ratio 1:0.95.

Thorax (Figures 13, 23-26): Setae of dorsocentral and acrostichal series generally more strongly developed; usually with a larger pair of prescutellar acrostichal setae; anteroventral scutellar bristle weakly developed, usually less than one-half length of apical scutellar bristles; length of basitarsus longer than combined length of remaining tarsomeres for each leg; capitellum of halter comparatively darker, mostly blackish gray, with pale coloration restricted to less than one-half total surface. Wing (Figure 16) with apex bluntly rounded; vein R_{2+3} evenly arched on basal three-fourths, thereafter shallowly dipping toward vein R_{4+5} ; costal vein ratio 27.5; vein M ratio 1.31.

Abdomen (Figures 14, 15, 17, 18): Dorsum usually lighter in color than mesonotum; length of third tergum only slighter shorter than combined length of fourth and fifth terga; fifth tergum truncate apically, not longer than wide; male terminalia as in Figures 14, 15, 17, 18.

TYPE-LOCALITY.—PERU. *Moquegua*: Yacango (a village in the arid zone, Torata District, Mariscal Nieto Province, Department of Moquegua, in the valley of the Rio Osmore, elevation 1875 m).



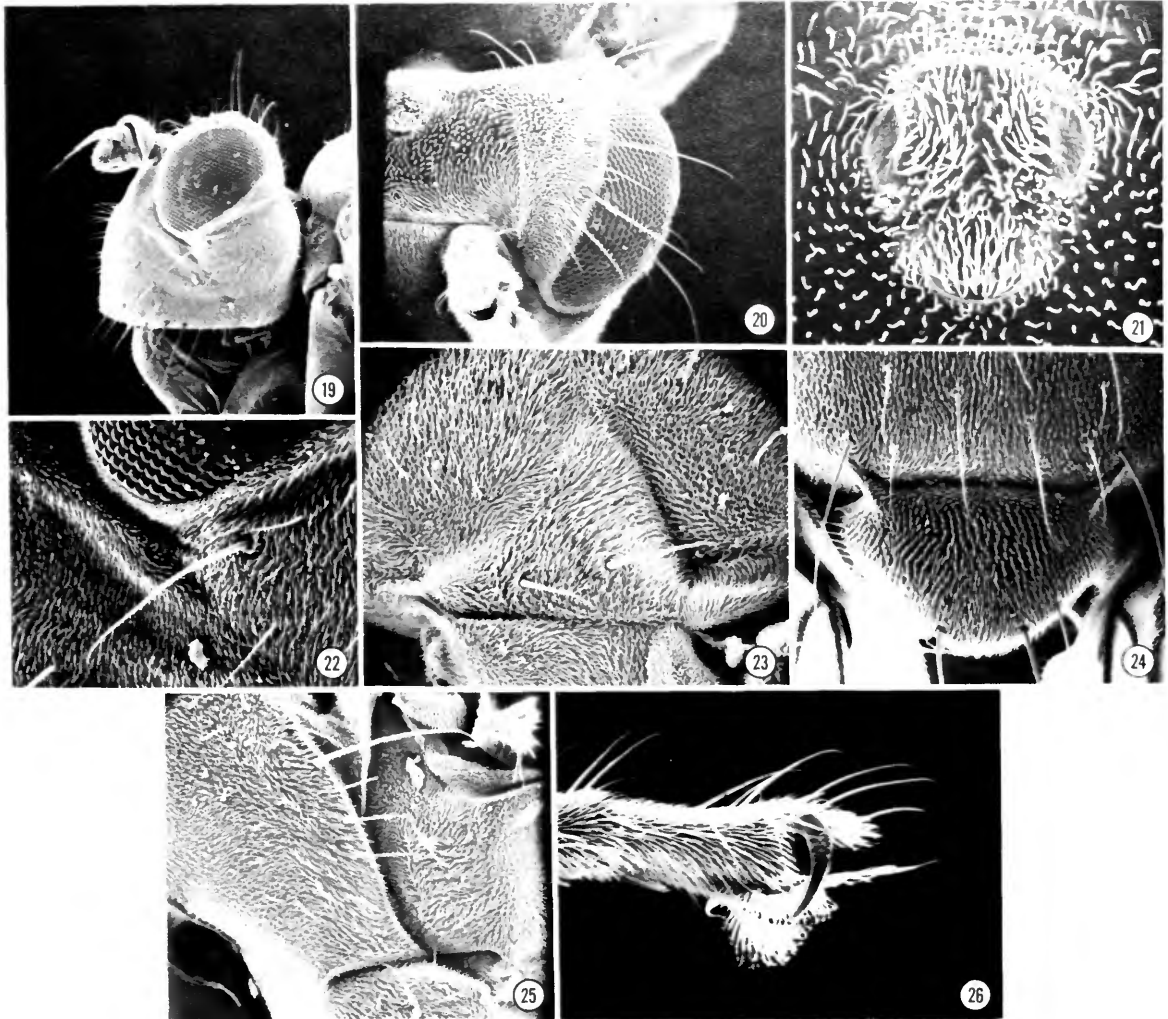
FIGURES 11-18.—*Diedrops hitchcocki*: 11, head, lateral aspect; 12, same, anterior aspect; 13, thorax, dorsal aspect; 14, internal male genitalia, lateral aspect; 15, same, posterior aspect; 16, wing; 17, fifth tergites, ventral aspect; 18, epandrium and cerci, posterior aspect.

PRIMARY TYPE MATERIAL.—Holotype male is labeled “5 IX [IX crossed out] X 1965 Yacango MOQUEGUA, PERU 197 Coll. J. C. Hitchcock, Jr. [day, crossing out of IX, and “197” handwritten]/♂/a red rectangle/HOLOTYPE *Diedrops hitchcocki* Mathis & Wirth [red; handwritten].” The holotype is double mounted (minute nadel in a cork base), is in good condition (a few setae of the head missing), and is in the National

Museum of Natural History, Smithsonian Institution, USNM 71116.

GEOGRAPHIC DISTRIBUTION.—This species is known only from the type-locality.

REMARKS.—Setae, especially the larger ones, of the major setal tracks are apparently more stable in this species than in its congener. My sampling, however, is limited to the series from the type-locality.



FIGURES 19–26.—*Diedrops hitchcocki*: 19, head, lateral aspect; 20, same, dorsal aspect of left side; 21, ocelli, dorsal aspect; 22, genal bristle, lateral aspect; 23, notopleuron and bristles, lateral aspect; 24, scutellum, dorsal aspect; 25, mesopleuron, dorsum of sternopleuron, and bristles, lateral aspect; 26, midleg, lateral aspect of fifth tarsomere, claws, and pulvilli.

Genus *Physemops* Cresson

Physemops Cresson, 1934:211 [type-species: *Psilephydra nemorosa* Cresson, by original designation and monotypy].—Wirth, 1968:20 [catalog of Neotropical species]; 1970:170–177 [review].—Mathis, 1977:555, 556 [generic key and discussion].

DIAGNOSIS.—Specimens of *Physemops* resemble those of *Dagus*, *Psilephydra*, and *Diedrops* but may be distinguished by the following combination of

characters: ocellar bristles variable, present or absent (see species group diagnoses); posterolatero-ocline fronto-orbital bristle 1, sometimes weakly developed; arisal length variable from about twice combined length of first 3 antennal segments to 3 to 4 times length of latter, usually with setula-like rays, sometimes in 2 rows; third antennal segment short to normally long; face shield-like, shallowly and uniformly protrudent; facial

setae mostly short, those along oral margin longer especially laterally, uniformly scattered, sometimes with a larger pair at midheight, lacking facial series extending from mid-dorsal facial prominence to posteroventral angle; genal bristle lacking; prescutellar acrostichal setae generally lacking; scutellar bristles with anterior pair distinctly smaller than posterior pair, usually the former less than one-half the latter; humeral callus bare of setulae; anterior notopleural bristle weaker than posterior one; posterior notopleural bristle inserted at level distinctly above that of anterior bristle; propleuron bare of setulae; sternopleural bristle weak as compared with mesopleural bristle; apices of vein R_{2+3} and R_{4+5} at normal distance apart, distance between them about equal to that between veins R_{4+5} and M ; forefemur lacking row of spinelike setae.

MALE TERMINALIA.—Epiandrium variously shaped, providing excellent characters at the species level, usually well sclerotized, with no evident surstyli along ventral margin, the latter probably fused indistinguishably with epiandrium; gonite in lateral view much longer than wide, usually with posterior, narrow projection; aedeagal apodeme usually small, straplike, frequently concealed in lateral view; aedeagus variously shaped.

PHYLOGENETIC CONSIDERATIONS.—As established earlier (Figure 27, with supportive character evidence), the genus *Physemops* is a monophyletic assemblage, with the genus *Dagus* as its probable sister group. Within *Physemops* the lineages are arranged cladistically into two species groups, here called the *nemorosus* and *panops* groups. Each group comprises three species. The *nemorosus* group is established by the following character evidence:

15. *Color of halter*: Generally the halteres are pale colored, usually yellowish, but in species of the *nemorosus* group the capitellum is black.
 16. *Ocellar bristles*: The presence of a pair of divergent, usually proclinate ocellar bristles is the generalized condition. Their absence, as in this species group, is a derived character.
 17. *Size of the second and third terga of males*: Terga 2–5 of males are normally subequal in length. Males of the *nemorosus* group, however, have enlarged second and third terga.
- Frequently the fourth tergum is partially, and the fifth tergum is completely concealed by the enlarged third.
18. *Vein CuA_1* : This vein, along the posterior margin of the discal cell, is generally more-or-less straight. In all members of this group, however, the vein is distinctly bowed posteriorly.
- Within the *nemorosus* group, the three species are related cladistically as indicated in Figure 27. *Physemops nemorosus* and *P. azul* are sister species, and these two together form the sister group of *P. wheeleri*. The monophyly and sister group relationship of *nemorosus-azul* is established by:
19. *Eye vestiture*: Of all the species of Dagini, these two are the only ones with microsetulose eyes. The generalized condition is for the eyes to be bare.
 20. *Size of fronto-orbital bristle*: The generalized condition is for at least one well-developed, fronto-orbital bristle, subequal with either vertical bristle. In specimens of these two species, the single fronto-orbital is much reduced, not well differentiated from surrounding setulae.
- Physemops wheeleri* is readily distinguished from its sister group and its monophyly corroborated by:
21. *Size of branching arisal rays*: In specimens of *P. wheeleri*, the double row of branching rays is very conspicuous, with the longer rays subequal in length of the width of the third antennal segment. The generalized condition is for the rays to be considerably shorter, less than one-half the width of the third antennal segment and usually much shorter.
- The second species group of *Physemops*, the *panops* group, appears to have retained more plesiotypic characters, but its monophyly is established by the following synapotypy:
22. *Distance between apical scutellar bristles*: Generally, the gap separating the apical scutellar bristles is greater than that between the anterolateral scutellar bristle and the apical scutellar bristle on the same side. In species of the *panops* group, however, the apical scutellar bristles are approximate, with the distance between them distinctly less than that between either apical bristle and the anterolateral scutellar bristle of the same side.
- Within the *panops* group, *P. maldonadoi* and *P. panops* are apparently sister species, and together they are the sister group of *P. fairchildi*. The monophyly and sister group relationship of *P. maldonadoi* and *P. panops* are established as follows:

