

A Phylogenetic Study of the Tribe
Dryxini Zatwarnicki
(Diptera: Ephydriidae)

WAYNE N. MATHIS
and
TADEUSZ ZATWARNICKI

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*Wayne N. Mathis
and Tadeusz Zatwarnicki*



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A B S T R A C T

Mathis, Wayne N., and Tadeusz Zatwarnicki. A Phylogenetic Study of the Tribe Dryxini Zatwarnicki (Diptera: Ephydriidae). *Smithsonian Contributions to Zoology*, number 617, 101 pages, 154 figures, 2 tables, 2002.—The shore-fly tribe Dryxini is revised, including a cladistic analysis at the generic level, and now includes eight genera. Two of the genera, *Omyxa* and *Papuama*, are new, as are their respective type species. Of the remaining six genera, the species are revised for *Dryxo* Robineau-Desvoidy, *Corythophora* Loew, *Oedenops* Becker, and the subgenus *Phaiosterna* Cresson of the genus *Paralimna* Loew. In addition, the species of *Afrolimna* Cogan, *Oedenopiforma* Cogan, and the *limbata* group (*Paralimna*) are reviewed. This study revealed the following synonyms: two genus-group names: *Karema* Cresson (1929) = *Corythophora* Loew (1862), and *Cyphops* Jaenicke (1867) = *Dryxo* Robineau-Desvoidy (1830); and seven species-group names: *Karema loewella* Cresson (1929) = *Corythophora longipes* Loew (1862), *Cyphops fasciatus* Jaenicke (1867) and *Dryxo spreta* Osten Sacken (1882) = *Dryxo lispoidea* Robineau-Desvoidy (1830), *Paralimna ligabuei* Canzoneri (1987) = *Paralimna madecassa* Giordani Soika (1956), *Oedenops aurantiacus* Giordani Soika (1956) and *Oedenops flavitarsis* Miyagi (1977) = *Oedenops isis* Becker (1903), and *Paralimna (Phaiosterna) vidua* Giordani Soika (1956a) = *Ephydra bicolor* Macquart (1851). Six new species are described in four genera (type locality in parentheses): *Dryxo brahma* (Sri Lanka. Colombo: Negombo), *D. freidbergi* (Cameroon. Kribi (beach), Rt. N7), *D. india* (India. Nedungadu), *Omyxa scuta* (Iran. 40 km SE Minab), *Paralimna (Phaiosterna) longiseta* (Dominican Republic. Azua: near Pueblo Viejo (18°24.8'N, 70°44.7'W)), and *Papuama ismayi* (Papua New Guinea. Central Province: Daramouka Village).

The cladistic analysis was based on 45 morphological characters and resulted in nine most parsimonious cladograms of 55 steps with consistency and retention indices of 0.83 and 0.83, respectively. The tribe is divided into four basal sublineages in the strict consensus cladogram. The first sublineage comprises a single genus (number of species indicated in parentheses), *Afrolimna* (2), which is Afrotropical in distribution. The second sublineage likewise includes a single genus, *Paralimna* (>85), including *Phaiosterna* as a subgenus. *Paralimna* currently has greater species diversity than the rest of the tribe combined; it is pantropical, with numerous species ranging into subtropical regions. The third sublineage comprises three genera: *Dryxo* (9), *Corythophora* (2), and *Omyxa* (1), with *Corythophora* as the sister group to *Dryxo* and *Omyxa*. Genera of this sublineage occur only in the Old World, with greatest species diversity in Africa. The three genera of the fourth sublineage are *Papuama* (2), *Oedenops* (3), and *Oedenopiforma* (3). In this sublineage, *Papuama* is the sister group to *Oedenops* and *Oedenopiforma*. *Oedenops* is also pantropical and subtropical in distribution, but *Papuama* occurs in the Australasian/Oceanian and Oriental regions, and *Oedenopiforma* occurs in the Old World, primarily Africa and Australia.

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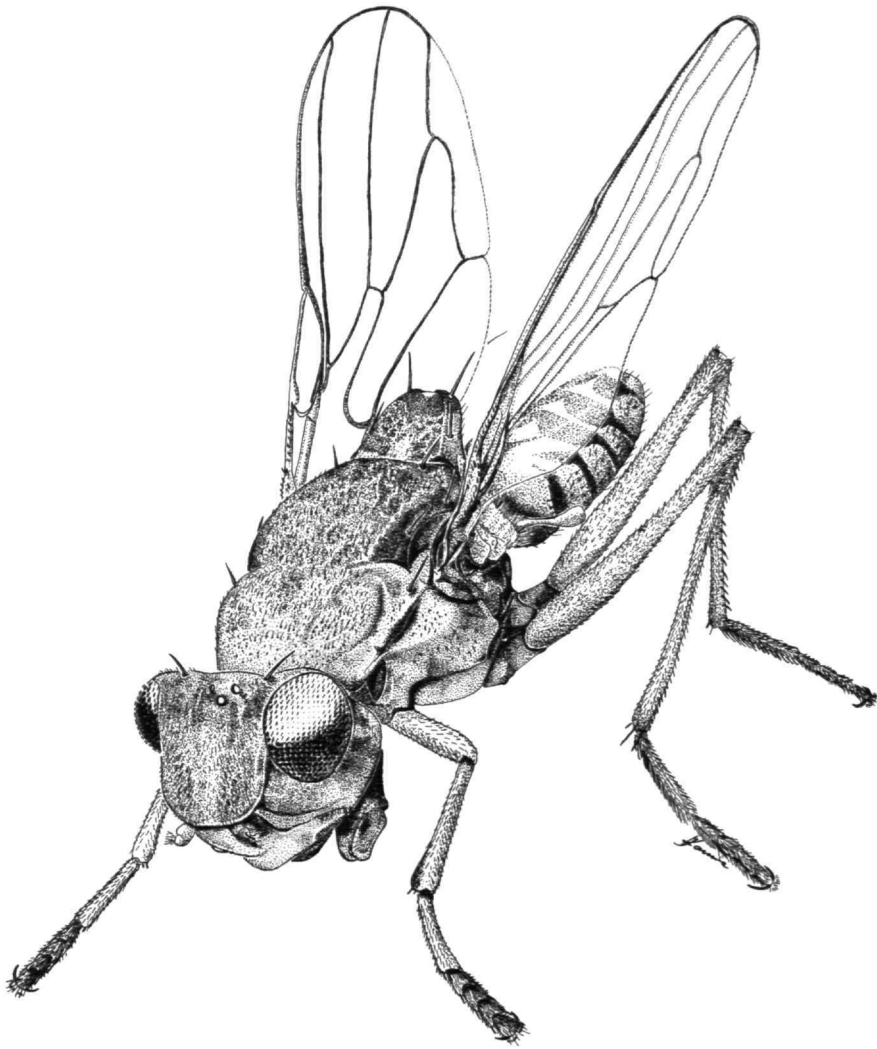


FIGURE 1.—Frontispiece of *Dryxo brahma*, new species (Kadaimparu, Sri Lanka, ♀).

A Phylogenetic Study of the Tribe Dryxini Zetwornicki (Diptera: Ephydriidae)

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Introduction

Like other tribes of the shore-fly family Ephydriidae, Dryxini Zetwornicki occurs in both the Old and New Worlds, and a few of the included genera, such as *Paralimna* Loew and *Oedenops* Becker, are equally widespread. Most genera of Dryxini, however, are found only in the Old World, and the Afrotropical Region is especially rich in genera and species. Conversely, no genus of this tribe occurs exclusively in the New World, even at the subgeneric level.

Despite being relatively widespread, comparatively diverse, and often abundant, there are no studies on the phylogenetic relationships within the tribe, and most of the included genera have never been revised. To remedy in part this gap in our understanding, we initiated this phylogenetic study of Dryxini. Our objectives are to provide a phylogeny and classification at the generic level and to present species revisions for *Dryxo* Robineau-Desvoidy, *Corythophora* Loew, *Oedenops*, and the subgenus *Phaiosterna* Cresson of the genus *Paralimna*. The species of *Afrolimna* Cogan and *Oedenopiforma* Cogan, and of the *limbata* group (*Paralimna*), are also reviewed.

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The origin of a taxon is not always reliably indicated by its present diversity and/or abundance, and classifications that are not based on phylogenetic relationships can likewise be misleading. Thus, conducting research on the phylogeny of Dryxini has applications that transcend simply knowing the relationships among the component lineages or providing the basis for a classification that facilitates the storage and retrieval of information.

Dryxini, which Zetwornicki (1992) first proposed, is the most recent tribe in the nomenclatural history of shore flies. It comprises all the taxa formerly included in the tribe Notiphilini Bigot, with the exception of the genus *Notiphila* Fallén. In the most recent world catalog of shore flies (Mathis and Zetwornicki, 1995), five genera and 101 species were included in Dryxini, with the vast majority, more than 85 species, being in the genus *Paralimna*. Although Dryxini is moderately diverse, we know that *Paralimna* alone is far richer in species than present numbers would indicate. Here we describe six new species, three in *Dryxo*, one in *Omyxa*, one in *Paralimna* (*Phaiosterna*), and one in *Papuama*. Two of these genera, *Omyxa* and *Papuama*, are also newly described.

Genera that are revised at the species level are provided with a "Historical Review" as a subsection under the generic treatment.

METHODS.—The descriptive terminology, with the exceptions noted in Mathis (1986), Mathis and Zetwornicki (1990a), and below, follows that published in the *Manual of Nearctic Diptera* (McAlpine, 1981). Although many specimens of Dryxini are among the largest in the Ephydriidae, study and illustration of the male terminalia required use of a compound microscope. For most structures of the male terminalia, we have followed the terminology used by other workers in Ephydriidae (see references in Mathis, 1986, and Mathis and Zetwornicki, 1990a, 1990b), for example, the terminology for surstylus, which in Dryxini is divided into a presurstylus (surstylus) and a postsurstylus (clasper). Zetwornicki (1996) has suggested

that these structures correspond with the pregonostylus and the postgonostylus and that the subepandrial plate is the same as the medandrium. The terminology for structures of the male terminalia is provided directly on Figures 6–8 and is not repeated for comparable illustrations of other species.

Alternative spellings for some localities are cited in parenthesis, especially for locality names that were transliterated into English. States of the United States in the “Distributions” sections are abbreviated as follows: AK=Arkansas, AZ=Arizona, CA=California, FL=Florida, GA=Georgia, IA=Iowa, IL=Illinois, LA=Louisiana, MO=Missouri, MS=Mississippi, NJ=New Jersey, OK=Oklahoma, TN=Tennessee, TX=Texas, UT=Utah.

The species descriptions are composite and are not based solely on the holotypes. Four head and two venational ratios used in the descriptions are defined below (all ratios are averages of three specimens (the largest, the smallest, and one other)).

1. Frons width-to-length ratio is the frons width divided by the frons length. Length is measured from the anterior margin of the frons to the posterior margin of the posterior ocelli; width is measured at the level of the anterior ocellus.
2. Face width-to-height ratio is the narrowest width between the eyes, divided by the facial height.
3. Gena-to-eye ratio is the genal height measured at the maximum eye height, divided by the eye height.
4. Eye width-to-height ratio is the eye width divided by the eye height, where both measurements are the longest distances taken with the eye oriented laterally.
5. Costal-vein ratio is the straight-line distance between the apices of veins R_{2+3} and R_{4+5} divided by the distance between the apices of veins R_1 and R_{2+3} .
6. M-vein ratio is the straight-line distance along vein M between crossvein dm-cu and r-m, divided by the distance apicad of crossvein dm-cu.

The phylogenetic analysis was performed with the assistance of Hennig86[®], a computerized algorithm that produces cladograms by parsimony. Character data were polarized primarily using outgroup procedures. We did not include autapomorphies in the cladistic analysis (they were made inactive) because that would have skewed the consistency and retention indices, but we listed them on the cladogram and included them as part of generic treatments and phylogenetic considerations to document the monophyly of the lineages, particularly at the generic level.

ACKNOWLEDGMENTS.—Although most specimens for this study, including the primary types, are in the National Museum of Natural History, Smithsonian Institution, numerous others were borrowed, particularly type specimens of the species previously described. To our colleagues and their institutions listed below who loaned specimens, we express our sincere thanks. Without their cooperation this study could not have been completed.

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| AM | Australian Museum, Sydney, Australia (Daniel J. Bickel, David K. McAlpine; including collections formerly housed at the School of Public Health and Tropical Medicine, University of Sydney) |
| AMNH | American Museum of Natural History, New York, New York, USA (David A. Grimaldi) |
| ANIC | Australian National Insect Collection, Canberra, Australia (David K. Yeates) |
| ANSP | Academy of Natural Sciences, Philadelphia, Pennsylvania, USA (Jon K. Gelhaus and Donald F. Azuma) |
| BAR | personal collection of M. Bartak (University of Agriculture, Praha, Czech Republic) |
| BMNH | The Natural History Museum (formerly the British Museum (Natural History)), London, England (Brian Pitkin and John E. Chaine) |
| BPBM | Bernice P. Bishop Museum, Honolulu, Hawaii, USA (Neal L. Evenhuis) |
| CAS | California Academy of Sciences, San Francisco, California, USA (Paul H. Arnaud, Jr.) |
| CNC | Canadian National Collection, Ottawa, Canada (James E. O'Hara and Bruce Cooper) |
| CU | Cornell University, Ithaca, New York, USA (James K. Liebherr) |
| DEI | Deutsches Entomologisches Institut, Eberswalde, Germany (Frank Menzel and Joachim Ziegler) |
| HNHM | Hungarian Natural History Museum, Budapest, Hungary (László Papp) |
| HUS | Hokkaido University, Sapporo, Hokkaido, Japan (Masaki Suwa and Ishiro Miyagi) |
| INHS | Illinois Natural History Survey, Champaign, Illinois, USA (Donald W. Webb) |
| IRSN | Institut Royal de Sciences Naturelles, Bruxelles, Belgium (Patrick Grootaert) |
| KU | Snow Entomological Museum, University of Kansas, Lawrence, Kansas, USA (Steve Ashe and George W. Byers) |
| MCV | Museo Civico di Storia Naturale de Venezia, Venice, Italy (Enrico Ratti and Leone Rampini) |
| MCZ | Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA (Philip D. Perkins) |
| MNHN | Muséum National d'Histoire Naturelle, Paris, France (Loïc Matile) |
| MRAC | Musée Royal de l'Afrique Centrale (Koninklijk Museum voor Midden-Afrika), Tervuren, Belgium (Eliane De Coninck) |
| NMNH | National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA |
| NMSA | Natal Museum, Pietermaritzburg, South Africa (David A. Barraclough) |
| NMSAC | National Museum, Prague, Czech Republic (Jan Jezek) |
| NMW | Naturhistorisches Museum, Wien, Austria (Ruth Contreras-Lichtenberg) |
| NNIC | Namibian National Insect Collection, State Museum, Windhoek, Namibia (Ashley H. Kirk-Spriggs) |
| NRS | Naturhistoriska Riskmuseet, Stockholm, Sweden (Thomas Pape) |
| NSF | Naturmuseum Senckenberg, Frankfurt, Germany (W. Tobias) |
| TZ | personal collection of Tadeusz Zatwarnicki, Department of Zoology, University of Agriculture, Wrocław, Poland |
| UMO | University Museum, Oxford University, Oxford, England (John W. Ismay) |
| USNM | collections of the former United States National Museum, now in the NMNH |
| UZMC | Zoologisk Museum, Copenhagen, Denmark (Verner Michelsen and Rudolf Meier) |
| ZIL | Zoological Institute, Museum of Zoology and Entomology, Lund University, Lund, Sweden (Roy Danielsson) |
| ZMA | Instituut voor Taxonomische Zoologie, Zoologisch Museum, Universiteit van Amsterdam, Amsterdam, Netherlands (Ben Brugge) |
| ZMHU | Zoologisches Museum, Humboldt Universität, Berlin, Germany (Marion Kotrba, Hubert Schumann, and Hella Wendt) |
| ZMUM | Zoological Museum, Moscow University, Moscow, Russia (Marina G. Krivosheina) |

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Systematics

Tribe DRYXINI Zatwarnicki

Dryxini Zatwarnicki, 1992:85 [type genus: *Dryxo* Robineau-Desvoidy, 1830].—Mathis and Zatwarnicki, 1995:115–127 [world catalog].

DIAGNOSIS.—*Dryxini* is the sister group of *Notiphilini*, and the tribe is distinguished from *Notiphilini* and other shore-fly tribes by the following combination of characters: ocellar seta stronger than the weak pseudopostocellar seta; reclinate fronto-orbital seta well developed, proclinate setae reduced or lacking; eye appearing bare; face wide, transversely arched, and generally projected anteriorly; facial setae in 1 or 2 serial rows running more or less parallel to parafacial; gena high (secondarily short in some species); subcranial cavity moderately large and cavernous; dorsocentral setae 4 (1+3; secondarily reduced in some genera of *Dryxini* (*Corythophora*, *Dryxo*, and *Omyxa*) (3 setae in *Notiphilini*, 1+2; a synapomorphy for *Notiphilini*); prescutellar acrostichal setae present, well developed; postsutural supra-alar setae strong, longer than posterior notopleural

seta; posterior notopleural seta at same level as anterior seta; ventral anepisternal seta elongate, twice length of dorsal seta (a synapomorphy for *Notiphilini*+*Dryxini*); costa elongate, extended to vein M (costa short, extended only to vein R_{4+5} in *Notiphilini*; a synapomorphy for *Notiphilini*); midtibia with prominent, erect, extensor setae on dorsal surface (a synapomorphy for *Notiphilini*+*Dryxini*); abdominal tergites fasciate (a synapomorphy for *Notiphilini*+*Dryxini*); male terminalia with surstylus divided into presurstylus (surstylus) and postsurstylus (clasper); presurstylus with apex angulate and bifurcate; subepandrial plate reduced (a synapomorphy for *Notiphilini*+*Dryxini*); pre- and postgonite reduced and/or lacking (structure remaining may represent fused and/or reduced pre- and postgonite); and hypandrium connected basally with postsurstylus, not with epandrium.

DESCRIPTION.—Small to very large shore flies of the subfamily *Hydrelliinae*, body length 1.65–11.20 mm, general body facies robust.

Head: Fronto-orbital setae reclinate and/or proclinate; reclinate fronto-orbital seta 1, well developed, inserted mediad of proclinate setulae; proclinate fronto-orbital setae moderately to greatly reduced, usually 2, inserted laterad of reclinate seta or lacking; pseudopostocellar seta greatly reduced or lacking, divergent to widely divergent if present; both inner and outer vertical setae usually well developed, sometimes inner vertical weakly developed; ocellar seta stronger than weakly developed pseudopostocellar seta. Pedicel lacking prominent, elongate setae; arista bearing numerous long, dorsally projected, hair-like branches. Face wide, transversely arched, usually projected anteriorly from antennal base; ventral facial margin flat or very shallowly emarginate; facial setae, if present, inserted near lateral margins, usually in vertical series somewhat parallel with parafacial setae, setae inclinate, frequently reduced in size or lacking; clypeus short, wide, band-like. Eye round to slightly oval with slight to conspicuous oblique orientation; appearing bare of interfacetal setulae. (We have discovered, using scanning electron microscopy, that most if not all shore flies have at least some interfacetal setulae.) Gena high; genal seta frequently reduced in size, inserted near ventral margin; subcranial cavity moderately large and cavernous.

Thorax: Acrostichal setae generally reduced, sometimes lacking, in 2–8 regular or irregular rows if present; only prescutellar acrostichal setae well developed, insertion moderately widely apart; dorsocentral setae usually 4 (1+3), anterior setae sometimes lost secondarily, leaving 1 posterior seta; posteriormost dorsocentral seta inserted laterad of alignment of dorsocentral track; presutural supra-alar seta usually present (secondarily lost in *Corythophora*, *Dryxo*, and *Omyxa*); postsutural supra-alar seta usually present, well developed (secondarily lost in *Dryxo freidbergi* (described herein) and *Papuama ismayi* (described herein)); postalar seta 1, well developed; scutellum with 2 setae inserted along lateral margins; disc of scutellum with few to numerous setulae;

postpronotal seta 1 or 2, sometimes lost secondarily (*Dryxo margaretae* Cogan, *D. digna* Osten Sacken, *D. lispoidea* Robineau-Desvoidy, and *Omyxa* (described herein)), larger seta postero-clinate, 2nd seta, if present, shorter, inclinate; notopleural setae usually 2 (secondarily reduced to 1 in *Corythophora*, *Dryxo*, and *Omyxa*), posterior seta at same level as anterior seta; anepisternum usually with 2 large setae along posterior margin, ventral seta usually elongate, sometimes twice length of dorsal seta, extended posteriorly to level of halter (dorsal seta secondarily reduced or lacking in *Corythophora* and in some species of *Dryxo*). Wing generally hyaline to faintly infuscate, patterned in some species of *Paralimna*; costal vein elongate, extended to vein M; vein R_{2+3} long, extended past midpoint of 2nd costal section. Midtibia with 1–4 prominent, erect, extensor setae along dorsal surface; tarsal claws regularly developed, relatively short, shallowly curved; pulvillar pads present, normally developed. Halter generally whitish yellow.

Abdomen: Tergites usually with fasciate pattern (secondarily unicolorous in *Oedenops*, *Oedenopiforma*, and *Pap-*

uama). Male terminalia: epandrium inverted U-shaped; presurstylus lobate or L-shaped; postsurstylus setulose with apex bent and bifurcate; subepandrial plate reduced; pregonite and postgonite reduced and/or lacking (remaining structure, which may be a composite of pre- and postgonites, termed a gonite); hypandrium frequently concave, connected basally with postsurstylus, not epandrium.

DISCUSSION.—In addition to the synapomorphies listed earlier (see tribal diagnosis) and those in the “Phylogenetic Considerations” section (beginning on page 94) that indicate a sister-group relationship for Dryxini and Notiphilini, Dryxini is further characterized by the following autapomorphies that establish the monophyly of the tribe: (1) gena high (secondarily short in some species of *Paralimna*); (2) face wide, transversely arched, and generally projected anteriorly; (3) male terminalia with surstylus divided into a presurstylus (surstylus) and a postsurstylus (clasper); presurstylus with apex angulate and bifurcate; (4) pregonite and postgonite reduced and/or lacking; (5) hypandrium connected basally with postsurstylus, not with epandrium.

Key to Genera of DRYXINI

1. Notopleuron bearing 1 large seta [Figures 1, 19]; presutural supra-alar seta lacking [Figures 19, 47]; mid- and hindfemora moderately long to very long, subequal to abdomen length [Figure 1] 2
- Notopleuron bearing 2 setae [Figure 5]; presutural supra-alar seta usually present [Figures 81, 92, 118] (lacking in *Papuama* and in one species of *Oedenops*); mid- and hindfemora normally developed, much shorter than abdomen 4
2. Ocellar seta present, although short, inserted slightly in front of anterior ocellus [Figures 17, 18]; reclinate fronto-orbital seta present [Figure 18]; anepisternum bearing 1 well-developed seta along posterior margin; vein R_1 bare along dorsum; R stem vein lacking setulae; crossvein dm-cu normally developed, nearly straight, forming acute inner angle with vein M (southern Afrotropical) *Corythophora* Loew
- Ocellar seta lacking [Figures 45, 46]; reclinate fronto-orbital seta lacking [Figure 46]; anepisternum bearing 2 or 3 thin, long, hair-like setae along posterior margin; vein R_1 bearing several setulae along dorsum; R stem vein basad of humeral crossvein bearing several pale, thin setulae on ventral surface; crossvein dm-cu moderately long to long, sinuous 3
3. Arista bearing 7–9 long dorsal hairs [Figures 54, 55]; katapisternum lacking row of slender setae along dorsal margin, and katapisternal seta reduced; crossvein dm-cu shallowly sinuous, generally forming angle with adjacent margin of wing; mid- and hindfemora normally developed, much shorter than length of abdomen (India, Iran, Oman) *Omyxa*, new genus
- Arista bearing 12 or more long dorsal hairs [Figures 45, 46]; katapisternum bearing row of slender setae near dorsal margin, and katapisternal seta usually well developed (secondarily reduced or absent in some species); crossvein dm-cu sinuous, long, generally running parallel with adjacent margin of wing; mid- and hindfemora elongate, subequal to length of abdomen (Afrotropical, Australian, Oriental) *Dryxo* Robineau-Desvoidy
4. Katapisternal seta absent or very weakly developed 5
- Katapisternal seta present, usually well developed (sometimes pale) 6

5. Arista bearing 3–5 hairs [Figure 80] (Afrotropical, Australian (Queensland), Nearctic (southern), Neotropical, Oriental, Palearctic (Egypt, Israel, Japan)) *Oedenops* Becker
 Arista bearing 8 or more hairs (Australasian, Oriental) *Papuama*, new genus
6. Long facial setae 2 or 3, length subequal to combined length of pedicel and 1st flagellomere, if 2 setae, these well separated, dorsal seta at about midheight, ventral seta closer to oral margin than to dorsal seta. R stem vein bearing 1–3 (usually 2) setulae on dorsum (Afrotropical, Australian, Oriental) *Oedenopiiforma* Cogan
 Long facial seta 1 (if other long setae present, setae not as long or as separated as above, these usually arranged in a somewhat vertical series of short setulae). R stem vein lacking setulae 7
7. Forefemur lacking row of closely set, very short, somewhat blunt, tooth-like spines along anteroventral surface; anterior proclinate fronto-orbital seta larger than posterior seta; face, gena, anepisternum, anterior surface of tibiae, and basolateral surface of scutellum not silvery microtomentose as in combination below; forefemur lacking long setae or setae not as below (pantropical with occasional extensions into temperate zone) *Paralimna* Loew
 Forefemur bearing anteroventral row of very short, stout, tooth-like setae; proclinate fronto-orbital setae greatly reduced and subequal, setula-like; face, gena, anepisternum, anterior surface of tibiae, and basolateral surface of scutellum densely, silvery microtomentose; forefemur bearing 4 or 5 long setae along apical ½ of posteroventral surface, length approaching twice width of femur (Afrotropical) *Afrolimna* Cogan

Genus *Afrolimna* Cogan, new status

Afrolimna Cogan, 1968:322 [as a subgenus of *Paralimna*; type species: *Paralimna carolinika* Cogan, 1968, original designation].—Cogan, 1980:662 [Afrotropical catalog].—Mathis and Zatwarnicki, 1995:118 [world catalog].

DIAGNOSIS.—This genus is distinguished from other genera of Dryxini by the following combination of characters: gena high, height about ⅓ or more of eye height; 1st flagellomere short, length at most 1.5 times width; face, gena, anepisternum, anterior surface of tibiae, and basolateral surface of scutellum densely, silvery microtomentose; forefemur bearing 4 or 5 long setae on apical ½ of posteroventral surface, their length approaching twice width of femur; forefemur of both sexes bearing row of short, tooth-like setulae apically along anteroventral surface (very inconspicuous in *A. keiseri* (Cogan)); male terminalia (Figures 6–8) with presurstylus angulate, elbowed in posterior view; aedeagal apodeme in lateral view with prominent, distinctive, broad keel and long, nearly parallel-sided medial projection; and hypandrium angulate in lateral view.

DESCRIPTION.—Medium-sized to moderately large shore flies, body length 3.40–4.30 mm.

Head (Figures 3, 4): Frons shallowly arched anteroventrally, not projected forward, sparsely setulose; ocelli in equilateral triangle; both inner and outer vertical setae well developed; reclinate fronto-orbital seta, ocellar seta, and paravertical seta well developed; proclinate fronto-orbital setae 2, anterior seta much better developed, subequal to posterior notopleural seta, posterior seta much reduced, setula-like. First

flagellomere moderately broadly rounded; arista bearing 13 or 14 long hairs along length of dorsal surface. Face usually bearing 1 moderately well-developed facial seta and series of smaller setae or setulae ventrad. Parafacial at anterior margin of eye narrow, width much less than length of 1st flagellomere. Gena moderately high, height slightly greater than height of 1st flagellomere.

Thorax (Figure 5): Dorsocentral setae 4 (1+3 or 2+2), well developed, 2nd seta near or at transverse suture, posterior pair displaced laterally; only prescutellar acrostichal seta well developed and well separated, other acrostichal setulae inconspicuous, in numerous irregular rows; presutural supra-alar seta well developed, subequal in length to anterior dorsocentral seta; postpronotal seta well developed; notopleural setae 2, posterior seta much shorter, about ½ length of anterior seta; anepisternum bearing 2 large setae along posterior margin, dorsal seta shorter, sometimes up to ½ length of ventral seta; katepisternal seta well developed. Posterior margin of scutellum truncate, nearly flat. R stem vein lacking setulae; crossvein dm-cu regularly developed, nearly straight, about 3 times longer than apical section of vein CuA₁, and at distinct angle with posterior margin of wing. Forefemur bearing comb-like row of very short, stout, spine-like setulae along apical ½ of anteroventral surface (very inconspicuous in *A. keiseri*); foretibiae of male lacking several long, slender setae at apex on ventral surface; forebasitarsus lacking row of long, slender, pale setulae inserted along anterior surface; midtibia with 3 dorsal extensor setae (subapically, subbasally, and near mid-

dle); mid- and hindfemora normally developed, much shorter than abdomen.

Abdomen: Coloration variable with species, but lacking a distinctly fasciate pattern. Male terminalia: epandrium broadly and uniformly U-shaped in posterior view (Figures 6, 9), lateral arms slightly wider; cercus moderately broad to broad ventrally, pointed dorsally; presurstylus angulate in posterior view (Figures 6, 9), elbowed, medially oriented arm slightly to much wider than vertical portion, medial surface truncate to concave; postsurstylus in lateral view curved, slightly widened medially, thereafter narrowed, apex shallowly bifurcate; aedeagal apodeme in lateral view hemispherical with short dorsal and ventral arms, anteromedial margin of apodeme bearing distinctive, long, nearly parallel-sided projection longer than width of keel, prominent keel irregularly rounded; aedeagus wider basally, gradually narrowed to broad, angulate

apex in lateral view (Figures 8, 11); lateral aedeagal process shorter than or subequal to aedeagus in lateral view, apex either tapered to acute point or broadly rounded; hypandrium angulate, moderately shallow.

DISTRIBUTION (Figure 2).—Afrotropical: Madagascar, Nigeria, Sudan, Zaire, Zimbabwe.

DISCUSSION.—*Afrolimna* was first described as a subgenus within *Paralimna* (Cogan, 1968, 1980; Mathis and Zatzwar-nicki, 1995). Our cladistic analysis and determination that *Afrolimna* has a closer relationship with *Corythophora*, *Dryxo*, and *Omyxa* than with *Paralimna* alters its phylogenetic position within Dryxini, and thus, we accord it generic status.

As implied by the generic name, the genus is known only from the Afrotropical Region, where there are two described species for which we provide the following key, diagnoses, and illustrations.

Key to Species of *Afrolimna* Cogan

1. Notopleuron dusted with silvery microtomentum; wing of male immaculate, hyaline 1. *A. carolinika* (Cogan)
- Notopleuron dark brown, concolorous with remainder of mesonotum; wing of male with dark spot at level of crossvein dm-cu in cells r_1 and r_{2+3} 2. *A. keiseri* (Cogan)

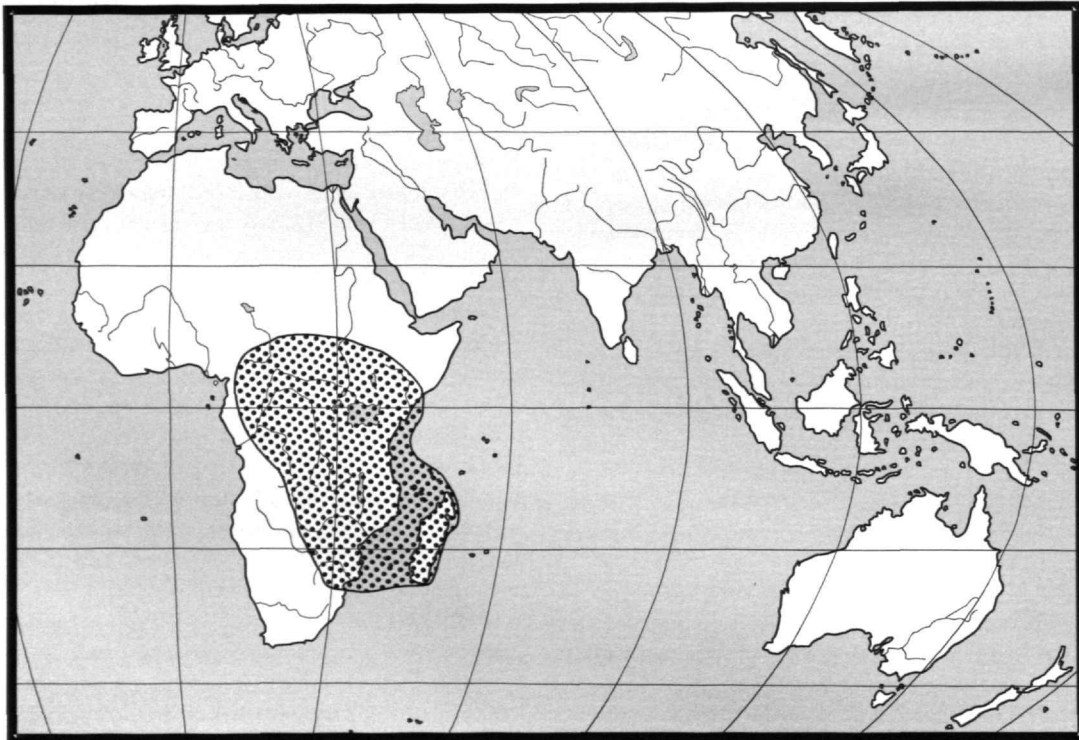


FIGURE 2.—Distribution map for *Afrolimna* (stippled).

1. *Afrolimna carolinika* (Cogan), new combination

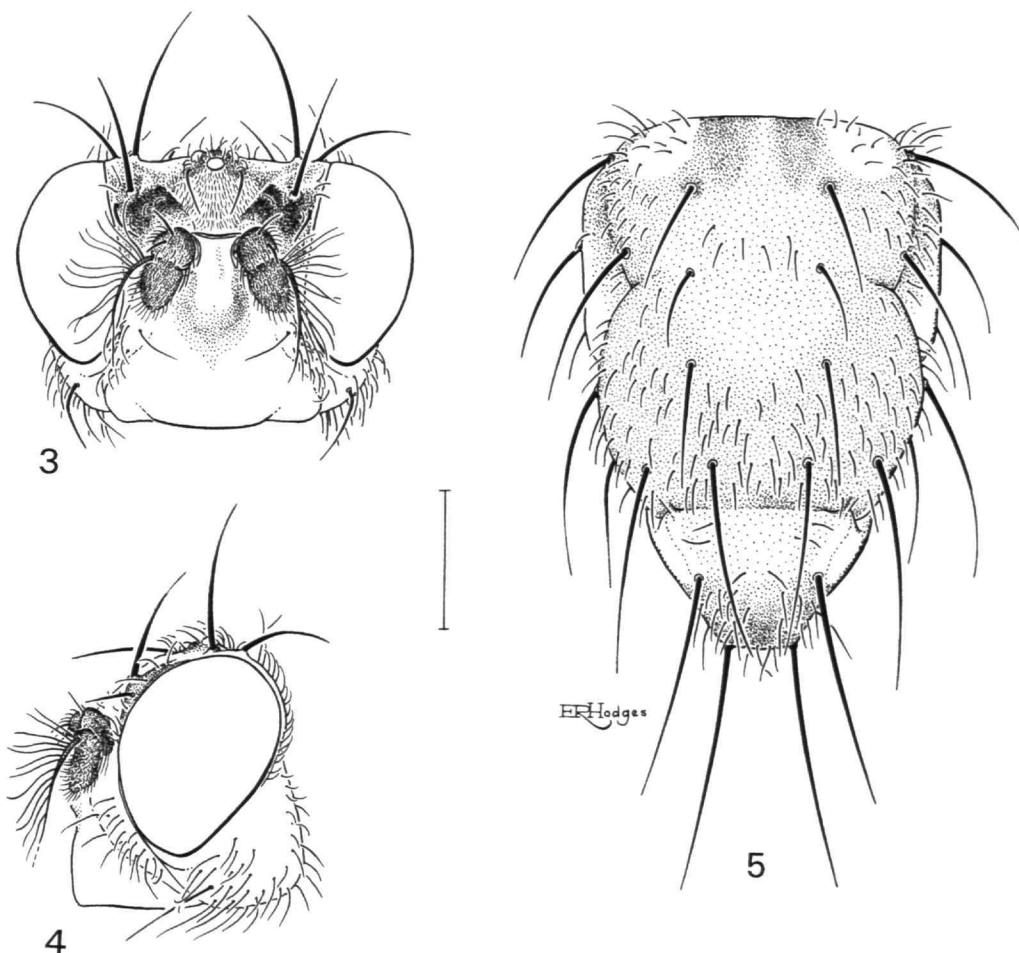
FIGURES 3-8

Paralimna (*Afrolimna*) *carolinika* Cogan, 1968:322; 1980:662 [Afrotropical catalog].—Mathis and Zatwarnicki, 1995:118 [world catalog].