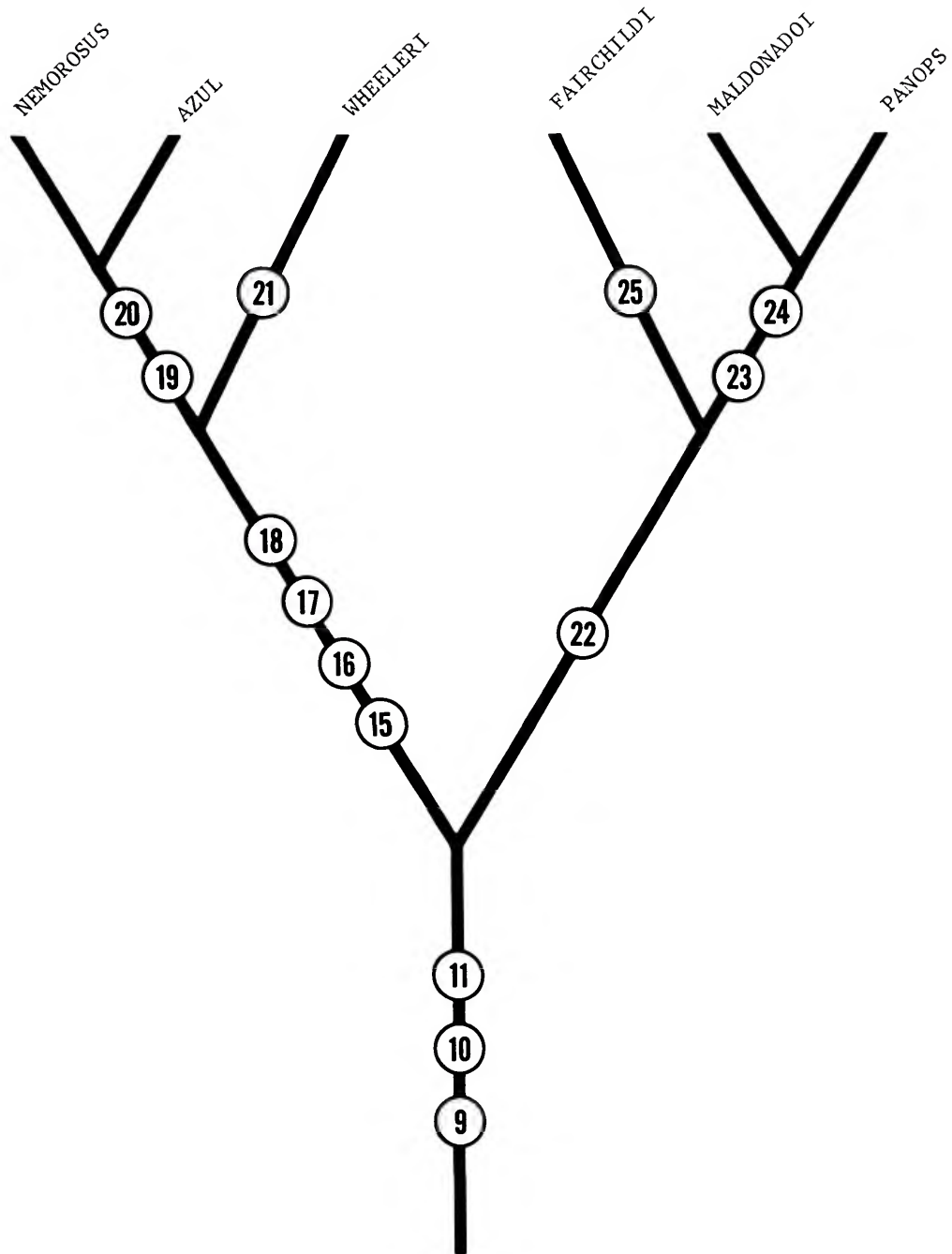


FIGURE 27.—Hypothetical phylogeny for species of genus *Physeomops* (based on character evidence in text).

23. *Color of antennal segments:* The generalized condition is for at least the basal two segments to be dark, usually black. Frequently the apical one is concolorous, although a pale, usually yellowish third antennal segment, is not uncommon. In specimens of *P. maldonadoi* and *P. panops*, however, the entire antenna is yellowish.
24. *Vestiture of arista:* Generally the arista vestiture includes one or two rows of very short setula-like rays, usually restricted to the basal one-half to two-thirds. In specimens of these two species, the branching rays are dorsad only, comparatively long, subequal to one-half the width of the third antennal segment, and extend along the basal two-thirds to three-fourths. This combination of features is unique to these two genera.

Physemops fairchildi is readily distinguished from its sister group, and its monophyly is established by the following:

25. *Vestiture of face:* The generalized condition is for the face to be at least partially tomentose, sometimes thinly so. In specimens of *P. fairchildi* the face is entirely shiny, devoid of tomentosity, a condition I interpret to be synapotypic.

ZOOGEOGRAPHIC DISTRIBUTION.—New World tropics: West Indies (Puerto Rico and Haiti); Mexico south to Colombia and Ecuador.

DISCUSSION.—*Physemops* was last revised by Wirth (1970), when five of the six known species were initially described. My treatment of the genus here is to an extent a synopsis of Wirth's study, particularly the descriptive aspects, although the key, cladistic synthesis, and arrangement of species are newly proposed.

Key to Species of *Physemops*

1. Halter capitellum black; ocellar bristles lacking; arista long, over twice combined length of first 3 antennal segments; vein CuA₁ along posterior margin of discal cell bowed posteriorly (the *nemorosus* group) 2
 - Halter capitellum mostly pale, usually yellowish; ocellar bristles present, conspicuous; arista shorter, usually not over twice combined length of first 3 antennal segments; vein CuA₁ along posterior margin of discal cell straight (the *panops* group) 4
2. Specimens entirely black except for eyes; arista pectinate, with 2 rows of rays; 1 pair of larger upper facial setae, porrect, divergent, inserted just below level of antennae; eye bare 5. ***P. wheeleri*** Wirth, 1970
 - Tibiae, tarsi, and usually third antennal segment pale, yellowish; arista macropubescent; facial setae more or less subequal in size; eyes with microsetulae 3
3. Arista three times or more combined length of first 3 antennal segments; third antennal segment lighter than first and second segments, yellowish brown; face bronzy dorsally, subshiny to shiny, becoming more pollinose ventrally, silvery 4. ***P. nemorosus*** (Cresson), 1914
 - Arista just over twice combined length of first 3 antennal segments; third antennal segment brightly orange; face bronzy dorsally, shiny, becoming greenish ventrally, subshiny 3. ***P. azul*** Wirth, 1970
4. Second and third antennal segments, tibiae yellowish to yellowish orange; face at most subshiny, thinly to densely tomentose, silvery 5
 - Entirely black except for third antennal segment and tarsi; face shiny, lacking tomentose vestiture 6. ***P. fairchildi*** Wirth, 1970

5. Face black except for silvery tomentose vestiture; mesonotum not granulose, more or less unicolorous, becoming shinier and more thinly setulose on scutellum 7. *P. maldonadoi* Wirth, 1970
 Face yellowish except for silvery tomentose vestiture; mesonotum coarsely granulose, distinctly two-toned, scutum appearing grayish brown, sometimes greenish, scutellum silvery blue to purplish blue
 8. *P. panops* Wirth, 1970

The *nemorosus* Group

DIAGNOSIS.—Specimens of this group are similar to those of the *panops* group but may be distinguished by the following combination of characters: ocellar bristles lacking; arista long, over twice combined length of first 2 antennal segments; capitellum of halter black; vein CuA_1 along posterior margin of discal cell bowed posteriorly; vein R_{2+3} curved posteriorly apically toward vein R_{4+5} ; second and third terga enlarged, first, fourth, and fifth terga much less than one-half length of either second or third terga, partially concealed.

3. *Physemops azul* Wirth

Physemops azul Wirth, 1970:172.

DIAGNOSTIC DESCRIPTION.—Resembling *P. nemorosus* but differing from it and other congeners as follows: wing length 1.75 mm; third antennal segment, tibiae, and basal tarsomeres pale, yellowish; face iridescent, with bluish to greenish metallic reflections; otherwise body mostly black.

Head: Vestiture of frons and mesonotum very sparse, appearing subshiny, lacking overt sculpturing, with extremely fine rugose markings; posterolaterocline fronto-orbital bristle weakly developed, barely evident; arista moderately long, at most twice combined length of first 3 antennal segments, with 2 rows of short setula-like rays extending nearly to apex; third antennal segment moderately long, nearly twice length of second; face densely tomentose, tomentum silvery; facial setae uniform in size, lacking pair of porrect setae near dorsum and larger setae along oral margin; eye with microsetulae.

Thorax: Dorsocentral and acrostichal series with anterior setae larger; scutellum broadly

rounded, disc with poorly defined lateral margins, anterolateral scutellar bristles short, less than one-half apical pair; costal vein ratio 6.25; vein M ratio 1.7.

TYPE-LOCALITY.—MEXICO. *Oaxaca:* Valle Nacional.

PRIMARY TYPE MATERIAL.—Holotype female is labeled "Above Valle Nacional Oaxaca, Mex May 15, 1963 [handwritten]/HOLOTYPE *Physemops azul* ♀ W. W. Wirth [red; species name and sex handwritten]." The holotype is glued to the side of a pin, is in excellent condition, and is in the National Museum of Natural History, Smithsonian Institution, USNM 70664.

GEOGRAPHIC DISTRIBUTION.—This species is known only from the type-locality.

REMARKS.—*Physemops azul* and *P. nemorosus* are sister species as indicated in Figure 27, with supportive character evidence as listed.

4. *Physemops nemorosus* (Cresson)

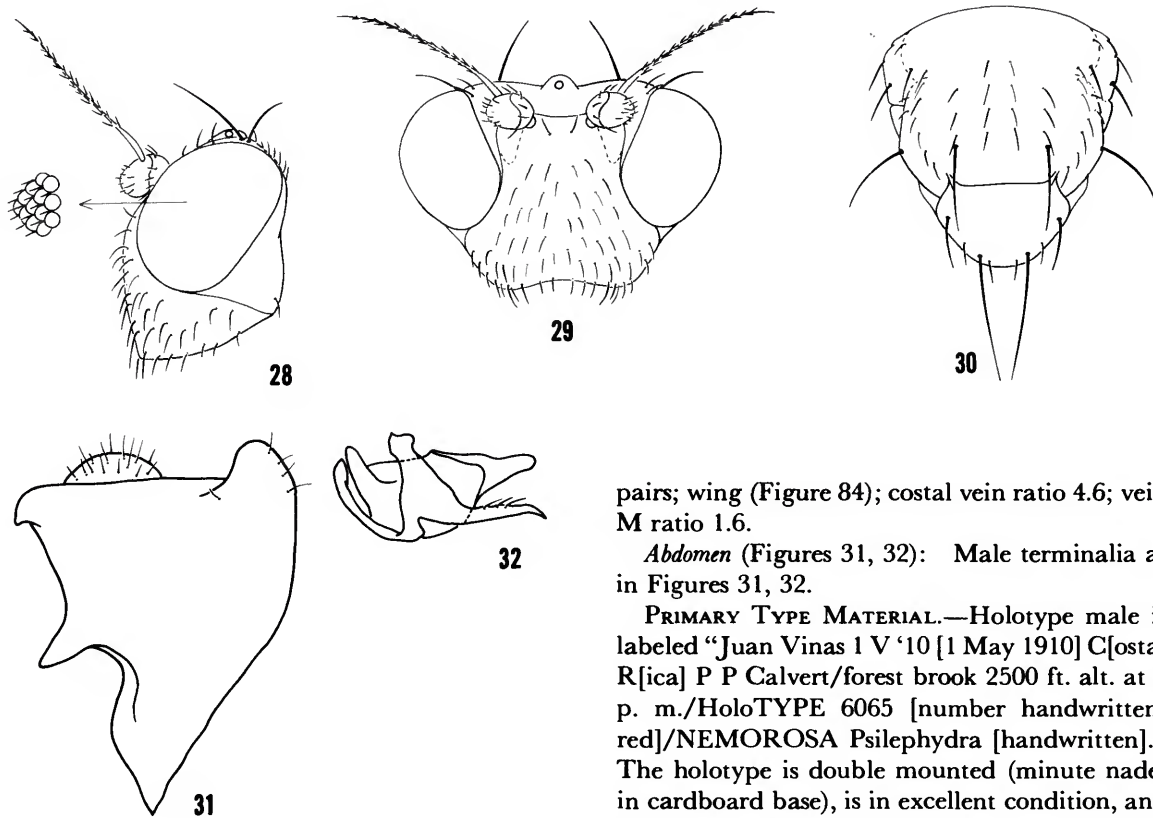
FIGURES 28–41, 84

Psilephydra nemorosa Cresson, 1914:244; 1918:64 [review, figure of head].

Physemops nemorosus.—Cresson, 1934:211 [combination; designated as type-species of *Physemops*].—Wirth, 1968:20 [catalog of Neotropical species].

DIAGNOSTIC DESCRIPTION.—Resembling *P. azul* Wirth but differing from it and other congeners as follows: wing length 2.00 mm; body entirely black except for brown eye and ventral portion of face, which is silvery.

Head (Figures 28, 29, 33–38): Vestiture of frons and mesonotum sparsely tomentose, appearing subshiny to shiny, sculpturing fine, finely reticulate rugose; posterolaterocline fronto-orbital bristle weakly developed, barely evident; arista long, approximately 3 times combined



FIGURES 28–32.—*Physemops nemorosus*: 28, head, lateral aspect; 29, same, anterior aspect; 30, thorax, dorsal aspect; 31, epandrium and cercus, lateral aspect; 32, internal male genitalia, lateral aspect.

length of first 3 antennal segments, with 2 rows of short setula-like rays extending nearly to apex; third antennal segment short, at most slightly longer than second; face 2-toned, dorsum sparsely tomentose, mostly subshiny, black, ventral half becoming more densely tomentose, silvery; eye with microsetulae; facial setae uniform in size, lacking pair of porrect setae near dorsum and larger setae along oral margin.

Thorax (Figures 30, 39–41, 84): Dorsocentral and acrostichal series with anterior setae weakly developed; scutellum broadly rounded, disc with poorly defined lateral margins, anterolateral scutellar bristles small, less than one-half apical

pairs; wing (Figure 84); costal vein ratio 4.6; vein M ratio 1.6.

Abdomen (Figures 31, 32): Male terminalia as in Figures 31, 32.

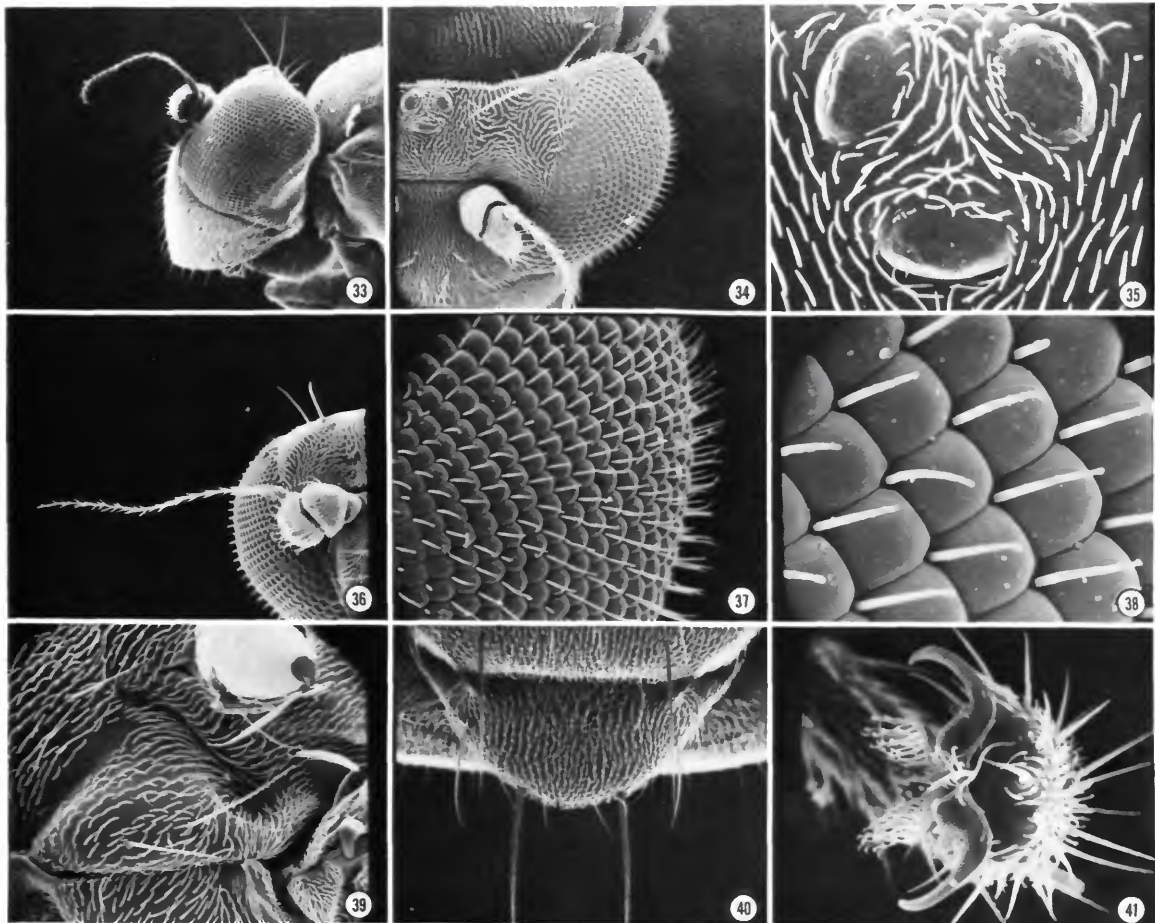
PRIMARY TYPE MATERIAL.—Holotype male is labeled “Juan Vinas 1 V ‘10 [1 May 1910] C[osta] R[ica] P P Calvert/forest brook 2500 ft. alt. at 4 p. m./HoloTYPE 6065 [number handwritten; red]/NEMOROSA Psilephydra [handwritten].” The holotype is double mounted (minute nadel in cardboard base), is in excellent condition, and is in the Academy of Natural Sciences of Philadelphia, ANSP 6065.

NATURAL HISTORY.—Wirth’s field notes (16 Jan 1965; pers. comm.) noted that on the island of Dominica, specimens of this species were observed “swarming in spray at waterfall of brook into Layou River.”

GEOGRAPHIC DISTRIBUTION.—Circumcaribbean and South American. Mexico (Oaxaca) south through El Salvador, Honduras, Nicaragua, Costa Rica, and Panama to Ecuador (Chimborazo) and Brazil (São Paulo). Lesser Antilles, Dominica.

REMARKS.—This species and *P. azul* are sister species (see “Phylogenetic Considerations” under *Physemops*). They are also the smallest species of the genus.

This is the most widespread species of *Physemops*, yet despite its distribution and abundance, nothing is known of its natural history or immature stages.



FIGURES 33-41.—*Physemops nemorosus*: 33, head, lateral aspect; 34, same, dorsal aspect of left side; 35, ocelli, dorsal aspect; 36, antenna, anterior aspect; 37, compound eye with sensory setae; 38, same, enlargement; 39, notopleuron and bristles, lateral aspect; 40, scutellum and bristles, dorsal aspect; 41, midleg, apex of fifth tarsomere, claws, and pulvilli.