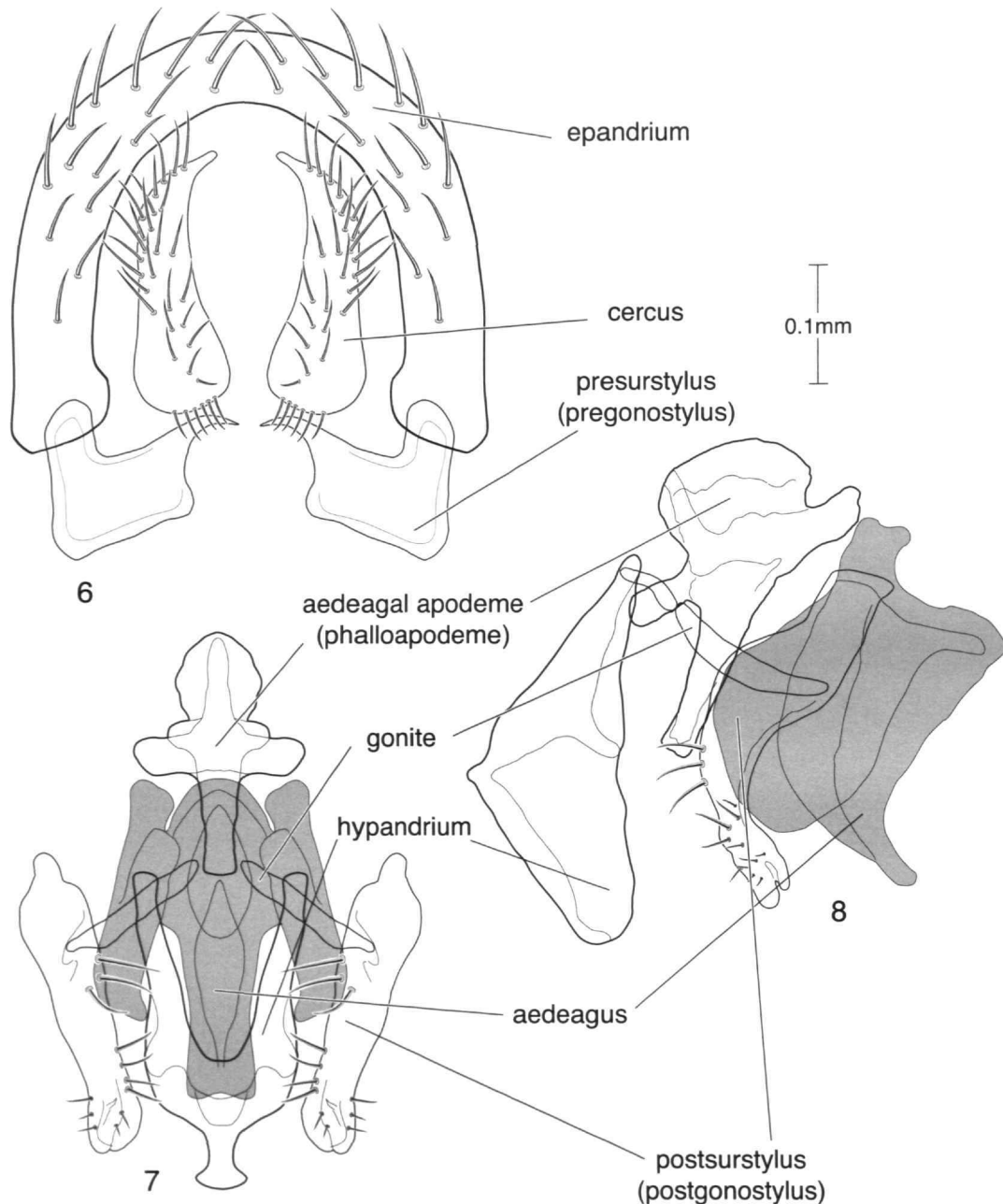
DIAGNOSIS.—This species is distinguished from *Afrolimna keiseri* by the characters indicated in the key and by the following characters from the male terminalia (Figures 6-8): epandrium uniformly U-shaped in posterior view (Figure 6), width even throughout; cercus greatly widened ventrally, pointed anteromedially; presurstylus angulate in posterior view (Figure 6), elbowed, medially oriented arm much wider than vertical portion, medial surface concave with dorsomedial angle projected, acutely pointed; postsurstylus in lateral view curved, slightly widened medially, thereafter narrowed, apex shallowly bifurcate; aedeagal apodeme with prominent

keel and long, almost parallel-sided medial projection as long as width of keel; aedeagus horn-shaped in lateral view (Figure 8), wide basally, tapering to posteriorly oriented, pointed apex; lateral aedeagal process as long as aedeagus in lateral view, broadly and unevenly rounded apically; and hypandrium angulate, moderately deep.

TYPE MATERIAL.—The holotype male of *Paralimna carolinika* Cogan is labeled "Holo-type [round label with red margin]/Chipinda Pools Tsetse Fly Ops. S. Rhodesia [Zimbabwe] Lower Lundi R. 22.X.1960 R. Goodier 1329 [all data except "Tsetse Fly Op. S. Rhodesia" and "19" of the year date are handwritten]/Pres by R. Goodier. B.M. 1961-72./*Paralimna carolinika* sp.n det. B.H. Cogan 1966 [species name and "sp.n" handwritten]." The holotype is pinned directly, is in excellent condition, and is deposited in BMNH. Two female paratypes (BMNH) bear the same label data as the holotype. Other



FIGURES 3-5.—*Afrolimna carolinika* (Cogan): 3, head, anterior aspect; 4, same, lateral aspect; 5, mesonotum, dorsal aspect. Scale=0.5 mm.



FIGURES 6-8.—Male terminalia of *Afrolimna carolinika* (Cogan): 6, epandrium, cerci, and presurstyli, posterior aspect; 7, internal male terminalia, ventral aspect; 8, same, lateral aspect.

paratypes are as follows: NIGERIA. Zungeru, Feb 1912, J.W.S. Macfie (2♀; BMNH). SUDAN. Yirol, 28 Feb 1954, E.T.M. Reid (1♂; BMNH).

OTHER SPECIMENS EXAMINED.—Afrotropical: ZAIRE. Kasongo, Aug 1959, P.L.G. Benoit (1♂; USNM).

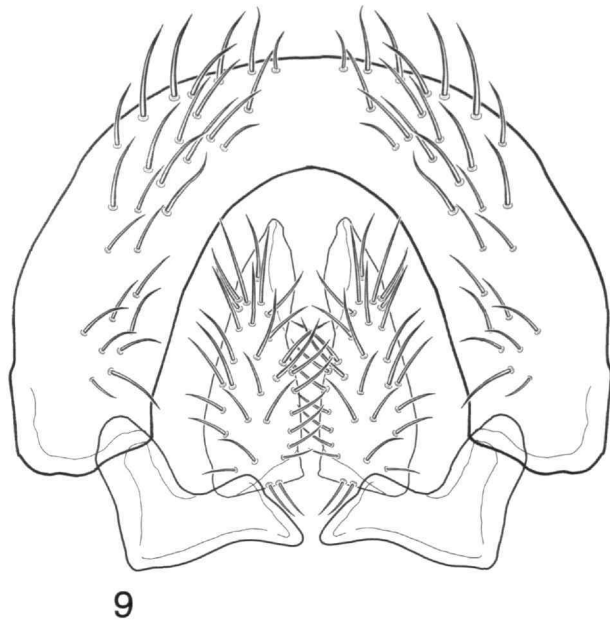
DISTRIBUTION.—Afrotropical: Nigeria, Sudan, Zaire, Zimbabwe.

2. *Afrolimna keiseri* (Cogan), new combination

FIGURES 9-11

Paralimna (*Afrolimna*) *keiseri* Cogan, 1968:323; 1980:662 [Afrotropical catalog].—Mathis and Zatwarnicki, 1995:118 [world catalog].

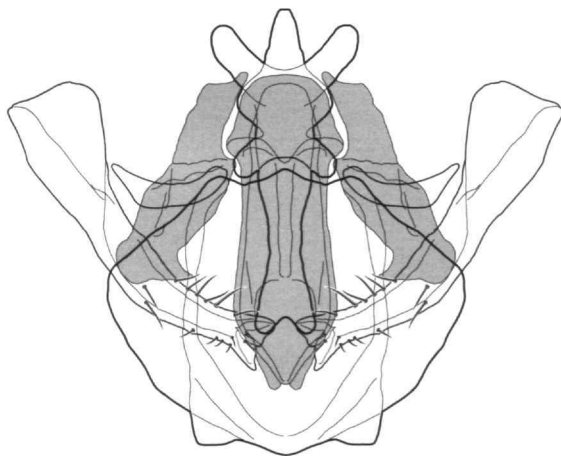
DIAGNOSIS.—This species is distinguished from *Afrolimna carolinika* by the characters indicated in the key and by the fol-



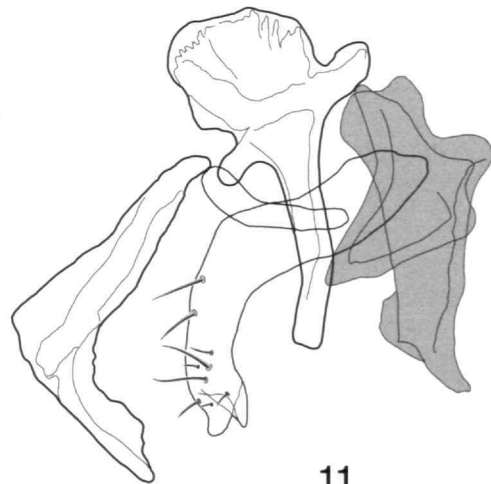
9

FIGURES 9–11.—Male terminalia of *Afrolimna keiseri* (Cogan): 9, epandrium, cerci, and presurstyli, posterior aspect; 10, internal male terminalia, ventral aspect; 11, same, lateral aspect.

0.1mm



10



11

lowing characters from the male terminalia (Figures 9–11): epandrium broadly and uniformly U-shaped in posterior view (Figure 9), lateral arms slightly wider; cercus moderately broad ventrally, pointed anteriorly; presurstylus angulate in posterior view (Figure 9), elbowed, medially oriented arm only slightly wider than vertical portion, medial surface truncate and with 90° dorsomedial angle not projected; postsurstylus in lateral view curved, slightly widened medially, thereafter narrowed, apex shallowly bifurcate; aedeagal apodeme with prominent keel, keel irregularly rounded and bearing long, almost parallel-sided medial projection longer than width of keel; aedeagus

wider basally, gradually narrowed to broad, angulate apex in lateral view (Figure 10); lateral aedeagal process shorter than aedeagus in lateral view, tapered to acute point apically; and hypandrium angulate, moderately shallow.

TYPE MATERIAL.—The holotype male of *Paralimna keiseri* Cogan is labeled "Holo-type [round label with red margin]/ Madagascar [Toliara] Sud Sept-Lacs 100m dct Tuléar 13-16.II.58 B.Stuckenber." The holotype is double mounted (minuten in a rectangular block of polyporus), is in good condition, and is deposited in the NMSA. Six paratypes (2♂, 4♀; BMNH) bear the same locality data as the holotype.

OTHER SPECIMENS EXAMINED.—Afrotropical. MADAGASCAR. *Toliara*: South Berenty Reserve, 20 Apr 1991, A. Freidberg, F. Kaplan (2♂; USNM).

DISTRIBUTION.—Afrotropical: Madagascar.

Genus *Corythophora* Loew

Corythophora Loew, 1862b:13 [type species: *Corythophora longipes* Loew, 1862, monotypy].—Bezzi, 1908a:195 [synonymy with *Dryxo* Robineau-Desvoidy].

Karema Cresson, 1929:182 [type species: *Karema loewella* Cresson, 1929 (= *Corythophora longipes* Loew), original designation].—Cogan, 1968: 356–358 [revision]; 1980:661 [Afrotropical catalog].—Mathis and Zatwarnicki, 1995:116–117 [world catalog]. [New synonym.]

DIAGNOSIS.—This genus is distinguished from other genera of Dryxini, especially *Dryxo*, which is similar, by the following combination of characters: ocellar seta present, although short, inserted slightly in front of anterior ocellus; reclinate fronto-orbital seta present; notopleuron bearing 1 large seta; presutural supra-alar seta lacking; anepisternum with 1 well-developed seta along posterior margin; katapisternal seta reduced and lacking row of slender setae along dorsal margin; vein R_1 bare along dorsum; R stem vein lacking setulae; vein R node bearing 3–5 setulae on dorsum; crossvein dm-cu normally developed, nearly straight, forming nearly 90° inner angle with vein M; forefemur of both sexes lacking row of short, peg-like setulae apically along anteroventral surface; and mid- and hindfemora elongate, subequal to length of abdomen.

DESCRIPTION.—Medium-sized to large shore flies, body length 3.40–6.60 mm.

Head: Frons shallowly arched anteroventrally, not projected forward, sparsely setulose; ocelli in isosceles triangle, distance between posterior pair shorter than between anterior ocellus and either posterior ocellus; inner vertical seta and reclinate fronto-orbital seta well developed; ocellar and paraverticlar setae weakly developed or absent. First flagellomere acutely rounded; arista bearing 10–14 long hairs along length of dorsal surface. Face lacking conspicuous facial setae. Parafacial at anterior margin of eye narrow, width much less than length of 1st flagellomere. Gena high, height subequal to combined length of 1st flagellomere and pedicel.

Thorax: Anterior dorsocentral setae lacking, only posteriormost pair present (0+1); acrostichal setulae poorly developed, inconspicuous, in 2 rows; presutural supra-alar seta lacking; postpronotal seta well developed; notopleural seta 1; anepisternum bearing 1 large seta at posterior margin, dorsal seta lacking; katapisternal seta weakly developed, hair-like. Posterior margin of scutellum broadly rounded. Wing with apex of costa at subcostal break bearing 2 short, stout setae; vein R_1 bare along dorsum; R stem vein lacking setulae; vein R node bearing 3–5 long, pale setulae on dorsum; crossvein dm-cu regularly developed, nearly straight, longer than apical section of vein CuA_1 , and at distinct angle with adjacent mar-

gin of wing. Forefemur of male lacking comb-like row of short, stout, tooth-like, sometimes flattened setae along apical ½ of anteroventral surface; foretibia of male lacking several long, slender setae at apex on ventral surface; midtibia bearing 4 dorsal extensor setae (basally, subbasally, subapically, and apically); mid- and hindfemora greatly elongate, subequal to length of abdomen; midtibia bearing 2 ventroapical setae and 1 posteroapical seta; foretarsus with mostly cylindrical tarsomeres, not distinctly flattened; forebasitarsus lacking row of long, slender, pale setulae inserted along anterior surface.

Abdomen: Coloration with distinctly fasciate pattern. Male terminalia: cercus ovoid to allantoid, bearing numerous setulae along medial margin; presurstylus a narrow, band-like process at ventral margin of cercus; aedeagus in lateral view wide basally, at midlength narrowed to slender process; aedeagal apodeme elongate, with long process extended beyond portion bearing keel and with secondary, short process extended externally at about midlength; hypandrium wide and robust, lateral margin with emargination and processes.

HISTORICAL REVIEW.—*Corythophora*, as a generic name, has been largely overlooked until now. For more than 90 years, *Corythophora* was treated as a junior synonym of *Dryxo* (Bezzi, 1908a). This oversight, which was perpetuated in the literature, is typical of interpreting a written description without studying the primary types. Limited or essentially no access to the types of *Corythophora longipes* Loew was undoubtedly the primary impediment to recognizing the identity and thus the nomenclatural precedence of *Corythophora*. Like Bezzi, Cresson (1929) also did not examine Loew's type series, and he and all subsequent authors have accepted Bezzi's determination that *Corythophora* was a junior synonym of *Dryxo*. As a result, most previous treatments of the species included in *Corythophora* since Bezzi were published under the name of *Karema* (Cresson, 1929; Wirth, 1956, 1960; Cogan, 1968, 1980; Canzoneri and Raffone, 1987; Canzoneri and Rampini, 1994; and Mathis and Zatwarnicki, 1995). Of these treatments, Cogan's revision (1968) was the most comprehensive and included illustrations.

We borrowed and studied Loew's type and here consider *Corythophora* to be the senior synonym of *Karema* Cresson, as the type species for both generic names, *Corythophora longipes* Loew and *Karema loewella* Cresson, are conspecific.

DISTRIBUTION (Figure 12).—Afrotropical: Angola, Botswana, Cameroon, Chad, Ethiopia, Ghana, Kenya, Madagascar, Malawi, Namibia, Nigeria, Sierra Leone (Northern Province: Bumbuna), South Africa (Cape Province, Natal, Transvaal), Sudan, Swaziland, Tanzania, Zaire, Zimbabwe.

PHYLOGENETIC RELATIONSHIPS.—Cresson (1929:182) suggested that *Corythophora* (as *Karema*) is related to *Dryxo* and is a "connectant" between the latter and *Paralimna*. He also made a comparison with the genus *Parydra* Stenhammar. Although the latter relationship with *Parydra* is untenable, being based on convergent characters, Cresson's primary suggestion

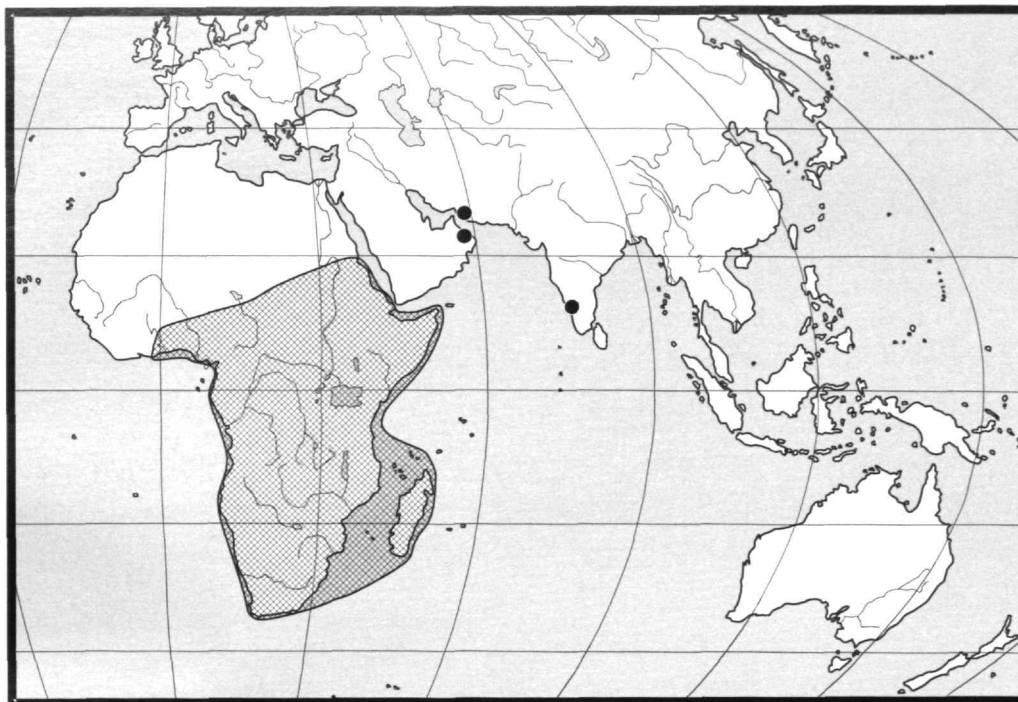


FIGURE 12.—Distribution map for *Corythophora* (hatched) and *Omyxa* (dots).

is confirmed and further documented by our research. *Dryxo*, with *Omyxa* as its immediate sister group, forms a lineage that is the sister group to *Corythophora*.

Unambiguous autapomorphies for *Corythophora* are (1) anepisternum with 1 large seta at posterior margin; (2) katepister-

nal seta reduced; (3) vein R node bearing 2–3 long, posteriorly directed setulae on dorsum; (4) adeagal apodeme with long projection extended from near articulation with hypandrium; (5) midtibia bearing 4 erect setae along dorsum; and (6) posterior margin of scutellum broadly rounded.

Key to Species of *Corythophora* Loew

- 1. Femora and tibiae mostly yellowish to ferruginous, fore- and hind femora with some grayish microtomentum dorsally toward base; ocellar seta long, length 2–3 times distance between anterior ocellus and either posterior ocellus; apical scutellar setae nearly parallel sided (Madagascar) 3. *C. flavipes* (Cogan)
- Femora and tibiae almost entirely black; ocellar seta short, length subequal to distance between anterior ocellus and either posterior ocellus; apical scutellar setae cruciate (widespread Africa) 4. *C. longipes* Loew

3. *Corythophora flavipes* (Cogan), new combination

FIGURES 13–16

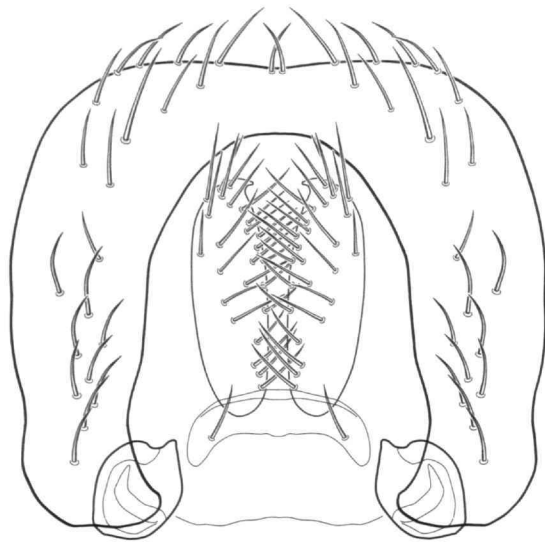
Karema flavipes Cogan, 1968:357; 1980:661 [Afrotropical catalog].—Mathis and Zatwarnicki, 1995:116 [world catalog].

DIAGNOSIS.—This species is distinguished from its congener by the characters indicated in the key.

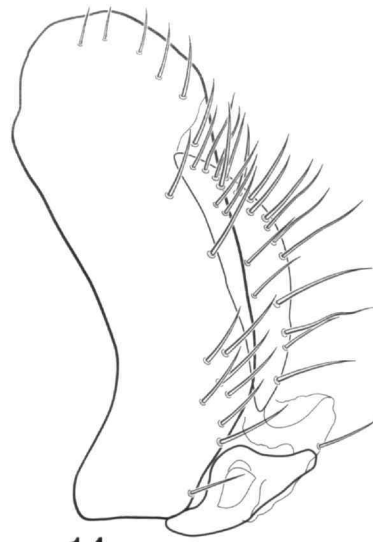
DESCRIPTION.—Moderately large to large shore flies, body length 4.40–6.60 mm.

Head: Head squarish, especially in lateral view. Frons wider than long, with distinct, sparsely microtomentose, rect-

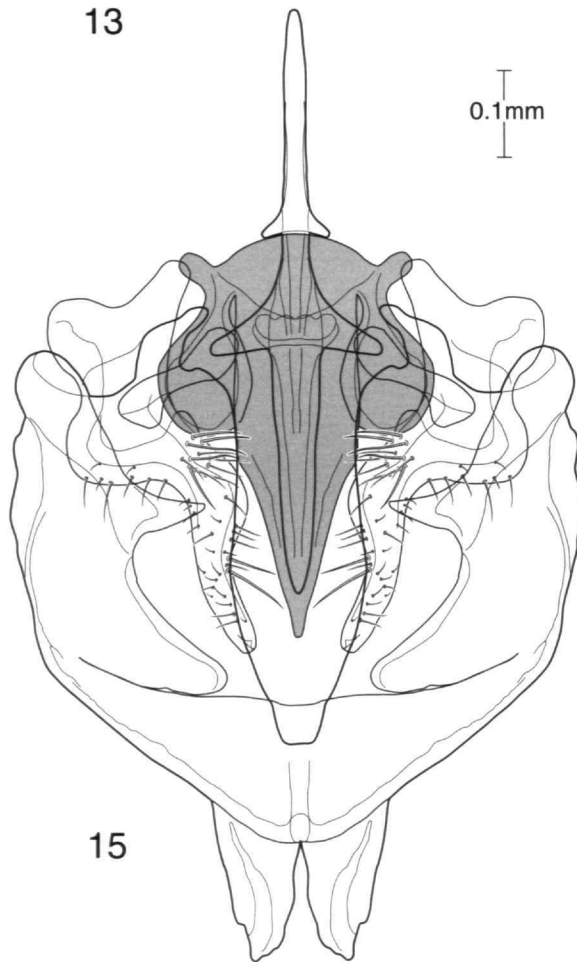
angular, blackish brown mesofrons extended broadly to anterior margin; frons laterad of mesofrons densely microtomentose with distinct golden brown and whitish gray spots. Ocellar seta long, length 2–3 times distance between anterior ocellus and either posterior ocellus, mostly proclinate and slightly divergent; outer vertical seta comparatively long, about 2/3 or more length of inner vertical seta. Antenna rather short, black; arista bearing 10–12 dorsal rays. Face mostly lightly golden, antennal grooves silvery gray. Gena high, silvery gray; gena-to-eye ratio 0.51–0.60.



13



14



15



16

FIGURES 13–16 (opposite).—Male terminalia of *Corythophora flavipes* (Cogan): 13, epandrium, cerci, and presurstyli, posterior aspect; 14, same, lateral aspect; 15, internal male terminalia, ventral aspect; 16, same, lateral aspect.

Thorax: Mesonotum generally gray to black, darker laterally, with distinct stripes in acrostichal and dorsocentral tracks that converge posteriorly; scutellum frequently two toned, apex blackish brown, anterior portion gray to silvery gray anterolaterally or golden on anterior portion; pleural areas mostly silvery gray to silvery white; anepisternum with distinct, large golden spot toward posterodorsal angle. Apical scutellar setae parallel sided. Wing faintly golden brown, mostly hyaline; costal-vein ratio 0.24–0.25; M-vein ratio 1.1–1.2. Legs mostly yellowish to reddish yellow, with some surfaces darker; femora reddish yellow with basodorsal areas blackish, especially on fore- and hindfemora, and invested with grayish white microtomentum; posterobasal surface of hindfemur shiny black; tibiae generally reddish yellow, apical portion blackish; tarsi becoming progressively darker apically, basitarsomere reddish yellow, apical tarsomere blackish brown.

Abdomen: Tergite 1 blackish brown at middle, lateral margins gray; tergite 2 gray but with extensive brown area from middle and extended laterally; tergites 3 and 4 distinctly fasciate, with wide, dark brown band extended across anterior $\frac{2}{3}$ or more of tergite, usually extended more posteriorly at middle, frequently dark coloration broadly extended to posterior margin; male tergite 5 entirely blackish brown; female tergite 5 fasciate across anterior margin. Male terminalia (Figures 13–16): epandrium in posterior view (Figure 13) broadly inverted U-shaped with dorsal margin somewhat truncate and wide, ventrally extended arms comparatively wide; presurstyli in posterior view (Figure 13) joined medially, forming band-like structure at ventral margin of cerci; postsurstylus in lateral view (Figure 16) shallowly concave along wide, basal margin, thereafter narrowed at midlength to long, curved, slightly tapered process; aedeagus in lateral view (Figure 16) with basal $\frac{1}{2}$ enlarged, margin toward aedeagal apodeme extended and broadly rounded, and apical $\frac{1}{2}$ greatly narrowed and shallowly curved anteriorly, aedeagus in ventral view (Figure 15) with lateral, rounded lobes subbasally, thereafter gradually tapered apically to acute point; aedeagal apodeme in lateral view (Figure 16) with extended fan-like structure enlarged, broadly rounded; hypandrium in ventral view (Figure 15) wide, obtusely pointed at anterior margin, apex comparatively more narrowly rounded in lateral view (Figure 16).

TYPE MATERIAL.—The holotype male of *Karema flavipes* Cogan is labeled "Holo-type [round label with red submargin]/Madagascar[,] Est[,] Ambodivoangy 20m[,] dct Maroantsetra 16-20.III.58 B.Stuckenberg/♂/[red triangle]/Karema flavipes sp. n. det. B. H. Cogan 1967 [species name and "1967" handwritten]." The holotype is double mounted (minuten in rectangular block of silicon), is in excellent condition, and is deposited in the MNHN. One paratype (♂; NMSA) bears the same locality label data as the holotype. Other paratypes are as fol-

lows: MADAGASCAR. *Antsiranana:* Sambirano, Lokobe, Nossi-Bé (6 m), 9–23 Nov 1957, B.R. Stuckenberg (1♀; BMNH). *Fianarantsoa:* Ranomafana, Dec 1955, B.R. Stuckenberg (1♀; NMSA). *Toamasina:* Mananara, Est Ivontaka (15 m), 10–14 Mar 1958, B.R. Stuckenberg (1♂, 2♀; BMNH, NMSA); Maroansetra, Sahasoa, Fanpanambo (80 m), 26–29 Mar 1958, B.R. Stuckenberg (1♂, 1♀; BMNH); Maroansetra, Navana-Antongil (6 m), 20–25 Mar 1958, B.R. Stuckenberg (1♀; NMSA). *Toliara:* Ranohira (860 m), 26 Jan–4 Feb 1958, B.R. Stuckenberg (1♂, 2♀; BMNH, NMSA); Tuléar (=Toliara), Sept-Lacs (100 m), 13–16 Feb, B.R. Stuckenberg (3♂; BMNH, NMSA).

OTHER SPECIMENS EXAMINED.—Afrotropical. MADAGASCAR. *Antsiranana:* Sambirano, Lokobe, Nossi-Bé (6 m), 9–23 Nov 1957, B.R. Stuckenberg (2♀; NMSA). *Fianarantsoa:* Ranomafana (7 km W; 900 m), 1 Feb–8 Oct 1988, 1990, W.E. Steiner (43♂, 36♀; USNM). *Mahajanga:* Mahajunga (=Mahajanga; km 530), Oct 1949, R.P. (1♀; NMSA). *Toamasina:* Mananara, Est Ivontaka (15 m), 10–14 Mar 1958, B.R. Stuckenberg (1♀; NMSA); Maroantsetra, Est Ambodivoangy (20 m), 16–20 Mar 1958, B.R. Stuckenberg (3♀; NMSA); Maroansetra, Sahasoa, Fanpanambo (80 m), 26–29 Mar 1958, B.R. Stuckenberg (1♀; NMSA). *Toliara:* Betroka (23°16'S, 46°5'E), 1 Aug 1948, A.R. (1♂; NMSA); South Berenty Reserve, 20 Apr 1991, A. Freidberg, F. Kaplan (1♂; USNM).

DISTRIBUTION.—Afrotropical: Madagascar.

4. *Corythophora longipes* Loew

FIGURES 17–22

Corythophora longipes Loew, 1862b:13.—Cresson, 1929:181 [synonymy with *Dryxo ornata* (Macquart)].

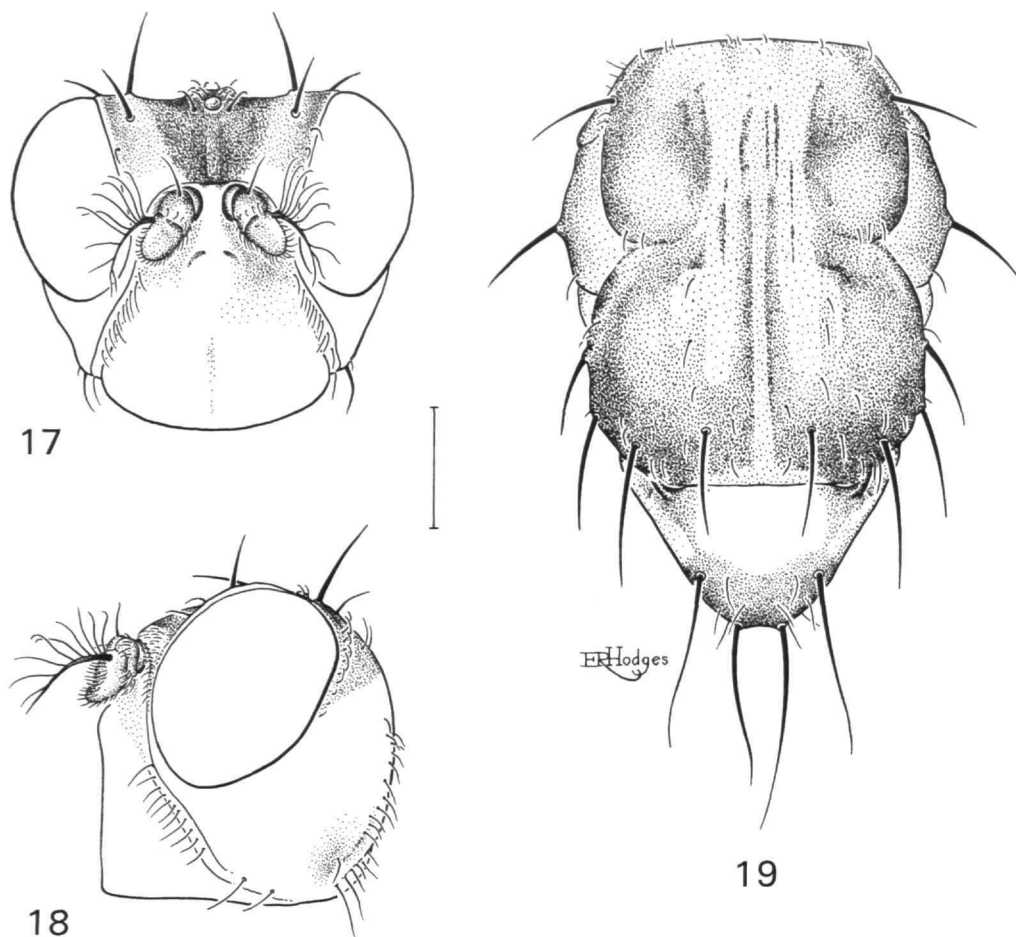
Dryxo longipes.—Bezzi, 1908b:187 [generic combination].

Karema loewella Cresson, 1929:182.—Wirth, 1956:388 [list, South Africa (Botswana, Cape Province, Natal, Transvaal)]; 1960:393 [list, Namibia].—Giordani Soika, 1956b:490 [list, Zaire].—Cogan, 1968:357 [revision]; 1980:661 [Afrotropical catalog].—Canzoneri and Raffone, 1987:70 [list, Kenya].—Canzoneri and Rampini, 1994:245 [list, Sierra Leone].—Mathis and Zatwarnicki, 1995:117 [world catalog]. [New synonym.]

DIAGNOSIS.—This species is distinguished from its congener by the characters indicated in the key.

DESCRIPTION.—Medium-sized to large shore flies, body length 3.40–6.0 mm.

Head (Figures 17, 18): Head squarish, especially in lateral view. Frons wider than long, with distinct, sparsely microtomentose, rectangular, blackish brown mesofrons extended broadly to anterior margin; frons laterad of mesofrons densely microtomentose with distinct golden brown and whitish gray spots. Ocellar seta short, length subequal to distance between anterior ocellus and either posterior ocellus, proclinate; outer vertical seta short, about $\frac{1}{2}$ length of inner vertical seta. Antenna rather short, black; arista bearing 10–12 dorsal rays. Face mostly lightly golden, antennal grooves silvery gray. Gena high, silvery gray; gena-to-eye ratio 0.52–0.56.

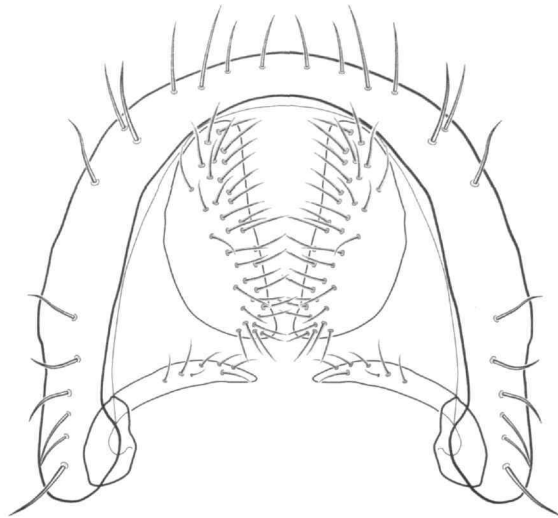


FIGURES 17-19.—*Corythophora longipes* Loew: 17, head, lateral aspect; 18, same, anterior aspect; 19, mesonotum, dorsal aspect. Scale=0.5 mm.

Thorax (Figure 19): Mesonotum generally dark gray to black, darker laterally; scutellum frequently two-toned, apex blackish brown, anterior portion gray to silvery gray anterolaterally or golden on anterior portion; pleural areas mostly silvery gray to silvery white; anepisternum with some faint, golden coloration. Apical scutellar setae cruciate. Wing faintly golden brown, mostly hyaline; costal-vein ratio 0.23-0.28; M-vein ratio 0.95-1.0. Femora and tibiae almost entirely black, only femoral apex and extreme base of tibiae yellowish; ventral surface of femora bare, shiny, dorsal surface moderately densely microtomentose; tibiae silvery white, extensively and densely microtomentose, especially anterobasal and posterobasal surfaces, and appearing reflective; tarsi black, mostly covered with moderately dense, gray to whitish gray microtomentum.

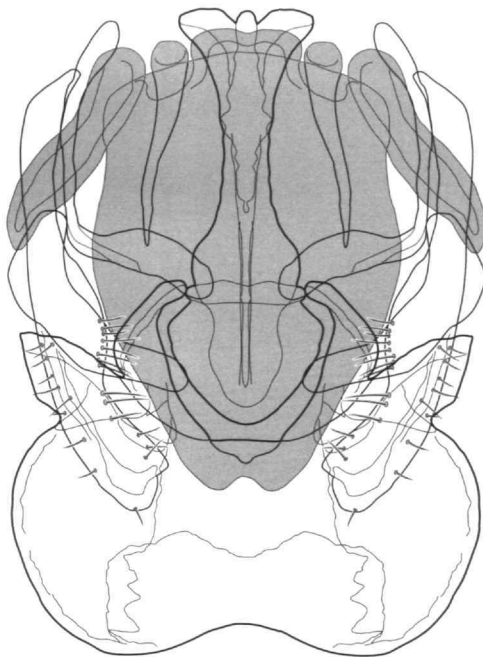
Abdomen: Tergite 1 dark brown at middle, lateral margins gray; tergite 2 mostly gray; tergites 3 and 4 distinctly fasciate,

with wide, dark brown band extended across anterior $\frac{1}{2}$ - $\frac{2}{3}$ of tergite, usually extended more posteriorly at middle, but some specimens with band weaker at middle; male tergite 5 with only anterolateral corners dark brown, remainder gray, female tergite 5 fasciate across anterior margin; some specimens with golden to silvery microtomentum on ventral surface of tergite, usually adjacent to dark band. Male terminalia (Figures 20-22): epandrium in posterior view (Figure 20) U-shaped, with dorsal margin rounded and ventrally extended arms comparatively narrow; presurstyli in posterior view (Figure 20) not fused medially, appearing as 2 narrow, band-like processes extended medially, with apices pointed; postsurstylus in lateral view (Figure 22) long and comparatively narrow, not enlarged basally, shallowly curved, apex bilobed; aedeagus in lateral view (Figure 22) with basal $\frac{1}{2}$ - $\frac{2}{3}$ greatly enlarged, margin away from aedeagal apodeme extended and broadly rounded, and apical $\frac{1}{2}$ greatly narrowed and shallowly curved posteri-



20

0.1mm



21



22

FIGURES 20–22.—Male terminalia of *Corythophora longipes* Loew: 20, epandrium, cerci, and presurstyli, posterior aspect; 21, internal male terminalia, ventral aspect; 22, same, lateral aspect.

only, aedeagus in ventral view (Figure 21) shield-like, lateral margins lacking conspicuous lobes and at midlength gradually tapering to bilobed apex (rounded notch at apex); aedeagal apodeme with extended fan-like structure only slightly enlarged and narrowly rounded; hypandrium in ventral view (Fig-

ure 21) broad with rounded lateral margins, anterior margin concave medially.

TYPE MATERIAL.—The holotype female of *Corythophora longipes* Loew is labeled “[South Africa.] ‘Caffraria’ 446. [handwritten]/332. [handwritten]/ *Corythophora longipes*

[typewritten]/Naturhistoriska Riksmuseet Stockholm Loan no 798/96 [light bluish green label].” The holotype is directly pinned, is in good condition (hindtarsus on left side missing and some setae on head missing), and is deposited in the NRS.