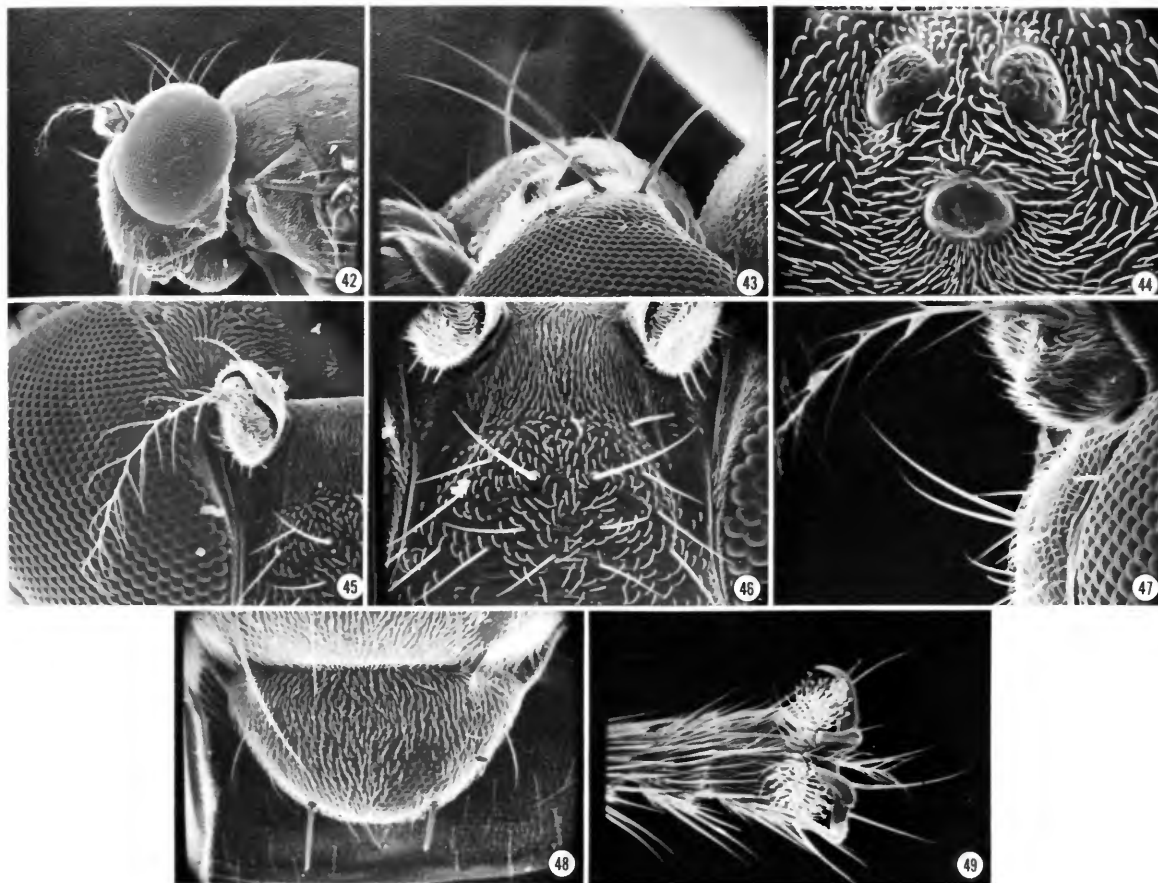
5. *Physemops wheeleri* Wirth

FIGURES 42-49, 85

Physemops wheeleri Wirth, 1970:176.

DIAGNOSTIC DESCRIPTION.—Resembling *P. nemorosus* (Cresson) and *P. azul* Wirth but differing from them and other congeners as follows: wing length 2.90 mm; body entirely black except for brownish eye.

Head (Figures 42-47): Vestiture of frons and mesonotum moderately sparse, appearing subshiny to shiny, finely reticulate rugose sculpturing; posterolaterocline fronto-orbital bristle well developed; arista with 2 rows of pectinate rays, larger rays subequal to length of third antennal segment; third antennal segment short, at most slightly longer than second segment; face with 1 pair of setae inserted just below dorsal margin of facial prominence, divergent, porrect;



FIGURES 42-49.—*Physemops wheeleri*: 42, head, lateral aspect; 43, same, lateral aspect of dorsum; 44, ocelli, dorsal aspect; 45, antenna, anterior aspect; 46, frons (prefrons), anterior aspect; 47, same, lateral aspect; 48, scutellum, dorsal aspect; 49, midleg, ventral aspect of fifth tarsomere, claws, and pulvilli.

facial setae along oral margin distinctly longer than other facial setae; eye bare.

Thorax (Figures 48, 49, 85): Dorsocentral and acrostichal series with anterior setae weak; scutellum broadly rounded, disc poorly defined laterally, anterolateral scutellar setae weak, less than one-half apical pair; wing (Figure 85); costal vein ratio 9.8; vein M ratio 1.8.

TYPE-LOCALITY.—PANAMA. *Canal Zone* [former]: Las Cruces Trail.

PRIMARY TYPE MATERIAL.—Holotype female is

labeled “Las Cruces Trail Canal Zone Feb 1958/ M R Wheeler Collector/ ♀ HOLOTYPE *Physemops wheeleri* W. W. Wirth [red; species name and sex handwritten].” The holotype is double mounted (glued to a paper point), is in excellent condition, and is in the National Museum of Natural History, Smithsonian Institution, USNM 70668.

GEOGRAPHIC DISTRIBUTION.—Panama (several localities) (see Wirth, 1970) south to Ecuador (Santo Domingo de los Colorados).

REMARKS.—Specimens of this species are easily recognized by the double row of long arista rays.

Although this species is well accommodated in the *nemorosus* group, as characterized here, it has apparently retained several characters of the generalized ground plan of the genus, some of which are secondarily plesiotypic with regard to the *nemorosus* group, for example: (1) the single posterolaterocline fronto-orbital bristle is well developed, and (2) the pair of facial setae inserted just below the dorsal facial prominence that is divergent and porrect. Both characters are used in the generic diagnosis and at the generic level are synapotypic, but within the *nemorosus* group they are plesiotypic.

The *panops* Group

DIAGNOSIS.—Specimens of the *panops* group are similar to those of the *nemorosus* group but may be distinguished by the following combination of characters: ocellar bristles present, conspicuous; arista moderately long, usually not over twice combined length of first 3 antennal segments; capitellum of halter mostly pale, usually yellowish; vein CuA_1 along posterior margin of discal cell more or less straight, not distinctly bowed posteriorly; vein R_{2+3} curved anteriorly apically; abdominal terga 2–5 more or less subequal in length.

6. *Physemops fairchildi* Wirth

Physemops fairchildi Wirth, 1970:173.

DIAGNOSTIC DESCRIPTION.—Resembling *P. panops* Wirth and *P. maldonadoi* Wirth but differing from them and other congeners as follows: wing length 2.10 mm; body entirely black except for third antennal segment and basal tarsomeres, which are pale, yellowish, and ventral portion of face, which is whitish.

Head: Posterolaterocline fronto-orbital bristle well developed; arista relatively short, less

than twice combined length of first 3 antennal segments, with setulae restricted to basal one-fourth or less, otherwise bare; third antennal segment normally developed, slightly less than twice length of second segment; dorsum of facial prominence bare, shiny, thereafter ventrally tomentose, tomentum whitish to silvery white; facial setae of uniform size except for distinct pair of divergent, porrect setae inserted just below dorsal margin of facial prominence.

Thorax: Dorsocentral and acrostichal series with anterior setae well developed; mesonotum with finely developed sculpturing, finely reticulate rugose; scutellum moderately acutely rounded, disc triangular, almost as long as wide, anterolateral scutellar bristles large, more than one-half length of apical pair; costal vein ratio 6.6; vein M ratio 1.6.

TYPE-LOCALITY.—PANAMA. *Panama Province:* Cerro Campana.

PRIMARY TYPE MATERIAL.—Holotype male is labeled "Cerro Campana Rep. Panama July 1967 W. W. Wirth/HOLOTYPED ♂ *Physemops fairchildi* W. W. Wirth [red; species name, sex, and "HO" handwritten]." The holotype is double mounted (minute nadel in a polyporus block), is in excellent condition, and is in the National Museum of Natural History, Smithsonian Institution, USNM 70665.

GEOGRAPHIC DISTRIBUTION.—Panama (type-locality) south to Colombia (vicinity of Bogotá and Medellín).

REMARKS.—Wirth's field notes indicate that the holotype was collected by sweeping over rocks near a small mountainous stream at about 547 m elevation. Specimens from Colombia were collected at high elevations between 2438 and 2652 m.

Physemops fairchildi is apparently the sister group to the stem lineage that gave rise to *P. maldonadoi* and *P. panops*. The relationship is as depicted in Figure 27, with supportive character evidence as indicated.

7. *Physemops maldonadoi* Wirth

FIGURES 50-55, 86

Physemops maldonadoi Wirth, 1970:173.

DIAGNOSTIC DESCRIPTION.—Resembling *P. fairchildi* Wirth and *P. panops* Wirth but differing from them and other congeners as follows: wing length 2.34 mm; antennal segments pale, yellowish, tibiae and tarsi pale, yellowish brown to yellowish; face mostly whitish to silvery white; otherwise body mostly black.

Head (Figures 50, 51): Posterolaterocline fronto-orbital bristle well developed; arista moderately long, but less than twice combined length of first 3 antennal segments, with long setula-like rays on dorsal surface of basal one-half to two-thirds, longest about one-half width of third antennal segment normally developed, slightly less than twice length of second segment; dorsum of facial prominence sparsely tomentose, becoming more densely tomentose ventrally, tomentum whitish to silvery white; facial setae uniform in size except for distinct pair of divergent, porrect setae inserted just below dorsal margin of facial prominence.

Thorax (Figures 52, 86): Dorsocentral and acrostichal series with anterior setae weakly developed; mesonotum with finely developed sculpturing, finely reticulate rugose; scutellum moderately acutely rounded, disc lacking sharp lateral margins, anterolateral scutellar bristles small, less than one-half apical pair; wing (Figure 86); costal vein ratio 3.4; vein M ratio 2.1.

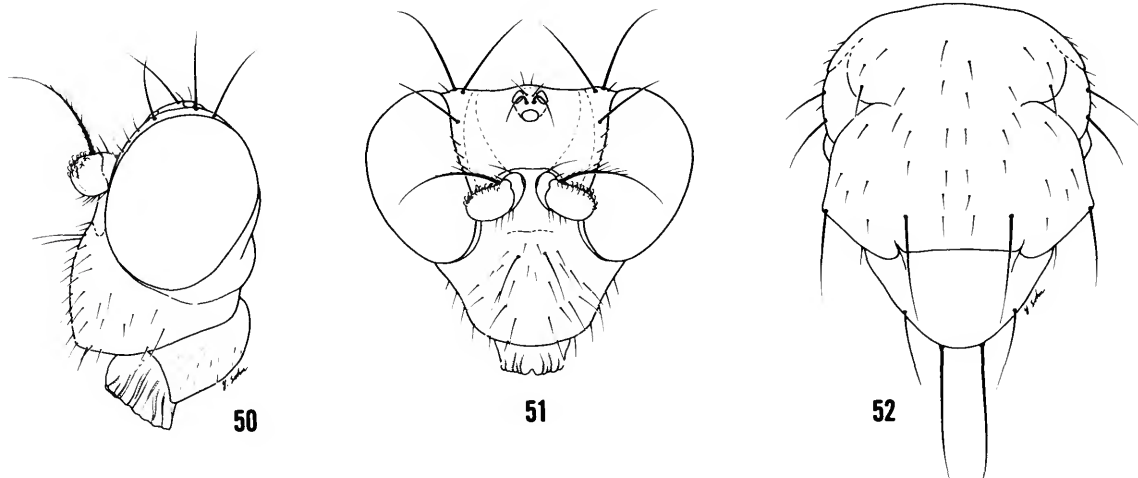
Abdomen (Figures 53-55): Male terminalia as in Figures 53-55.