The holotype female of *Karema loewella* Cresson is labeled “[South Africa. Transvaal:] Barberton. 12.8.16 [12 Aug 1916] H.K.Munro. [date handwritten; label with black submargin]/TYPE ♀ Karema LOEWELLA E.T.Cresson, Jr. [red label; species name and gender handwritten]/Karema loewella Cresson HOLOTYPE No: 976 [species name, author, and number handwritten in red ink].” The holotype is double mounted (minuten in polyporus rectangular block), is in fair condition (several setae of head and thorax, especially on right side, lacking; right wing removed, glued to locality label), and is deposited in the NMSA. A female paratype (1♀; ANSP) bears the same locality label data as the holotype.

OTHER SPECIMENS EXAMINED.—Afrotropical. ANGOLA. *Cunene*: Rocadas, Cunene (river), 19–22 Feb 1972 (6♂, 7♀; BMNH). *Namibe*: Moçâmedes (2 mi N), 29 Feb 1972 (1♂, 1♀; BMNH). *Without Further Locality*: Bruco, 26 Feb–2 Mar 1972 (17♂, 13♀; BMNH, TZ).

BOTSWANA. River Nata (20°12'S, 26°11'E), 23 Apr 1972 (1♀; BMNH). River Semowane (20°25'S, 26°23'E), 23–24 Apr 1972 (1♀; BMNH).

CAMEROON. *West Cameroons*: Bolo, 30 Jan 1970, F.H.L. Disney (1♂; BMNH).

CHAD. W. Goulem, 8–9 Aug 1958, G.B. Popov (1♂; BMNH).

ETHIOPIA. Ever, 30 Oct 1968, R. Kano (1♂, 1♀; BMNH).

GHANA. Akosombo, 22–25 Jun 1973, L. Knutson (1♀; USNM).

KENYA. Biretwo (40 km E Eldoret), 12 May 1991, A. Freidberg, F. Kaplan (9♂, 6♀; USNM).

MALAWI. Cholo, R.C. Wood (1♂, 1♀; BMNH). Nyungwi, 26 Nov 1909, J.B. Davey (1♂; ANSP).

NIGERIA. *Niger*: Zungeru, Feb 1912, J.W.S. Macfie (8♂, 7♀; BMNH).

SOUTH AFRICA. *Cape Province*: Grahamstown, 28 Apr 1953, B.R. Stuckenberg (2♂; NMSA); Kraaifontein, Mara, Jun 1918, H.G. Breijer (1♀; NMSA). *Natal*: Ingwavuma, Nduma Reserve (1♂, 1♀; BMNH, NMSA); Durban, 26 Apr 1919, C.N. Barker (1♂; BMNH); Maqonqo (28°20'S, 30°26'E; 1200 m; grassland with dongas), Vaalkop Farm, 17 Feb 1992, A.E. Whittington (2♀; NMSA); Mhlopheni Nature Reserve (29°01'09"S, 30°24'56"E; 900 m; Acacia thornveld), 15 Mar 2000, T. Dikow, J.G.H. Londt (1♂, 2♀; USNM); Nagel Dam, 19 May 1955, B.R. Stuckenberg (1♀; BMNH); Oribi Gorge Reserve, Umzimkulwana Valley, 21–28 Nov 1960, B.R. and P. Stuckenberg (1♂; NMSA); Sileza Forest Reserve (sandy hillside), 4 Nov 1996, M.E. Irwin (1♀; INHS); Tugela Ferry, 18 Feb 1979, J.G.H. Londt (1♀; NMSA); Tugela Ferry (20 km W; Malaise trap), 26–27 Feb 1977, R.M. Miller (1♂; NMSA); Tugela Ferry (4 km N; trees and grass near stream), 18 Feb 1979, J.G.H. Londt (1♀; NMSA); Zululand, lower Umfolozi River, 1922, H.H. Curson (1♂, 3♀; BMNH). *Transvaal*: Kruger

Park (Timbetene Tswiri waterholes; savanna woodland near Skukuza), 9 Dec 1972, B.R. and P. Stuckenberg (2♀; NMSA); Kruger Park, Tshorwane, Dec 1972, B.R. and P. Stuckenberg (1♀; NMSA); Rio Limpopo (23°00'S, 27°57'E), 25–26 Apr 1972 (1♂, 3♀; BMNH); Waterbert, Jul 1948, O. Beyer (1♂; BMNH).

SUDAN. Katire (12 km W), 28 Aug 1980, A.L. Armstrong (1♀; USNM). W. Darfur, Jebel Marra, Killing (2134 m), 7 Apr 1932, M. Steele (2♂; ANSP, BMNH).

SWAZILAND. Mbuluzone River, 28 Mar 1984, P. Kelly, J. Cory (2♂; BMNH). Mluwla Pools, 17 Mar 1984, P. Kelly, J. Cory, (1♀; BMNH). Sihoye, Mar 1984, P. Kelly, J. Cory (2♀; BMNH). Sihoye Stream, 29 Mar 1984, P. Kelly, J. Cory (2♀; BMNH).

TANZANIA. Bukoba, 10 Apr 1912, C.C. Gowdey (1♂; BMNH).

ZAIRE. Ituri Kasenyi (Lac Albert), 5 Jul 1953, J. Verbeke (1♂; IRSN). Kongold (25°25'S, 23°E), 8 Feb 1974, R. Baker (1♀; BMNH). Matadi (19.3 km N), 28 Jul 1957 (1♂; USNM). *Kivu*: Rutshuru, Sep–Oct 1934, 1936, Delville (5♂, 13♀; MRAC, ZMHU). *Ile Idjwi*: Shashi-Busibu, 15 Apr 1953, J. Verbeke (1♂, 2♀; IRSN); Uvira, Kawezi, 23 May 1958, G. Marlier (2♂, 1♀; MRAC).

ZIMBABWE. Balla-Balla, Apr 1931, A. Cuthbertson (1♀; AMNH). Lower Lundi River (Chipinda Pools), 22 Oct 1960, R. Goodier (1♀; BMNH).

DISTRIBUTION.—Afrotropical: Angola, Botswana, Cameroon, Chad, Ethiopia, Ghana, Kenya, Malawi, Namibia, Nigeria, Sierra Leone (Northern Province: Bumbuna), South Africa (Cape Province, Natal, Transvaal), Sudan, Swaziland, Tanzania, Zaire, Zimbabwe.

Genus *Dryxo* Robineau-Desvoidy

Dryxo Robineau-Desvoidy, 1830:787 [type species: *Dryxo lispoidea* Robineau-Desvoidy, 1830, monotypy].—Becker, 1926:92–93 [review].—Cogan and Wirth, 1977:332 [Oriental catalog].—Cogan, 1980:661 [Afrotropical catalog]; 1984:144 [Palearctic catalog].—Mathis, 1989:644 [Australasian/Oceanian catalog].—Mathis and Zatwarnicki, 1995:115–116 [world catalog].

Blepharitaris Macquart, 1844:411 [as a genus; type species: *Blepharitaris ornatus* Macquart, 1844, monotypy].—Jones, 1906:169 [discussion].—Bezzi, 1908a:195 [synonymy].

Cyphops Jaenicke, 1867:367 [as a genus; type species: *Cyphops fasciatus* Jaenicke, 1867, monotypy].—Cogan and Wirth, 1977:332 [Oriental catalog; subgeneric status].—Mathis, 1989:644 [Australasian/Oceanian catalog].—Mathis and Zatwarnicki, 1995:115 [world catalog]. [New synonym.]

DIAGNOSIS.—This genus is distinguished from other genera of Dryxini, especially *Corythophora* and *Omyxa*, to which it is similar, by the following combination of characters: ocellar seta lacking; reclinate fronto-orbital seta lacking; notopleuron bearing 1 large seta; presutural supra-alar seta lacking; anepisternum bearing 2 or 3 thin, long, hair-like setulae along posterior margin; katepisternum bearing 1 well-developed seta (secondarily reduced or absent) and row of slender setae near dorsal margin; vein R₁ bearing several setulae along dorsum; R

stem vein basad of humeral crossvein bearing several pale, thin setulae on ventral surface; vein R node lacking setulae; crossvein dm-cu long, sinuous, paralleling posterior margin of wing, with obtuse inner angle with vein M; forefemur of both sexes lacking row of short, peg-like setulae apically along anteroventral surface; and mid- and hindfemora elongate, subequal to length of abdomen.

DESCRIPTION.—Moderately large to very large shore flies, body length 4.70–11.20 mm.

Head: Frons projected forward as a shield-like, nearly flat plate, densely setulose; ocelli in equilateral or isosceles triangle, and if latter, with distance between posterior pair shorter than between anterior ocellus and either posterior ocellus; both inner and outer vertical setae well developed; reclinate fronto-orbital seta, ocellar seta, and paraverticilar seta absent. First flagellomere with apex moderately rounded; arista bearing 12–16 long hairs along length of dorsal surface. Face bearing 4 or 5 moderately short, thin facial setae. Parafacial at anterior margin of eye very wide, width greater than length of 1st flagellomere. Gena very high, height greater than combined length of 1st flagellomere and pedicel.

Thorax: Anterior dorsocentral setae absent, only posterior-most pair present (0+1); acrostichal setulae poorly developed, inconspicuous, in 2 rows; prescutellar acrostichal setae absent; presutural supra-alar seta absent; postpronotal seta well developed; notopleural seta 1; anepisternum bearing 2 or 3 thin, poorly developed, hair-like setae along posterior margin, middle seta longest; katapisternal seta well developed; katapisternum also bearing row of 6–10 long, slender, hair-like setae posterodorsad of larger seta. Posterior margin of scutellum truncate, nearly flat. Wing with apex of costa at subcostal break bearing 2 short, stout setae; R stem vein basad of humeral crossvein bearing several pale, thin setulae on ventral surface; vein R node lacking setulae; crossvein dm-cu long, sinuous, general orientation parallel with posterior margin of wing, inner angle with vein M at almost 90°. Forefemur of male lacking comb-like row of short, stout, slightly flattened setae along apical ½ of anteroventral surface; foretibia of male lacking several long, slender setae at apex on ventral surface; midtibia with 3 dorsal extensor setae (basally, subbasally, and apically); mid- and hindfemora greatly elongate, subequal to length of abdomen; midtibia bearing 2 ventroapical setae and 1 posteroapical seta; tarsomeres bearing long setae anteroapically and posteroapically, length of setae subequal to width of tarsomere at apex; forebasitarsus lacking row of long, slender, pale setulae inserted along anterior surface; foretarsomeres 2–5 mostly cylindrical to only slightly flattened.

Abdomen: Coloration with distinctly fasciate pattern. Male terminalia: epandrium in posterior view as wide or wider than high, broadly inverted U-shaped, dorsum essentially truncate to shallowly rounded, extended arms usually wider than dorsal base; cercus much longer than wide, usually wider basally, somewhat oval, bearing numerous short setulae; presurstylus of two types, narrowly somewhat L-shaped and bearing

setulae along medial curvature or as a ventrally extended broad process; postsurstylus usually broader apically, apex broadly bifurcate; aedeagus quite variable, dorsum irregular, sometimes bearing short process; aedeagal apodeme with extended keel long and rounded, moderately deep to short, if deep, keel pointed; gonite in lateral view quadrate to mostly linear and shallowly curved; hypandrium wider than long, shallowly depressed.

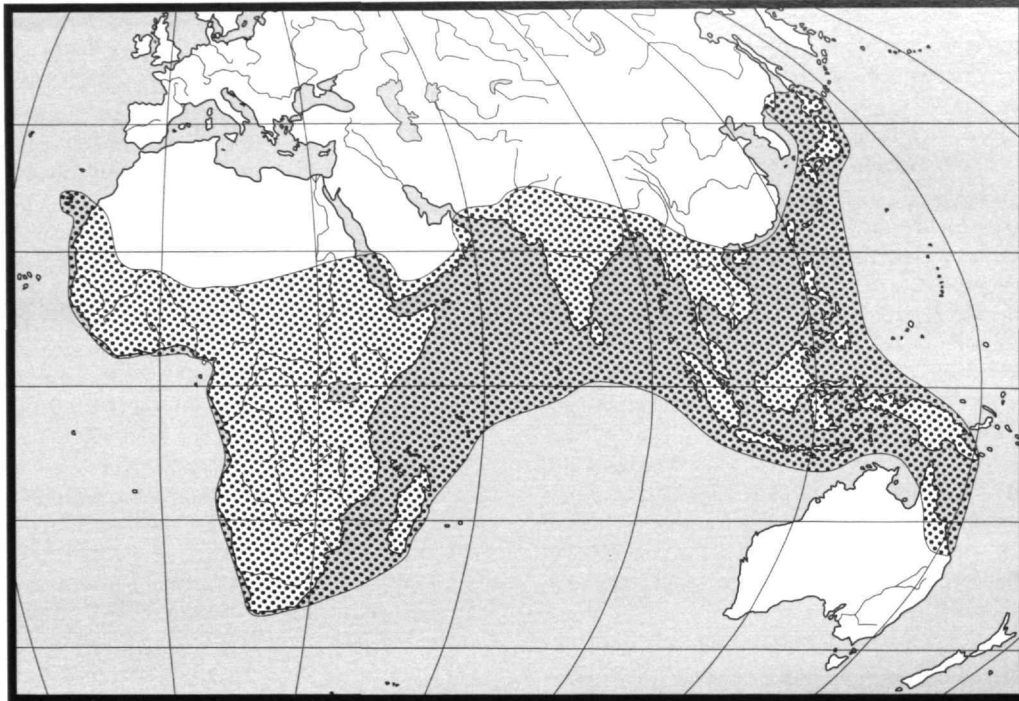
HISTORICAL REVIEW.—*Dryxo*, the type genus of the tribe Dryxini, includes species that are among the largest of shore flies, with body lengths that sometimes exceed 11 mm. Robineau-Desvoidy (1830) described *Dryxo* early in the nomenclatural history of shore flies from specimens that were collected on the Indonesian island of Sumatra. Since then, that species, *D. lispoidea*, has often been misidentified, in part because the type series was lost (we designate a neotype herein). Additional species were described by Macquart (1844), Jaenicke (1867), Osten Sacken (1882), Cresson (1936), Cogan (1968), and Miyagi (1977). Until now, Cogan's revision of *Dryxo* from the Afrotropical Region has been the most complete study of the genus, and it was the first to provide illustrations of the male terminalia.

Our study of *Dryxo* clearly indicates that the subgenera, as previously characterized (Cogan and Wirth, 1977), are unwarranted. The species of *Dryxo* are relatively similar to each other, and no evident gap is apparent in their external morphology or, from what we can determine, in their natural history. Moreover, the characters that Jaenicke (1867) proposed to characterize *Cyphops* are quite variable within species of the genus and are not consistent with any phylogenetic division. We have therefore placed *Cyphops* as a junior synonym of *Dryxo*, and for the same reasons, we continue to recognize *Blepharitaris* Macquart, the second oldest genus-group name, as a junior synonym of *Dryxo*, following the precedent of Bezzi (1908a) and of subsequent workers on the genus.

Dryxo is a rather peculiar generic name that Robineau-Desvoidy (1830) treated as a feminine noun of Greek derivation. The late George C. Steyskal, a classical scholar, advised us to follow Robineau-Desvoidy's precedent in considering *Dryxo* to be feminine.

DISTRIBUTION (Figure 23).—All species are from the Old World tropics and subtropics (Afrotropical, Australasian/Oceanian, Oriental, and southern Palearctic Regions) with one species, *D. nudicorpus* Miyagi, also occurring in China, Japan, and Russia (Far East).

Afrotropical: Angola, Botswana, Burundi, Cameroon, Chad, Ethiopia, Ghana, Kenya, Liberia, Madagascar, Malawi, Mozambique, Namibia, Niger, Nigeria, Rwanda, Sierra Leone (Northern Province: Bumbuna; Western Area: Sussex), Somalia, South Africa (Cape Province, Natal, Transvaal), Sudan, Swaziland, Tanzania, Uganda, Yemen, Zaire, Zambia, Zimbabwe. Australasian/Oceanian: Australia (Queensland), Papua New Guinea (Bismarck Archipelago, Central). Oriental: India (Karnataka, Orissa, Rajasthan, Tamil Nadu, Uttar Pradesh),

FIGURE 23.—Distribution map for *Dryxo*.

Indonesia (Java, Sulawesi, Sumatra), Philippines (Luzon, Mindanao, Samar), Sri Lanka, Taiwan, Thailand. Palearctic: Canary Islands, China, Iran (Baluchistan), Japan (Hokkaido, Honshu, Ishikawa, Kyushu, Shikoku), Morocco, Russia (Far East).

DISCUSSION.—Species of *Dryxo* are among the largest of shore flies and are characterized by many derived character states that establish the monophyly of the genus. Synapomorphies that we have discovered are as follows: (1) ocellar seta absent; (2) reclinate fronto-orbital seta absent; (3) prescutellar acrostichal setae absent; (4) 6–10 large setae inserted posterodorsad of katepisternal seta; (5) R stem vein bearing several long, pale setulae; (6) short setulae along dorsum of vein R_1 ; (7) crossvein dm-cu long, sinuous, oriented parallel with posterior margin of wing, forming obtuse inner angle with vein M; and (8) tarsomeres bearing long setae anteroapically and posteroapically, length of setae subequal to width of tarsomere at apex.

Although we did not analyze the phylogenetic relationships among the species of *Dryxo* rigorously, some patterns are evident and are noted here. The species groups are informally designated, meaning that we do not recognize them in a classification as subgenera. The *ornata* group comprises three species: *D. brahma* (described herein), *D. margaretae* Cogan, and *D. ornata* (Maquart). This group is characterized and its monophyly is corroborated by several synapomorphies as

noted in the key that follows (see four synapomorphies in the first half of the first couplet). In addition, we suggest that the shape of the presurstylus is similar within the group and is probably another synapomorphy. The presurstylus is wide (best seen in posterior view), lacks a basomedial arm, and the medial margin is irregular, having one or two notches or shallow breaks.

A second species group, the *lispoidea* group, also includes three species: *D. digna*, *D. lispoidea*, and *D. nudicorpus*. This group is characterized by the three characters noted in the key (last half of couplet 5). The presurstylus in this group has a basomedial arm that is especially well developed in *D. lispoidea* and *D. nudicorpus*. A well-developed basomedial arm is probably a plesiomorphic character, however, as it occurs in other species of *Dryxo* (*D. woodi* Cresson), in its sister group, *Omyxa*, and elsewhere, such as in *Paralimna*.

The other three species of *Dryxo* are unplaced in species groups, although *D. woodi* and *D. freidbergi* (described herein) may be closely related, as their adults are quite similar externally and both species occur in the Afrotropical Region. *Dryxo india* (described herein) appears to be a comparatively derived species, as evidenced by the unusually flattened tarsomeres of the male and by the shape of the structures of the male terminalia (quadrated presurstylus and angulate aedeagal apodeme, especially the keel).

Key to Species of *Dryxo* Robineau-Desvoidy

1. Tergites 3 and 4 with dark band along posterior margin, at least in middle, band sometimes connected laterally with anterolateral spot or spot separate; tergite 1 with medial patch of short, dorsally erect setulae; male hindbasitarsus and 2nd hindtarsomere bearing long, slender setae dorsally; katapisternal seta well developed, length subequal to notopleural seta (the *ornata* group) 2
 Tergites either with dark band toward anterior margin (at most with very thin dark area along posterior margin) or lacking band; tergite 1 with sparse, inconspicuous, dorsally erect setulae; male hindtarsi lacking long, slender setae dorsally; katapisternal seta usually greatly reduced, much weaker than notopleural seta, or lacking 4
2. Inner vertical seta much reduced, about ½ length of outer vertical seta; male hindbasitarsus bearing bush-like, long, slender setae along entire length of dorsum (Oriental) 5. *D. brahma*, new species
 Inner vertical seta subequal to or slightly longer than outer vertical seta; male hindbasitarsus bearing several long, slender setae toward base, setae becoming shorter and much fewer toward apex 3
3. Postpronotal seta absent; R stem vein bearing about 6 long, thin setulae along posterior margin basad of humeral crossvein (Afrotropical: Madagascar) 10. *D. margaretae* Cogan
 Postpronotal seta well developed; R stem vein bearing 2 or 3 long, thin setulae on dorsum along posterior margin basad of humeral crossvein (Afrotropical) 12. *D. ornata* (Macquart)
4. Postsutural supra-alar seta greatly reduced or absent; anepisternum lacking moderately long, slender setae along posterior margin (Afrotropical) 7. *D. freidbergi*, new species
 Postsutural supra-alar seta well developed; anepisternum bearing 1 or 2 moderately long, slender setae along posterior margin 5
5. Parafacial essentially uniformly concolorous; femora and tibia concolorous, faintly reddish, with sparse whitish microtomentum; mesonotum grayish tan to grayish brown, lacking dark brown spots or areas 6
 Parafacial with wide blackish brown to golden brown stripe immediately laterad of antennal base, contrasting distinctly with silvery gray remainder of parafacial; femora except apices gray, concolorous with pleural areas, contrasting with yellow tibiae; mesonotum with numerous small, dark brown spots at bases of setae and setulae, with 2 large, somewhat triangular dark brown spots at posterior margin of scutum, and with 2 spots on scutellum around bases of apical scutellar setae (the *lispoidea* group) 7
6. Foretarsomeres 2–5 of male greatly expanded apically, width of 2nd tarsomere greater than length, narrow basally at attachment with preceding tarsomere; tergites 3–5 of female with dark brown spot anterolaterally; wing of male lacking black spots (Oriental) 8. *D. india*, new species
 Foretarsomeres 2–5 of male normally developed, width of 2nd tarsomere far less than length; tergites 3–5 of female generally unicolorous, lacking darkened spot anterolaterally; wing of male with 2 blackened, microtomentose spots, 1 in cell dm at posterior margin adjacent to pointed convergence of crossvein dm-cu and vein CuA₁, and 1 at posterior margin adjacent to vein A₁+CuA₂ (Afrotropical) 13. *D. woodi* Cresson
7. Dark band on tergites 3–5 lacking narrow, medial extension to posterior margin; postpronotal seta present; scutellar disc, and in some specimens the frons, lacking a gray, medial, microtomentose stripe (Palearctic) 11. *D. nudicorpus* Miyagi
 Dark band on tergites 3–5 with narrow, medial extension to posterior margin; postpronotal seta absent; frons and scutellar disc mostly dark but with gray, medial, microtomentose stripe 8

8. Katepisternal seta well developed, subequal to notopleural seta; tergites 2–5 gray on ventral side, lacking blackish brown spot; anepisternum mostly gray, at most with brown spot near middle; 1 well-developed anepisternal seta on posterior margin (Oriental) 6. *D. digna* Osten Sacken
 Katepisternal seta weakly developed, much thinner and shorter than notopleural seta; tergites 2–5 with blackish brown spot on ventral side; anepisternum with large, wide, transverse, dark brown stripe; 2 weakly developed anepisternal setae along posterior margin (Australasian/Oriental, Oriental) 9. *D. lispoidea* Robineau-Desvoidy

5. *Dryxo brahma*, new species

FIGURES 1, 24–26

Dryxo lispoidea of authors, not Robineau-Desvoidy, 1830:787 [misidentification, in part].—Becker, 1926:93 [review, list, "Persisch-Belutschistan"].—Cogan and Wirth, 1977:332 [in part; Oriental catalog].—Cogan, 1984:144 [in part; Palearctic catalog].—Mathis and Zatwarnicki, 1995:116 [in part; world catalog].

DIAGNOSIS.—This species is distinguished from congeners by the following combination of characters: inner vertical seta much reduced, length about $\frac{1}{2}$ that of outer vertical seta; male hindbasitarsus with bush-like, long, slender setae along entire length of dorsum; 2nd hindtarsomere of male bearing long, slender setae on dorsal surface; katepisternal seta well developed, length subequal to notopleural seta; 3rd and 4th tergites with dark band along posterior margin, at least in middle, posterior band sometimes connected laterally with anterolateral spot or spot separate; and 1st tergite with medial patch of short, dorsally erect setulae.

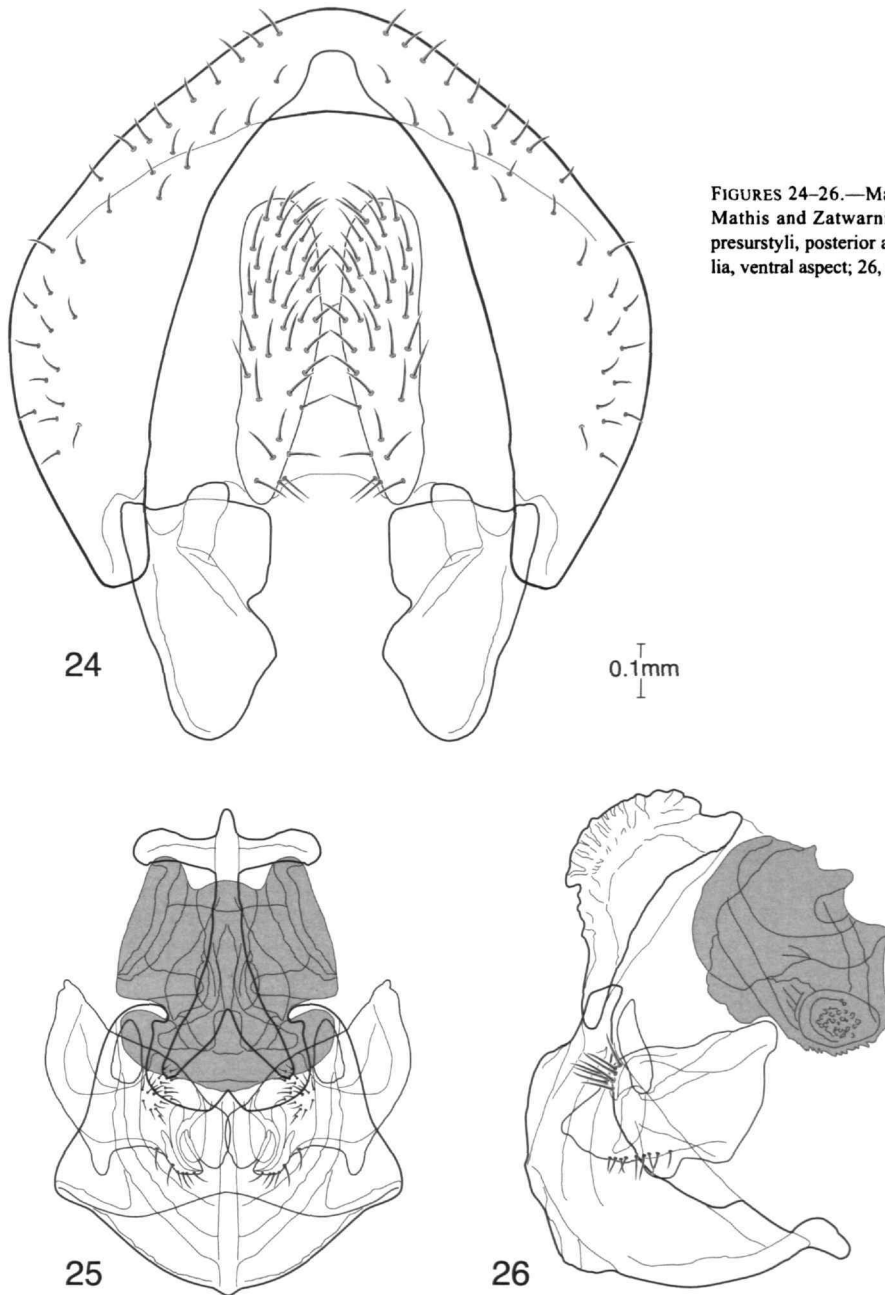
DESCRIPTION.—Large to very large shore flies (Figure 1), body length 7.00–11.20 mm; dorsum of head and thorax generally dark brown with some gray to yellowish gray; legs generally dark colored.

Head: Generally densely microtomentose. Frons mostly to almost entirely gray to tan, sometimes with some blackish brown maculations, especially posteriorly as short stripe laterad of ocelli and extended anterior and at vertex laterad; inner vertical seta short and thin, length about $\frac{1}{2}$ – $\frac{2}{3}$ that of outer vertical seta; ocelli arranged in equilateral triangle. Antenna blackish brown, usually with some gray to tan microtomentum dorsally; arista white to tannish white basally, bearing 11–13 dorsal rays. Face, parafacial, gena, and microtomentose portion of clypeus concolorous, whitish gray, contrasting with darker-colored frons; face bare except for series of setulae paralleling frontal suture; parafacial with transverse, golden brown to blackish brown stripe or maculation at level of antennal base, thereafter ventrally concolorous with face. Eye slightly higher than wide. Gena with anterior portion concolorous with face and parafacial, becoming whiter posteriorly, high, height slightly more than $\frac{1}{2}$ eye height; gena-to-eye ratio 0.57–0.63. Clypeus with dorsal $\frac{1}{2}$ of medial portion bare.

Thorax: Mesonotum generally mottled, gray to tannish gray, especially peripherally and along setal tracks, with bases of setae blackish brown; scutum with some blackish brown to blackish gray areas sometimes evident posteriorly; gray areas

as usually short stripes along acrostichal and dorsocentral tracks; scutellum with medial area gray, becoming blackish gray to blackish brown posteriorly and laterally and with dark brown areas at bases of lateral setae; anepisternum generally concolorous with rest of pleural area, sometimes slightly darker, lacking maculation in middle. Postsutural supra-alar seta well developed but slightly shorter than postalar seta; anepisternal setae 1–3, thinly developed; katepisternal seta well developed, length subequal to notopleural seta. Wing hyaline; R stem vein bearing 5–7 short, thin, pale setulae dorsally; vein R_1 with short, sparse setulae along dorsal length; costal-vein ratio 0.31–0.33; M-vein ratio 0.65–0.76. Leg color variable; femora blackish brown with moderately dense whitish gray microtomentum; tibiae blackish brown apically, basal portion yellowish red, thinly invested with whitish gray microtomentum; tarsi blackish brown dorsally, yellowish orange to orange ventrally, apical tarsomeres becoming blackish gray; forebasitarsomere of male normally developed, similar to basitarsomeres of mid- and hindlegs; foretarsomeres 2–5 of male normally developed, not greatly expanded apically, width much less than length; lateroapical setae of foretarsi of male tapered; hindbasitarsus and 2nd tarsomere of male bearing dense patch of long, slender setae along dorsum; tarsomeres of midleg bearing long setae lateroapically, aligned with plane of leg, length of setae subequal to width of tarsomere at apex.

Abdomen: Third and 4th tergites with dark band along posterior margin, at least in middle, posterior band sometimes connected laterally with anterolateral spot, or spot separate; 1st tergite with medial patch of short, dorsally erect setulae. Male terminalia (Figures 24–26): epandrium in posterior view (Figure 24) like a broadly pointed arch, narrow dorsally and slightly angulate, arms wider at dorsolateral level, ventrally becoming narrower; cercus ovoid, wider subdorsally; presurstylus in posterior view (Figure 24) broadly triangular, length nearly twice basal width, dorsomedial angle formed, not produced, medial margin irregular, with angulate indentation and extension; ventral apex rounded, lateral margin very shallowly convex; postsurstylus in lateral view (Figure 26) wide basally, produced at angle toward aedeagus, setulose lobe just beyond midlength, inner lobe of bilobed apex wider than outer lobe, essentially bare of setulae; aedeagus in lateral view (Figure 26) about equally wide throughout short length, inner surface irregularly convex, external surface irregularly concave with angulate indentation, apex truncate; aedeagal apodeme in lateral



FIGURES 24–26.—Male terminalia of *Dryxo brahma* Mathis and Zatwarnicki: 24, epandrium, cerci, and presurstyli, posterior aspect; 25, internal male terminalia, ventral aspect; 26, same, lateral aspect.

view (Figure 26) with keel moderately shallow and with long, narrow extension toward attachment with hypandrium, bifurcate arms at attachment with hypandrium long; hypandrium moderately wide and deep.

TYPE MATERIAL.—The holotype male is labeled “SRI LANKA:Col.Dist. Negombo[,] 7 May 1980/Collectors: W.N. Mathis[,] T. Wijesinhe[,] L. Jayawickrema/HOLOTYPEDryxo

brahma ♂ W.N. Mathis USNM & Zatwarnicki [red label; species name and “& Zatwarnicki” handwritten].” The holotype is pinned directly, is in good condition, and is deposited in the NMNH. The allotype female and 25 other paratypes (5♂, 20♀; USNM) bear the same locality label data as the holotype.

OTHER SPECIMENS EXAMINED.—Oriental. INDIA. Karnataka: Shimoga (568 m), 26 May–Oct 1936, 1937, P.S.

Nathan (17♂, 11♀; IRSN); Yelburga (near), 10 Dec 1974, K. Ghorpadé (1♂, 1♀; USNM). *Orissa*: Pottangi (21 km SE; 550 m), 4 Feb 1962, D.Q. Cavagnaro, E.S. Ross (1♀; CAS). *Rajasthan*: Rajaputana, Deesa (=Disa, 24°15'N, 72°10'E), Apr–7 Nov 1897, 1898, C.G. Nurse (9♂, 2♀; BMNH). *Tamil Nadu*: Anamali Hills, Cinchona, May 1964, T.R.S. Nathan (4♂; USNM); Coimbatore (11°N, 76°58'E), Mar–Oct 1947, 1955, 1957, P.S. Nathan (25♂, 22♀; BPBM, USNM); Coimbatore (25.8 km NW; 640 m), 8 Mar 1962, D.Q. Cavagnaro, E.S. Ross (3♀; CAS); Karaikal, Karubagaram, 19 Jan 1951, P.S. Nathan (1♀; IRSN); Karaikal, Kurunebaganan, Apr 1955, P.S. Nathan (3♂, 3♀; USNM); Karaikal, Pondicherry (11°56'N, 79°53'E), Mar 1964, T.R.S. Nathan (1♂; USNM); Madras (1♀; USNM); Nedungadu (10°58'N, 79°46'E), 29 Apr, P.S. Nathan (1♂; USNM); Nilgiri Hills, Cherangade (1067 km), Oct 1950, P.S. Nathan (1♂; IRSN). *Uttar Pradesh*: Dehra Dun Valley (700 m), 4–13 Aug 1978 (1♀; UZMC).

SRI LANKA. *Central Province*. Kandy: Kandy, 4 Jan 1924, E. Brunetti (2♀; BMNH). Mahaganay, 27 Nov 1890, Yerbury (2♂; BMNH). *Eastern Province*. Batticaloa: Batticaloa, 2 May 1980, L. Jayawickrema, W.N. Mathis, T. Wijesinha (1♂; USNM). *North Central Province*. Anuradhapura: Padawiya (=Pavaviya; 55 m), 2–8 Nov 1970, O.S. Flint, Jr. (1♂; USNM). *North Western Province*. Puttalam: Kadaimparu (24.1 km N Negombo; at shore of lagoon; locality 36), 31 Jan 1962, H. Andersson, P. Brinck, L. Cederholm (1♀; ZIL). *Southern Province*. Hambantota: Bundala, 25 Apr 1980, L. Jayawickrema, W.N. Mathis, T. Wijesinha (2♂; USNM). "Ceylon," Lichtwardt (1♂, 1♀; ANSP).

Paleartic. IRAN. *Baluchistan*: Bampur, Bazman-Farra, 4–20 Jul 1898 (1♂; ZMHU).

DISTRIBUTION.—Oriental: India (Karnataka, Orissa, Rajasthan, Tamil Nadu, Uttar Pradesh), Sri Lanka. Palearctic: Iran (Baluchistan).

ETYMOLOGY.—The specific epithet, *brahma*, is derived from the name of a Hindu caste and is a noun in apposition. The name is intended to recognize the magnificence of this species, especially its size and beauty.

REMARKS.—In recent catalogs (see species synonymy), this species was usually misidentified as *D. lispoidea*, the type species of the genus. Now that the identity of *D. lispoidea* has been clarified (see species treatment below), we here name and describe one of the species that was misidentified.

6. *Dryxo digna* Osten Sacken

FIGURES 27–29

Dryxo digna Osten Sacken, 1882:241.

Dryxo (Cyphops) digna.—Cogan and Wirth, 1977:332 [in part; Oriental catalog].—Mathis and Zatwarnicki, 1995:115 [in part; world catalog].

Cyphops dignus.—Cresson, 1929:182 [generic combination; list, Celebes, Philippines].

DIAGNOSIS.—This species is distinguished readily from congeners, especially *D. lispoidea*, which is similar, by the following combination of characters: frons and scutellar disc mostly

brown to blackish brown but with a gray, medial, microtomentose stripe; anepisternum mostly gray, at most with a brown spot near middle; 1 well-developed anepisternal seta along posterior margin; katapisternal seta well developed, subequal to notopleural seta; male hindtarsus lacking long, slender setae on dorsal surface; 1st tergite with sparse, inconspicuous, dorsally erect setulae; dark band on tergites 3–5 with a narrow, medial extension to posterior margin; postpronotal seta absent; and tergites 2–4 gray on ventral side, lacking blackish brown spot.

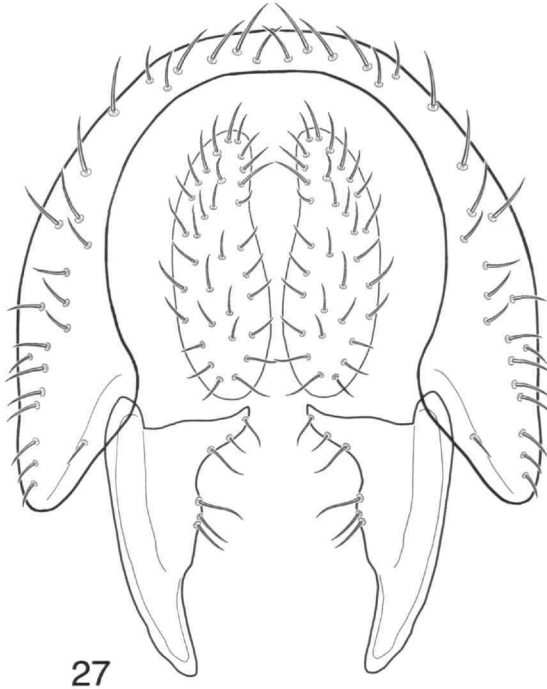
DESCRIPTION.—Large to very large shore flies, body length 7.20–9.30 mm; generally densely microtomentose, gray, with dark brown maculation pattern on dorsum.

Head: Generally densely microtomentose. Frons mostly dark brown, with a usually thin, gray, medial stripe; dark brown area laterad of ocellar triangle in V-shaped pattern, with its vertex posterior and its arms very broad; dark brown area adjacent to eye near vertex, extended from vertical setae forward to middle-width level of eye; inner vertical seta short and thin, length about $\frac{1}{2}$ – $\frac{2}{3}$ that of outer vertical seta; ocelli arranged in equilateral triangle. Antenna blackish brown; arista blackish brown, bearing 12–14 dorsal rays. Face, parafacial, gena, and clypeus concolorous, whitish gray, contrasting with darker colored frons; face bare except for series of setulae paralleling frontal suture; parafacial with transverse, golden brown to blackish brown stripe or maculation at level of antennal base, thereafter ventrally concolorous with face. Eye slightly higher than wide. Gena high, height slightly more than $\frac{1}{2}$ eye height, anterior portion concolorous with face and parafacial, becoming whiter posteriorly; gena-to-eye ratio 0.62–0.65.