TYPE-LOCALITY.—PUERTO RICO. Yauco-Lares Road, km 29.

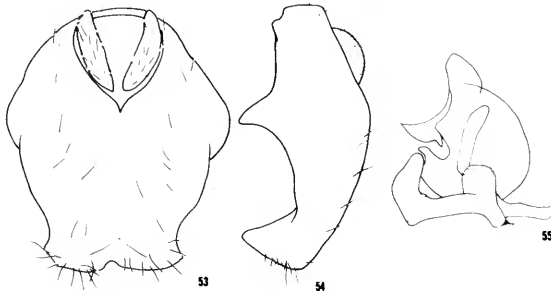
PRIMARY TYPE MATERIAL.—Holotype male is labeled "Yauco-Lares Rd., P[uerto]. R[ico]. Km. 29 Jan. 20, 1954/J. Maldonado [,] S. Medina Colls./HOLOTYPE *Physemops maldonadoi* W. W. Wirth [red; species name and sex handwritten]." The holotype is double mounted (glued to a paper point), is in excellent condition, and is in the National Museum of Natural History, Smithsonian Institution, USNM 70666.

GEOGRAPHIC DISTRIBUTION.—This species is known only from the type-locality.

REMARKS.—*Physemops maldonadoi* and *P. panops*



FIGURES 50-52.—*Physemops maldonadoi*: 50, head, lateral aspect; 51, same, anterodorsal aspect; 52, thorax, dorsal aspect.



FIGURES 53–55.—*Physemops maldonadoi*: 53, epandrium and cerci, posterior aspect; 54, same, lateral aspect; 55, internal male genitalia, lateral aspect.

are sister species as indicated in Figure 27, with supportive character evidence as listed.

8. *Physemops panops* Wirth

Physemops panops Wirth, 1970:175.

DIAGNOSTIC DESCRIPTION.—Resembling *P. maldonadoi* Wirth and *P. fairchildi* Wirth but differing from them and other congeners as follows: wing length 2.4 mm; antennal segments pale, yellowish; tibiae and tarsi pale, yellowish brown to yellowish, facial prominence yellow with very sparse tomentose vestiture, otherwise body mostly black.

Head: Posterolaterocline fronto-orbital bristle well developed; arista moderately long, but less than twice combined length of first 3 antennal segments, with long setula-like rays on dorsal surface of basal one-half to two-thirds, longest ray about one-half width of third antennal segment; third antennal segment normally developed, slightly less than twice length of second segment; tomentum of face sparse dorsally, becoming denser ventrally and laterally, tomentum whitish to silvery white; facial setae uniform in size except for distinct pair of divergent, porrect setae inserted just below dorsal margin of facial prominence.

Thorax: Dorsocentral series with anterior setae moderately well developed, acrostichal series weakly developed anteriorly; mesonotum conspicuously sculptured, reticulate rugose, especially evident on scutellum, with iridescent metallic reflections, scutum silvery to faintly golden, scutellum more purplish to bluish; scutellum with lateral margins at basal one-fourth somewhat parallel, then angling inward distinctly for remainder of length to pointed apex, anterolateral scutellum bristles long, more than one-half length of apical pair; costal vein ratio 4.3; vein M ratio 2.0.

TYPE-LOCALITY.—HAITI.

PRIMARY TYPE MATERIAL.—Holotype male is labeled “Haiti W B Heed/Kenscoff 4000 ft/Feb 1956/HOLOTYPE ♂ *Physemops panops* W. W. Wirth [red; species name, sex, and “HO” handwritten].” The holotype is double mounted (glued to a paper point), is in good condition (some setae of the head missing), and is in the National Museum of Natural History, Smithsonian Institution, USNM 70667.

GEOGRAPHIC DISTRIBUTION.—This species is known only from the type-locality.

REMARKS.—*Physemops panops* and *P. maldonadoi* are sister species, as indicated in Figure 27, with supportive character evidence as listed.

Genus *Dagus* Cresson

Dagus Cresson, 1935:345 [type-species: *Ephydra rostrata* Cresson, by original designation and monotypy].—Wirth, 1968:24 [catalog of Neotropical species].

DIAGNOSIS.—Specimens of *Dagus* resemble those of *Psilephydra*, *Physemops*, and *Diedrops* but may be distinguished by the following combination of characters: ocellar bristles present, well developed; laterocline fronto-orbital bristles 3, anterior bristle smaller, about one-half length of posterior bristles; arista moderately long but not twice length of first 3 antennal segments, very small setulae dorsally on basal two-thirds; third antennal segment nearly twice length of second

segment; face with ventral portion distinctly protrudent, uniformly arched vertically and transversely; mostly subshiny, thinly tomentose, becoming more densely tomentose ventrally and laterally; facial setae sparse but with prominent series extending from facial carina to posteroventral angle of face, larger bristles of this series porrect and anaclinate; genal bristle present, conspicuous; prescutellar acrostichal setae usually lacking; anterior scutellar setae small, less than one-half length of posterior pair; dorsocentral bristles stronger postsuturally, but usually with 1 or 2 larger setae at suture or presuturally; posterior one; posterior notopleural bristle inserted at level distinctly above that of anterior bristle; propleuron bare of setulae; sternopleural bristle weakly developed, especially as compared to mesopleural bristle; apex of vein R_{2+3} well separated from vein R_{4+5} , distance between these two about equal to that between veins R_{4+5} and M ; pulvilli lacking or greatly reduced; tarsal claws comparatively long, straight, oriented anteriorly, frequently held together throughout length.

MALE TERMINALIA.—Epandrium, in posterior view, triangular, abbreviated dorsally, not forming cercal cavity around cerci, ventral angle with median cleft, lateral view of epandrium with dorsal one-third wide, thereafter ventrally narrowing rapidly to form rather narrow apex; cerci placed at dorsal margin of epandrium, lacking cercal cavity; gonite with 2 posterior projections, each bearing 1 or more setae; aedeagal apodeme about twice as long as wide, roughly oval; aedeagus long and slender, length subequal to that of epandrium.

PHYLOGENETIC CONSIDERATIONS.—See “Phylogenetic Considerations” under tribe Dagini and genus *Physemops* (pages 4 and 11, respectively).

GEOGRAPHIC DISTRIBUTION.—New World tropics between 30° north latitude and 10° south latitude.

DISCUSSION.—When Cresson (1935:345) selected the name “*Dagus*” for his new genus, he indicated that the name was derived from a Greek word meaning “a puppet.” Cresson’s latinized

transliteration of the Greek word was unfortunately in error and has caused confusion as to its proper gender. The correct transliteration is “*Dagys*,” and as such it would be feminine, but “*Dagus*,” with its masculine termination in the published form is supported by the rules [ICZN, 1964, art. 30 (a)(i)(3)], which state: “If a genus group name is a Greek word latinized with a change of termination, it takes the gender appropriate to that termination.” Consequently, the generic name is to be treated as masculine, and the correct combination of the type-species is *Dagus rostratus* (Cresson).

9. *Dagus rostratus* (Cresson)

FIGURES 56–72, 87

Ephydra pygmaea Williston, 1896:402 [preoccupied, Haliday, 1833:174].

Ephydra rostrata Cresson, 1918:66 [new name for *E. pygmaea* Williston; figure of head].

Dagus rostrata.—Cresson, 1935:346 [designated as type-species of *Dagus*].

DIAGNOSTIC DESCRIPTION.—As in generic diagnosis but with the following details: length 1.54 to 2.49 mm.

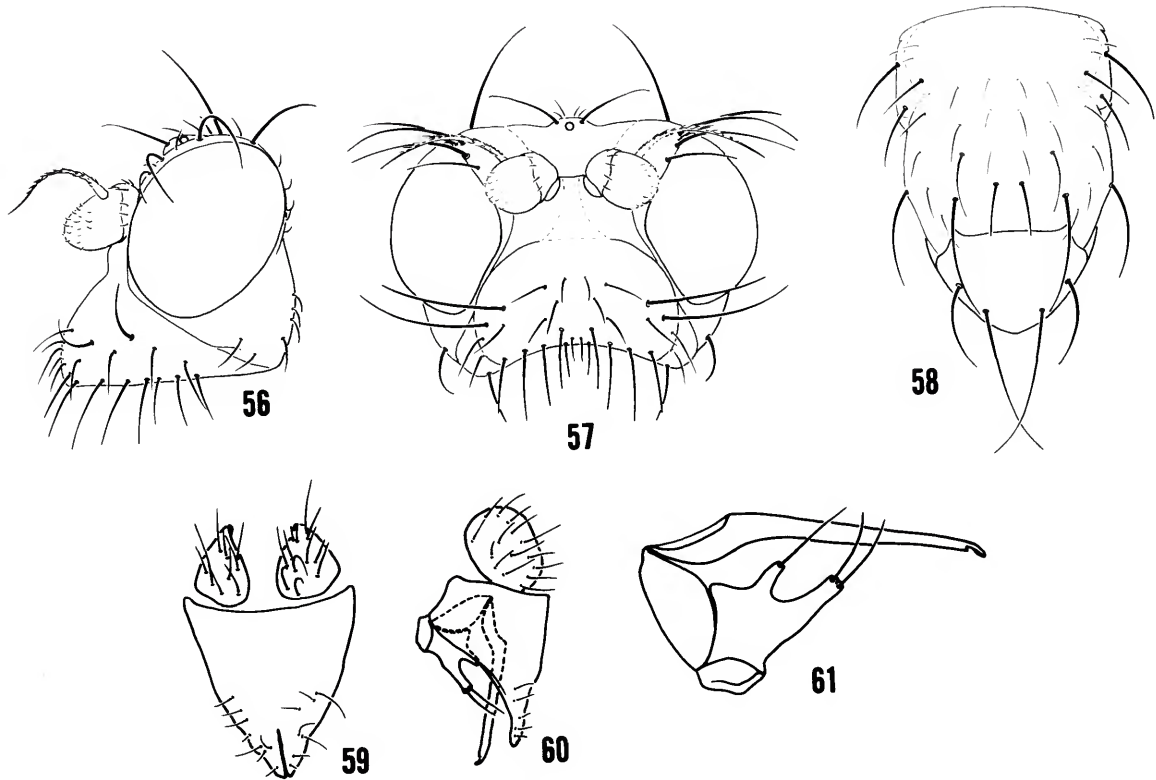
Head (Figures 56, 57, 62–67): Parafrons densely tomentose, appearing as velvety anterior wedges, distinctly contrasting with mesofrons and fronto-orbits; face lacking antennal foveae.

Thorax (Figures 58, 68–72, 87): Acrostichal setae conspicuous, especially posterior pair; apicolateral setae of fourth tarsomere of foreleg not as conspicuous or curved; wing as in Figure 87.

Abdomen (Figures 59–61): Male terminalia as in Figures 59–61.

TYPE-LOCALITY.—WEST INDIES. *Saint Vincent*: Perseverance Valley.

Primary Type Material.—Lecotype male, herein designated, is labeled “Co-type [disk with yellow border]/Windward side St. Vincent, W[est]. I[ndies]. H. H. Smith./W. Indies 1907–



FIGURES 56-61.—*Dagus rostratus*: 56, head, lateral aspect; 57, same, anterior aspect; 58, thorax, dorsal aspect; 59, epiandrium and cerci, posterior aspect; 60, same plus internal male genitalia, lateral aspect; 61, internal male genitalia, lateral aspect.

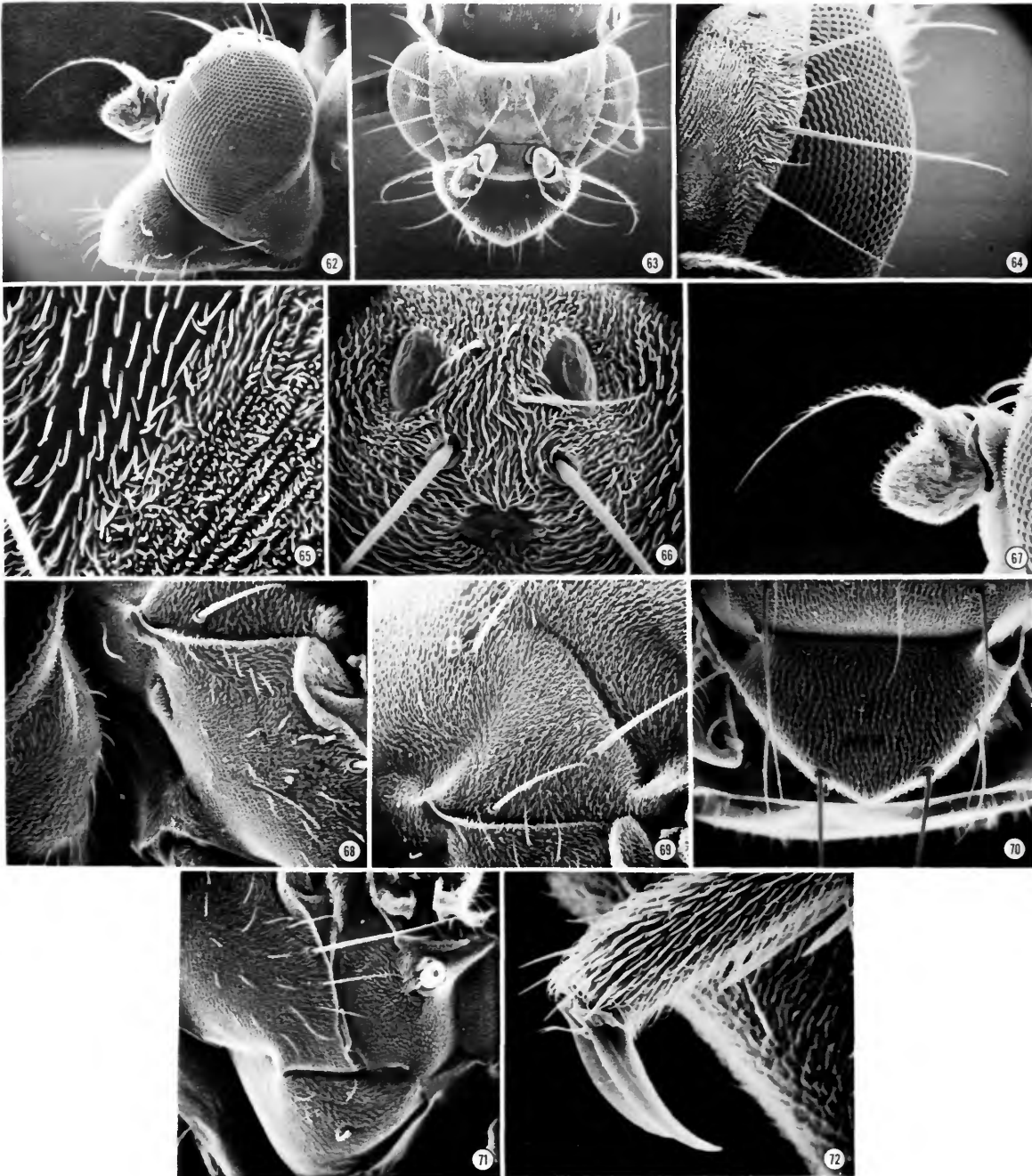
66./1000 feet./*Ephydra pygmaea* Will [handwritten; two submarginal red borders]/LECTO-TYPE ♂ *Ephydra pygmaea* Williston by W. N. Mathis [handwritten; red].” The lectotype is double mounted (minute nadel in cardboard base), is in good condition (the apical segment of the right antenna is missing), and is in the British Museum (Natural History). I have also examined seven other syntypes (1♂, 6♀; BMNH), which are here designated as paralectotypes.

GEOGRAPHIC DISTRIBUTION.—West Indies (Cuba, Dominica, Jamaica, Saint Vincent); Mexico south through Costa Rica (Cartago; Cresson, 1918:66), to Venezuela (Rancho Grande) and

Brazil (without specific locality; Cresson, 1935: 346).

REMARKS.—This is a distinctive species and is not likely to be confused with any others of the tribe.

Both Williston (1896) and Cresson (1918) initially placed this species in the genus *Ephydra*, as it has three fronto-orbital bristles, lacks conspicuous pulvilli, and the tarsal claws are relatively straight and long. The similarity of these characters with those of *Ephydra*, however, is due to convergence, as was later observed by Cresson (1935), who proposed the genus *Dagus* to accommodate the species.



FIGURES 62-72.—*Dagus rostratus*: 62, head, lateral aspect; 63, same, dorsal aspect; 64, same dorsal aspect of left side; 65, tomentosity of mesofrons (sparse) and parafrons (dense), dorsal aspect; 66, ocelli and bristles, dorsal aspect; 67, antenna, lateral aspect; 68, propleuron and mesopleuron, lateral aspect; 69, notopleuron and bristles, lateral aspect; 70, scutellum, dorsal aspect; 71, mesopleuron, sternopleuron, and bristles, lateral aspect; 72, midleg, apex of fifth tarsomere and claws.

Genus *Psilephydra* Hendel

Psilephydra Hendel, 1914:99 [type-species: *Psilephydra cyanoprosopa* Hendel, by original designation and monotypy].—Cresson, 1918:63 [diagnosis, subfamilial placement].—Mathis and Wirth, 1976:128 [comparison with *Diedrops*].—Cogan and Wirth, 1977:338 [catalog of Oriental species].

DIAGNOSIS.—Specimens of *Psilephydra* are similar to those of *Diedrops*, *Physemops*, and *Dagus* but may be distinguished by the following combination of characters: ocellar bristles present, well developed; orientation of fronto-orbital bristles variable, 1-2, development variable; arista moderately long, length nearly twice combined length of first 3 antennal segments, apex virtually bare of vestiture, basal two-thirds with some dorsal, minute setulae or nearly bare; third antennal segment longer than second, but not twice length of latter; face generally shieldlike, either shallowly and uniformly protrudent over entire height or with lower two-thirds slightly but distinctly more protrudent (best seen in profile); facial setae variable; genal bristle variable; prescutellar acrostichal setae lacking; scutellar bristles with anterior pair smaller, length as compared to apical pair variable; humeral callus either bare of setulae or with 1 setula; notopleural bristles variable; propleuron bare of setulae; sternopleural bristle variable; apices of veins R_{2+3} and R_{4+5} normal, distance between them about equal to that between veins R_{4+5} and M; vestiture of forefemur variable.

MALE TERMINALIA.—Epandrium shieldlike, forming cercal cavity dorsally; surstyli either distinct or apparently fused to ventral margin; gonite in lateral view with ventral and anterior projections, both slender; aedeagal apodeme long and very slender; aedeagus either about as wide

as long or longer than wide.

PHYLOGENETIC CONSIDERATIONS.—The characterization of *Psilephydra* and the evidence used to establish its monophyly are not entirely satisfactory, and I am recognizing the genus as much for convenience as for soundness of phylogenetic or taxonomic evidence. Still I suspect that the two species comprising *Psilephydra* are closely related and may well represent a monophyletic lineage. As noted earlier, the character evidence to corroborate the monophyly of *Psilephydra* is based solely on characters of the male genitalia. Moreover, there are other characters, including several external ones, which resemble those of other genera within the tribe, apparently by convergence. Thus, there is considerable margin for reinterpretation of the relationships, and ultimately I was persuaded to recognize the genus, with its present composition, by two factors. First, the male genitalia of both included species are more similar to each other than to others within the tribe; and second, both species are the only known species of the tribe to occur in the Old World, and specifically in the Orient.

Because I am somewhat ambivalent as to the monophyly and cohesiveness of *Psilephydra* I have not diagrammed the lineage with its two species, although there is an abundance of characters that could be used as evidence to substantiate each species lineage (see key and species diagnoses).

GEOGRAPHIC DISTRIBUTION.—Old World: Japan, Ryukyu Islands, and Taiwan.

DISCUSSION.—Our knowledge of this genus is limited to descriptive taxonomic data and the brief synthesis of phylogenetic relationships presented here. The ecology, natural history, and description of the life-cycle stages are lacking for both species.