Thorax: Mesonotum generally blackish brown; scutum with some gray areas marginally, along transverse suture, and as small, usually short stripes along acrostichal and dorsocentral tracks; scutellum with medial stripe and lateral margins whitish gray to gray except for dark brown areas around base of lateral scutellar setae; anepisternum with faint, small, dark brown spot near middle. Postsutural supra-alar seta well developed but slightly shorter than postalar seta; anepisternal setae 1 or 2, well developed; katapisternal seta well developed. Wing hyaline; R stem vein bearing 5–7 short, thin, pale setulae dorsally; costal-vein ratio 0.31–0.34; M-vein ratio 0.42–0.51. Legs mostly dark colored; femora and tibiae blackish brown to brown with moderately dense, gray microtomentum; tarsi yellowish orange to reddish orange ventrally, gray to yellowish gray dorsally, apical tarsomeres becoming blackish gray; forebasitarsomere of male swollen over most of length, especially as compared to basitarsomeres of mid- and hindlegs; foretarsomeres 2–5 of male moderately wide apically, width nearly equal to length; lateral setae of foretarsomeres, especially in males, parallel sided or even slightly wider to apex, apex pointed; hindbasitarsus of male lacking long, slender setae on dorsum; tarsomeres of midleg bearing long setae lateroapically, aligned with plane of leg, length of setae subequal to width of tarsomere at apex.

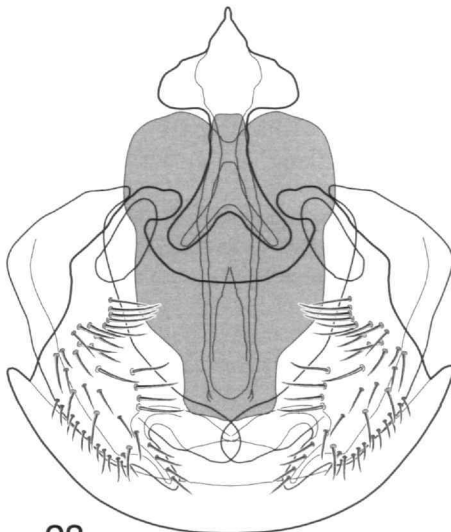
Abdomen: Tergites 1 and 2 mostly densely microtomentose, gray; tergite 1 with faint dark brown area medially; tergite 2 with a brown to blackish brown spot laterally; tergites 3 and 4 with wide, dark brown band along anterior margin and with medial projection extended posteriorly to posterior margin; tergite 5 with dark brown band and shallow extension medi-

ally; ventral surface entirely gray, densely microtomentose. Male terminalia (Figures 27–29): epandrium in posterior view (Figure 27) rounded arch-shaped, narrow dorsally, arms becoming wider ventrally; cercus ovoid, wider subventrally; presurstylus in posterior view (Figure 27) narrowly triangular, twice as long as wide, dorsomedial angle narrowly produced,

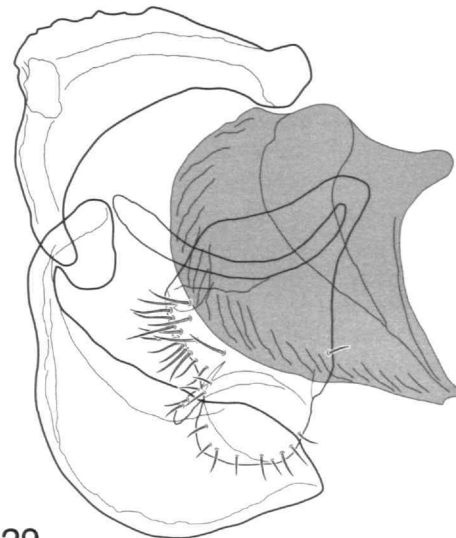


27

0.1mm



28



29

FIGURES 27–29.—Male terminalia of *Dryxo digna* Osten-Sacken: 27, epandrium, cerci, and presurstyli, posterior aspect; 28, internal male terminalia, ventral aspect; 29, same, lateral aspect.

medial margin irregular, ventral apex narrowly pointed, lateral margin shallowly and evenly arched; postsurstylus in lateral view (Figure 29) narrowed basally, becoming wider to subapical widest level and thereafter apical extension short, parallel sided, and broadly truncate apically, in ventral view (Figure 28) with inner lobe of bilobed apex longer, wider, and essentially bare of setulae; aedeagus in lateral view (Figure 29) as long as wide, inner margin rounded, external margin with short, narrow, rounded projection; aedeagal apodeme in lateral view (Figure 29) with keel very shallow; hypandrium moderately wide and deep.

TYPE MATERIAL.—The lectotype male of *Dryxo digna* Osten Sacken, here designated to stabilize and make more universal the use of this name, is labeled "Dryxo digna O.S. ♂ type [handwritten]/Philippinen [handwritten]/Coll. O.S. [handwritten]/ coll. Oldenberg/Coll. Osten-Sacken/Syntypus [red label; "1972" handwritten on the underside]/Typus [maroon-red label with pencil mark through it]/LECTOTYPE ♂ *Dryxo digna* Osten Sacken By Mathis & Zatwarnicki [handwritten except for "LECTOTYPE" and "By"; label with black submarginal border]." The lectotype is pinned directly, is in good condition (posterior margin of wings torn, thorax cracked around pin), and is deposited in the DEI. There are also six paralectotypes (4♂, 2♀; DEI) that are here designated.

OTHER SPECIMENS EXAMINED.—PHILIPPINES. *Luzon*. Quezon: Maliao, C.F. Baker (1♂; USNM). Laguna: Los Baños, C.F. Baker (1♂; USNM).

DISTRIBUTION.—Oriental: Philippines (Luzon, Mindanao).

REMARKS.—Species of *Dryxo* are frequently widespread, and thus we would not be surprised to find this species occurring beyond the islands of the Philippines, although it is presently known only from there.

7. *Dryxo freidbergi*, new species

FIGURES 30–32

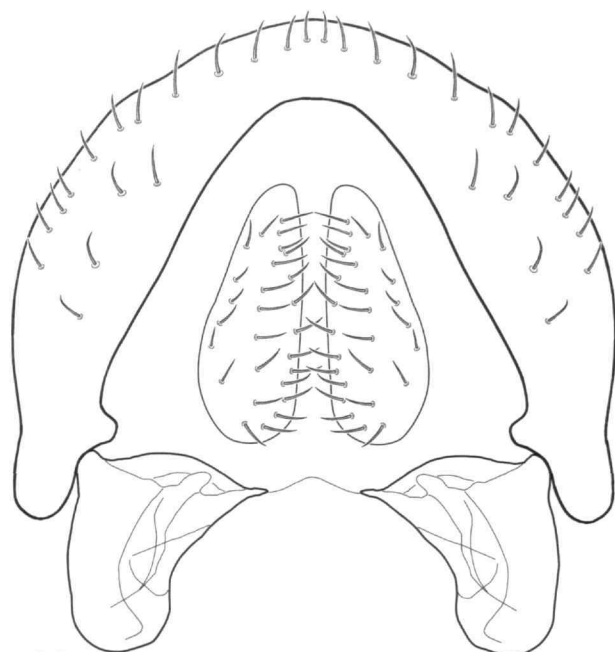
DIAGNOSIS.—This species is distinguished from congeners by the following combination of characters: parafacial with wide, blackish brown stripe immediately laterad of antennal base contrasting distinctly with silvery gray remainder of parafacial; mesonotum with numerous small, dark brown spots at bases of setae and setulae, 2 large, somewhat triangular, dark brown spots at posterior margin of scutum, and 2 spots on scutellum around bases of apical scutellar setae; postsutural supra-alar seta greatly reduced or absent; anepisternum lacking moderately long, slender setae along posterior margin; katepisternal seta usually greatly reduced, much weaker than notopleural seta, or lacking; femora except apices gray, concolorous with pleural areas, contrasting with yellow tibiae; male hindtarsi lacking long, slender setae on dorsal surface; tergites with dark band toward anterior margin, at most with a very thin, dark area along posterior margin; and 1st tergite with sparse, inconspicuous, dorsally erect setulae.

DESCRIPTION.—Large to very large shore flies, body length 5.90–6.45 mm; generally white with some brown coloration dorsally and with apices of legs yellowish.

Head: Generally densely microtomentose. Frons mostly silvery white to silver with some golden areas medially, anterior of anterior ocellus; length of inner and outer vertical setae about coequal, both reduced and about equal to length of pedicel; ocelli arranged either in equilateral or slightly isosceles triangle, usually with distance between posterior ocelli shorter than between either posterior ocellus and anterior ocellus. Antenna blackish brown to black; scape and pedicel sometimes with considerable fine, grayish to brownish microtomentum, especially dorsally; arista silvery white, bearing 8 or 9 dorsal rays. Face white to faintly tannish white, bare except for series of setulae paralleling frontal suture; parafacial concolorous with face except for a wide, brown to blackish brown stripe immediately laterad of antennal base. Eye slightly higher than wide. Gena high, anterior portion concolorous with face and parafacial, becoming whiter posteriorly; gena-to-eye ratio 0.50–0.54. Clypeus mostly bare medially, shiny black, becoming densely microtomentose laterally, especially along ventral margin.

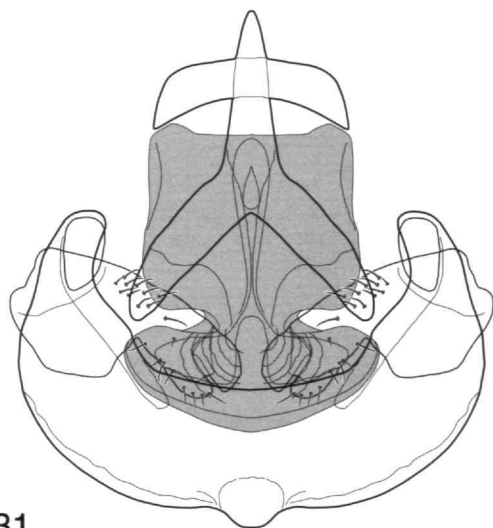
Thorax: Mesonotum with small dark brown spots at bases of setae and setulae, 2 large, somewhat triangular to quadrate dark brown spots toward posterior margin of scutum, varying amounts of dark brown areas medially and along setal tracks (none consistently expressed), and 2 spots on scutellum at bases of apical scutellar setae; postsutural supra-alar seta greatly reduced or absent; anepisternum either lacking moderately long, slender setae along posterior margin or bearing 1 small, slender seta; katepisternal seta usually greatly reduced, much weaker than notopleural seta, or lacking. Wing hyaline; R stem vein bearing 4–6 short, thin setulae dorsally; costal-vein ratio 0.44–0.50; M-vein ratio 0.72–0.84. Femora except apices microtomentose, whitish gray, concolorous with pleural areas, contrasting with yellow to yellowish orange tibiae with faint and thin white microtomentum; male foretarsi similar to female, unmodified; forebasitarsomere of male similar to basitarsomeres of mid- and hindlegs; some lateroapical setae of forebasitarsomere of male parallel sided and bluntly rounded apically; hindtarsi lacking long, slender setae on dorsal surface.

Abdomen: Generally whitish gray and lacking bands, but with some brown to golden brown along extreme posterior margin; sometimes tergites 2 and/or 3 with some dark brown irregular maculations anterolaterally; 1st tergite with sparse, inconspicuous, dorsally erect setulae. Male terminalia (Figures 30–32): epandrium yellowish to yellowish orange, frequently exposed and conspicuous from dorsal angle, in posterior view (Figure 30) rounded arch-shaped, narrow dorsally, arms wider at dorsolateral level, ventrally becoming narrower; cercus ovoid, wider subventrally; presurstylus in posterior view (Figure 30) broadly triangular, length only slightly more than basal width, dorsomedial angle very narrowly produced, medial margin irregularly concave, ventral apex broadly rounded, lateral margin very shallowly arched; postsurstylus in lateral view

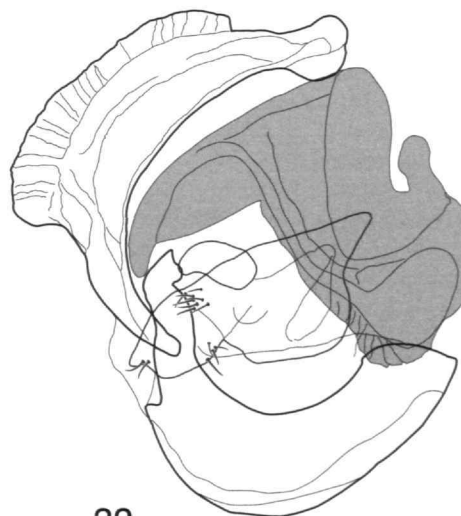


30

0.1mm



31



32

FIGURES 30–32.—Male terminalia of *Dryxo freidbergi* Mathis and Zatwarnicki: 30, epandrium, cerci, and presurstyli, posterior aspect; 31, internal male terminalia, ventral aspect; 32, same, lateral aspect.

(Figure 32) wide basally, becoming narrower to apex, with sub-apical, angulate indentation, in ventral view with both lobes of bilobed apex of about equal size, inner lobe essentially bare of setulae; aedeagus in lateral view (Figure 32) with base very wide, immediately narrowed, especially on inner surface, external surface with recurved, narrow lobe at midlength, apex irregularly and relatively broadly rounded; aedeagal apodeme in lateral view (Figure 32) with keel very shallow, ridge-like, bi-

furcate arms at attachment with hypandrium long; hypandrium moderately wide and deep.

TYPE MATERIAL.—The holotype male is labeled "CAMEROON Kribi (beach) Rt. N7 28,29.XI.1987 [28–29 Nov 1987] A. FREIDBERG/HOLOTYPE *Dryxo freidbergi* ♂ W.N.Mathis & Zatwarnicki USNM [red label; species name, gender symbol, and "& Zatwarnicki" handwritten]." The holotype is pinned directly, is in excellent condition, and is deposited in the

NMNH. The allotype female and six other paratypes (3♂, 2♀; USNM) bear the same locality data as the holotype.

DISTRIBUTION.—Afrotropical: Cameroon.

ETYMOLOGY.—The specific epithet, *freidbergi*, is a genitive patronym to honor one of the collectors of this new species from Africa.

8. *Dryxo india*, new species

FIGURES 33–35

DIAGNOSIS.—This species is distinguished from congeners by the following combination of characters: mesofrons yellowish orange to grayish tan; inner vertical seta subequal in length to outer vertical seta; scape and pedicel reddish, 1st flagellomere black; parafacial lacking transverse stripe; mesonotum generally concolorous with frons, lacking dark spots at bases of setae and lacking maculation pattern; postsutural supra-alar seta well developed; anepisternal seta and katepisternal setae well developed although slender, subequal; legs mostly yellowish orange to orange; femora extensively whitish gray basally; tarsomeres black apically and laterally; foretarsomeres 2–5 of male greatly expanded apically, width equal to length, and narrow at attachment with preceding tarsomere; hindbasitarsus of male lacking long, slender setae on dorsum; 2nd hindtarsomere of male lacking long setulae along dorsum; 3rd and 4th tergites lacking dark band; and 1st tergite with medial patch of short, dorsally erect setulae.

DESCRIPTION.—Large to very large shore flies, body length 7.60–8.70 mm; head and thorax generally tan to whitish tan dorsally, abdomen mostly whitish gray; legs yellowish orange, becoming darker brown apically and whitish basally.

Head: Generally densely microtomentose. Frons yellowish orange to grayish tan; inner vertical seta subequal in length to outer vertical seta; ocelli arranged in isosceles triangle, with distance between posterior ocelli longer than between either posterior ocellus and anterior ocellus. Antenna with scape and pedicel faintly reddish orange with thin dusting of whitish gray microtomentum; 1st flagellomere blackish brown to black; arista silvery white, bearing 11–14 dorsal rays. Face, parafacial, gena, and clypeus concolorous, creamy white, contrasting with darker-colored frons; face bare except for series of setulae paralleling frontal suture; parafacial lacking transverse stripe, dorsal ½ slightly tannish; essentially uniformly concolorous with face, lacking stripe. Eye slightly higher than wide. Gena high, height slightly more than ½ eye height, anterior portion concolorous with face and parafacial, becoming whiter posteriorly; gena-to-eye ratio 0.56. Clypeus mostly microtomentose, medial portion with dorsal ½ or more bare, somewhat shiny.

Thorax: Mesonotum yellowish tan to whitish tan, lacking darkened spots at bases of setae and lacking maculation pattern; postsutural supra-alar seta well developed but slightly shorter than postalar seta; anepisternal and katepisternal setae well developed although slender, subequal in length. Wing hyaline; R stem vein bearing 4–6 short, thin setulae dorsally; costal-vein ratio 0.40–0.44; M-vein ratio 0.57–0.61. Legs mostly

yellowish orange to orange; femora extensively whitish gray basally; tarsomeres black apically and laterally, apical tarsomere almost entirely black; foretarsomeres 2–5 of male greatly expanded apically, width equal to length, narrow basally at attachment with preceding tarsomere; lateroapically, setae of foretarsomeres of male tapered evenly; hindbasitarsus of male lacking long, slender setae on dorsum; 2nd hindtarsomere of male bearing short setulae, none clustered; tarsomeres of mid-leg bearing long setae lateroapically, aligned with plane of leg, length of setae subequal to width of tarsomere at apex.

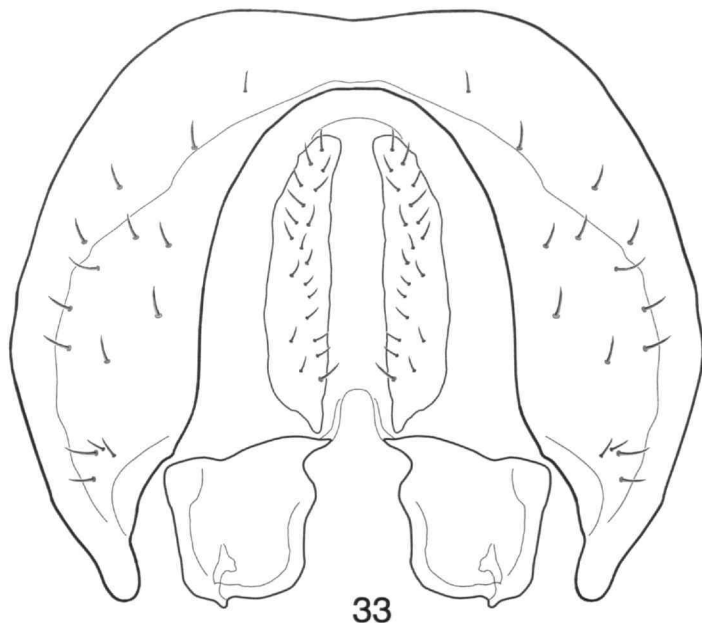
Abdomen: Dorsum mostly grayish white, lacking darkened bands anteriorly or posteriorly; male with slightly darkened area anterolaterally on 2nd tergite, this area also bearing denser patch of setulae, those inserted more toward anterolateral margin longer, more erect; female with dark brown spot anterolaterally. Male terminalia (Figures 33–35): epandrium frequently exposed and conspicuous from dorsal angle, in posterior view (Figure 33) rounded arch-shaped, narrow dorsally and shallowly emarginate, arms widest subventrally, thereafter ventrally becoming narrower, bluntly pointed; cercus narrowly hemispherical, dorsal apex rounded, ventral apex pointed; presurstylus in posterior view (Figure 33) irregularly quadrate, width dorsally only slightly more than length, dorsomedial angle very narrowly produced, apex acutely pointed, medial margin sinuous, ventral margin nearly flat, with shallow papilla-like point near middle, lateral margin nearly straight; postsurstylus in lateral view (Figure 35) C-shaped with curved dorsal extension attached to aedeagus, ventral portion wider and with apex only very shallowly bifurcate; aedeagus in lateral view (Figure 35) with base moderately wide, becoming wider to widest width subapically, thereafter narrowed immediately to rounded apex; aedeagal apodeme in lateral view (Figure 35) L-shaped, with keel very shallow, ridge-like, and pointed ventroapically, bifurcate arms at attachment with hypandrium short; hypandrium short, moderately wide and deep.

TYPE MATERIAL.—The holotype male is labeled “Nedungadu S. India 4-II P.S. Nathan/HOLOTYPE *Dryxo india* ♂ W.N.Mathis & Zatwarnicki [red label; species name and “& Zatwarnicki” handwritten].” The holotype is pinned directly, is in good condition, and is deposited in the NMNH.

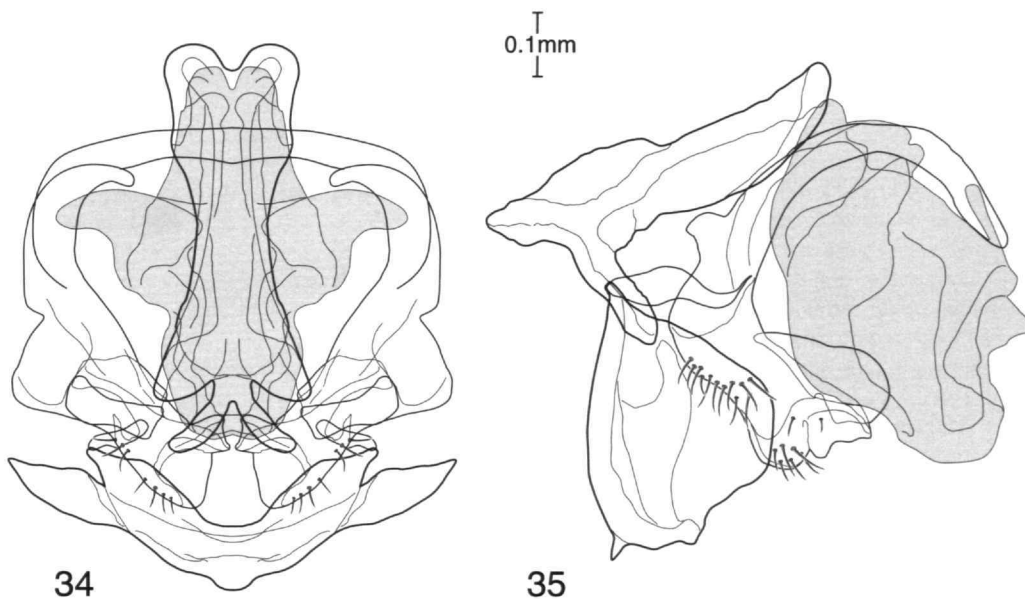
OTHER SPECIMENS EXAMINED.—INDIA. *Karnataka:* Shimoga (568.5 m; trapped by 200 Petromax lamp), River Tunga, 29 May 1936, P.S. Nathan (5♂, 9♀; IRSN); Shimoga, 20 Jan–29 May 1936, P.S. Nathan (3♀; IRSN). *Tamil Nadu:* Karaikal (10°55'N, 79°45'E), Jul 1956, P.S. Nathan (13♂, 17♀; BMNH); Kurumbagaram, Karaikal, Jul–Dec 1951, 1952, P.S. Nathan (4♂, 8♀; BMNH); Tranquebar (=Tarangambadi, 11°02'N, 79°51'E), Jul–Dec 1952, P.S. Nathan (7♂, 9♀; BMNH, IRSN); Walayar Forests (10°51'N, 76°51'E), South Malabar, 5 Aug 1956, P.S. Nathan (2♂, 1♀; BMNH).

DISTRIBUTION.—Oriental: India (Karnataka, Tamil Nadu).

ETYMOLOGY.—The specific epithet, *india*, is a noun in apposition and refers to the Indian subcontinent where this species occurs, perhaps exclusively.



FIGURES 33–35.—Male terminalia of *Dryxo india* Mathis and Zatwarnicki: 33, epandrium, cerci, and presurstyli, anterior aspect; 34, internal male terminalia, ventral aspect; 35, same, lateral aspect.



9. *Dryxo lispoidea* Robineau-Desvoidy

FIGURES 36–38

Dryxo lispoidea Robineau-Desvoidy, 1830:787.—Becker, 1926:93 [review, list, "Persisch-Belutschistan"].—Cogan and Wirth, 1977:332 [in part; Oriental catalog].—Cogan, 1984:144 [in part; Palearctic catalog].—Mathis and Zatwarnicki, 1995:116 [in part; world catalog].

Cyphops fasciatus Jaennicke, 1867:368. [New synonym.]

Dryxo (Cyphops) fasciatus.—Cogan and Wirth, 1977:332 [generic combination].—Mathis, 1989:644 [Australasian/Oceanian catalog].—Mathis and Zatwarnicki, 1995:115 [world catalog].

Dryxo spreta Osten Sacken, 1882:242. [New synonym.]

Dryxo digna of authors, not Osten Sacken [misidentification].—Cresson, 1929:182 [synonymy with *D. spreta*].—Cogan and Wirth, 1977:332 [in part; Oriental catalog].—Mathis and Zatwarnicki, 1995:115 [in part; world catalog].

DIAGNOSIS.—Although Cresson (1929) synonymized *D. spreta* (= *D. lispoidea*) with *D. digna*, a precedent followed by subsequent workers, this species is readily distinguished from *D. digna* and other congeners by the following combination of characters: frons and scutellar disc mostly brown to blackish

brown but with a gray, medial, microtomentose stripe; anepisternum with a large, wide, transverse, dark brown stripe; 2 weakly developed anepisternal setae along posterior margin; katepisternal seta usually greatly reduced, much weaker than notopleural seta; male hindtarsi lacking long, slender setae on dorsal surface; 1st tergite with sparse, inconspicuous, dorsally erect setulae; dark band on tergites 3–5 with narrow, medial extension to posterior margin; postpronotal seta absent; and tergites 2–5 with blackish brown spot on ventral side.

DESCRIPTION.—Large to very large shore flies, body length 5.50–9.00 mm; dorsum of head and thorax generally dark brown, with some gray to yellowish gray; legs generally dark colored.

Head: Generally densely microtomentose. Frons mostly dark brown, with some tan and gray coloration; dark brown area in V-shaped pattern, with its vertex posterior and its arms very broad; dark brown area adjacent to eye near vertex, extended from vertical setae forward to middle-width level of eye; inner vertical seta short and thin, length about $\frac{1}{2}$ – $\frac{2}{3}$ that of outer vertical seta; ocelli arranged in equilateral triangle. Antenna blackish brown; arista blackish brown, bearing 12–14 dorsal rays. Face, parafacial, gena, and clypeus concolorous, whitish gray, contrasting with darker-colored frons; face bare except for series of setulae paralleling frontal suture; parafacial with transverse, golden brown to blackish brown stripe or maculation at level of antennal base, thereafter ventrally concolorous with face. Eye slightly higher than wide. Gena high, height slightly more than $\frac{1}{2}$ eye height; anterior portion concolorous with face and parafacial, becoming whiter posteriorly; gena-to-eye ratio 0.62–0.65.

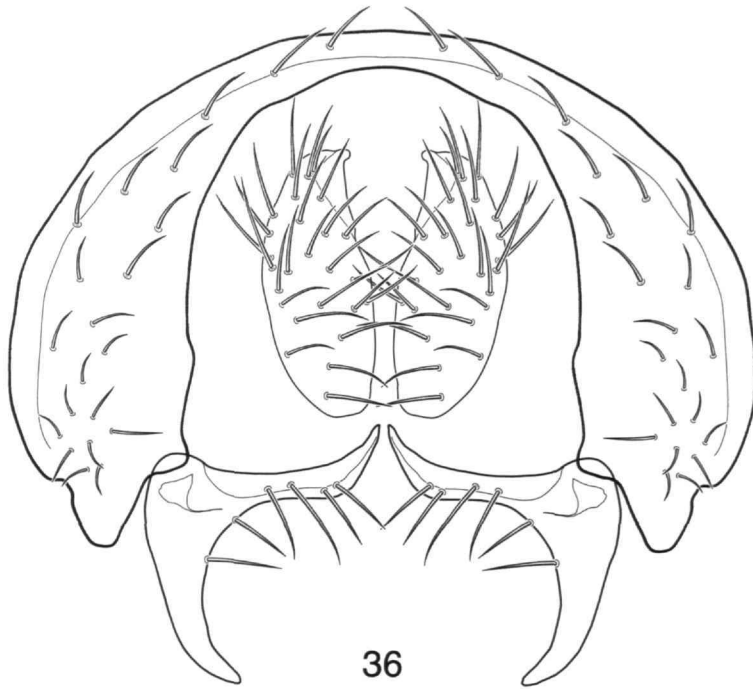
Thorax: Mesonotum generally blackish brown; scutum with some gray areas marginally, along transverse suture, and as small, usually short stripes along acrostichal and dorsocentral tracks; scutellum with medial stripe and lateral margins whitish gray to gray except for dark brown areas around base of lateral scutellar setae; anepisternum with dark brown spot near middle. Postsutural supra-alar seta well developed but slightly shorter than postalar seta; anepisternal setae 1 or 2, weakly developed, thin; katepisternal seta very weakly developed, smaller than anepisternal seta(e). Wing hyaline; R stem vein bearing 5–7 short, thin, pale setulae dorsally; costal-vein ratio 0.41–0.44; M-vein ratio 0.71–0.77. Legs mostly dark colored; femora and tibiae blackish brown to brown with moderately dense gray microtomentum; tarsi yellowish orange to orange ventrally, dorsally gray to yellowish gray, apical tarsomeres becoming blackish gray; forebasitarsomere of male normally developed, similar to basitarsomeres of mid- and hindlegs; foretarsomeres 2–5 of male normally developed, not greatly expanded apically, width much less than length; some lateroapical setae of foretarsi of male parallel sided and with broadly rounded apices; hindbasitarsus of male lacking long, slender setae on dorsum; tarsomeres of midleg bearing long setae lateroapically, aligned with plane of leg, length of setae subequal to width of tarsomere at apex.

Abdomen: Tergites 1 and 2 mostly gray, posterior margin of tergite 2 dark brown and sometimes with medial stripe dark brown; tergites 2–5 with dark brown band along anterior margin, posterior margin of brown band with medial projection extended to posterior margin; lateral margin gray to whitish gray; ventral surface usually with brown maculation, usually more evident on tergites 2–5. Male terminalia (Figures 36–38): epandrium in posterior view (Figure 36) rounded arch-shaped, narrow dorsally, arms wider at dorsolateral level, ventrally becoming narrower; cercus ovoid, wider subventrally, pointed dorsomedially; presurstylus in posterior view (Figure 36) deeply bifurcate, each arm long and slender, medial arm oriented medially, apex turned dorsomedially and bearing 5 or 6 setulae extended ventrally, lateral arm oriented ventrally, gradually tapering to medially oriented apex; postsurstylus in lateral view (Figure 38) narrow basally, becoming wider at midlength and with a swelling along anterior margin, margin bearing several setulae, postsurstylus thereafter narrowed before becoming wider at ventral margin, ventral margin bifurcate with posterior lobe slightly wider, posteroventral margin bearing 5 or 6 setulae; aedeagus in lateral view (Figure 38) narrow basally, immediately becoming wider, with broad apex truncate; aedeagal apodeme in lateral view (Figure 38) with keel very shallow, ridge-like, and developed on half attached to base of aedeagus only; hypandrium moderately wide and deep.

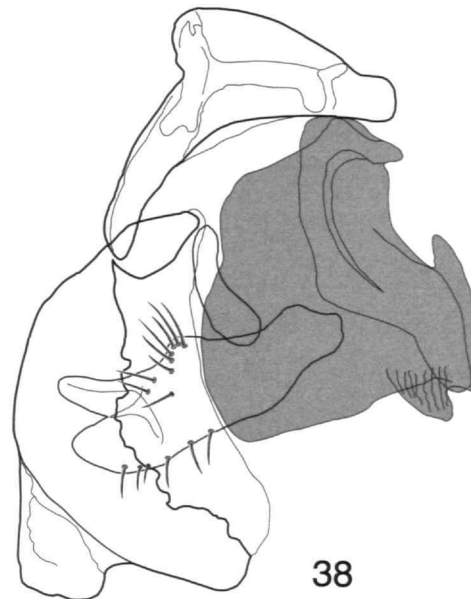
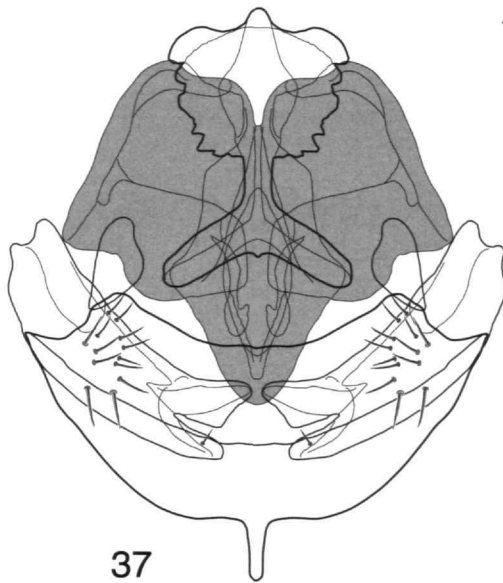
TYPE MATERIAL.—The neotype of *Dryxo lispoidea* Robinseau-Desvoidy, here designated, is the lectotype male of *Cyphops fasciatus* and bears labels as indicated below for that specimen. The original type series of *Dryxo lispoidea* was collected on the island of Sumatra and apparently has been destroyed (the second author and Volker Hollmann, pers. comm., 1995, after they visited Paris and consulted with L. Matile). As it is likely that the type specimens represented this species, based in part on distribution, we are fixing its name as the senior objective synonym by designating the lectotype of *Cyphops fasciatus* as the neotype for *Dryxo lispoidea*.

The lectotype male of *Cyphops fasciatus* Jaenicke, here designated to stabilize and make more universal the use of this name, is labeled "Mas[culus]. Wiesb. Java. Fritz [handwritten]/von Heyden [collection]/Typus [red label with black border]/*Cyphops fasciatus* Jaen[nicke] Java [handwritten, square label with black border]/LECTOTYPE ♂ *Cyphops fasciatus* Jaenicke By Mathis & Zatwarnicki [handwritten except for "LECTOTYPE" and "By"; label with black submarginal border]." The lectotype is pinned directly, is in poor condition (partially eaten by dermestids), and is deposited in the NSF.

The lectotype male of *Dryxo spreta* Osten Sacken, here designated to stabilize and make more universal the use of this name, is labeled "Dryxo spreta O.S. type. [handwritten]/Philippinen Coll. Osten-Sacken/D 419. [handwritten]/spreta O.S. [handwritten]/Becker det./Syntypus [red label; number "1972" on the underside]/TYPUS [pink label]/LECTOTYPE ♂ *Dryxo spreta* Osten Sacken By Mathis & Zatwarnicki [handwritten except for "LECTOTYPE" and "By"; label with black submar-



0.1mm



FIGURES 36–38.—Male terminalia of *Dryxo lispoidea* Robineau-Desvoidy: 36, epandrium, cerci, and presurstyli, posterior aspect; 37, internal male terminalia, ventral aspect; 38, same, lateral aspect.

ginal border].” The lectotype is pinned directly, is in poor condition (right eye caved in, thorax cracked toward right of pin, left hindleg missing), and is deposited in the DEI. There is also a male paralectotype (DEI) that is here designated.

OTHER SPECIMENS EXAMINED.—Australasian/Oceanian. AUSTRALIA. *Queensland*: Byfield State Forest, 3 Jan 1976, G. Daniels (9♂, 4♀; AM); Claudie River near Mt. Lamond, 27 May–24 Dec 1966, 1971, D.K. McAlpine (6♂, 4♀; AM).

PAPUA NEW GUINEA. *Central Province*: Goldie River, Barracks (shaded stream), 11 Aug 1985, J.W. Ismay (10♂, 4♀; USNM). Iomari Creek, 12 Feb 1982, J.W. Ismay (1♂; BMNH). Kokoda (366 m), Sep–Oct 1933, L.E. Cheesman (7♂, 9♀; BMNH). *Bismarck Archipelago*: Neu-Pommern (=New Britain), Kinigunan, C. Ribbe (1♂; ANSP). Ralum, 1896–1897, S. Dahl (8♂, 2♀; ANSP, ZMHU).

Oriental. INDIA. *Orissa*: Pottangi (21 km SE; 18°34'N, 82°58'E; 550 m), 4 Feb 1962, D.Q. Cavagnaro, E.S. Ross (1♀; CAS). *Tamil Nadu*: Cinchona, Anamali Hills, May 1964, T.R.S. Nathan (1♂, 2♀; USNM).

INDONESIA. *Sulawesi*: Samanga, Nov 1895, H. Fruhstorfer (1♂, 1♀; ANSP).

Sumatra: Landkat District, Bekulab River, Tambunan-A, (Malaise trap), 3 Jul–9 Aug 1985, M.E. Irwin (3♂, 10♀; INHS, USNM); Sandaran Agong, Korinchi Lake (747 m), May–Jun 1914 (1♀; BMNH). Fort de Kock (920 m), E. Jacobson (1♂, 2♀; BMNH).

PHILIPPINES. *Luzon*. Quezon: Malinao, C.F. Baker (1♂, 2♀; AMNH, USNM); Luzon, Inugan, 6 Jun 1918, G. Böttcher (1♀; DEI). *Samar*: Osmena, Aug 1945, J. Laffoon (1♂; USNM).

SRI LANKA. *Sabaragamuwa Province*. Ratnapura: Uggalkaltota (107 m; irrigation bungalow), 31 Jan–8 Feb 1970, D.R. Davis, W. Rowe (1 ex (abdomen missing); USNM). *Uva Province*. Monaragala: Wattagama (km 13), 11–20 Dec 1967, P. Karunaratne (1♀; BMNH).

TAIWAN. Kankau, 12 Nov, H. Sauter (3♂, 10♀; BMNH, DEI, ZMHU). Koshun, Aug 1908 (2♀; ANSP). Koshun, Jun–Aug 1908 (7♂, 32♀; HNHM).

THAILAND. *Chanthaburi*: Khao Sai Dao Tai, Jan–Feb 1988, W.L. Abbott (1♀; USNM); South Khao Sok National Park, Route 401, 22 Oct 1993, A. Freidberg, F. Kaplan (1♀; USNM). *Krabi*: Huai Waterfall (riverbanks, open area; 2 km before National Park), 24 Oct 1997, P. Grootaert (1♂, 1♀; IRSN). *Trang*: Kachong (rocky banks on large river), 24 Oct 1997, P. Grootaert (1♂, 2♀; IRSN).

DISTRIBUTION.—Australasian/Oceanian: Australia (Queensland), Papua New Guinea (Bismarck Archipelago, Central). Oriental: India (Orissa, Tamil Nadu), Indonesia (Java, Sulawesi, Sumatra), Philippines (Luzon, Mindanao, Samar), Sri Lanka, Taiwan, Thailand.