Key to Species of *Psilephydra*

- Larger species, length 2.50–3.15 mm; fronto-orbital bristles weak, distinctly smaller than vertical bristles; genal bristle lacking; anterior notopleural bristle weaker than posterior bristle; forefemur with row of short, spinelike setae along posteroventral surface (Taiwan) 10. *P. cyanoprosopa* Hendel, 1914

Smaller species, length 2–2.60 mm; fronto-orbital bristles strong, subequal to vertical bristles; genal bristle present, well developed; anterior notopleural bristle subequal to posterior bristle; forefemur lacking row of spinelike setae along posteroventral surface (Japan and Ryukyu Islands)
 11. *P. fluvialis* (Miyagi), 1977

10. *Psilephydra cyanoprosopa* Hendel

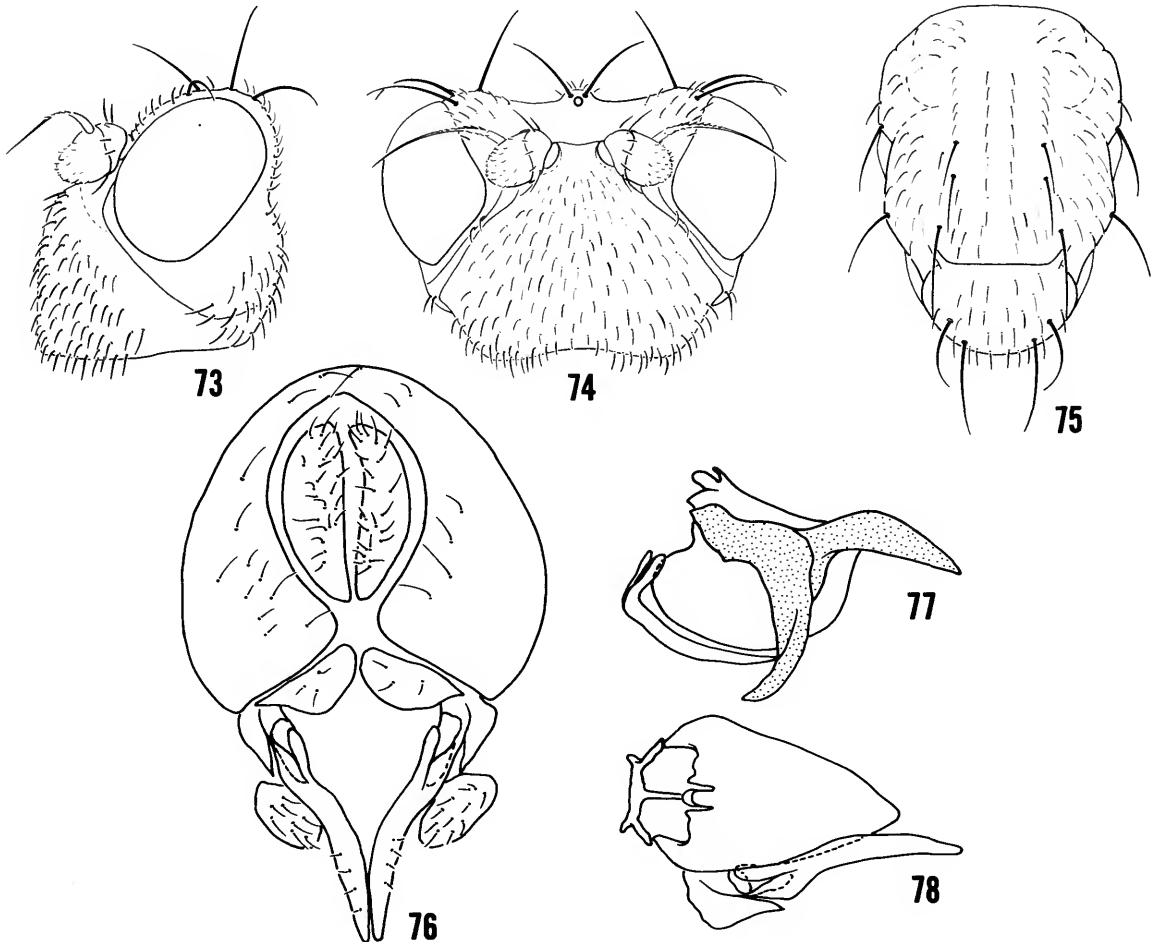
FIGURES 73–78, 88

Psilephydra cyanoprosopa Hendel, 1914:100.—Cogan and Wirth, 1977:338 [catalog of Oriental species].

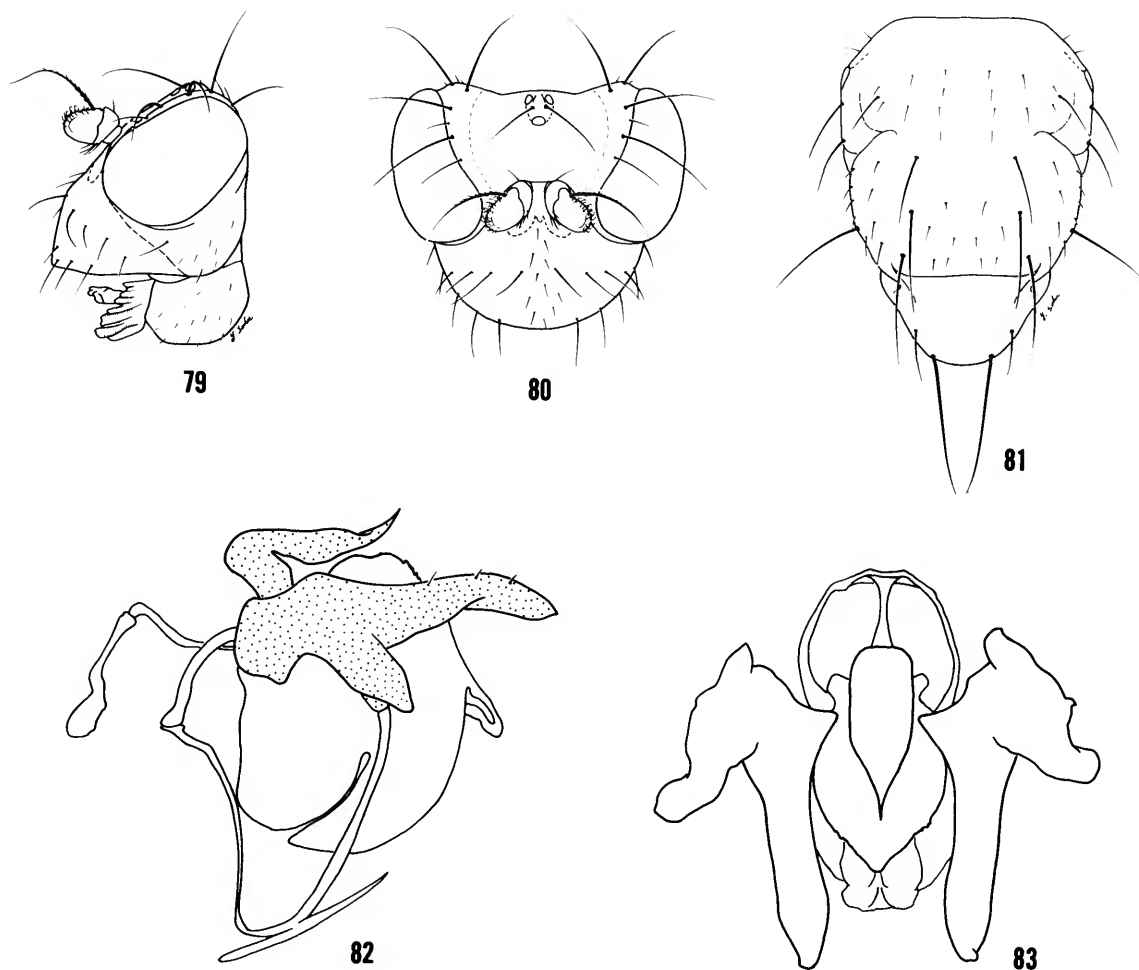
Psilephydra cyanocephala [sic] Cresson, 1934:211 [misspelling of specific epithet].

DIAGNOSTIC DESCRIPTION.—Resembling *P. fluvialis* but differing from it as follows: length 2.47 to 3.15 mm.

Head (Figures 73, 74, 79, 80): Frons generally dull, tomentose, brownish, mesofrons with some metallic reflections, greenish blue; fronto-orbital



FIGURES 73–78.—*Psilephydra cyanoprosopa*: 73, head, lateral aspect; 74, same, anterior aspect; 75, thorax, dorsal aspect; 76, male terminalia, posterior aspect; 77, internal male genitalia, lateral aspect; 78, same, dorsal aspect.



FIGURES 79-83.—*Psilephydra fluviialis*: 79, head, lateral aspect; 80, same, anterodorsal aspect; 81, thorax, dorsal aspect; 82, internal male genitalia, lateral aspect; 83, same, dorsal aspect.

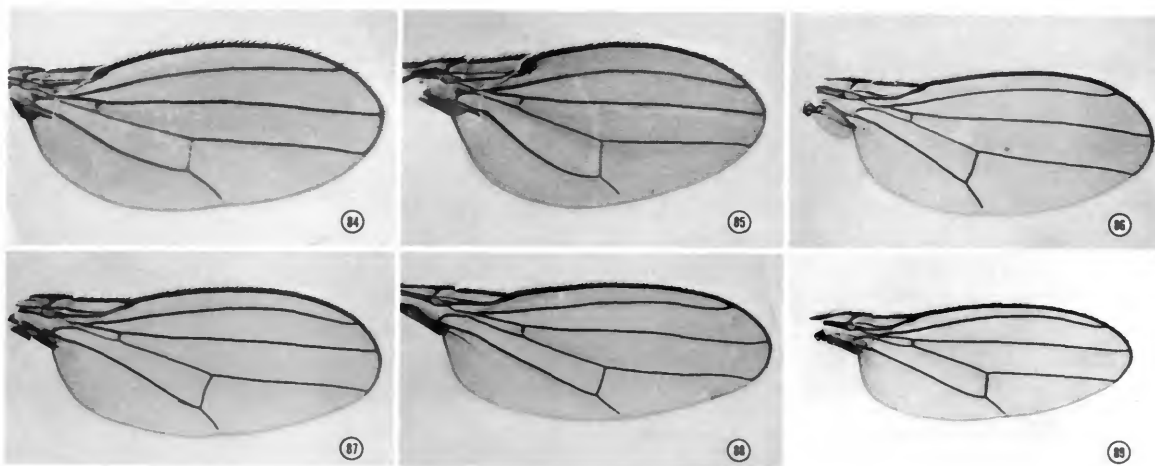
bristles posterolaterocline, weakly developed, 1-2; arista mostly bare, microsetulae sparse and restricted to basal one-third; face shallowly and evenly protrudent, subshiny to shiny, mostly silvery but with considerable greenish blue reflections; facial setae uniformly small, including those along oral margin, moderately densely distributed, lacking series extending from dorsal facial prominence to posteroventral angle of face; genal bristle lacking.

Thorax (Figures 75, 88): Anterior scutellar bristle slightly longer than one-half length of posterior pair; humeral callus bare of setulae;

anterior notopleural bristle weakly developed as compared to posterior one; posterior notopleural bristle inserted at about same level as anterior bristle; sternopleural bristle weakly developed as compared with mesopleural bristle; forefemur with row of short, spinelike setae along posteroventral surface; apicolateral setae of fourth tarsomere of foreleg as on other tarsomere; wing (Figure 88); costal vein ratio 4.72; vein M ratio 1.92.

Abdomen (Figures 76-78): Male terminalia as in Figures 76-78.

TYPE-LOCALITY.—TAIWAN. Hoozan.



FIGURES 84-89.—Wings: 84, *Physemops nemorosus*; 85, *Physemops wheeleri*; 86, *Physemops maldonadoi*; 87, *Dagus rostratus*; 88, *Psilephydra cyanoprosopa*; 89, *Psilephydra fluvialis*.

PRIMARY TYPE MATERIAL.—Lectotype male, here designated, is labeled “Hoozan Formosa H. Sauter, 1911/7. I. [“7” handwritten = (?) 7 Jan] /*Psilephydra cyanoprosopa* H. det. Hendel [species name handwritten]/Coll. Hendel/LECTO-TYPE *Psilephydra cyanoprosopa* Hendel by W. N. Mathis [red, handwritten].” The lectotype is pinned directly, is in fair condition (some setae missing; dirty), and is in the Naturhistorisches Museum, Vienna. Hendel’s original description mentioned 12 syntypes. Of these I have examined the lectotype, a second male (NMW), and a female (ANSP) (here designated as paralectotypes). The remaining nine specimens are presumably in Vienna, although this has not been confirmed.

GEOGRAPHIC DISTRIBUTION.—TAIWAN.

REMARKS.—This is a very distinctive species within *Dagini* and is not likely to be confused with any other.

11. *Psilephydra fluvialis* (Miyagi), new combination

FIGURES 79-83, 89

Lamproscatella fluvialis Miyagi, 1977:88.

DIAGNOSTIC DESCRIPTION.—Resembling *P. cyanoprosopa* but differing from it as follows: length

2.02 to 2.60 mm.

Head (Figures 79, 80): Frons generally with vestiture and coloration similar throughout, very thinly tomentose, subshiny to shiny, parafrons not distinguished; fronto-orbital bristles laterocline, well developed, 2; arista with microsetulae along dorsum of basal two-thirds; face shallowly protrudent, although lower two-thirds slightly but distinctly more protrudent, thinly tomentose, especially dorsomedially which is subshiny, with bronzy to greenish blue reflections; facial setae with marginal ones conspicuously larger and with distinct series of larger setae extending from dorsal facial prominence to posteroventral angle of face; genal bristle present, well developed.

Thorax (Figures 81, 89): Anterior scutellar bristle comparatively small, about one-third length of apical pair; humeral callus with 1 setula; anterior notopleural bristle subequal in size to posterior bristle; posterior notopleural bristle inserted at distinctly higher level than anterior bristle; sternopleural bristle fairly strong, subequal to mesopleural bristle; sternopleural bristle fairly strong, subequal to mesopleural bristle; forefemur lacking row of short, spinelike setae along posteroventral surface; apicolateral setae of fourth tarsomere of foreleg stout, curved inward; wing (Figure 89); costal vein ratio of 5.60; vein M ratio 1.65.

Abdomen (Figures 82, 83): Male terminalia as in Figures 82, 83.

TYPE-LOCALITY.—JAPAN. *Shikoku Island*: Nametoko, Ehime-ken.

PRIMARY TYPE MATERIAL.—Holotype male is apparently labeled "Nametoko Sept. 10 1962/JAPONIA Shikoku I. MIYAGI." The holotype is double mounted (minute nadel in a paper rectangle) and is in the Entomological Institute, Hokkaido University. I have not examined the holotype but have studied a female paratopotype. The data cited here are presumed to be like those on the holotype specimen.

GEOGRAPHIC DISTRIBUTION.—Japan (Honshu and Shikoku Islands) and the Ryukyu Islands (Okinawa-honto).

REMARKS.—My attempt to determine the identity of this species for a separate study on the Old World *Lamproscatella* Hendel was the action that prompted this paper. Through the kindness of Dr. I. Miyagi, I was sent a male and female paratype of his new species, and after examining them, I have concluded that they cannot be included in the genus *Lamproscatella* but are more closely related to *Psilephydra* and represent a second species of that genus.

Literature Cited

- Cogan, B. H.
 1980. Family Ephydriidae. In R. W. Crosskey, editor, *Catalogue of the Diptera of the Afrotropical Region*, 71: 655–669. London: British Museum (Natural History).
- Cogan, B. H., and W. W. Wirth
 1977. Family Ephydriidae. In M. D. Delfinado and D. E. Hardy, editors, *A Catalog of the Diptera of the Oriental Region, Volume III: Suborder Cyclorrhapha (Excluding Division Aschiza)*, pages 321–339. Honolulu: The University Press of Hawaii.
- Cresson, E. T., Jr.
 1914. Descriptions of New Genera and Species of the Dipterous Family Ephydriidae, I. *Entomological News*, 25(6):241–250, 1 plate.
 1918. Costa Rican Diptera Collected by Philip P. Calvert, Ph.D., 1909–1910, Paper 3: A Report on the Ephydriidae. *Transactions of the American Entomological Society*, 44:39–68, 1 plate.
 1930. Studies in the Dipterous Family Ephydriidae, Paper III. *Transactions of the American Entomological Society*, 56:93–131.
 1931. Descriptions of New Genera and Species of the Dipterous Family Ephydriidae, Paper IX. *Entomological News*, 42(4):104–108.
 1934. Descriptions of New Genera and Species of the Dipterous Family Ephydriidae, XI. *Transactions of the American Entomological Society*, 60:199–222, 1 plate.
 1935. Descriptions of New Genera and Species of the Dipterous Family Ephydriidae. *Transactions of the American Entomological Society*, 61:345–372.
- Dahl, R. G.
 1959. Studies on Scandinavian Ephydriidae (Diptera: Brachycera). *Opuscula Entomologica*, supplement, 15: 224 pages, 84 figures.
- Haliday, A. H.
 1833. Catalogue of Diptera Occurring about Holywood in Downshire. *The Entomological Magazine* (London), 1:147–180.
- Hendel, F.
 1914. H. Sauter's Formosa-Ausbeute: Acalyptrate Musciden (Dipt.), III. *Supplementa Entomologica*, 3:90–117, 7 figures.
- Hennig, W.
 1973. 31, Diptera (Zweiflügler). In M. Beier, editor, volume IV: Arthropoda, second half: Insecta, second edition, Part 2: Spezielles. In J.-G. Helmcke et al., editors, *Handbuch der Zoologie*, 337 pages, 143 figures. Berlin: Walter de Gruyter.
- ICZN
 1964. *International Code of Zoological Nomenclature Adopted by the XV International Congress of Zoology*. Pages xx+176. London: International Trust for Zoological Nomenclature.
- Mathis, W. N.
 1977. Key to the Neotropical Genera of Parydrinae with a Revision of the Genus *Eleleides* Cresson (Diptera: Ephydriidae). *Proceedings of the Biological Society of Washington*, 90(3):553–565, 13 figures.
 1979a. Studies of Ephydriinae (Diptera: Ephydriidae), II: Phylogeny, Classification, and Zoogeography of Nearctic *Lamproscatella* Hendel. *Smithsonian Contributions to Zoology*, 295:1–41, 52 figures.
 1979b. Ephydriinae (Diptera: Ephydriidae): A New Perspective. In D. L. Deonier, editor, *First Symposium on the Systematics and Ecology of Ephydriidae (Diptera)*, pages 47–60, 5 figures, 1 table. Oxford, Ohio: The North American Benthological Society.
 1980. Studies of Ephydriinae (Diptera: Ephydriidae), III: Revisions of Some Neotropical Genera and Species. *Smithsonian Contributions to Zoology*, 303:1–50, 77 figures.
- Mathis, W. N., and G. E. Shewell
 1978. Studies of Ephydriinae (Diptera: Ephydriidae), I: Revisions of *Parascatella* Cresson and the *triseta* Group of *Scatella* Robineau-Desvoidy. *Smithsonian Contributions to Zoology*, 285:1–44, 62 figures, 1 table.
- Mathis, W. N., and K. W. Simpson
 1981. Studies of Ephydriinae (Diptera: Ephydriidae), V: The Genera *Cirrula* Cresson and *Dimecoenia* Cresson in North America. *Smithsonian Contributions to Zoology*, 329:1–51, 119 figures, 1 table.
- Mathis, W. N., and W. W. Wirth
 1976. A New Neotropical Shore Fly Genus with Two New Species (Diptera: Ephydriidae). *The Pan-Pacific Entomologist*, 52(2):126–132, 15 figures.
- Miyagi, I.
 1977. Ephydriidae (Insecta: Diptera). In *Fauna Japonica*, 113 pages, 49 plates, 500 figures.
- Sturtevant, A. H., and M. R. Wheeler
 1954. Synopses of Nearctic Ephydriidae (Diptera). *Transactions of the American Entomological Society*, 79:151–257.

Williston, S. W.

1896. On the Diptera of St. Vincent (West Indies). *The Transactions of the Entomological Society of London*, 1896:253-446, 7 plates.

Wirth, W. W.

1965. Family Ephydriidae. In A. Stone et al., editors, A Catalog of the Diptera of America North of Mexico. *United States Department of Agriculture, Agriculture Handbook*, 276: 1696 pages.
1968. Family Ephydriidae. In N. Papavero, editor, *A Catalogue of the Diptera of the Americas South of the United States*, 77:1-43. São Paulo: Departamento de

Zoologia, Secretaria da Agricultura.

1970. A Revision of the Neotropical Genus *Physemops* Cresson (Diptera: Ephydriidae). *The Pan-Pacific Entomologist*, 46(3):170-177.

Wirth, W. W., and A. Stone

1956. Aquatic Diptera. In R. L. Usinger, *Aquatic Insects of California*, pages 372-482, 64 figures. Berkeley: University of California Press.

Zetterstedt, J. W.

1837. Conspectus familiarum, generum et specierum dipterorum, in fauna insectorum Lapponica descriptorum. *Isis* [Oken's], 1837:28-67.

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Illustrations must not be included within the manuscript but must be submitted separately as original art (not copies). All illustrations (photographs, line drawings, maps, etc.) can be intermixed throughout the printed text. They should be termed **Figures** and should be numbered consecutively. If several "figures" are treated as components of a single larger figure, they should be designated by lowercase italic letters (underlined in copy) on the illustration, in the legend, and in text references: "Figure 9 \underline{h} ." If illustrations are intended to be printed separately on coated stock following the text, they should be termed **Plates** and any components should be lettered as in figures: "Plate 9 \underline{b} ." Keys to any symbols within an illustration should appear on the art and not in the legend.

A few points of style: (1) Do not use periods after such abbreviations as "mm, ft, yds, USNM, NNE, AM, BC." (2) Use hyphens in spelled-out fractions: "two-thirds." (3) Spell out numbers "one" through "nine" in expository text, but use numerals in all other cases if possible. (4) Use the metric system of measurement, where possible, instead of the English system. (5) Use the decimal system, where possible, in place of fractions. (6) Use day/month/year sequence for dates: "9 April 1976." (7) For months in tabular listings or data sections, use three-letter abbreviations with no periods: "Jan, Mar, Jun," etc.

Arrange and paginate sequentially EVERY sheet of manuscript—including ALL front matter and ALL legends, etc., at the back of the text—in the following order: (1) title page, (2) abstract, (3) table of contents, (4) foreword and/or preface, (5) text, (6) appendices, (7) notes, (8) glossary, (9) bibliography, (10) index, (11) legends.