REMARKS.—Since Cresson (1929), *Dryxo spreta* has been considered conspecific with, and thus a junior synonym of *D. digna*. The two species are indeed similar and are apparently closely related, and although characterized by many similarities, including synapomorphies, they are readily distinguished

from each other using external characters as well as structures of the male terminalia (see diagnosis and description).

Specimens of other species were often misidentified as *D. lipsoidea*, especially specimens on the Indian subcontinent, where a few species of *Dryxo* are apparently sympatric.

10. *Dryxo margaretae* Cogan

FIGURES 39–41

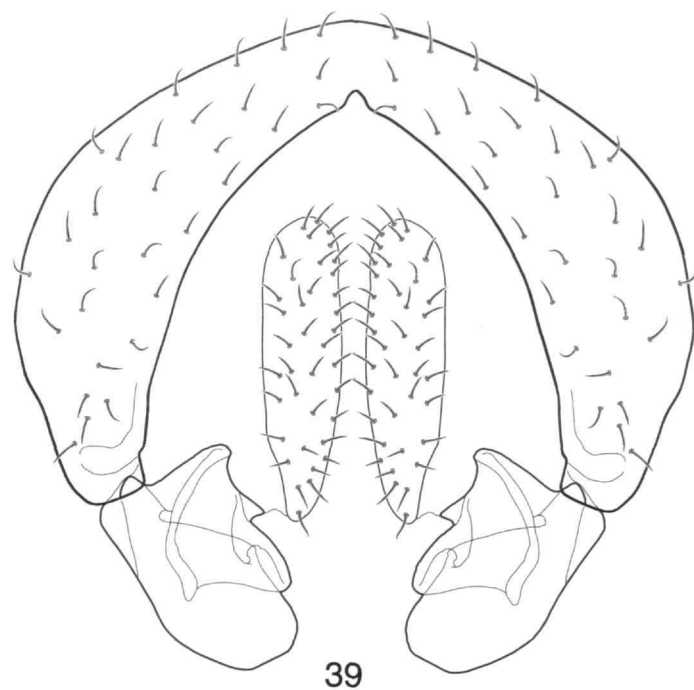
Dryxo margaretae Cogan, 1968:360; 1980:661 [Afrotropical catalog].—Mathis and Zatwarnicki, 1995:116 [world catalog].

DIAGNOSIS.—This species is distinguished from congeners by the following combination of characters: inner vertical seta subequal or slightly longer than outer vertical seta; postpronotal seta absent; R stem vein bearing about 6 long, thin setulae along posterior margin basad of humeral crossvein; male hindbasitarsus with several long, slender setae toward base, setae becoming shorter and much sparser toward apex; male 2nd hindtarsomere bearing long, slender setae on dorsal surface; katapisternal seta well developed, length subequal to notopleural seta; tergites 3 and 4 with dark band along posterior margin, at least in middle, band sometimes connected laterally with anterolateral spot or spot separate; and tergite 1 with medial patch of short, dorsally erect setulae.

DESCRIPTION.—Large to very large shore flies, body length 7.10–9.30 mm; generally blackish brown dorsally but with considerable areas gray.

Head: Generally densely microtomentose. Frons mostly to almost entirely gray to tan, sometimes with some blackish brown maculation, especially posteriorly as 2 short, parallel stripes extended obliquely anterolaterally from posterior ocellus and adjacent lateral area of vertex; inner vertical seta subequal or slightly longer than outer vertical seta; ocelli arranged in equilateral triangle. Antenna blackish brown, usually with some gray to tan microtomentum dorsally; arista white to tannish white basally, bearing 11–13 dorsal rays. Face, parafacial, gena, and microtomentose-covered portion of clypeus concolorous, whitish gray, contrasting with darker-colored frons; face bare except for series of setulae paralleling frontal suture; parafacial with transverse, golden brown to blackish brown stripe or maculation at level of antennal base, thereafter ventrally concolorous with face. Eye slightly higher than wide. Gena high, height slightly more than ½ eye height, anterior portion concolorous with face and parafacial, becoming whiter posteriorly; gena-to-eye ratio 0.52–0.56. Clypeus with dorsal ½ of medial portion bare.

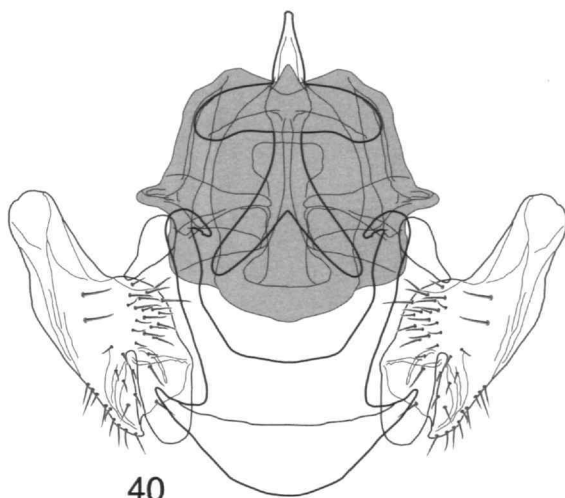
Thorax: Mesonotum generally mottled, mostly dark brown, with some gray to tannish gray areas, especially peripherally and along setal tracks, bases of setae blackish brown; scutum mostly brown to blackish brown, with some gray areas sometimes evident, usually as short stripes along acrostichal and dorsocentral tracks; scutellum generally and extensively blackish brown, only mediobasal, somewhat triangular area whitish gray; anepisternum generally concolorous with rest of



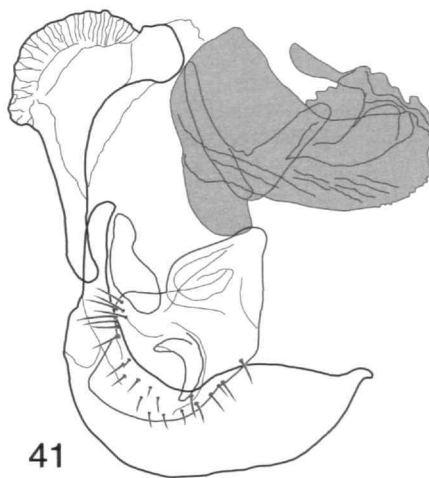
39

FIGURES 39-41.—Male terminalia of *Dryxo margaretae* Cogan: 39, epandrium, cerci, and presurstyli, posterior aspect; 40, internal male terminalia, ventral aspect; 41, same, lateral aspect.

0.1mm



40



41

pleural area, sometimes slightly darker, lacking maculation in middle. Postsutural supra-alar seta well developed but slightly shorter than postalar seta; anepisternal setae 1-3, thinly developed; katepisternal seta well developed, length subequal to notopleural seta. Wing hyaline; R stem vein bearing 5-7 short, thin, pale setulae dorsally; vein R_1 with short, sparse setulae along length; costal-vein ratio 0.29-0.33; M-vein ratio 0.56-0.62. Leg color variable; femora blackish brown with moderately dense whitish gray microtomentum; tibiae blackish brown apically, basal portion yellowish red, thinly invested with whitish gray microtomentum; tarsi blackish brown dor-

sally, yellowish orange to orange ventrally, apical tarsomeres becoming blackish gray; forebasitarsomere of male normally developed, similar to basitarsomeres of mid- and hindlegs; foretarsomeres 2-5 of male normally developed, not greatly expanded apically, width much less than length; lateroapical setae of foretarsi of male tapered; hindbasitarsus and tarsomere 2 of male bearing sparse patch of long, slender setae posterodorsally; hindtarsomere 2 of male bearing some long setae along dorsum; tarsomeres of midleg bearing long setae lateroapically, aligned with plane of leg, length of setae subequal to width of tarsomere at apex.

Abdomen: Tergites 3 and 4 with dark band along posterior margin, at least in middle, band sometimes connected laterally with anterolateral spot, or spot separate; 1st tergite with medial patch of short, dorsally erect setulae. Male terminalia (Figures 39–41): epandrium in posterior view (Figure 39) rounded arch-shaped, narrow dorsally and slightly angulate, arms wider at dorsolateral level, ventrally becoming narrower; cercus ovoid, wider subventrally; presurstylus in posterior view (Figure 39) broadly triangular, length about 1.5 times basal width, dorso-medial angle narrowly produced, short, medial margin with 2 step-like processes, ventral apex broadly rounded, lateral margin very shallowly arched; postsurstylus in lateral view (Figure 41) wide and angulate basally, bearing shallow, setulose lobe just beyond midlength; inner lobe of bilobed apex wider and slightly longer than outer lobe, essentially bare of setulae; aedeagus in lateral view (Figure 41) with base moderately wide, immediately narrowed, especially on inner surface, external surface with recurved, narrow lobe at midlength, apex irregularly and relatively broadly rounded; aedeagal apodeme in lateral view (Figure 41) with keel shallow, ridge-like, with long, narrow extension toward attachment with hypandrium, bifurcate arms at attachment with hypandrium long; hypandrium somewhat wide and deep.

TYPE MATERIAL.—The holotype male is labeled "Holo-type [round label with red submargin]/Madagascar[.] [Tamatave:] Est[,] Sahasoa Fampanambo 80m[,] dct Maroanetra[,] 26–29.III.58[,] B.Stuckenberg/Dryxo margaretae sp. n. det. B. H. Cogan 1967 [species name and "1967" handwritten]." The holotype male is pinned directly, is in excellent condition (right midleg missing), and is deposited in the MNHN. Two paratypes (1♂, 1♀; NMSA) bear the same locality data as the holotype. Other paratypes are as follows: MADAGASCAR. *Toamasina*: Moramanga (=Mamaranga), Perinet (Niagarakely Forst., Dec 1955, B.R. Stuckenberg (2♂, 1♀; BMNH, NMSA).

OTHER SPECIMENS EXAMINED.—Afrotropical. MADAGASCAR. *Fianaratsoa*: Ranomafana (600 m), 18–20 Jan 1990, W.E. Steiner (1♂, 2♀; USNM); Ranomafana (7 km W; 900 m), 8–21 Oct 1988, 20–24 Mar 1990, W.E. Steiner (7♂, 4♀; USNM). *Toamasina*: Maroanetra, Dec 1949, J. Vadon (3♀; MRAC).

DISTRIBUTION.—Afrotropical: Madagascar.

REMARKS.—Like many plant and animal species that occur there, *D. margaretae* is apparently endemic to Madagascar.

11. *Dryxo nudicorpus* Miyagi

FIGURES 42–44

Dryxo nudicorpus Miyagi, 1977:35.—Cogan, 1984:144 [Palaearctic catalog].—Krivoshchina, 1987:123 [review, Russia (Far East)].—Mathis and Zatwarnicki, 1995:116 [world catalog].

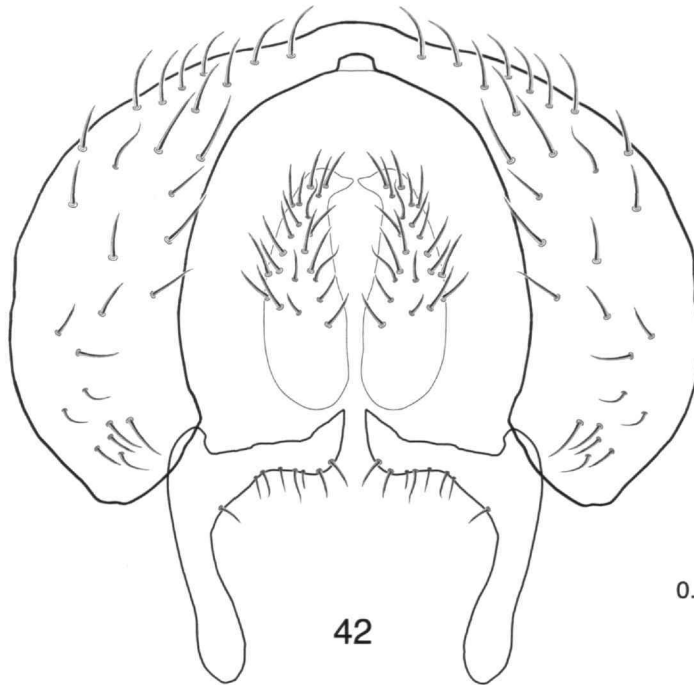
DIAGNOSIS.—This species is distinguished from congeners by the following combination of characters: frons and mesonotum mostly blackish brown, sometimes with medial, vertical, gray stripe; postpronotal seta present; scutellar disc and, in

some specimens, frons lacking medial, microtomentose, gray stripe; katepisternal seta greatly reduced, much weaker than notopleural seta or lacking; postsutural supra-alar seta present, well developed; anepisternum bearing 2 long, slender setae along posterior margin; legs, especially femora and tibiae, mostly grayish black to black; male hindtarsi lacking long, slender setae on dorsal surface; tergites with band toward anterior margin, at most with very thin, dark area along posterior margin; tergite 1 with sparse, inconspicuous, dorsally erect setulae; tergites 3–5 with prominent dark bands along anterior margin; and dark bands of tergites 3–5 lacking narrow, medial extension to posterior margin.

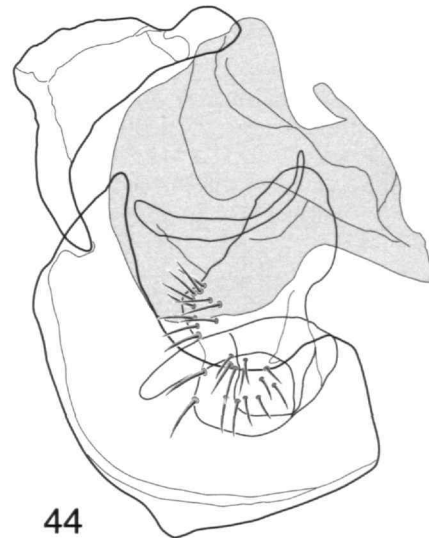
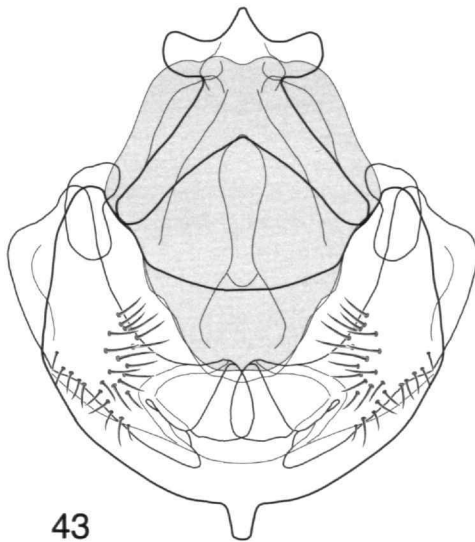
DESCRIPTION.—Large shore flies, body length 7.45–7.90 mm; generally blackish brown dorsally but with considerable areas gray.

Head: Generally densely microtomentose. Frons mostly to entirely brownish black, at most with thin gray stripe anterior of anterior ocellus and slightly lighter areas at lateral margin; inner vertical seta short and thin, length about ½ that of outer vertical seta; ocelli arranged in equilateral triangle. Antenna blackish brown to black; arista blackish brown to black, bearing 13–16 dorsal rays. Face, parafacial, gena, and clypeus concolorous, whitish gray to silvery gray, contrasting with darker-colored frons; face bare except for series of setulae paralleling frontal suture; parafacial with transverse, blackish brown stripe or maculation at level of antennal base, thereafter ventrally concolorous with face, dark coloration merged and concolorous with lateral margins of frons. Eye slightly higher than wide. Gena high, slightly more than ½ eye height, anterior portion concolorous with face and parafacial, becoming whiter posteriorly; gena-to-eye ratio 0.62–0.65.

Thorax: Mesonotum generally blackish brown except for gray postpronotum, area just laterad of postsutural supra-alar seta, and faint stripes, especially anteriorly, in dorsocentral track; pleural areas uniformly gray; scutellum more or less evenly rounded, not conspicuously truncate; postpronotal seta well developed; presutural supra-alar seta lacking; postsutural supra-alar seta well developed; anepisternum bearing 2 well-developed setae, anepisternum with faint, small, dark brown spot near middle. Postsutural supra-alar seta well developed but slightly shorter than postalar seta; anepisternal setae 1 or 2, well developed; katepisternal seta weakly developed, thin; lacking row of long, thin setae dorsad of katepisternal seta. Wing hyaline; R stem vein bearing 6–8 short, thin, pale setulae dorsally; costal-vein ratio 0.31–0.34; M-vein ratio 0.42–0.51. Legs mostly dark colored; femora and tibiae blackish brown to black with moderate to heavy gray microtomentum; tarsi black with some yellowish orange to reddish orange ventrally; forebasitarsomere of male relatively swollen over most of length, especially as compared to basitarsomeres of mid- and hindlegs; foretarsomeres 2–5 of male moderately wide apically, width nearly equal to length; lateral setae of foretarsomeres, especially in males, parallel sided or even slightly wider to apex, apex pointed; hindbasitarsus of male lacking long, slender se-



FIGURES 42-44.—Male terminalia of *Dryxo nudicarpus* Miyagi: 42, epandrium, cerci, and presurstyli, posterior aspect; 43, internal male terminalia, ventral aspect; 44, same, lateral aspect.



tae on dorsum; tarsomeres of midleg bearing long setae lateroapically, aligned with plane of leg, length of setae subequal to width of tarsomere at apex.

Abdomen: Anterior margin of tergites 3-5 brownish black, posterior margin of band curved and pointed medially. Male terminalia (Figures 42-44): epandrium in posterior view (Figure 42) rounded arch-shaped, narrow dorsally, arms wider at

dorsolateral level, becoming narrower ventrally; cercus ovoid, wider subventrally, pointed dorsomedially; presurstylus in posterior view (Figure 42) deeply bifurcate, each arm long and slender, medial arm bearing 5 or 6 short setulae extended ventrally, arm oriented medially, apical portion becoming wider, apex turned dorsomedially, lateral presurstylar arm oriented ventrally, mostly parallel sided but apical portion slightly ex-

panded and narrowly rounded at apex; postsurstylus in lateral view (Figure 44) narrow basally, becoming wider at midlength and with a swelling along anterior margin, swelling bearing several setulae, thereafter slightly narrowed before becoming wider at ventral margin, ventral margin bifurcate with both lobes broadly developed and subequal in size, ventrolateral surface bearing numerous setulae; aedeagus in lateral view (Figure 44) narrow basally, immediately becoming wider, with broad apex truncate; aedeagal apodeme in lateral view (Figure 44) with keel moderately shallow, ridge-like, and developed on half attached to base of aedeagus only; hypandrium moderately wide and deep.

TYPE MATERIAL.—The holotype male is labeled “Jyozankei 17-VII-1961/Japonia Hokkaido I, MIYAGI/-type *Dryxo nudicorpus* I. Miyagi [red label; all except for “-type” handwritten].” The holotype is pinned directly, is in poor condition (damaged in shipment; wings, most legs, and most setae missing; legs and wing fragments glued on a label below specimen), and is deposited in the HUS.

OTHER SPECIMENS EXAMINED.—Palearctic. JAPAN. *Ishikawa*: Oono, Kanazawa, 11 Jun 1964, H. Kurahashi (1ex; BMNH). Label data in Japanese kanji that we were unable to read (5♀; BMNH).

CHINA. Shan-hai-Kwan (in mountains), 1 Sep 1906, F.M. Thomson (1♂, 2♀; BMNH).

RUSSIA. *Far East*: Juzhnoe Primor'ye, Lazovski zapovednik (25 km SE L'azo), 31 Jul 1986 (2♂; ZMUM). Primurskiy Kraj, Pokrovka (48°31'N, 134°55'E), Suj-fun, 2 Aug 1935, A. Mishchenko (1♀; ZMUM). Pristan Bulochna, 10 viorst vyshe Ust-komenogorsk, 9 Jul 1914, Kazantseva (2♀; ZMUM).

DISTRIBUTION.—Palearctic: China, Japan (Hokkaido, Honshu, Ishikawa, Kyushu, Shikoku), Russia (Far East).

REMARKS.—This is the only species of *Dryxo* that extends into temperate climates.

We continue to interpret, recognize, and treat this species' epithet, *nudicorpus*, as a noun in apposition, as apparently Miyagi did when first describing this species. *Corpus* is a Latin noun meaning “body.”

12. *Dryxo ornata* (Macquart)

FIGURES 45–50

Blepharitarsis ornatus Macquart, 1844:411.

Dryxo ornata.—Bezzi, 1908a:194 [generic combination].—Wirth, 1955:53 [list, Tanzania (Ngaruka)]; 1956:388 [list, Mozambique, South Africa (Natal, Transvaal), Zimbabwe]; 1960:393 [list, Namibia].—Giordani Soika, 1956b:490 [list, Zaire].—Cogan, 1968:359–360 [revision]; 1980:661 [Afrotropical catalog]; 1984:144 [Palearctic catalog].—Canzoneri and Meneghini, 1969:163 [list, Zaire].—Canzoneri and Rampini, 1994:245 [list, Sierra Leone].—Mathis and Zatwarnicki, 1995:116 [world catalog].

Dryxo ornatus.—Becker, 1926:93 [review, list, Canary Islands].

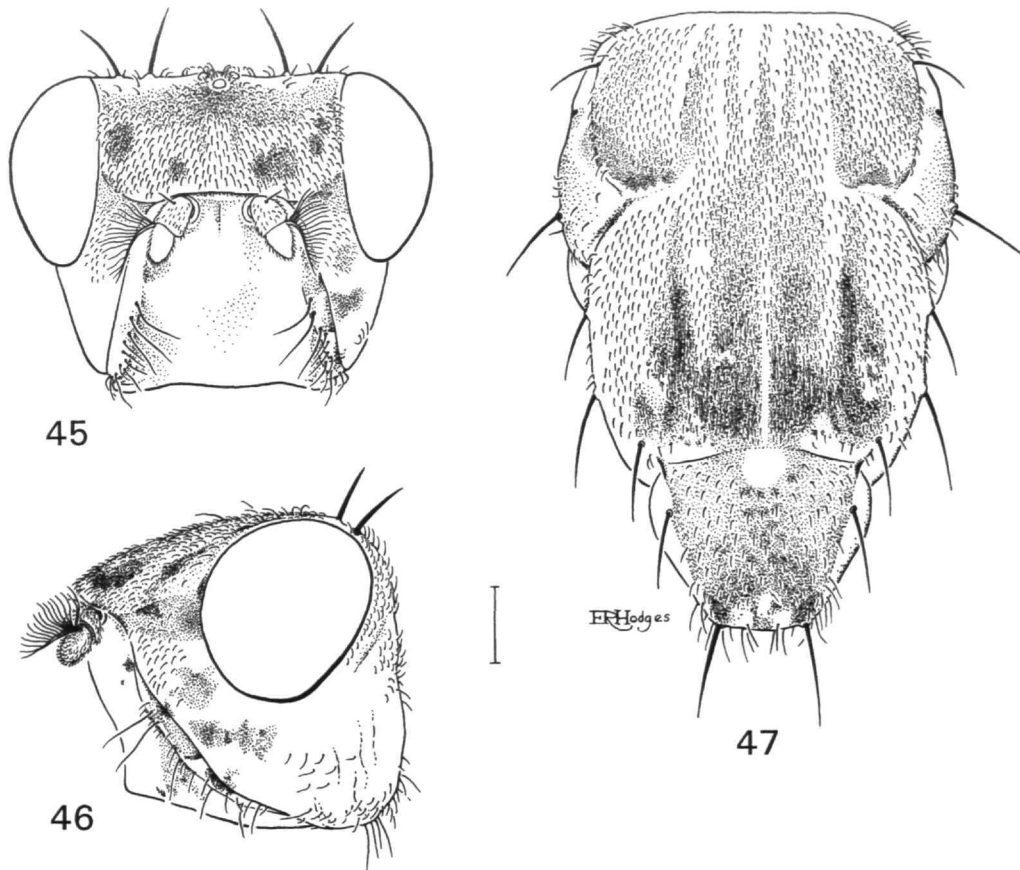
DIAGNOSIS.—This species is distinguished from congeners by the following combination of characters: inner vertical seta subequal or slightly longer than outer vertical seta; postpronotal seta present, well developed; R stem vein bearing 2 or 3

long, thin setulae along posterior margin basad of humeral crossvein; male hindbasitarsus with several long, slender setae toward base, setae becoming shorter and much sparser toward apex; male hindtarsomere 2 bearing long, slender setae on dorsal surface; katepisternal seta well developed, length subequal to notopleural seta; tergites 3 and 4 with dark band along posterior margin, at least in middle, band sometimes connected laterally with anterolateral spot, or spot separate; and tergite 1 with medial patch of short, dorsally erect setulae.

DESCRIPTION.—Moderately large to very large shore flies, body length 4.75–8.85 mm; generally blackish brown dorsally but with considerable areas gray.

Head (Figures 45, 46): Generally densely microtomentose. Frons mostly to almost entirely gray to tan, sometimes with some blackish brown maculation, especially posteriorly as 1 or 2 short, anteriorly directed stripes of variable shape laterad of ocelli and from vertex; inner vertical seta subequal or slightly longer than outer vertical seta; ocelli arranged in equilateral triangle. Antenna blackish brown, usually with some gray to tan microtomentum dorsally; arista white to tannish white basally, bearing 11–13 dorsal rays. Face, parafacial, gena, and microtomentose-covered portion of clypeus concolorous, whitish gray, contrasting with darker-colored frons; face bare except for series of setulae paralleling frontal suture; parafacial with transverse, golden brown to blackish brown stripe or maculation at level of antennal base, thereafter ventrally concolorous with face. Eye slightly higher than wide. Gena high, height slightly more than ½ eye height, anterior portion concolorous with face and parafacial, becoming whiter posteriorly; gena-to-eye ratio 0.52–0.56. Clypeus with dorsal ⅓ of medial portion bare.

Thorax (Figure 47): Mesonotum generally mottled, partially to mostly dark brown, with some gray to tannish gray areas, especially peripherally and along setal tracks, bases of setae blackish brown; scutum with anterior ½ extensively gray with brown to blackish brown maculation, latter becoming much darker with some gray areas sometimes evident, usually as short stripes along acrostichal and dorsocentral tracks; scutellum generally and extensively blackish brown, only mediobasal, somewhat triangular area whitish gray; anepisternum generally concolorous with rest of pleural area, sometimes slightly darker, lacking maculation in middle. Postsutural supra-alar seta well developed but slightly shorter than postalar seta; anepisternal setae 1–3, thinly developed; katepisternal seta well developed, length subequal to notopleural seta. Wing hyaline; R stem vein bearing 5–7 short, thin, pale setulae dorsally; vein R₁ with short, sparse setulae along length; costal-vein ratio 0.32–0.36; M-vein ratio 0.56–0.58. Leg coloration variable; femora and tibiae generally concolorous, blackish brown with moderately dense whitish gray microtomentum; tarsi blackish brown dorsally, yellowish orange to orange ventrally, apical tarsomeres becoming blackish gray; forebasitarsomere of male normally developed, not swollen, similar to basitarsomeres of mid- and hindlegs; foretarsomeres 2–5 of male normally developed, not greatly expanded apically, width



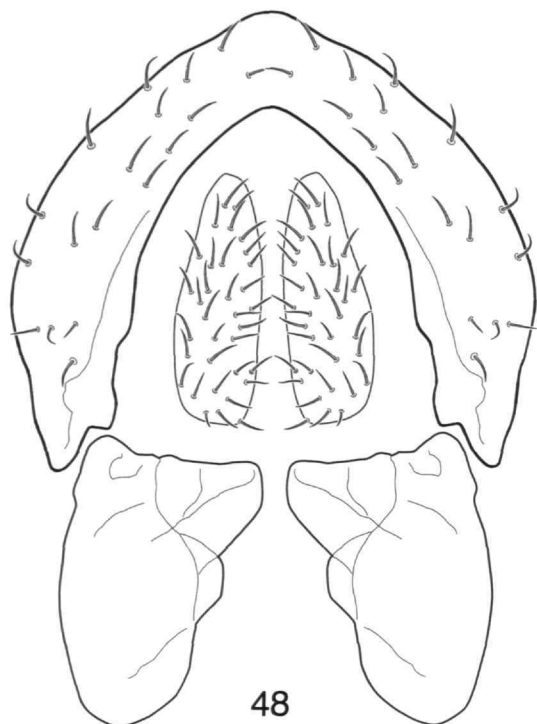
FIGURES 45–47.—*Dryxo ornata* (Macquart): 45, head, lateral aspect; 46, same, anterior aspect; 47, mesonotum, dorsal aspect. Scale=0.5 mm.

much less than length; lateroapical setae of foretarsi of male tapered; hindbasitarsus of male bearing sparse patch of long, slender setae posterodorsally; hindtarsomere 2 of male bearing some long setae along dorsum; tarsomeres of midleg bearing long setae lateroapically, aligned with plane of leg, length of setae subequal to width of tarsomere at apex.

Abdomen: Tergites 3 and 4 with dark band along posterior margin, at least in middle, band sometimes connected laterally with anterolateral spot or spot separate; 1st tergite with medial patch of short, dorsally erect setulae. Male terminalia (Figures 48–50): epandrium in posterior view (Figure 48) like a broadly pointed arch, narrow dorsally and slightly angulate, arms wider at dorsolateral level, ventrally becoming narrower; cercus ovoid, wider subventrally; presurstylus in posterior view (Figure 48) broadly triangular, length about 1.5 times basal width, dorsomedial angle broadly produced, short, medial margin with shallow lobe at midlength, ventral apex broadly rounded, lateral margin very shallowly arched; postsurstylus in lateral view (Figure 50) narrow, pointed basally, bearing

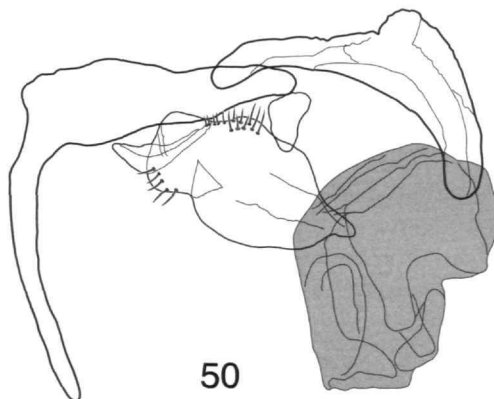
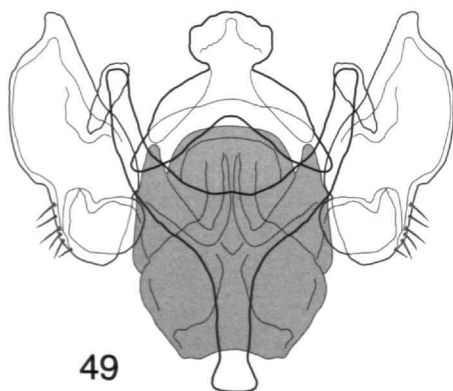
very shallow, setulose lobe just beyond midlength, both lobes of bilobed apex about equal in size, inner lobe essentially bare of setulae; aedeagus in lateral view (Figure 50) about equally wide throughout length, inner surface irregularly convex, external surface irregularly concave with angulate indentation, apex truncate; aedeagal apodeme in lateral view (Figure 50) with keel shallow, ridge-like, with long, narrow extension toward attachment with hypandrium, bifurcate arms at attachment with hypandrium long; hypandrium somewhat narrow and shallow.

TYPE MATERIAL.—The syntypes of *Blepharitarsis ornatus*, which were collected at “D’Afrique, Shubar” (=Sierra Leone?), were not located and may well not exist. The second author and Volker Hollmann, who visited MNHN in 1995, were unable to find any specimen(s) (pers. comm., 1995). Lacking a primary type, we have followed Cogan’s concept of this species, as he was the last revisor. Cogan’s concept was and is generally recognized (see references in species synonymy), and the species is easily identified. Thus, we have not deemed it necessary to



FIGURES 48–50.—Male terminalia of *Dryxo ornata* (Macquart): 48, epandrium, cerci, and presurstyli, posterior aspect; 49, internal male terminalia, ventral aspect; 50, same, lateral aspect.

0.1mm



designate a neotype. This is a common and widespread Afrotropical species and is the only species of *Dryxo* known thus far from Sierra Leone.

OTHER SPECIMENS EXAMINED.—Afrotropical. ANGOLA. *Cuanza Sul*: Cachoeiras (20 mi SW Gabela), 18–19 Mar 1972 (5♂, 11♀; BMNH). *Cunene*: Rocadas, Cunene (River), 19–22 Feb 1972 (6♂, 6♀; BMNH, TZ). *Namibe*: Rio Giraul (16.1 km NE Moçâmedes), 27–29 Feb 1972 (1♂; BMNH); Moçâmedes (3.2 km N), 29 Feb 1972 (1♂, 2♀; BMNH); Tun-

davala (12.9–16.1 km NW Sá da Bandeira, 27–29 Mar 1972 (1♂; BMNH). Bruco, 26 Feb–2 Mar 1972 (1♂; BMNH). Landana (=Caçongo; 5°14'S, 12°8'E), Port Congo (1♀; AMNH).

BOTSWANA. River Nata (20°12'S, 26°11'E), 23 Apr 1972 (1♂; BMNH).

BURUNDI. Burburi (2000 m), 10 Oct 1948, F.J. Francois (1♂, 1♀; IRSN). Lestrade (2♂, 2♀; MRAC). Rumonge (sur la rive du Lac Tanganyika; 780 m), 13 Feb 1934, 1949, A. Lestrade, F.J. Francois (8♂, 7♀; IRSN, MRAC). Rumongi River, Lac

Tanganyika, 16 Sep 1948, F.J. Francois (10♂, 3♀; IRSN). Usumbura (780 m), 19 Apr 1953, F. Francois (6♂, 3♀; IRSN).

CAMEROON. Kribi (route N7, beach), 28–29 Nov 1987, A. Freidberg, F. Kaplan (10♂, 17♀; USNM).

CHAD. Ouli Bangala, Logone, 1 Mar 1966, J.C. Hitchcock, Jr. (1♂, 2♀; USNM). West Goulem, 8–9 Aug 1958, G.B. Popov (1♀; BMNH).

ETHIOPIA. Dire-Dana, 19 Feb 1911, Kovács (1♀; HNHM). Ever, 30 Oct 1968, R. Kano (3♂, 3♀; BMNH). Lake Langano, 13 Dec 1989, A. Freidberg, F. Kaplan (2♂; TZ, USNM). Lake Langano (7°27'N, 39°11'E), 27 Jul 1973, R. Baker (1♂; BMNH). Urso (=Hurso; 9°36'N, 41°38'E), Mar 1911, Kovács (3♂, 2♀; HNHM).

GHANA. *Capital District*: Accra, 3 Aug 1942, F.M. Snyder (1♀; AMNH). *Eastern*: Koforidua, Apr 1921, J.F. Corson (1♂, 1♀; BMNH). *Northern*: Yapi, Mar 1916, J.J. Simpson (4♂, 3♀; BMNH). *Without Further Locality*: Kpong, Apr 1922, J.W.S. Macfie (1♀; BMNH).

KENYA. *Coast*: Bura (3°30'S, 38°18'E; 1060 m), Mar 1911, Ch. Alluard, R. Jannel (1♂; MNHN); Lusinga Island (Victoria–Ntanzam NE), 1904, Ch. Alluard (1♀; MNHN); Vall. Dierrer (=Dierra; 2°35'S, 39°57'E), Jun 1911, Kovács (8♂, 32♀; HNHM); Voi (3°23'S, 38°34'E; 600 m), Mar 1911, Ch. Alluard, R. Jannel (2♂; MNHN). *Eastern*: Tsavo National Park (East), 4–7 Apr 1968, B. Cogan, A. Hutson (1♂; BMNH). *Without Further Locality*: Tana Bridge (sand bank), 1–2 Jul 1948, Van Someren (4♂, 5♀; BMNH).

LIBERIA. Bendu, Robertsport, 26 Feb–5 Mar 1943, F.M. Snyder (2♀; AMNH).

MADAGASCAR. *Toamasina*: Fenerive (lagoon shore), Dec 1955, B.R. Stuckenberg (1♂, 1♀; NMSA). *Toliara*: Ranohira (860 m), 26 Jan–4 Feb 1958, B.R. Stuckenberg (1♂; NMSA).

MALAWI. Chisi, near Nkhata Bay, 15 Oct 1908, J.B. Davey (1♀; BMNH). Central Angoniland, R. Limpembe (2♂, 2♀; BMNH). Cholo, R.C. Wood (2♂; ANSP). Deep Bay, 3 Oct 1909, J.B. Davey (1♀; ANSP). Kasungu National Park, Lifupa Camp (1000 m), 9–10 Dec 1980, J.G.H. Londt, B.R. Stuckenberg (1♀; NMSA). Kota Kota, 13 Sep 1919, W.A. Lamborn (1♂; BMNH). Lake Shore, 4 Aug 1909, J.B. Davey (1♂; ANSP).

MOZAMBIQUE. Amont de Tambara Alfiate (rail station), 1929, P. Lesne (1♀; MNHN). Env. de Chemba, Bas Sangadze, 1929, P. Lesne (1♀; MNHN). Env. de Vila Pery Cabeca de Velho, bords du Mzingaze, 1929, P. Lesne (1♂; MNHN).

NAMIBIA. Huans River (river bed), 31 Jan 1969, B. Lamoral (1♂; NMSA). Kamanjab (43.5 km ESE), Otjitambi Farm, 13–15 Feb 1972 (19♂, 18♀; BMNH). Naukluft Park, Naukluft spring (24°15'78"S, 16°14'08"E; Malaise trap), 28–30 Nov 1997, Kirk-Spriggs and Marais (1♀; NNIC). Swakop River, (4.8 km S Okahandja), 7 Apr 1972 (2♀; BMNH). Satanplatz (1300 m), 17–18 Dec 1933, K. Jordan (1♀; BMNH).

NIGERIA. *Kwara*: Ilorin, 21 Feb 1912, J.W.S. Macfie (2♂, 2♀; ANSP, BMNH). Agundele, 5 May 1912, J.W.S. Macfie (1♀; ANSP). Between Ilorin and Bude Egba, 24 May 1912, J.W.S. Macfie (1♂; ANSP).

NIGER. Zungeru, 1 Feb–15 Mar, 1911, 1912, J.W.S. Macfie (8♂, 5♀; AMNH, BMNH). Alagua, 1912, J.W.S. Macfie (1♀; BMNH). Shao, 14 Mar 1912, J.W.S. Macfie (1♀; BMNH).

RWANDA. Kisenyi (près emb. river Sebeya), 4 Apr 1953, J. Verbeke (5♂, 6♀; IRSN). River Sange, 10 Feb 1904 (1♀; IRSN).

SIERRA LEONE. Kaniki, 22 May 1912, J. Simpson (1♂, 1♀; ANSP, BMNH). Kayima, 29 Jul 1919, J.J. Simpson (1♀; BMNH). Lungi, 14 Jul 1959, C.P. Hoyt (1♀; BMNH).

SOMALIA. Hargeisa, Mar 1949, K.M. Guithard (1♂, 1♀; BMNH).

SOUTH AFRICA. *Cape Province*: Clanwilliam (3 mi W; Olifantes River), 6 Jan 1972 (3♂, 1♀; BMNH); Cogman's Kloof, Ashton–Montagu Road (along river), 11 Jan 1983, R. Miller, P. Stabbins (1♀; NMSA); Dohne, 11 May 1925, H.K. Munro (5♂, 2♀; ANSP, DEI, NMSA); Dwyka R. Merweville–Koup Road, 2 Jan 1972 (3♂; BMNH); Groblershoop (12 km E; banks of Orange River), 19 Mar 1982, J. Londt, L. Schoeman (1♀; NMSA); Muizenberg, 3 Apr 1935, M. Bequaert (1♂; IRSN); Port Shepstone (30°45'N, 30°27'E), 27 Aug 1920, H.K. Munro (1♀; NMSA). *Natal*: Durban, 13 May 1919, C.N. Barker (1♂; ANSP); Illovo, 8 Jun 1919, W.H. (8♂, 4♀; ANSP, DEI, NMSA); F Toppin Umsindasi Ubombo, Sep 1910 (4♀; NMSA); Muden, 1 Oct 1956, B.R. Stuckenberg (1♀; NMSA); Nagel Dam, 19 May 1955, B.R. Stuckenberg (1♂; NMSA); Pietermaritzburg, Town Bush, 31 May 1957, T. Schofield (4♂, 1♀; NMSA); Ramsgate, 6–16 Jan 1983, J.G.H. Londt (2♂, 1♀; NMSA); Umvoti River (mouth), 13 Mar 1963, T.W. Schofield (1♂, 1♀; NMSA). *Transvaal*: Barberton, 12 Aug 1916, H.K. Munro (5♂, 2♀; ANSP, DEI, NMSA); Kruger Park (Timbetene Twiri waterholes; savanna woodland near Skukuza), 9 Dec 1972, B.R. and P. Stuckenberg (6♂, 5♀; NMSA); N.E. Zoutpansberg District, Jul–Aug 1916, H.G. Breyer (2♀; NMSA); River Magalakwena (23°26'S, 28°37'E), 26 Apr 1972 (1♂; BMNH).

SUDAN. *Darfur*: Jebel Marra, Karanga (2012 m), 23 Apr 1932, M. Steele (4♂, 3♀; ANSP, BMNH).

SWAZILAND. Mbuluzone River, 28 Mar 1984, P. Kelly, J. Cory (1♂, 3♀; BMNH).

TANZANIA. *Arusha*: Tarangiri National Park (1158 m), 23 Jan 1970, M.E. Irwin, E.S. Ross (2♂, 1♀; USNM). *Kagera*: Bukoba (1°20'S, 31°49'E), 10 Jun 1912, C.C. Gowdey (3♂, 3♀; ANSP, BMNH). *Kigoma*: Kigoma, Sep–Dec 1918, R. Mayné (4♀; MRAC). *Mara*: Katona, Shirati (1°08'S, 33°59'E), Feb–May 1909, L. Oldenberg (64♂, 18♀; ANSP, DEI, HNHM). *Zanzibar*: Chukusani, 12 Oct 1911, W.M. Adero (1♂; BMNH). *Without Further Locality*: Old Shinyanga, 29 Oct 1952, E. Burt (1♂, 3♀; BMNH).

UGANDA. Entebbe, 16 Jul 1912, C.C. Gowdey (3♂, 10♀; BMNH). Ruwenzori Range, Kilembe (1311 m), Dec 1934 (1♂; BMNH).

YEMEN. Jebel Harir (1585 m), 26 Oct–6 Nov 1937, F.B. Brittin, H. Scott (2♂, 2♀; BMNH).

ZAIRE. *Kivu*: Kasongo, Lualaba River, Jul 1959, P.L.G. Benoit (1♂, 1♀; MRAC); Kasongo, Pongo River, Oct 1959, P.L.G. Benoit (3 ex; MRAC); Lake Tanganyika, Lueba near Baraka, 19 Aug 1927, R. Bois (9♂, 12♀; BMNH); Rutshuru (Miss. Prophylactique), 30 Jul 1937 (2♂; MRAC); Uvira, 16 Mar–30 Nov 1927, 1953, 1954, 1958, P. Basilewsky, N. Lelup, G. Marlier, C. Seydel (1♂, 1♀, 9ex; MRAC); Kolembalembe, Baraka, Jul 1918, R. Mayné (13 ex; MRAC). *Shaba*: Mpala (780 m), Aug 1953, H. Bomans (8 ex; MRAC). *Without Further Locality*: Albert National Park (=Virunga National Park): Bitshumbi (925 m), 15 Apr 1936, L. Lippens (1♂, 1♀; MRAC); Ishango, 11–14 Dec 1935, H. Damas (3♂, 1♀; MRAC); Kamande (925 m), 8 Apr 1935, 4 May–18 Nov 1935, H. Damas (91♂, 130♀; MRAC); Kamande Lemera (925 m), 20 Nov 1935, H. Damas (5♂, 13♀; MRAC); Kitembo (925 m), 4 Apr 1936, L. Lippens (1♂, 7♀; MRAC); Embouch, Rutshuru, 18 Jan 1936, H. Damas (1♂; MRAC); Rwindi River (1000 m), 9 Feb–25 Apr 1936, L. Lippens (1♀; MRAC); Talia (925 m), 7 Apr 1936, L. Lippens (3 ex (abdomens missing); MRAC); Mabwe (r. E lac Upemba; 585 m), 12 Jan–15 Aug 1947, 1949, G.F. de Witte (2♂; MRAC); Beni (1200 m), 17 Sep 1953, F.J. Francois (1♂, 3♀; IRSN); Ituri Kasenyi (Lac Albert), 2–5 Jul 1953, J. Verbeke (4♂, 1♀; IRSN); Kivu Ile Idjwi, Shashi-Busibu, 15 Apr 1953, J. Verbeke (1♂, 2♀; IRSN). Kongold (25°25'S, 23°E), 8 Feb 1974, R. Baker (1♂, 1♀; BMNH). Lomami-Loputa, 1935, Bouvier (2♀; MRAC). L.S.T.M., 1904 (1♂; BMNH). Matadi, 18 Nov 1903, Dutton, Todd, Christy (1♀; BMNH).

ZAMBIA. Kafu N.W.R. (945 m; on mud by river bank), 1 Sep 1913 (1♀; BMNH). Luangwa Valley, Mvuvia (at waterhole), 17 Sep 1910 (1♀; BMNH).

ZIMBABWE. Balla-Balla, Mar 1931, A. Cuthbertson (1♂, 1♀; AMNH). Loagundi (on wet sand), 6 Oct 1931, J.H. Bath (1♀; AMNH). Sunny Bank, Golden Valley, 14 Feb 1931, W.L. Williams (1♂; AMNH). Lower Lundi River (Chipinda Pools), 22 Oct 1960, R. Goodier (3♂, 6♀; BMNH). Triangle, 21 Oct 1963, A.L. Moore (1♀; USNM). Wankie, 26 Jan 1926, R.H.R. Stevenson (2♀; NMSA). *Umtali* (=Mutatre): Mutambara, 26 Dec 1952, N.S. Myers (2♀; NMSA).

Palaearctic. CANARY ISLANDS. Gomera, 1889, Simony (5♂, 3♀; ANSP, ZMHU).

IRAN. Chashmeh-ye Sargaz (1650 m), 20–21 May 1977 (1♀; NMSAC). Minab (40 km SE), 21 May 1973 (14♂, 15♀; NMSAC). Rudan (17 km N, road tunnel no. 7), 15 May 1977 (3♂, 7♀; NMSAC).

MOROCCO. Aoulouz, 9 May 1992, M. Hradsky (1♀; BAR).

DISTRIBUTION.—Afrotropical: Angola, Botswana, Burundi, Cameroon, Chad, Ethiopia, Ghana, Kenya, Liberia, Malawi, Mozambique, Namibia, Nigeria, Rwanda, Sierra Leone (Northern Province: Bumbuna; Western Area: Sussex), Somalia, South Africa (Cape Province, Natal, Transvaal), Sudan, Swaziland, Tanzania, Uganda, Yemen, Zaire, Zambia, Zimbabwe. Palaearctic: Canary Islands, Iran, Morocco.

REMARKS.—We have examined one female specimen that is possibly from Sri Lanka. The specimen is labeled "Nalanda,"

and in gazetteers available to us, "Nalanda" is located in central Sri Lanka, which would be a new record from that country as well as from the Oriental Region. The specimen (1♀; ANSP), however, bears minimal label data, and it could have been mislabeled, the name "Nalanda" may be a place name that is used elsewhere, including Africa, or we may not have interpreted the label data correctly; thus, we are hesitant to extend the known distribution of this species to the Oriental Region based on this single specimen.

13. *Dryxo woodi* Cresson

FIGURES 51–53

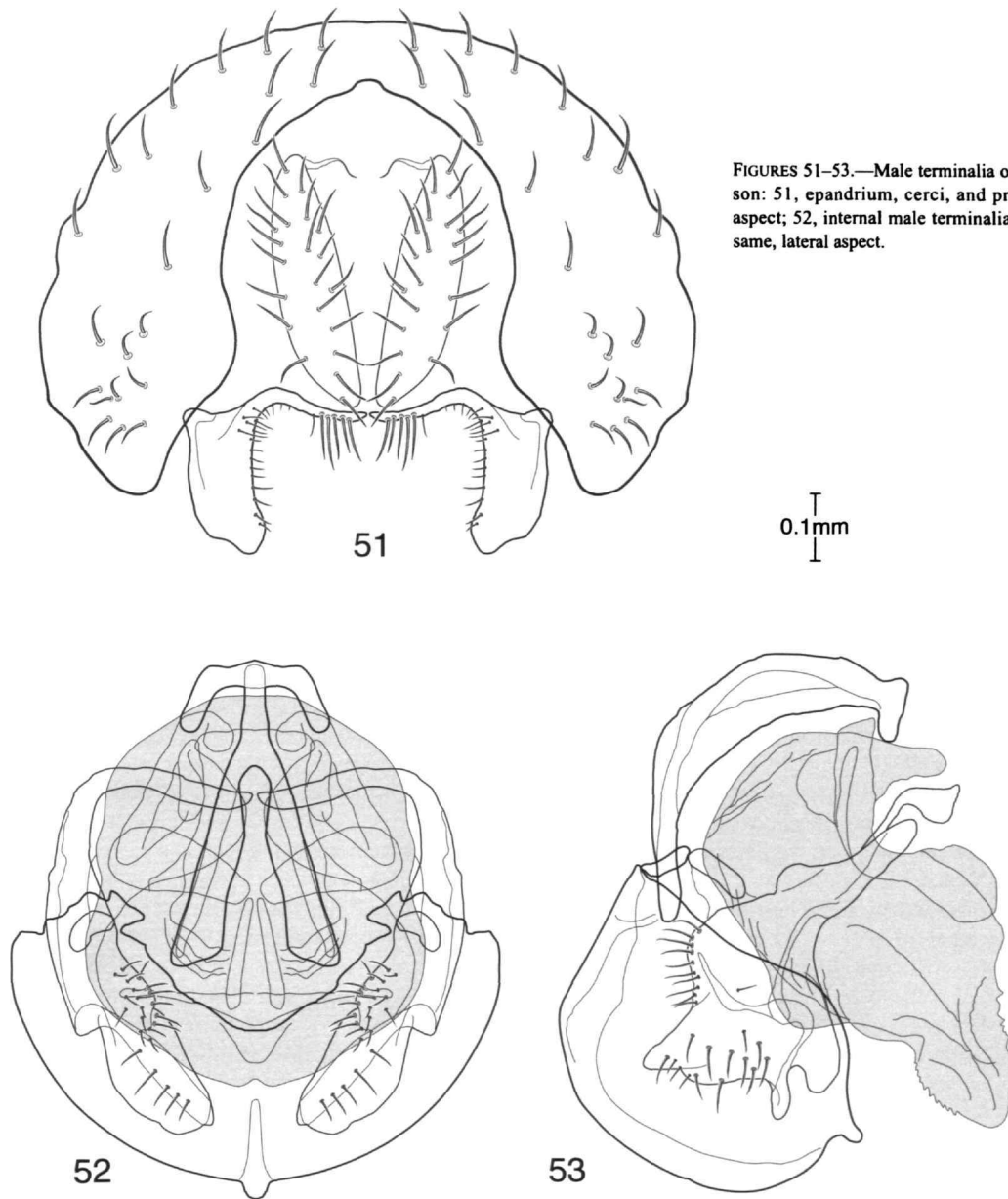
Dryxo woodi Cresson, 1936:266.—Cogan, 1968:362 [revision]; 1980:661 [Afrotropical catalog].—Mathis and Zatwarnicki, 1995:116 [world catalog].

DIAGNOSIS.—This species is distinguished from congeners by the following combination of characters: parafacial essentially uniformly concolorous; mesonotum grayish tan to grayish brown, lacking dark brown spots or areas; postsutural supra-alar seta well developed; anepisternum with weakly developed, moderately long, slender setae along posterior margin; katapisternal seta moderately well developed but more weakly developed than notopleural seta; femora and tibia concolorous, faintly reddish, with sparse whitish microtomentum; male hindtarsi lacking long, slender setae on dorsal surface; tergites with dark band toward anterior margin, at most with very thin, dark area along posterior margin; tergite 1 with sparse, inconspicuous, dorsally erect setulae.

DESCRIPTION.—Large to very large shore flies, body length 7.40–7.80 mm; generally tan, especially dorsally, to cream colored.

Head: Frons faintly mottled, whitish gray to tannish gray with some slightly darker areas posteriorly, laterad of ocellar triangle; inner and outer vertical setae well developed, about coequal in length; ocelli arranged in equilateral triangle. Antenna with scape and pedicel faintly yellowish red with sparse whitish microtomentum; 1st flagellomere black with moderately sparse (lateral) to dense (medial surface) gray microtomentum; arista mostly silvery white, base faintly brown, bearing 14 or 15 dorsal rays. Face silvery gray; parafacial wide, width subequal to length of pedicel and 1st flagellomere, mostly uniformly concolorous with face but with some tan coloration dorsally, lacking distinct stripe laterad of antennal base. Eye slightly higher than wide. Gena high, concolorous with face and parafacial; gena-to-eye ratio 0.47–0.55. Clypeus mostly microtomentose, concolorous with face, dorsal 1/3 of medial portion bare, subshiny.

Thorax: Mesonotum whitish gray to tan, lacking darkened areas or spots at bases of setae and setulae; scutum mostly uniformly colored, sometimes with broad, faintly defined stripes on either side of medial and along dorsocentral track; scutellum generally concolorous with scutum, no darkened areas at base of lateral setae; postsutural supra-alar seta well developed but slightly shorter than postalar seta; anepisternum lacking mod-



FIGURES 51–53.—Male terminalia of *Dryxo woodi* Cresson: 51, epandrium, cerci, and presurstyli, posterior aspect; 52, internal male terminalia, ventral aspect; 53, same, lateral aspect.

erately long, slender setae along posterior margin; katapisternal seta usually greatly reduced, much weaker than notopleural seta, or lacking. Wing hyaline; costal-vein ratio 0.38–0.41; M-vein ratio 0.49–0.51; wing of male with 2 blackened, microtomentose spots, 1 in cell dm at posterior margin, adjacent to pointed convergence of crossvein dm-cu and vein CuA_1 , and 1 at posterior margin, adjacent to vein $A_1 + CuA_2$. Femora and tibia concolorous, faintly reddish, with sparse whitish microtomentum; male hindtarsi lacking long, slender setae on dorsal

surface; foretarsus of male unmodified, similar to that of female; forebasitarsomere of male normally developed, similar to that of female, not conspicuously swollen; lateroapical setae of forebasitarsomere of male tapered, sharply pointed apically.

Abdomen: Dorsum and venter of tergites generally uniformly whitish gray to tan and lacking darkened areas, such as bands or spots, except for dark medial area toward anterior of 5th tergite of male. Male terminalia (Figures 51–53): epandrium in posterior view (Figure 51) rounded arch-shaped, nar-

row dorsally, arms widest subapically, thereafter becoming narrowed and moderately pointed at ventral apex; cercus ovoid, both apices equally narrowly rounded; presurstylus in posterior view (Figure 51) deeply bifurcate, each arm long, medial arm very slender, oriented medially with slight arch basally, thereafter straight, bearing patch of setulae extended ventrally toward apex of medial arm, lateral arm thickly developed (compared to medial arm) oriented ventrally, parallel sided throughout most of length, apex slightly narrowed to bluntly rounded ventral apex; postsurstylus in lateral view (Figure 53) very narrow basally, thereafter gradually expanded to very wide, truncate apex, apical margin sinuous with distinct papilla-like projection, bearing numerous setulae on midlength swelling along anterior margin, lacking bifurcation apically; aedeagus in lateral view (Figure 53) somewhat narrow basally, immediately becoming wider for most of length, with dorsal margin moderately deeply incised toward base, narrow apex moderately pointed; aedeagal apodeme in lateral view (Figure 53) slender and shallowly arched, with keel very shallow, lacking ridge-like extension, developed into T-like apex attached to base of aedeagus, apex attached to hypandrium evenly narrow throughout length; hypandrium short, moderately wide and quite deep.

TYPE MATERIAL.—The holotype female (not a male, as indicated in the original publication) of *Dryxo woodi* Cogan is labeled "Type [round label with red submargin]/704 [handwritten]/[MALAWI] Nyasaland[,] Cholo R.C. Wood TYPE No. Dryxo WOODI ♂ [sic] E.T. Cresson, Jr, [red label; species name and gender handwritten]/Pres. by Imp. Inst. Ent. B.M. 1935-481." The holotype is double mounted (pin in rectangular piece of celluloid), is in fair condition (left wing removed, some pieces glued to celluloid piece), and is deposited in BMNH. There is also an allotype male and two female paratypes in BMNH and a male and female paratype in the ANSP.

DISTRIBUTION.—Afrotropical: Malawi (known thus far from only the type locality, Cholo).

REMARKS.—The labels of the holotype female and allotype male were probably mixed up by Cresson or through subsequent curation by other workers. Specimens of this species are large, the structures of the male and female terminalia are easily distinguished, and it is unlikely that Cresson or subsequent workers misidentified the gender of these two specimens. We have left the status of the specimens as currently labeled. These specimens, including the two paratypes, are conspecific.

Omyxa, new genus

TYPE SPECIES.—*Omyxa scuta*, new species, by present designation.

DIAGNOSIS.—This genus is distinguished from other genera of Dryxini, especially *Dryxo* and *Corythophora*, which are similar, by the following combination of characters: ocellar seta lacking; reclinate fronto-orbital seta lacking; arista bearing 7–9 long dorsal hairs; notopleuron bearing 1 large seta on posterior ¼ (near posteroventral angle); presutural supra-alar seta

lacking; anepisternum with 2 thin, long, hair-like setae along posterior margin; katepisternum with thin, hair-like seta, lacking row of slender setae near dorsal margin; vein R₁ bearing several setulae along dorsum; R stem vein basad of humeral crossvein bearing several pale, thin setulae on ventral surface; crossvein dm-cu moderately long, shallowly sinuous, general orientation at distinct angle with posterior margin of wing, forming acute inner angle with vein M; forefemur of male and female lacking row of short, peg-like setulae apically along anteroventral surface; and mid- and hindfemora moderately elongate, although not subequal to length of abdomen.

DESCRIPTION.—Medium-sized to large shore flies, body length 3.80–5.10 mm.

Head: Frons projected forward as a shield-like, squarish, nearly flat plate, densely setulose; ocelli in isosceles triangle, with distance between posterior pair shorter than distance between anterior ocellus and either posterior ocellus; both inner and outer vertical setae present, but only outer seta well developed; reclinate fronto-orbital seta, ocellar seta, and paraverticlar seta lacking. First flagellomere with apex moderately rounded; arista short, stout, bearing 7–9 long hairs along length of dorsal surface and at apex. Face mostly bare, bearing row of short, pale setulae in shallow groove paralleling parafacial. Parafacial at anterior margin of eye moderately wide, width subequal to height of 1st flagellomere. Gena high, height slightly greater than combined length of 1st flagellomere and pedicel.

Thorax: Anterior dorsocentral setae lacking, only posteriormost pair present (0+1); acrostichal setulae poorly developed, inconspicuous, in 2 rows; prescutellar acrostichal setae lacking; presutural supra-alar seta lacking; postpronotal seta lacking; notopleural seta 1, inserted at posterior ⅓; anepisternum bearing 2 thin, poorly developed, hair-like setae along posterior margin; katepisternal seta greatly reduced or absent; katepisternum lacking row of 6–10 long, slender, hair-like setae dorsad of larger seta. Posterior margin of scutellum truncate, nearly flat. Vein R stem vein basad of humeral crossvein bearing several pale, thin setulae on ventral surface; crossvein dm-cu moderately long, shallowly sinuous, generally oriented at distinct angle with adjacent margin of wing, inner angle with vein M acute. Forefemur of male and female lacking row of short, peg-like setulae apically along anteroventral surface; foretibia of male lacking several long, slender setae at apex on ventral surface; midtibia bearing 3 dorsal extensor setae (basally, subbasally, and apically); mid- and hindfemora moderately elongate, although not subequal to length of abdomen; midtibia bearing 2 ventroapical setae and 1 posteroapical seta; tarsomeres bearing long setae anteroapically and posteroapically, length of setae subequal to width of tarsomere at apex; forebasitarsus lacking row of long, slender, pale setulae inserted along anterior surface; foretarsomeres 2–5 distinctly flattened.

Abdomen: Coloration with distinctly fasciate pattern. Male terminalia (Figures 57–60): Presurstyli robust, large, in posterior view (Figure 57) irregularly triangular, length subequal to

length of cerci; postsurstylus bearing setulose, rounded lobe just beyond midlength; aedeagus becoming broader apically; aedeagal apodeme with keel relatively shallow but extended along most of length; hypandrium moderately wide and deep, deeply incised subbasally.

DISTRIBUTION (Figure 12).—See "Distribution" of monotypic species.

PHYLOGENETIC RELATIONSHIPS.—This genus is the sister group of *Dryxo*, and the two genera share the following synapomorphies that establish their sister-group relationship: (1) ocellar seta lacking; (2) reclinate fronto-orbital seta lacking; (3) anepisternum with 2 or 3 thin, long, hair-like setae along posterior margin; (4) vein R_1 bearing several setulae along dorsum; (5) R stem vein basad of humeral crossvein bearing several pale, thin setulae on ventral surface; (6) crossvein dm-cu moderately long, shallowly sinuous (more pronounced in *Dryxo*; more shallowly sinuous and shorter in *Omyxa*); and (7) midtibia bearing 3 erect extensor setae on dorsal surface (basally, subbasally, and apically). (These setae, especially those toward the base, are easily knocked off, and often the only evidence for the setae is their sockets.)

DISCUSSION.—*Omyxa*, for the present, is monotypic, although other species may occur on the Arabian Peninsula and

adjacent lands. The Diptera fauna, shore flies in particular, in this area is both poorly sampled and poorly known.

ETYMOLOGY.—*Omyxa* is an arbitrary combination of letters and is considered feminine.

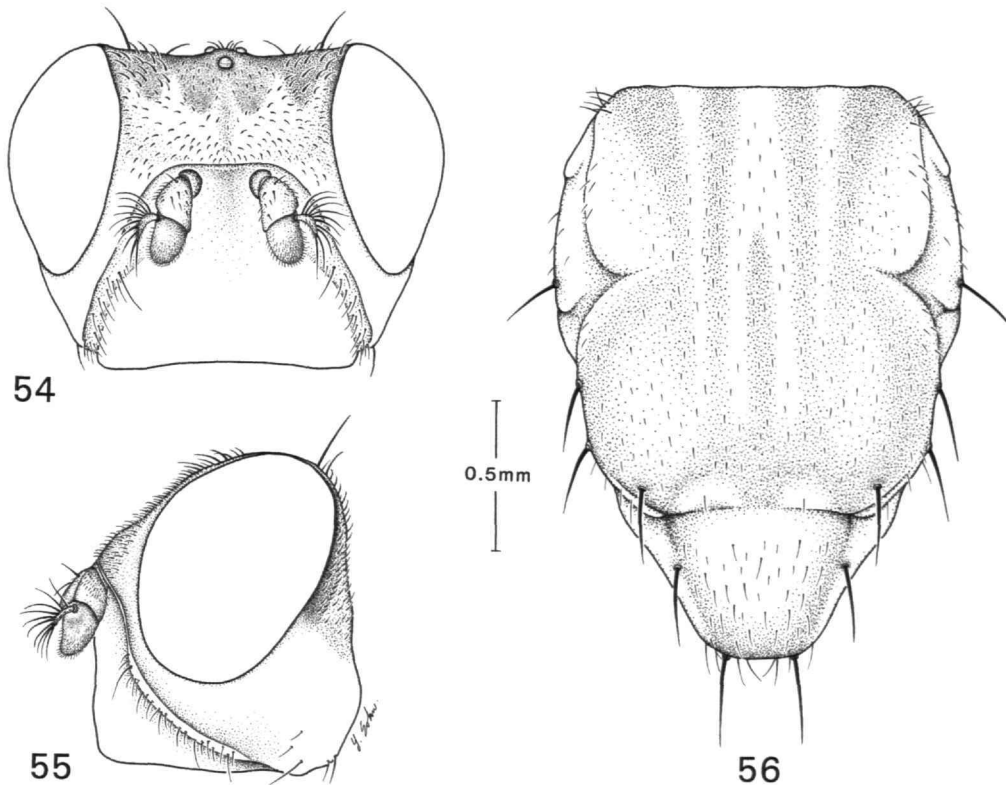
14. *Omyxa scuta*, new species

FIGURES 54–60

DIAGNOSIS.—As the only known species, the generic diagnosis will serve to distinguish this species. Should additional species be discovered, the structures of the male terminalia will undoubtedly be diagnostic.

DESCRIPTION.—As in generic description but with details as follows: medium-sized to large shore flies, body length 3.80–5.10 mm; body mostly microtomentose except posterior portion of frons and mesonotum.

Head (Figures 54, 55): Generally densely microtomentose except for posterior portion of frons. Frons more or less square, shield-like, bearing numerous setulae and with distinctive color pattern, anterior portion whitish yellow to whitish tan, abruptly differentiated from black to blackish brown posterior portion of frons, demarcation line zigzagged from lateral margin to me-



FIGURES 54–56.—*Omyxa scuta* Mathis and Zatwarnicki: 54, head, anterior aspect; 55, same, lateral aspect; 56, mesonotum, dorsal aspect.

dial, oriented posteromedially then anteromedially, medial thinly but deeply incised to anterior ocellus; inner vertical seta short, thin, about $\frac{1}{2}$ size of outer vertical seta (these with apex apparently broken). Antenna essentially concolorous with anterior margin of frons, 1st flagellomere slightly darker; 1st flagellomere short, length subequal to combined length of scape and pedicel; arista extended beyond apex of 1st flagellomere, bearing 7–10 dorsal hairs, these more curved toward apex. Face concolorous with anterior portion of frons but duller and uniformly colored, dorsal portion of face between antennal bases vertical, not projected, thereafter ventrally flared anteriorly to oral margin, generally lacking setae or setulae except bearing row of short, thin, pale-colored setulae in vertical groove parallel to parafacial. Parafacial moderately wide, slightly less than width of pedicel at apex, concolorous with face; gena high, becoming wider posteriorly from parafacial, also becoming more silvery white, lacking a prominent genal seta; gena-to-eye ratio 0.38. Clypeus band-like, black with gray microtomentum; palpus short, mostly black but with some gray microtomentum.

Thorax (Figure 56): Mesonotum generally concolorous with posterior portion of frons, with only very sparse microtomentum, mostly blackish brown to black with thin gray stripes medially and laterally, these more evident anteriorly, basolateral margin of scutellum gray, microtomentose; pleuron ventrad of postpronotum and notopleuron, including femora and tibiae, uniformly silvery gray. Wing hyaline with mostly brown veins; costal-vein ratio 0.41; M-vein ratio 1.0. Legs mostly black with dense, whitish gray microtomentum; tarsi with some yellowish orange coloration; foretarsus with tarsomeres 2–5 blackish brown, distinctly flattened, forebasitarsomere much paler than apical tarsomeres.

Abdomen: Tergites 2–4 (and perhaps tergite 5, dissected before observation on it) with blackish brown bank along anterior margin, otherwise grayish, microtomentose. Male terminalia (Figures 57–60): generally robust externally, thickly sclerotized; epandrium U-shaped in posterior view (Figure 57), arms extended ventrally, becoming slightly wider ventrally; cercus narrowly ovoid, almost 4 times longer than wide, widest just above midheight, dorsal margin rounded, ventral margin narrowed; presurstylus in posterior view (Figure 57) irregularly triangular, medial margin with dorsal $\frac{1}{2}$ moderately deeply concave, dorsomedial portion produced into narrow, short process, with similar process meeting it from other side, ventral portion pointed, lateral margin shallowly arched and in lateral view sharply angulate, higher than wide, basal $\frac{2}{3}$ squarish, projected posteriorly to just below midheight, forming 90° angle, posterodorsal surface invaginated, ventral $\frac{1}{3}$ mostly oriented ventrad, parallel sided, ventral margin sharply truncate; post-surstylus in lateral view (Figure 58) relatively short, length about twice width, bilobed on ventral $\frac{1}{3}$; aedeagus in lateral view (Figure 60) narrow basally at attachment with aedeagal apodeme, dorsal margin irregular, projected laterally as a flap, apicodorsal portion with an upcurved, short projection, immediately ventrad with a more truncate process, and ventral mar-

gin large, broadly curved, in dorsal view base of aedeagus much wider than apex, becoming slightly wider to about midlength, thereafter tightly recurved, forming a short, lateral process, then angled medially to wider, capitate apex; aedeagal apodeme in lateral view (Figure 60) with only apices curved posteriorly toward attachments with aedeagus and hypandrium, anterior crest long, irregularly arched; hypandrium in lateral view (Figure 60) angulate, anterior $\frac{3}{4}$ wide, anterior margin truncate, in ventral view (Figure 59) deeply incised subbasally, with narrowly angulate lateral processes.

TYPE MATERIAL.—The holotype male is labeled "S. Iran 40 km SE Minab 21. 5 1973 [21 May 1973]/Loc. no. 205 Exp. Mus. Nat Praha/Cat. No. 33751 [pink label with black submargins; handwritten]." The holotype is double mounted (minuten in a small block of cork), is in good condition (some setae missing), and is deposited in NMSAC. The allotype female and six paratypes (4 σ , 2 f ; NMSAC, USNM) bear the same locality data as the holotype but with different catalog numbers (NMSAC 33747–33754). Other paratypes are as follows: Oriental. INDIA. *Tamil Nadu*: Coimbatore, Jul 1956, P.S. Nathan (1 σ , 1 f ; BMNH); Karaikal (10°55'N, 79°45'E), Jul 1956, P.S. Nathan (8 σ , 12 f ; BMNH, USNM); Kurumbagaram, Karaikal, Jul–Dec 1952, P.S. Nathan (2 σ , 3 f ; BMNH); Walayar Forests (10°51'N, 76°51'E), South Malabar, 5 Aug 1956, P.S. Nathan (10 σ , 7 f ; BMNH, USNM). Palearctic. OMAN. Al Gharbi (650 m), 10 Apr 1985, P. Ardö (1 σ ; ZIL).

DISTRIBUTION (Figure 12).—Oriental: India (Tamil Nadu). Palearctic: Iran, Oman.

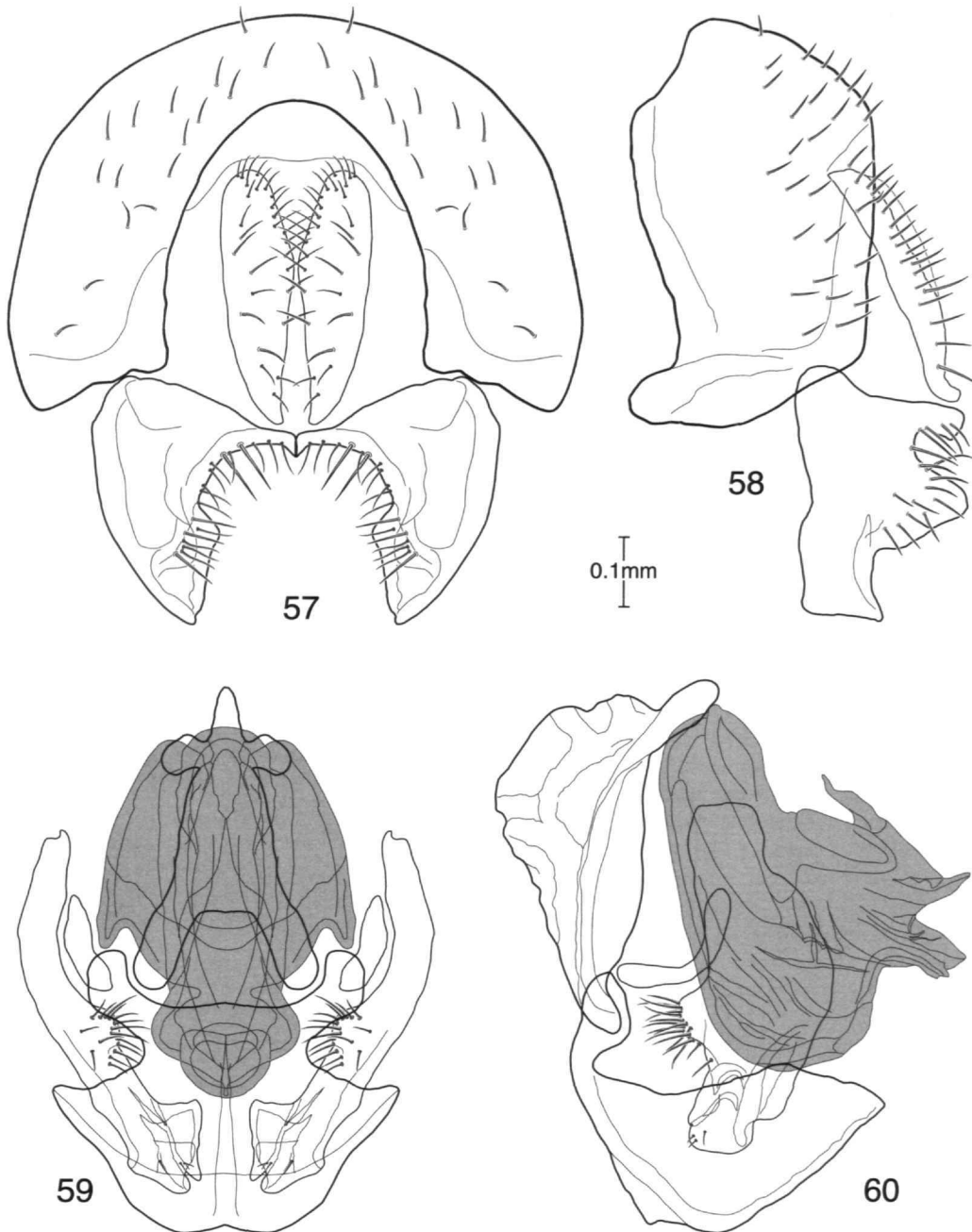
ETYMOLOGY.—The specific epithet, *scuta*, refers to the shield-like frons of this species.

Genus *Oedenopiforma* Cogan

Oedenopiforma Cogan, 1968:319 [as a subgenus of *Paralimna*; type species: *Paralimna madecassa* Giordani Soika, 1956a, original designation].—Cogan, 1980:663 [Afrotropical catalog, as a subgenus of *Paralimna*].—Mathis and Zatwarnicki, 1995:117 [world catalog, accorded generic status].

DIAGNOSIS.—This genus is distinguished from other genera of Dryxini by the following combination of characters: arista bearing 8 or more dorsal hairs; proclinate fronto-orbital setae greatly reduced and subequal, setula-like; facial setae 2 or 3, if 2, these well spaced, dorsal seta at about midheight, ventral seta closer to oral margin than dorsal seta; dorsocentral setae 4 (1+3), anterior seta well developed; presutural supra-alar seta present; notopleuron bearing 2 large setae (anterior notopleural seta well developed); anepisternal and katepisternal setae well developed; forefemur bearing anteroventral row of very short, stout, spine-like setae (difficult to see) along apical $\frac{1}{2}$; and mid- and hindfemora normally developed, much shorter than length of abdomen.

DESCRIPTION.—Small to moderately small shore flies, body length 1.65–2.85 mm; densely microtomentose, gray to brown dorsally, usually becoming darker ventrally.



FIGURES 57–60.—Male terminalia of *Omyxa scuta* Mathis and Zatwarnicki: 57, epandrium, cerci, and presurstyli, posterior aspect; 58, same, lateral aspect; 59, internal male terminalia, ventral aspect; 60, same, lateral aspect.

Head: Frons shallowly arched anteroventrally, not projected forward, sparsely setulose; ocelli in isosceles triangle, distance between posterior pair longer than between anterior

ocellus and either posterior ocellus; ocellar seta, inner vertical seta, and reclinate fronto-orbital seta well developed; proclinate fronto-orbital setae greatly reduced, subequal in length,

anterior seta not conspicuously larger than posterior seta; paraverticlar seta well developed, subequal to length of posterior notopleural seta. First flagellomere broadly rounded; arista bearing 6–8 long hairs along dorsal surface. Face with 2 or 3 long (subequal to length of large, reclinate seta), inclinate (but not cruciate) facial setae on ventral $\frac{1}{2}$ of face and 3 or 4 smaller setulae interspersed along same vertical alignment as larger setae, facial setae and setulae vertically aligned, parallel with parafacial. Parafacial at anterior margin of eye narrow, width much less than length of 1st flagellomere. Gena high, height subequal to combined length of 1st flagellomere and pedicel.

Thorax: Dorsocentral setae 4 (1+3), well developed, posterior pair displaced laterally; acrostichal setulae well developed, conspicuous, in about 8 irregular rows; presutural supraalar seta well developed, subequal in length to anterior, dorsocentral seta; postpronotal seta well developed; notopleural setae 2, posterior seta shorter; anepisternum variable, bearing 1 large seta along posterior margin and with dorsal seta reduced, or (usually) bearing 2 setae with apical seta $\frac{1}{4}$ – $\frac{1}{2}$ length of larger, ventral seta; katapisternal seta well developed. Posterior margin of scutellum truncate, nearly flat. R stem vein bearing 1–3 (usually 2) setulae, these oriented posteriorly; crossvein dm-cu regularly developed, nearly straight, longer than apical section of vein CuA_1 , and at distinct angle with posterior margin of wing. Forefemur bearing comb-like row of short, stout, spine-like setulae along apical $\frac{1}{2}$ of anteroventral surface; foretibia of male bearing several long, slender setae at apex on ventral surface; forebasitarsus with row of long, slender, pale setulae inserted along anterior surface; midtibia with 3 dorsal extensor setae (subapically, subbasally, and near middle); mid- and hindfemora normally developed, much shorter than length of abdomen.

Abdomen: Lacking pattern of fascia. Male terminalia: epandrium in posterior view a broad to moderately narrow inverted U, bearing setulae toward posterior margin; cercus ovoid, dorsum in posterior view slightly narrower than venter, bearing numerous setulae, especially on medial portion; presurstylus in posterior view wider than high, bearing few to many short to long setulae; postsurstylus slightly curved anteriorly in lateral view, base wider than apex, especially in lateral view, with preapical notch, bearing setulae in patches along inner curva-

ture; aedeagus simple, usually broad basally, apex pointed to truncate; aedeagal apodeme with conspicuous, moderately deep to deep keel; hypandrium wider than long (best seen in posterior view), shallowly and sometimes irregularly curved in lateral view.

HISTORICAL REVIEW.—*Oedenopiforma* was first described by Cogan (1968) as a subgenus of *Paralimna* and initially included only two species, *O. madecassa* (Giordani Soika, 1956a), the type species, and *O. argentea*, which Cogan described in the same paper. Other than Cogan's (1980) Afrotropical catalog and our world catalog (Mathis and Zatwarnicki, 1995), there are no further references to the genus and species. Consistent with our catalog, herein we accord generic status to this taxon, but we also expand the generic concept to include two additional species, *Paralimna uniseta* Malloch and *P. ligabuei* Canzoneri. The latter species is Afrotropical in distribution, like the two originally included species, and *P. uniseta* is known thus far only from Australia. Structurally, *P. uniseta* is more divergent from the other three species (see first couplet of key and description of male terminalia).

None of the included species is common in collections available to us, and virtually nothing is known about their natural history.

DISTRIBUTION (Figure 61).—Australasian/Oceanian: Australia (New South Wales, Northern Territory, Western Australia). Afrotropical: Kenya, Madagascar, Namibia, Nigeria, Rwanda, South Africa (Transvaal), Sudan, Zaire. Palearctic: Iran.

DISCUSSION.—*Oedenopiforma* is characterized by several synapomorphies that confirm the monophyly of the genus. Among derived character states that we have discovered are the following: (1) forefemur bearing comb-like row of short, stout, spine-like setulae along apical $\frac{1}{2}$ of anteroventral surface; (2) R stem vein bearing 1–3 (usually 2) setulae; and (3) abdomen lacking a pattern of fascia.

Specimens of *Oedenopiforma* are relatively scarce in collections, and despite concerted effort over a number of years, including examination of thousands of specimens of Dryxini from major museums throughout the world, we were able to locate only a few specimens. In this review, we recognize three species of *Oedenopiforma*, one of which, *O. madecassa*, has two junior synonyms, one newly proposed herein.

Key to Species of *Oedenopiforma* Cogan

1. Facial series of setae 3; paraverticlar setae greatly reduced or lacking. Stem vein bearing 1 long setula, length equal to twice width of vein at level of insertion. Forefemur bearing minute, peg-like setulae anteroventrally (Australia) 17. *O. uniseta* (Malloch)
- Facial series of setae 2, these well separated; paraverticlar setae moderately to well developed (with same orientation as inner vertical seta although smaller). Stem vein bearing 1–3 (usually 2) setulae, length of each about equal to width of vein at level of insertion. Forefemur bearing conspicuous, peg-like setulae anteroventrally 2

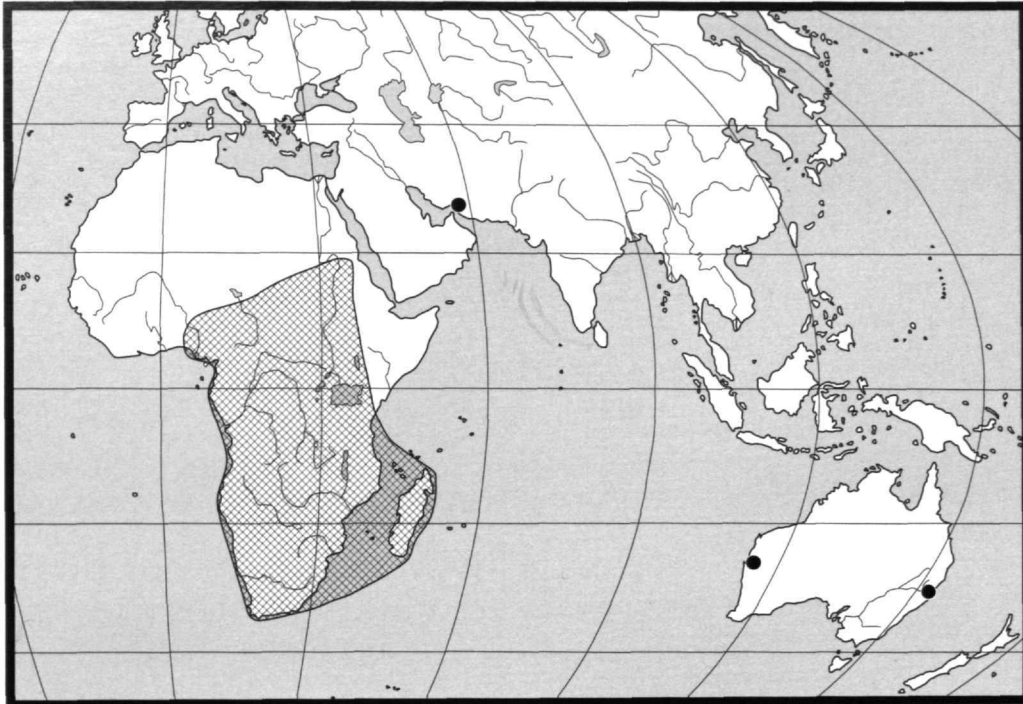


FIGURE 61.—Distribution map for *Oedenopiforma* (hatched and dots).

2. Face in both sexes yellow to orangish yellow, distinct from grayish yellow, microtomentose antenna; forefemur of male lacking row of setulae as above; apex of foretibia and forebasitarsus of male bearing long, pale setulae (widespread Africa) 15. *O. argentea* (Cogan)
 Face and antenna of male appearing velvety, densely microtomentose, dark brown; face of female silvery gray; antenna of female dark brown (Madagascar, South Africa, Sudan) 16. *O. madecassa* (Giordani Soika)

15. *Oedenopiforma argentea* (Cogan)

FIGURES 62–65

Paralimna (*Oedenopiforma*) *argentea* Cogan, 1968:322; 1980:663 [Afrotropical catalog].

Oedenopiforma argentea.—Mathis and Zatwarnicki, 1995:117 [catalog, generic recombination].

DIAGNOSIS.—This species is distinguished from congeners by the following combination of characters: in both sexes face yellow to orangish yellow, distinct from grayish yellow, microtomentose antenna; facial series of setae 2, these well separated; and forefemur of male lacking row of long, fine, pale, ventrally oriented setulae along anteroventral surface.

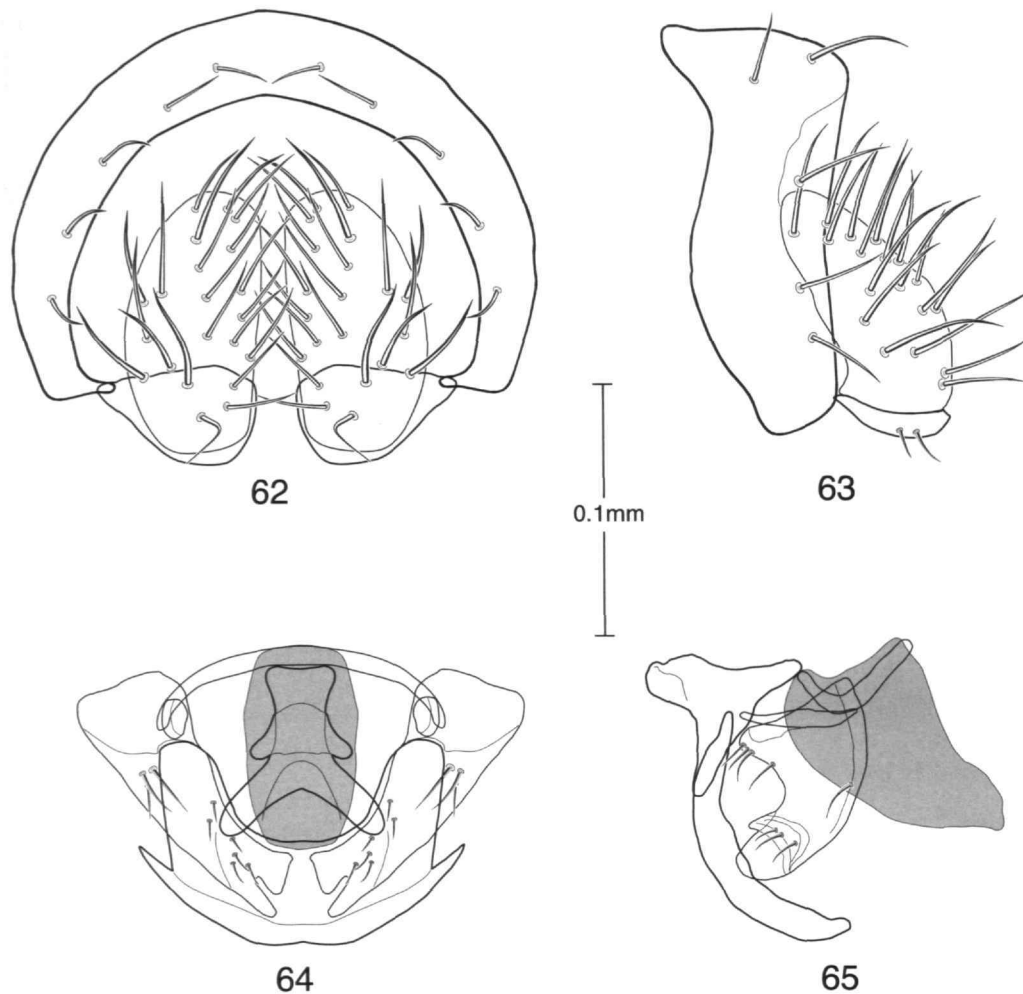
DESCRIPTION.—Small to moderately small shore flies, body length 1.80–2.30 mm.

Head: Paraverticral seta well developed, about 1/3–1/2 length of inner vertical seta. Arista with 7 or 8 dorsal rays. Face yellow to orangish yellow in both sexes, distinct from grayish yellow,

low, microtomentose antenna; facial series of setae 2, these well separated. Gena-to-eye ratio 0.34–0.35.

Thorax: Stem vein bearing 1–3 (usually 2) setulae dorsally along posterior margin, length of each about equal to width of vein at level of insertion; costal-vein ratio 0.35–0.36; M-vein ratio 0.90–0.94. Forefemur of male lacking row of long, fine, pale, ventrally oriented setulae along anteroventral surface; apex of foretibia and forebasitarsus of male bearing long, pale setulae.

Abdomen: Male terminalia (Figures 62–65): epandrium wider than high in posterior view (Figure 62), evenly rounded, semicircular, width even, bearing setulae of equal length toward posterior margin, in lateral view (Figure 63) much wider dorsally, thereafter ventrad narrowed abruptly, anterior margin sinuous; cercus ovoid, bearing numerous setulae, especially medially; presurstylus horizontal tear-drop-shaped, much wider medially, narrowed laterally, bearing several long setu-



FIGURES 62–65.—*Oedenopiforma argentea* (Cogan): 62, epandrium, cerci, and presurstyli, posterior aspect; 63, same, lateral aspect; 64, internal male terminalia, ventral aspect; 65, same, lateral aspect.

lae; postsurstylus with truncate to very shallowly arched basal margin, base twice apical width, bearing 2 or 3 subapical setulae at level of preapical notch, bearing 3 or 4 setulae on basal $\frac{1}{3}$ of inner curvature; aedeagus with apex pointed in lateral view (Figure 65); aedeagal apodeme with moderately wide and deep keel, extended processes about equal in length in lateral view (Figure 65); hypandrium wider than long, bluntly rounded anteriorly, with lateral pointed process at anterolateral corner, thereafter posteriorly parallel sided, posterior margin broadly emarginate, excavate.

TYPE MATERIAL.—The holotype female of *Paralimna argentea* Cogan is labeled "Pres. by Imp.BurEnt./Holo-type [round label with red margin]/N. Nigeria. Ilorin. 22.2. 191 Dr. J.W.Scott-Macfie./1920-271/Paralimna argentea sp.n. ♀ det B.H.Cogan 1966 [species name, gender, and "sp.n." handwrit-

ten]." The holotype is double mounted (pin in a rectangular piece of celluloid), is in fair condition (pin fold in much of mesonotum), and is deposited in BMNH.

OTHER SPECIMENS EXAMINED.—Afrotropical. KENYA. Lake Victoria (10 km S Kisumu), 19 Nov 1986, A. Freidberg (3♂, 1♀; USNM).

NAMIBIA. Ameib Farm (on vegetation around pools), 31 Jan–2 Feb 1972 (9♂, 5♀; BMNH). Kamanjab (43.5 km ESE), Otjitambi Farm, 13–15 Feb 1972 (80♂, 97♀; BMNH).

NIGERIA. *Kaduna*: Zaria, Samaru, 21 Feb–1 Nov 1967, 1968 (2♂; BMNH). *Kwara*: New Bussa, 12 Jan 1970, J.T. Medler (1♂; USNM). *Osun*: Ile-Ife, 20 May 1969, J.T. Medler (1♀; BMNH).

RWANDA. Kisenyi (près emb. riv. Sebeya), 4 Apr 1953, Verbeke (2♂, 7♀; MRAC).

SOUTH AFRICA. *Transvaal*: Kruger Park (Olifants River near Balule; riparian woodland), 9 Dec 1972, B.R. and P. Stuckenberg (1 ♀; NMSA).

ZAIRE. Elisabethville (light), 17 Dec 1949, C. Seydel (1 ♀; USNM).

Palaearctic. IRAN. Derpehan (12 km E Senderk), 11–12 May 1977 (13 ex; NMSAC).

DISTRIBUTION.—Afrotropical: Kenya, Namibia, Nigeria, Rwanda, South Africa (Transvaal), Zaire. Palaearctic: Iran.

REMARKS.—A male from Sri Lanka may also be this species, although the row of short, stout setae along the anteroventral surface is not as well developed. Label data for this male are Amp. Dist. Maha Oya, 1 May 1980, W.N. Mathis, T. Wijesinhe, L. Jayawickrema (1 ♂; USNM).

16. *Oedenopiforma madecassa* (Giordani Soika)

FIGURES 66–68

Paralimna madecassa Giordani Soika, 1956a:123.—Cogan, 1968:321 [revision]; 1980:663 [Afrotropical catalog].

Oedenopiforma madecassa.—Mathis and Zatwarnicki, 1995:117 [catalog, generic recombination].

Paralimna brunneifacies Giordani Soika, 1956a:123.—Cogan, 1968:321 [synonymy].

Paralimna ligabuei Canzoneri, 1987:84.—Mathis and Zatwarnicki, 1995:121 [world catalog]. [New synonym.]

DIAGNOSIS.—This species is distinguished from congeners by the following combination of characters: face and antenna of male appearing velvety, densely microtomentose, dark brown; face of female silvery gray; facial series of setae 2, these well separated; antenna of female dark brown; mesofrons of male dark brown anteriorly, becoming golden brown posteriorly; anterior fronto-orbits concolorous with anterior portion of mesofrons, not appearing velvety; scutum of male either mostly concolorous with scutellum except for golden brown anteromedial area or with disc of scutellum gray, contrasting with dark brown scutum; and forefemur of male usually bearing row of long, fine, pale, ventrally oriented setulae along anteroventral surface.

DESCRIPTION.—Small to moderately small shore flies, body length 1.65–2.40 mm.

Head: Paraverticilar seta well developed, length about $\frac{1}{3}$ – $\frac{1}{2}$ inner vertical seta. Arista with 6–8 dorsal rays. Face and antenna of male appearing velvety, densely microtomentose, dark brown; face of female silvery gray; antenna of female dark brown; facial series of setae 2, these well separated. Gena-to-eye ratio 0.26–0.36.

Thorax: Scutum of male mostly concolorous with scutellum except for golden brown anteromedial area. Stem vein bearing 1–3 (usually 2) setulae dorsally along posterior margin, length of each about equal to width of vein at level of insertion; costal-vein ratio 0.41–0.42; M-vein ratio 0.80–0.85. Forefemur bearing conspicuous, peg-like setulae anteroventrally; forefemur of male with row of long, fine, pale, ventrally oriented setulae along anteroventral surface.

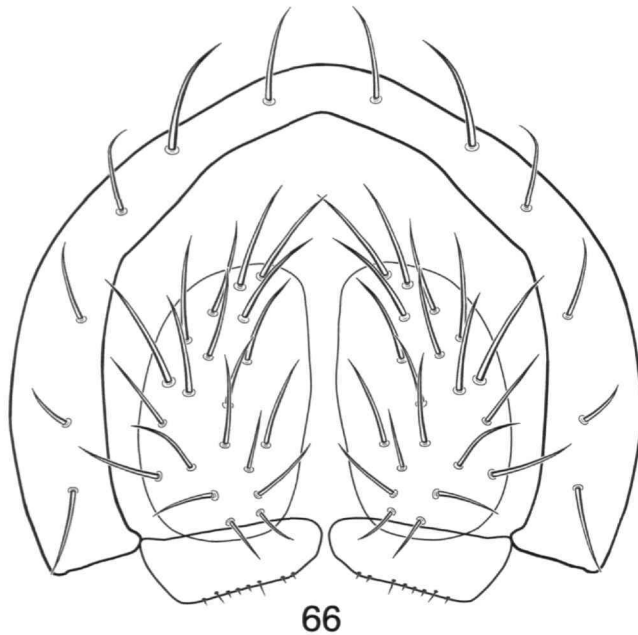
Abdomen: Male terminalia (Figures 66–68): epandrium about as wide as high in posterior view (Figure 66), dorsum more acutely rounded and more thinly developed than lateral arms, bearing several long setulae toward posterior margin; cercus broadly ovoid, only slightly narrower dorsally, bearing numerous long setulae, evenly scattered; presurstylus in posterior view (Figure 66) as a nearly parallel-sided, horizontal bar bearing tiny setulae along ventral margin, apex only slightly narrower than base; postsurstylus in lateral view (Figure 68) with truncate, nearly flat basal margin, base nearly twice apical width, bearing 2 or 3 subapical setulae at level of preapical notch and bearing 5 or 6 setulae on basal $\frac{1}{3}$ of inner curvature; aedeagus with apex irregularly truncate in lateral view (Figure 68); aedeagal apodeme with wide and moderately deep keel, extended processes about equal in length in lateral view (Figure 68); hypandrium in ventral view (Figure 67) wider than long, bluntly rounded V-shaped, apex of posteriorly extended arms with wide, medial process, posterior margin very broadly excavate.

TYPE MATERIAL.—The lectotype male of *Paralimna madecassa* Giordani Soika, here designated to stabilize and make more universal the use of this name, is labeled “HOLOTYPUS [pink label with black submarginal line]/COLL. MUS. CONGO Madagascar: [Tamatave:] Maroanetra[,] XII-1949 [Dec 1949] J. Vadon/HOLOTYPUS *Paralimna madecassa* Soika [red label; handwritten except for “HOLOTYPUS”].” The lectotype male is double mounted (minuten), is in good condition (right fronto-orbital seta missing, posterior portion of left wing destroyed), and is deposited in the MRAC. Although Giordani Soika (1956a:123) wrote that the two specimens comprising the type series are females, one of the syntypes that we are here designating as the lectotype is clearly a male.

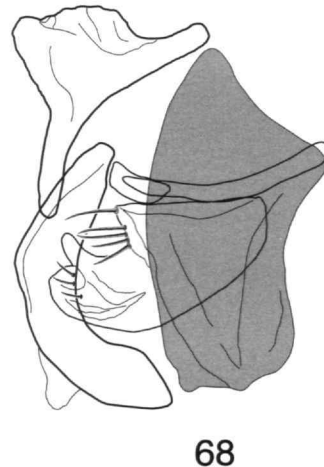
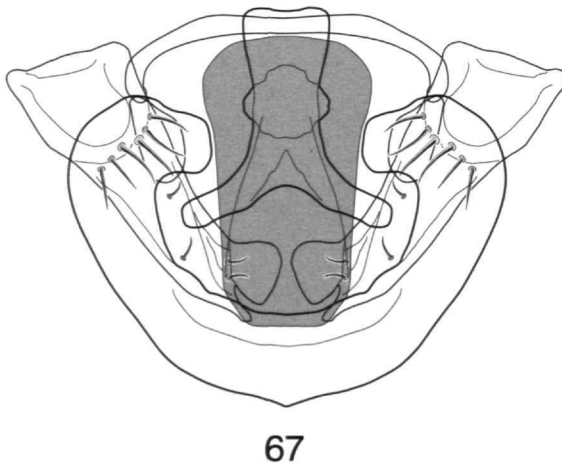
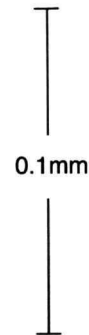
The lectotype female of *Paralimna brunneifacies* Giordani Soika, here designated to stabilize and make more universal the use of this name, is labeled “HOLOTYPUS [pink label with black submarginal line]/COLL. MUS. CONGO Madagascar: [Tamatave:] Maroanetra[,] XII-1949 [Dec 1949] J. Vadon/HOLOTYPUS *Paralimna brunneifacies* Soika [red label; handwritten except for “HOLOTYPUS”].” The lectotype female is double mounted (minuten), is in fair condition (right portion of mesonotum removed, right mid- and hindtarsi missing), and is deposited in the MRAC.

The holotype male of *Paralimna ligabuei* Canzoneri is labeled “[Sudan] Kartoum Barc (nilo) 6-xii-80 Leg. Rallo [handwritten]/HOLOTYPUS *Paralimna ligabuei* nov. det. Canzoneri S. [red label; species name handwritten]/MUSEO CIVICO DI STORIA NATURALE DI VENEZIA Materiale tipico descritto Inv. n. 03732 [red label; number handwritten].” The holotype is double mounted (minuten in a long, rectangular block of polyporus), is in fair condition (several setae missing; abdomen removed and dissected, and the parts are in an attached microvial), and is deposited in the MCV.

OTHER SPECIMENS EXAMINED.—Afrotropical. MADAGASCAR. *Antananarivo*: Ambatondrazaka, Centre Station Agric.,



FIGURES 66–68.—*Oedenopiforma madecassa* (Giordani Soika): 66, epandrium, cerci, and presurstyli, posterior aspect; 67, internal male terminalia, ventral aspect; 68, same, lateral aspect.



Alaotra (800 m), 24 Dec 1957, B.R. Stuckenberg (1♀; BMNH). *Toliara*: Ampanihy (250 m), 16–18 Feb 1958, B.R. Stuckenberg (1♀; BMNH); Morondava (black light near sand beach), 28–31 Mar 1990, W.E. Steiner, C. Kremen, V. Razafimahatratra (3♀; USNM); Ranohira (860 m), 26 Jan–4 Feb 1958, B.R. Stuckenberg (3♀; BMNH); Saint Augustin (6 m), 11–13 Feb 1953, B.R. Stuckenberg (2♂; BMNH, USNM); Fenerive (lagoon shore), Dec 1955, B.R. Stuckenberg (1♂; USNM).

SOUTH AFRICA. *Transvaal*: Kruger Park (Olifants River near Balule; riparian woodland), 9 Dec 1972, B.R. and P. Stuckenberg (1♂; NMSA).

DISTRIBUTION.—Afrotropical: Madagascar, South Africa (Transvaal), Sudan.

REMARKS.—This species is obviously sexually dimorphic, as noted in the diagnosis and description, and the pronounced dimorphism may have contributed to this species being described twice by the same author, on the same page, and based

on specimens from the same locality. Although the syntype series for *Paralimna madecassa*, including the lectotype, was stated to consist of females, the specimens are clearly males, which have densely microtomentose, dark brown faces; the syntypes of *P. brunneifacies*, also including the lectotype, are females with faces that are only moderately densely microtomentose and are mostly gray with contrastingly dark brown antennae. These conspicuous differences are normally associated with distinct species, but in this case, they indicate striking sexual dimorphism within the same species.

In addition to variation associated with sexual dimorphism, the coloration of the dorsum, the mesonotum in particular, apparently demonstrates some differences that may be geographically based and that may also have contributed to confusion about this species. This variation is evident in the holotype of *Paralimna ligabuei*, which was collected in Sudan. The holotype differs from specimens collected in Madagascar and South Africa by having the disc of the scutellum gray, contrasting with the dark brown scutum. In specimens from Madagascar and South Africa, the scutellum and scutum are both dark brown. Unfortunately the holotype and paratype from Sudan are the only specimens available to us, and thus, for the present, we lack adequate material to assess further the variation in color.

The two specimens of *P. ligabuei* are very similar to *Oedenopiforma madecassa*, as Canzoneri (1987:84) noted. The similarity Canzoneri described is especially evident externally in the coloration and vestiture of the sexually dimorphic male heads. The male heads of both species, especially the face, parafacials, and antennae, are densely microtomentose, dark brown to black, and appear velvety. The female heads are mostly gray, although the antennae are blackish brown to black, as in males. Although we confirm the similarities in color and the differences Canzoneri noted, our study of the structures of the male terminalia indicates that there is a single species represented in the specimens before us, including all appropriate primary types. All structures of the male terminalia are virtually identical, and the detailed similarity is the primary basis for our opinion that we are dealing with a single species.

17. *Oedenopiforma uniseta* (Malloch), new combination

FIGURES 69–71

Paralimna uniseta Malloch, 1925:325.—Bock, 1988:894–895 [revision].—Mathis, 1989:644 [Australasian/Oceanian catalog].—Mathis and Zatwarnicki, 1995:126 [world catalog].

DIAGNOSIS.—This species is distinguished from congeners by the following combination of characters: face and antenna of male densely microtomentose but not appearing velvety; antenna of male black; face of male yellowish tan to lightly rusty on ventral $\frac{2}{3}$ or more, whitish gray to gray dorsally just ventrad of antennal bases; facial series of setae 3; and forefemur of male with row of long (longest setae greater than width of fe-

mur), well-developed, black, ventrally oriented setae along posteroventral margin.

DESCRIPTION.—Small to moderately small shore flies, body length 1.80–2.85 mm.

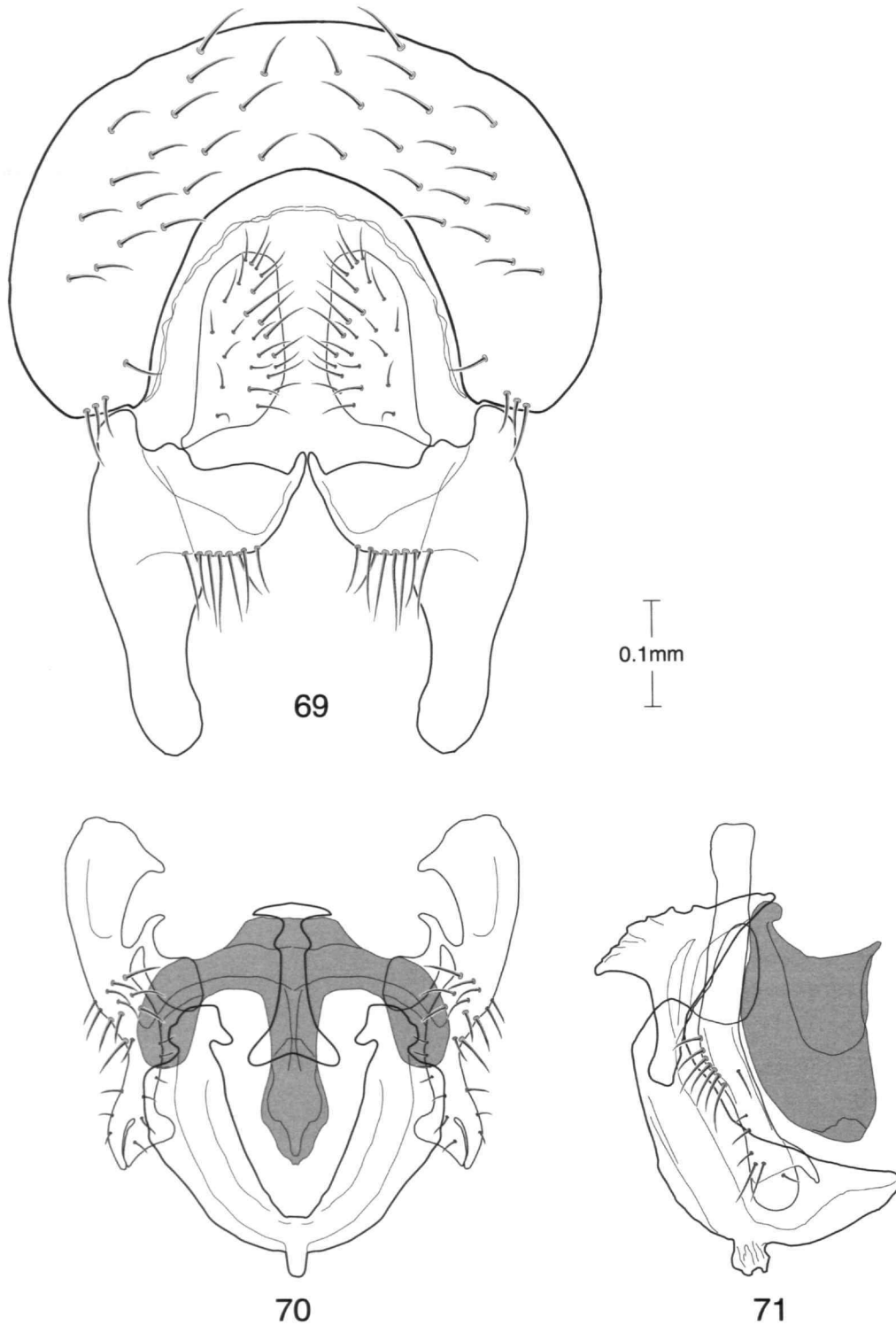
Head: Paraverticlar seta greatly reduced or lacking, no enlarged setae evident. Frons of male whitish gray to gray anteriorly; ocellar triangle and fronto-orbits tan to rusty brown. Face and antenna of male densely microtomentose but not appearing velvety; antenna of male black; face of male yellowish tan to lightly rusty on ventral $\frac{2}{3}$ or more, whitish gray to gray dorsally just ventrad of antennal bases. Arista with 9 or 10 dorsal rays. Facial series of setae 3. Gena-to-eye ratio 0.29–0.30.

Thorax: Mesonotum yellowish brown to rusty brown medially, especially between dorsocentral setal tracks, becoming grayer laterally; pleural areas gray dorsally, becoming yellowish brown to rusty brown ventrally. Stem vein bearing 1 long, thin setula dorsally along posterior margin; costal-vein ratio 0.33–0.35; M-vein ratio 1.0–1.05. Legs blackish brown to black, bearing gray black microtomentum; forefemur of male bearing inconspicuous row of tiny, tooth-like setulae along apical $\frac{1}{2}$ of anteroventral surface and with row of long (longest setae greater than width of femur), well-developed, black, ventrally oriented setae along posteroventral margin.

Abdomen: Male terminalia (Figures 69–71): epandrium in posterior view wider than high, dorsal portion with numerous, evenly scattered setulae, ventrally extended arms broad (Figure 69); cercus with ventrolateral extended process, otherwise like a trapezoid with rounded angles, densely setulose, especially medially; presurstylus large, robustly developed, like an inverted L, basomedial horizontal extension bearing a row of closely set setulae along ventral margin, lateroventral process vertical, bluntly rounded apically; postsurstylus in lateral view (Figure 71) long and narrow, width relatively even, bifurcate at ventral apex, bearing vertical row of setulae anteriorly near middle; aedeagus simple, in lateral view (Figure 71) with apex only slightly narrower than base, anterior margin rounded, posterior margin nearly straight; aedeagal apodeme with keel irregular, distinctly pointed ventrally, extended processes short; hypandrium wide, as a shallowly depressed bowl, bearing a short projection externally toward anterior margin.

TYPE MATERIAL.—The holotype male of *Paralimna uniseta* Malloch is labeled “[Australia.] N S. Wales[,] Fish River[,] 25.3.23 [25 Mar 1923] Health Dept./Det. J. R. Malloch Type *Paralimna uniseta* [“Type” and species name handwritten; label with black submarginal border]/*Paralimna uniseta* Malloch HOLOTYPE [red label; species name and author handwritten]/SPHTM Coll. [light blue label].” The holotype male is double mounted (pin in a rectangular block of polyporus), is in excellent condition, and is deposited in the AM.

OTHER SPECIMENS EXAMINED.—Australasian/Oceanian. AUSTRALIA. *New South Wales:* Bargo (5 km N), 20 Mar 1980, G.F. Hevel, J.A. Fortin (2♂; USNM); Mendooran (37 km N), Wingabutta Creek, 26 Mar 1971, D.K. McAlpine (1♀; AM). *Western Australia:* Mileura (29 km NW; 310 m), 6 Oct



FIGURES 69–71.—*Oedenopiforma uniseta* (Malloch): 69, epandrium, cerci, and presurstyli, posterior aspect; 70, internal male terminalia, ventral aspect; 71, same, lateral aspect.

1962, E.S. Ross, D.Q. Cavagnaro (1♂; USNM); Millstream, 7 Apr 1971, D.H. Colless (1♂; ANIC).

DISTRIBUTION.—Australasian/Oceanian: Australia (New South Wales, Northern Territory, Western Australia).

REMARKS.—This species and other undescribed species from Australia (represented by single male specimens) apparently form a species group that is distinguished by the characters in the first couplet of the key to species of *Oedenopiforma*. The group should be revised when additional specimens are available.

Genus *Oedenops* Becker

Oedenops Becker, 1903:178 [type species: *Oedenops isis* Becker, 1903, monotypy].—Becker, 1926:94 [review].—Cresson, 1929:180 [assigned to subfamily Notiphilinae (=Hydrelliinae)]; 1947a:37, 46 [generic key; review, Neotropical Region]; 1947b:106 [generic key, Afrotropical Region].—Curran, 1934:353 [key to nearctic genera].—Séguy, 1951:5 [generic key].—Wirth and Stone, 1956:465, 470 [generic key, review, Californian species].—Wirth, 1965:748 [Nearctic catalog]; 1968:16 [Neotropical catalog].—Cole, 1969:395–396 [generic key, list].—Cogan, 1980:662 [Afrotropical catalog]; 1984:148 [Palearctic catalog].—Mathis and Zatwarnicki, 1995:117–118 [world catalog].

DIAGNOSIS.—This genus is distinguished from other genera of Dryxini by the following combination of characters: arista bearing 3–6 hairs; presutural supra-alar seta present (lacking in *O. isis*); notopleuron bearing 2 large setae (anterior notopleural seta well developed); anepisternal and anterior dorsocentral setae well developed (dorsocentral setae 1+3); katapisternal seta absent; forefemur in both sexes bearing row of short, peg-like setulae apically along anteroventral surface; and mid- and hindfemora normally developed, much shorter than abdomen.

DESCRIPTION.—Small to moderately small shore flies, body length 1.70–2.65 mm; generally gray, often strikingly bicolored, rusty yellowish on head.

Head: Frons shallowly arched anteroventrally, not projected forward, sparsely setulose; ocelli in isosceles triangle, distance between posterior pair slightly longer than between anterior ocellus and either posterior ocellus; ocellar seta, inner vertical seta, and reclinate fronto-orbital seta well developed; proclinate fronto-orbital seta greatly reduced, frequently 1 or both lacking; paraverticilar seta greatly reduced or absent. First flagellomere broadly rounded; arista bearing 3–5 long hairs, mostly along basal ½ of dorsal surface. Face with 1–3 short, inclinate (but not cruciate) facial setae on ventral ½ of face and 3 or 4 smaller setulae interspersed along same vertical alignment as larger setae, facial setae and setulae vertically aligned, parallel with parafacial. Parafacial at anterior margin of eye narrow, width much less than length of 1st flagellomere. Gena high, height subequal to combined length of 1st flagellomere and pedicel.

Thorax: Dorsocentral setae 4 (1+3), well developed, posterior pair displaced laterally; presutural supra-alar seta usually well developed, subequal in length to anterior, dorsocentral seta (secondarily lost in *O. isis* and *O. aurantiacus*); acrostichal setulae poorly developed, inconspicuous, absent or, if present, in about 2 irregular rows; postpronotal seta well developed; no-

topleural setae 2, posterior seta shorter than anterior seta; anepisternum bearing 2 poorly developed setae along posterior margin, dorsal seta shorter; katapisternal seta poorly developed or absent. Posterior margin of scutellum truncate, nearly flat. Veins lacking setulae; costal section I lacking long setae; crossvein dm-cu regularly developed, nearly straight, longer than apical section of vein CuA₁, and at distinct angle with posterior margin of wing. Forefemur shallowly excavate along apical ½ of anteroventral surface, excavation bearing comb-like row of short, stout, tooth-like setulae along apical ½ of anteroventral surface; forefemur of male lacking comb-like row of short, stout, slightly flattened setae along apical ½ of anteroventral surface; foretibia of male lacking several long, slender setae at apex on ventral surface; forebasitarsus lacking row of long, slender, pale setulae inserted along anterior surface; midtibia with 2 dorsal, erect, extensor setae (subapically and subbasally); mid- and hindfemora normally developed, much shorter than length of abdomen.

Abdomen: Lacking fasciate pattern. Male terminalia: epanthrium inverted U-shaped, width of arms wider than dorsum in posterior view; cercus oval to distinctly wider ventrally; presurstyli almost touching or fused medially; postsurstylus angulate anteriorly near middle, apex slightly spatulate, shallowly bifurcate; aedeagus in lateral view with posterobasal, curved projection, usually slightly tapered toward apex, apical margin sometimes uneven; aedeagal apodeme with relatively narrow but long keel in lateral view; hypandrium shallowly curved in lateral view, relatively short, shallowly developed.

HISTORICAL REVIEW.—The nomenclatural history of the genus *Oedenops* is relatively recent and brief, as the genus was described early in this century and there are relatively few species. Becker (1903) first described *Oedenops* and its then only included species, *O. isis*, from specimens collected in Egypt. A year earlier, however, Coquillett (1902) had described the first species now placed in *Oedenops*, *O. nudus*, but in the genus *Paralimna*. Coquillett's species was first collected in the state of Tabasco, Mexico, and has since been found to occur more widely in both North and South America. It remains the only known species of *Oedenops* from the New World. Cresson (1929) recognized that Coquillett's species was closely related to *O. isis* and made the generic combination. Wirth (1956) described a second Old World species, *O. afrus*, from specimens collected in South Africa, and that same year Giordani Soika (1956a) described *O. aurantiacus* from specimens collected in Zaire. The latter species, however, is conspecific with *O. isis* and is thus a junior synonym. Giordani Soika was apparently unaware of the variability among specimens of *O. isis*, especially the pronounced sexual dimorphism. This same confusing variability may also have been a factor when Miyagi (1977) described a second junior synonym of *O. isis* as *O. flavitarsis*. Miyagi's species was based on specimens collected in Japan, which is rather distant from Egypt. No other species have been described in the genus.

Oedenops occurs worldwide in tropical zones and ranges into some temperate climates, such as the southwestern United

States and into Japan. There are relatively few species in the genus, but two of these, *O. isis* and *O. nudus*, are very widespread, occurring on more than one continent.

Nothing is known about the immature stages of *Oedenops*, and judging from the few specimens that we have collected or that were made available to us, adults are seldom collected and are relatively scarce in collections and perhaps in nature. Foote (1995) did report specimens of *Oedenops* as regularly occurring in stands of mangrove.

DISTRIBUTION (Figure 72).—Afrotropical: Cameroon, Ethiopia, Kenya, Madagascar (Toliara), Namibia, South Africa (Cape Province, Natal), Zaire. Australasian/Oceanian: Australia (Queensland). Nearctic: USA (AK, AZ, CA, FL, IA, IL, MO, MS, OK, TN, TX, UT). Neotropical: Brazil, Ecuador, Guatemala, Honduras, Mexico (Chiapas, Tabasco), Peru, Venezuela, West Indies (Barbados, Dominica, Dominican Republic, Puerto Rico, St. Vincent). Oriental: China, India (Karnataka),

Malaysia, Pakistan, Taiwan, Thailand, Vietnam. Palearctic: Egypt, Israel, Japan (Hokkaido, Honshu, Kyushu, Shikoku).

DISCUSSION.—Considerable variation is exhibited in specimens of *Oedenops*, especially the coloration of females, although the differences expressed are not strictly sexually dimorphic. The variation seems most evident on the face and mesonotum. The face of males tends to be more intensely colored, such as the yellowish orange to yellow coloration of *O. isis*. In females, often from the same locality, the face varies from almost as intensely colored, like the males, to being much paler and more subdued, frequently whitish gray.

Synapomorphies that we have discovered and that establish the monophyly of *Oedenops* are as follows: (1) only 3–6 arisal hairs; (2) setae on mesonotum generally reduced or absent; (3) katapisternal seta absent; and (4) abdomen lacking fasciate pattern.

The origins of this genus were likely in the Old World, where most of the species diversity occurs.

Key to Species of *Oedenops* Becker

1. Presutural supra-alar seta absent; antenna pale yellow in both sexes (Afrotropical, Australasian/Oceanian, Oriental, Palearctic) 19. *O. isis* Becker
Presutural supra-alar seta present; scape, pedicel, and 1st flagellomere (somewhat) brownish orange, dark gray, or black. 2
2. Male frons and dorsal facial region reddish brown, gena golden; female frons, gena, and face grayish yellow; 2 hair-like setae in facial series. Midfemur of male bearing a few scattered setulae along posteroventral margin (Nearctic, Neotropical) 20. *O. nudus* Coquillett
Male frons brown, face and gena mostly silvery white; female with face and gena, particularly latter, silvery gray; 2 or 3 hair-like setae in facial series. Midfemur of male bearing distinct, comb-like row of numerous, short setae along posteroventral margin (Afrotropical) 18. *O. afrus* Wirth

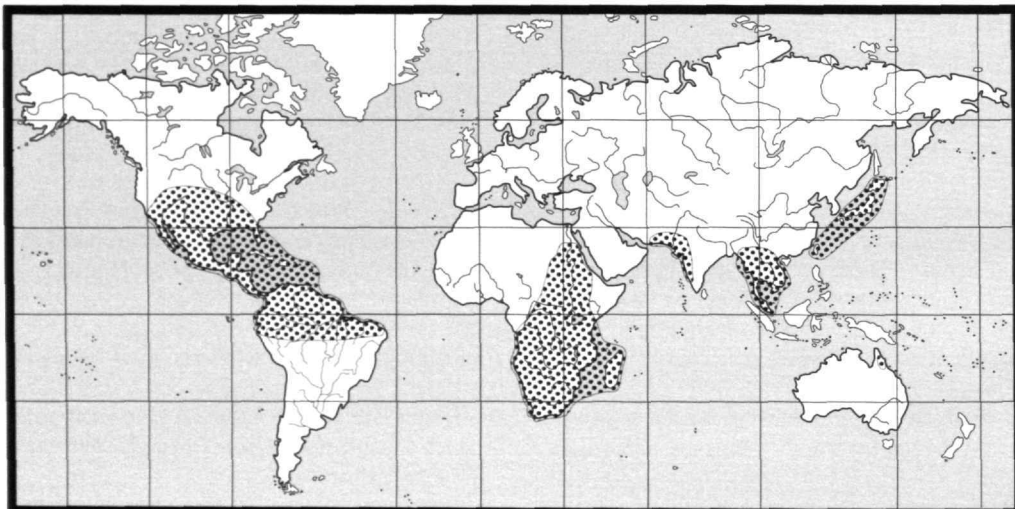


FIGURE 72.—Distribution map for *Oedenops*.

18. *Oedenops afrus* Wirth

FIGURES 73-75

Oedenops afra Wirth, 1956:387.—Cogan, 1968:355 [revision].

Oedenops afrus.—Cogan, 1980:662 [Afrotropical catalog].—Mathis and Zatzwarnicki, 1995:117 [world catalog].

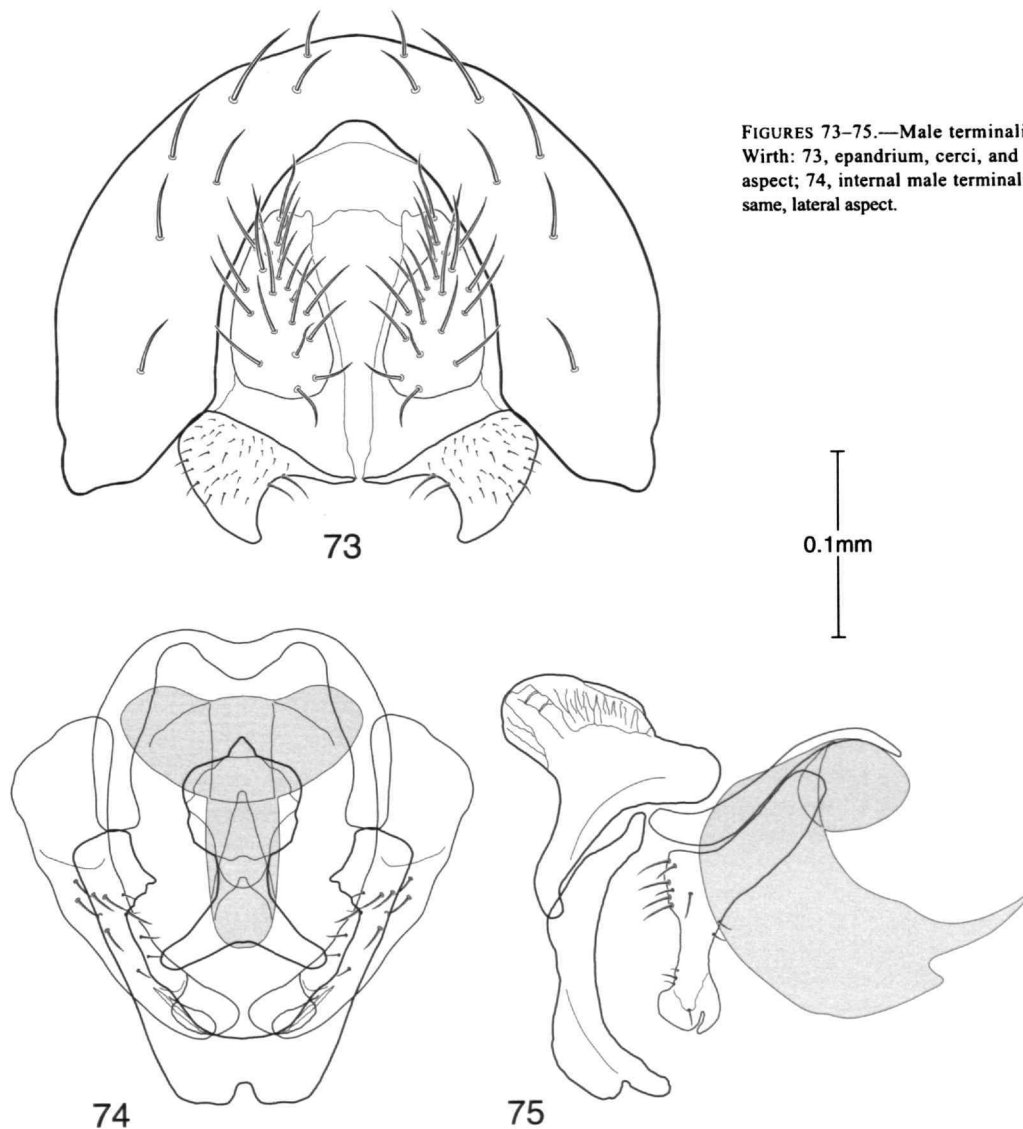
DIAGNOSIS.—This species is distinguished from congeners by the following combination of characters: male frons brown, face and gena mostly silvery white; female with face and gena, particularly latter, silvery gray; scape and pedicel and to a degree 1st flagellomere brownish orange, dark gray, or black; 2 or 3 hair-like setae in facial series; presutural supra-alar seta present; and midfemur of male bearing distinct, comb-like row of numerous short setae along posteroventral margin.

DESCRIPTION.—Moderately small shore flies, body length 2.10–2.35 mm; frons of male brown, face and gena silvery

white to silvery gray; face and gena of female silvery gray. Antenna dark gray to black. Presutural supra-alar seta present. Midfemur of male bearing comb-like row of numerous short setae along posteroventral margin.

Head: Frons of male brown with some faint blackish coloration on parafrons, fronto-orbits gray to brownish gray. Scape and pedicel gray, 1st flagellomere blackish gray; arista bearing 4 or 5 dorsally branching hairs. Face bearing 2 or 3 setae in vertical series; face and gena of male mostly silvery white, face sometimes with faint yellowish to tannish coloration, especially dorsally; face and gena of female silvery gray. Gena high; gena-to-eye ratio 0.43–0.54. Maxillary palpus black with whitish gray microtomentum.

Thorax: Mesonotum mostly grayish brown to brown, slightly darker through acrostichal tract and posterior portion



FIGURES 73-75.—Male terminalia of *Oedenops afrus* Wirth: 73, epandrium, cerci, and presurstyli, posterior aspect; 74, internal male terminalia, ventral aspect; 75, same, lateral aspect.

of scutum, becoming more grayish brown to gray laterally; pleural areas mostly gray. Presutural supra-alar seta present, subequal in length to anterior dorsocentral seta. Costal-vein ratio 0.33–0.35; M-vein ratio 0.80–0.86. Femora and tibiae gray; basal tarsomeres yellow, other tarsomeres becoming progressively darker, apical 1 or 2 tarsomeres brownish orange to brown; midfemur of male bearing comb-like row of numerous short setae along posteroventral margin.

Abdomen: Dorsum mostly gray, sometimes with some brownish coloration anteromedially. Male terminalia (Figures 73–75): epandrium broadly inverted U-shaped, lateral arms wider than dorsum in posterior view (Figure 73); cercus teardrop-shaped, widened ventrally, narrowed dorsally, dorsal apex pointed in posterior view (Figure 73); presurstylus with long, narrow, pointed projection medially, ventral margin pointed and slightly oriented medially, short; postsurstylus in lateral view (Figure 75) with angulate, shallow projection medially along anterior surface, apical portion clavate, very shallowly bifurcate; gonite long, narrow, sinuous in lateral view (Figure 75); aedeagal apodeme with long, moderately wide keel, irregularly rounded in lateral view (Figure 75); aedeagus with posterobasal projection wide, rounded apically, rest of aedeagus slightly curved, width even, apex acutely pointed and projected; hypandrium shallow and shallowly curved, anterior margin slightly narrowed in ventral view, notched medially (Figure 74).

TYPE MATERIAL.—The holotype male of *Oedenops afrus* Wirth is labeled "Port ALFRED [handwritten] South Africa [Cape Province:] 17-3-1953 [17 Mar 1953; day, month, and "53" handwritten][,] B.Stuckenberg/♂ HOLOTYPE *Oedenops afra* W.W.Wirth [red label; sex and species name handwritten]." The holotype is double mounted (minuten in a long, rectangular block of polyporus), is in good condition (the right wing is missing), and is deposited in the NMNH (USNM 62817).

OTHER SPECIMENS EXAMINED.—Afrotropical. KENYA. Lake Victoria, Kisumu (10 km S), 19 Nov 1986, A. Freidberg (5♂, 6♀; USNM).

NAMIBIA. Aus (3.2 km E), Plateau Farm, 14–17 Jan 1972 (1♀; BMNH). Dwyka River, Merweville–Koup Road, 2 Jan 1972 (31♂, 32♀; BMNH). Fish River Canyon (27°37'S, 17°36'E), 12–14 Jan 1972 (2♂, 2♀; BMNH). Helmeringhausen (25 mi W), Barby Farm, 17–18 Jan 1972 (1♀; BMNH). Kamanjab (27 mi ESE), Otjitambi Farm, 13–15 Feb 1972 (2♀; BMNH). Omaruru (53 km ENE), Otikoko Sud Farm, 10–13 Feb 1972 (1♂, 1♀; BMNH). Swakopmund, 26–30 Jan 1972 (3♂, 14♀; BMNH). Windhoek, Hoffnung Farm (lakeside vegetation), 7 Feb 1972 (1♂, 5♀; BMNH).

SOUTH AFRICA. *Cape Province:* Brandkop Area, Calvinia District, South-West Cape, 14 Oct 1964, B.R. and P. Stuckenberg (1♀; NMSA); Dwyka River, Merweville–Koup Island, 2 Jan 1972 (1♂; BMNH); Port St. Johns, 20–25 Nov 1961, B.R. and P. Stuckenberg (3♀; BMNH, NMSA, USNM); Steytlerville (7 km N; Groot River; Lucerne field), 30 Oct 1978, R.M. Miller (1♀; NMSA); Wit River Valley, Cambria Area (33°40'S, 24°34'E), Patensie District, 6 Dec 1967, B.R. and P. Stucken-

berg (1♂; NMSA). *Natal:* Ahrens, near Lilani, Apr 1962, B.R. and P. Stuckenberg (1♀; NMSA).

ZAIRE. *Kivu:* Kavimvira (Uvira; at light), Dec 1954, G. Marlier (1♀; MRAC).

DISTRIBUTION.—Afrotropical: Kenya, Namibia, South Africa (Cape Province, Natal), Zaire.

REMARKS.—This species, widespread in eastern and southern Africa, is the sister species to the other two species of *Oedenops*. A synapomorphy is the fringe-like row of closely set setulae along the posteroventral margin of the male midfemur. There are no conspicuous color differences between the sexes.

19. *Oedenops isis* Becker

FIGURES 76–78

Oedenops isis Becker, 1903:179; 1926:94 [review, list, Egypt].—Cresson, 1929:183 [synonymy with *O. nudus*]; 1947b:108 [removed from synonymy with *O. nudus*; list, Egypt (Island Elephantina), Sudan].—Wirth, 1956:388 [compared with *O. afrus* Wirth].—Cogan, 1968:355–356 [revision]; 1980:662 [Afrotropical catalog]; 1984:148 [Palearctic catalog].—Mathis and Zatwamicki, 1995:117–118 [world catalog].

Oedenops nudus of authors, not Coquillett [misidentification].—Cresson, 1929:183–184 [in part; discussion, synonymy of *O. isis* Becker with *O. nudus* (Coquillett)].

Oedenops aurantiacus Giordani Soika, 1956a:123.—Cogan, 1968:355 [revision]; 1980:662 [Afrotropical catalog].—Mathis and Zatwamicki, 1995:117 [world catalog]. [New synonymy.]

Oedenops flavitarsis Miyagi, 1977:46.—Cogan, 1984:148 [Palearctic catalog].—Mathis and Zatwamicki, 1995:117 [world catalog]. [New synonymy.]

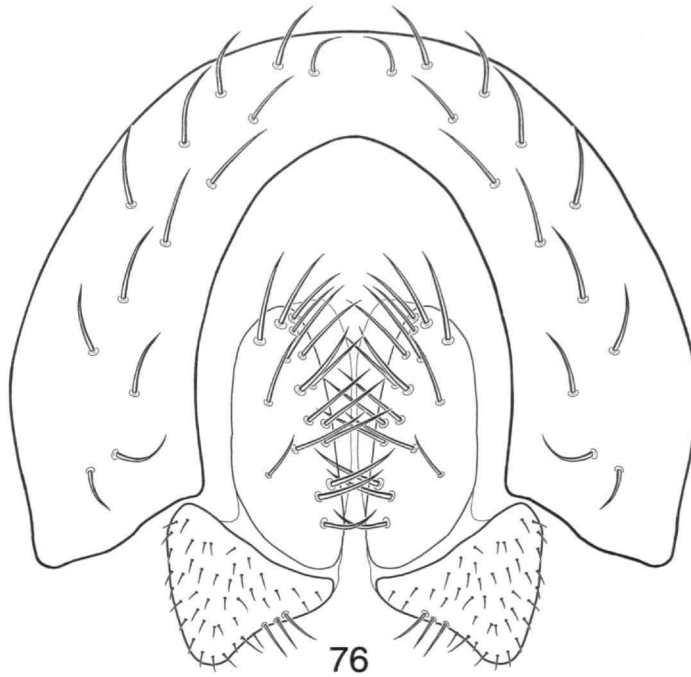
DIAGNOSIS.—This species is distinguished from congeners by the following combination of characters: antenna pale yellow in both sexes; presutural supra-alar seta absent; fore- and midlegs mostly yellow to yellowish orange; and midfemur of male bearing sparse, short row of setulae along posteroventral margin.

DESCRIPTION.—Small to moderately small shore flies, body length 1.70–2.40 mm.

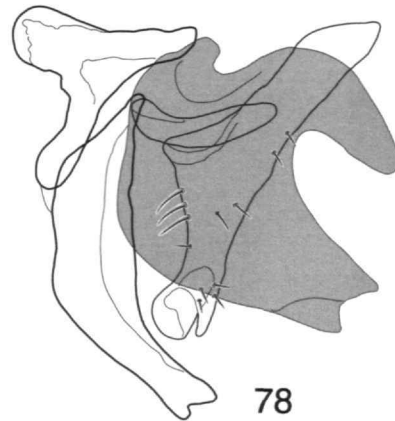
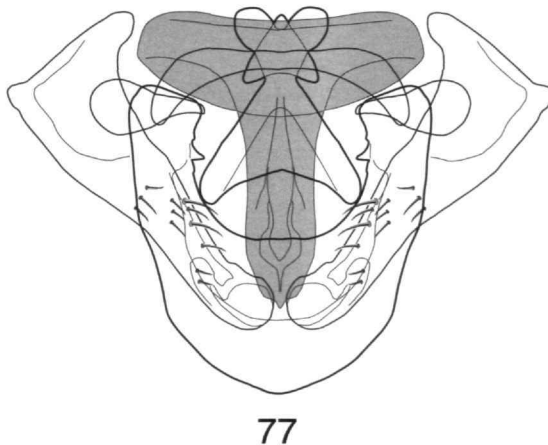
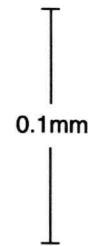
Head: Antenna pale yellow to orange in both sexes. Genito-eye ratio 0.38–0.40. Maxillary palpus faintly grayish yellow to yellow.

Thorax: Generally gray; occasionally with broad, yellowish brown to brown stripe between dorsocentral tracks of setae, more evident on posterior ½ of scutum; anepisternum yellowish gray, this coloration extended onto immediately adjacent sclerites in some specimens. Supra-alar seta lacking. Costal-vein ratio 0.25–0.27; M-vein ratio 0.75–0.80. Color of legs variable and somewhat sexually dimorphic; fore- and midleg of males and of some females mostly yellow to yellowish orange, only base of forefemur and apical tarsomere sometimes darkened, otherwise femora mostly gray, especially for females; hindfemur with basal ½ or more gray to blackish gray, apex yellowish; forefemur with row of short, stout, pale, tooth-like setulae along anteroventral surface at apical ½; midfemur of male bearing few scattered setulae along posteroventral margin.

Abdomen: Male terminalia (Figures 76–78): epandrium in posterior view inverted U-shaped (Figure 76), generally thick walled, each arm becoming wider ventrally; cercus hemispherical, bearing long setulae, ventral and dorsal apices about



FIGURES 76–78.—Male terminalia of *Oedenops isis* Becker: 76, epandrium, cerci, and presurstyli, posterior aspect; 77, internal male terminalia, ventral aspect; 78, same, lateral aspect.



equally rounded; presurstylus in posterior view triangular (Figure 76), bearing longer setulae along medial margin, somewhat fused dorsomedially with ventral margin of cercus; postsurstylus with anteroapical surface shallowly concave, posterior surface nearly flat, apex capitate, very shallowly bifurcate; aedeagus in lateral view (Figure 78) with relatively long posterodorsal projection narrowed and extended apically, rest of aedeagus wide basally, curved and becoming narrower posteriorly, apex shallowly concave; gonite rod-like, portion attached to hypandrium slightly curved in lateral view (Figure 78); aedeagal apodeme more or less triangular, with narrow, long

keel; hypandrium moderately concave, anterior margin broadly rounded and shallowly pointed in ventral view (Figure 77).

TYPE MATERIAL.—The lectotype male of *Oedenops isis* Becker, here designated to stabilize and make more universal the use of this name, is labeled “[Egypt] Assuan 44554. I.[Jan] [handwritten]/Typus [red label]/LECTOTYPE ♂ *Oedenops isis* Becker By Mathis and Zatwarnicki [handwritten except for “LECTOTYPE” and “By”]; label with black submarginal border]/Zool.Mus. Berlin [yellow label].” The lectotype is double mounted (of the two minuten, the lectotype is mounted on the minuten nearer the main pin in a rectangular block of pith; the

second, more outside specimen, a female, is here designated a paralectotype), is in good condition (some setae of the mesonotum missing or displaced), and is deposited in the ZMHU. The original description (Becker, 1903:179) cited "Insel Philae bei Assuan" as the type locality. In addition to the lectotype and female paralectotype there are five additional female paralectotypes, here designated, that have the same locality data and are deposited in the MNHN, USNM, and ZMHU.

The lectotype male (not a female as indicated in the original publication) of *Oedenops aurantiacus* Giordani Soika, here designated to stabilize and make more universal the use of this name, is labeled "HOLOTYPUS [light orange label with black submarginal border]/COLL. MUS[ÉE DU]. CONGO Madagascar: [Tamatave] Maroanetra[,] XII-1949 [Dec 1949][,] J. Vandon/HOLOTYPUS *Oedenops aurantiacus* Soika [species name and author handwritten]/LECTOTYPE *Oedenops aurantiacus* G. Soika ♂ By Mathis & Zatzwornicki [all except "LECTOTYPE" and "By" handwritten; label with black submarginal border]." The lectotype is double mounted (minuten in a long rectangular block of polyporus), is in poor condition (left wing missing, right wing folded, most setae of the mesonotum missing), and is deposited in the MRAC. Although the lectotype is labeled "HOLOTYPUS," Giordani Soika (1956a:123) recognized a type series of two "♀ ♀," neither of which was designated as the holotype, and thus the need for this lectotype designation.

The holotype male of *Oedenops flavitarsis* Miyagi is labeled "Japonia Kyushu I. MIYAGI Is. T[s]ushima 6, Aug. 1963/-type *Oedenopus* [sic] *flavitarsis* I. Miyagi [red label; all except "-type" handwritten]." The holotype is double mounted (minuten in a rectangular card), is in poor condition (damaged in shipment; wings on small rectangular card below specimen; abdomen removed and dissected, with the parts in an attached microvial), and is deposited in the HUS.

OTHER SPECIMENS EXAMINED.—Afrotropical. CAMEROON. Kribi (beach; route N7), 28–29 Nov 1987, A. Freidberg (3♂; USNM).

ETHIOPIA. Lake Langano, 13 Dec 1989, A. Freidberg, F. Kaplan (1♂; USNM).

MADAGASCAR. *Toamasina*: Fenerive (lagoon shore), Dec 1955, B.R. Stuckenberg (2♂, 5♀; BMNH, NMSA, USNM). *Toliara*: Morondava, 28–31 Mar 1990, W.E. Steiner, C. Kremen, V. Razafimahatratra (1♂, 1♀; USNM); Sud-Est Sainte Luce, Fort Dauphin (=Taolanaro; 10 m), 22–24 Feb 1958, B.R. Stuckenberg (6♂, 3♀; BMNH, NMSA, USNM); Saint Augustin (6 m), 11–13 Feb 1958, B.R. Stuckenberg (2♀; BMNH, NMSA).

NAMIBIA. Skeleton Coast Park. Kunene River mouth (17°15'97"S, 11°46.83'E), 17–18 Mar 1998, A.H. Kirk-Spriggs (1♀; NNIC).

Australasian/Oceanian. AUSTRALIA. *Queensland*: Deeral, Jan 1950, N.L.H. Krauss (1♀; USNM).

Oriental. CHINA. *Yunnan*: Jinhong, Lanchan River, 11 Mar 1999, P. Grootaert (1♂; IRSN).

INDIA. *Karnataka*: Mudigere (19 km W), 6 Apr 1980, A. Freidberg, W.N. Mathis (2♀; USNM).

MALAYSIA. Selangor, Kuala Lumpur (light), 8 Aug 1958, R. Trauo, (1♂; BMNH).

PAKISTAN. Lahore, Jun–Aug 1957, J. Maldonado (1♂; USNM).

THAILAND. Loei: Chiang Khan Mae Kong, 11 Feb 1999, P. Grootaert (1♀; IRSN); Na Haeo, 12 Feb 1999, P. Grootaert (3♀; IRSN).

TAIWAN. Anping, Sep 1908, H. Sauter (1♂; DEI).

VIETNAM. Prens (15 km from Da Lat; 11°56'N, 108°25'E), 15–19 Oct 1988, O. Mahunka, Vásárhelyi (1♂; HNHM). Hanoi, Song Hong (21°37'N, 104°44'E), 17 Jan 1986, O. Mahunka (4♂, 4♀; HNHM).

Palaearctic. EGYPT. Asswan, Jan (1♂, 5♀; USNM, ZMHU; lectotype and paralectotypes). Helwan, 31 Mar 1964, G. Steyskal (1♀; USNM). Elephantine, Reimoser (1♂; ANSP).

ISRAEL. Ein Avdat, 29 Mar 1980, A. Freidberg, W.N. Mathis (2♀; USNM).

DISTRIBUTION.—Afrotropical: Cameroon, Ethiopia, Madagascar (Toliara), Namibia, Sudan. Australasian/Oceanian: Australia (Queensland). Oriental: China, India (Karnataka), Malaysia, Pakistan, Taiwan, Thailand, Vietnam. Palaearctic: Egypt, Israel, Japan (Hokkaido, Honshu, Kyushu, Shikoku).

REMARKS.—Considerable variation is evident in facial and thoracic coloration. In specimens from some localities, the coloration appears to be sexually dimorphic, with the male face being deeply yellowish and the female's grayish white to gray. At other localities, the female face is also yellowish, varying from lightly grayish yellow to deeply yellow, quite similar to that of males. Likewise, the brown stripe between the dorsocentral setae varies from being restricted only to that area to having the brown coloration covering much of the mesonotum.

In addition to variation in color, two other factors probably contributed to the misidentifications and descriptions of the two junior synonyms. The first was Giordani Soika's mistaken determination of the sex of the lectotype, which is a male, not a female. With some sexual dimorphism evident in this species, mistaking the sex of the type series would hinder the accurate identification of this species. Although the male of *O. aurantiacus* is deeply reddish brown, the structures of the male terminalia are essentially identical to those of *O. isis*, and because variation is demonstrated within this species and the distributions are broadly sympatric, we believe that these specimens are conspecific and that the two names are thus synonyms.

The second problem apparently resulted from a lack of reliable comparative specimens or descriptions. Miyagi's (1977:46) diagnosis of *O. flavitarsis* adequately contrasted it with *O. nudus*, known from western North America. There was no comparison of *O. flavitarsis* with *O. isis*, however, perhaps because the latter was then known only from northern Africa, which is geographically and climatically more distant from Japan than is western North America. Our comparison of *O. flavitarsis* with *O. isis* revealed the conspecificity of the two type series and thus that these two names are likewise synonyms.

This species and *O. nudus* are sister species, as evidenced by the sexual dimorphism, especially the colorational differences between males and females, and by the tendency for a broad, brown stripe between the dorsocentral tracks, which is some-

times more evident on the posterior half of the scutum and which continues on to the scutellum. This species is distinguished from *O. nudus* by the absence of a prescutellar supra-alar seta and by its distribution in the Old World. *Oedenops nudus* occurs only in the New World.

20. *Oedenops nudus* (Coquillett)

FIGURES 79–84

Paralimna nuda Coquillett, 1902:182.—Aldrich, 1905:624 [Nearctic catalog].—Jones, 1906:178–179 [key, catalog].

Oedenops nudus.—Cresson, 1916:104 [tentative generic combination]; 1929:183 [in part; generic combination, synonymy of *O. isis* Becker with *O. nudus* (Coquillett)]; 1946:229 [review, Nearctic Region]; 1947a:46 [review, Neotropical Region].—Wirth and Stone, 1956:470 [list, California].—Wirth, 1956:388 [compared with *O. afrus* Wirth]; 1965:748 [Nearctic catalog]; 1968:16 [Neotropical catalog].—Cole, 1969:396 [list, western United States].—Mathis and Zatwarnicki, 1995:118 [world catalog].

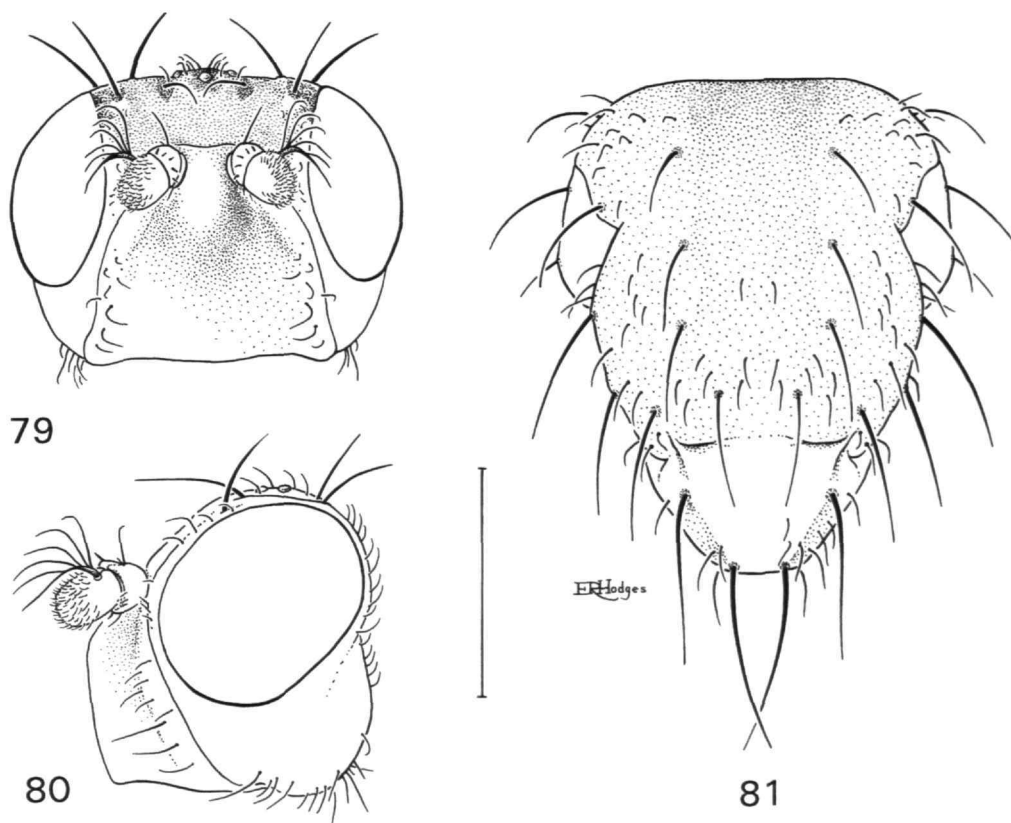
DIAGNOSIS.—This species is distinguished from congeners by the following combination of characters: Male frons and dorsal facial region reddish brown, gena golden; female frons, gena, and face grayish yellow. Antenna dark gray to blackish orange; 2 hair-like setae in facial series; presutural supra-alar

seta present; and midfemur of male bearing a few scattered setulae along posteroventral margin.

DESCRIPTION.—Moderately small shore flies, body length 2.00–2.65 mm.

Head (Figures 79, 80): Frons sexually dimorphic, male frons orange to rusty brown, concolorous with dorsal portions of face and broad stripe on mesonotum, female frons whitish gray to gray, concolorous with pleural areas. Antenna blackish gray to yellowish orange; scape grayish orange to blackish orange; pedicel paler than scape, more yellowish orange; 1st flagellomere mostly yellowish orange to orange, sometimes darkened basally; arista bearing 4–6 dorsally branching hairs. Face bearing 2 or 3 setae in vertical series; face and gena of female mostly silvery white to yellowish gray, face of male with dorsal portion concolorous with frons, ventral portion paler, more grayish. Gena high; gena-to-eye ratio 0.40–0.42. Maxillary palpus black with whitish gray microtomentum.

Thorax (Figure 81): Scutum bicolored, mostly whitish gray to gray but with broad stripe between dorsocentral setae tan to golden brown, brown coloration extended to scutellum and with short, narrower stripe laterad of posterior dorsocentral setae brown; pleural areas mostly whitish gray to gray. Presutural



FIGURES 79–81.—*Oedenops nudus* (Coquillett): 79, head, lateral aspect; 80, same, anterior aspect; 81, mesonotum, dorsal aspect. Scale = 0.5 mm.

supra-alar seta present, subequal in length to anterior dorsocentral seta. Costal-vein ratio 0.29–0.33; M-vein ratio 0.86–0.90. Femora whitish gray to gray; tibiae mostly gray; basal tarsomeres yellow, other tarsomeres becoming progressively darker, apical 1 or 2 brownish orange to brown; forefemur bearing short row of closely set, tooth-like setulae anteroventrally along apical ½; midfemur of male bearing few scattered setulae along posteroventral margin.

Abdomen: Dorsum mostly gray, sometimes with some brownish coloration anteromedially. Male terminalia (Figures 82–84): epandrium in posterior view (Figure 82) inverted U-shaped, lateral arms wider than dorsal portion, ventral margin broadly rounded; cercus in posterior view (Figure 82) ovate, ventral margin more broadly rounded than dorsal margin; presurstyli nearly touching medially, triangular, slightly longer than wide; postsurstylus with anterior margin angulate medially, dorsal extension narrowed to pointed apex, ventral extension truncate, very shallowly bifurcate apically; gonite very narrow, with apices slightly curved; aedeagal apodeme triangular in lateral view (Figure 84), keel long and relatively narrow, extensions short; aedeagus with posterobasal projection narrowly developed, curved posteriorly, acutely pointed, rest of aedeagus nearly parallel sided, slightly curved, broadly rounded apically; hypandrium with very irregular surface in lateral view (Figure 84), V-shaped in ventral view, pointed anteriorly (Figure 83).

TYPE MATERIAL.—Holotype male *Paralimna nuda* Coquillett is labeled "Mexico [handwritten]/Frontera 3.9 Tab[asco]/Coll Townsend/on moist sand at river edge [handwritten]/Type No 6641 U.S.N.M. [red label; number handwritten]/*Paralimna nuda* Coq. [handwritten; label with black submargin]." The holotype is double mounted (minuten in a rectangular block of pith), is in good condition, and is deposited in the NMNH (USNM 6641).

OTHER SPECIMENS EXAMINED.—Nearctic. UNITED STATES. *Arizona.* Cochise County: Chiricahua Mountains, Martyr Dam, 11 Jun 1951, M.R. Wheeler (1♂, 2♀; USNM); Fairbank, 13 Jun 1951, M.R. Wheeler (2♂, 2♀; USNM); San Pedro River (12 km E Sierra Vista; Hwy 90; 124 m), 3 Jun 1991, J. Gelhaus, C. Nelson (4♂, 3♀; ANSP). Coconino County: Bill Williams Fork, F.H. Snow (2♂, 2♀; ANSP). Maricopa County: Tempe, 19–24 Jun 1917, J.M. Aldrich (1♂, 2♀; ANSP). Santa Cruz County: Patagonia, 23–26 Aug 1953, M.R. Wheeler (1♀; USNM). Pima County: Tucson, Saguaro National Monument, 10 Apr 1935, A.L. Melander (2♂, 1♀; ANSP); Kits Peak (near 32°N, 111°32'W; 1097 m), Baboquivari Mountains, 7–9 Aug 1916 (4♂, 2♀; AMNH, ANSP). *Arkansas.* Jefferson County: Pine Bluff, 3 Sep 1952, M.R. Wheeler (1♀; USNM). Union County: Calion, 3 Sep 1952, M.R. Wheeler (1♂; USNM). *California.* Los Angeles County: Los Angeles, 8 Aug 1916, V. Duran (1♂; ANSP); Lake Elsinore, 2 Aug–21 Nov 1911, 1934, J.M. Aldrich, A.L. Melander (1♂, 2♀; ANSP). San Diego County: San Diego (lakeside), 4 Aug 1932 (3♂, 4♀; ANSP). *Florida.* Okaloosa County: Ft. Walton, 16 Jun 1953, M.R. Wheeler (1♀; USNM). *Illinois.* Morgan County: Meredosia, 20 Aug 1917 (1♂, 1♀; ANSP). *Mississippi.* Oktibbeha County: Mississippi State, 30 Oct 1922 (2♂, 1♀; ANSP). *Missouri.* Bollinger County: Patton, 4 Sep 1952,

M.R. Wheeler (1♂; USNM). Perry County: Lithium, 5 Sep 1952, M.R. Wheeler (1♀; USNM). *Oklahoma.* Kingfisher County: Kingfisher, 13 Sep 1952, M.R. Wheeler (1♂; USNM). *Tennessee.* Henry County: Paris Landing State Park, 29 Jul 1954, M.R. Wheeler (1♀; USNM). *Texas.* Bastrop County: Bastrop, 4 Nov 1951, M.R. Wheeler (1♀; USNM). Culberson County: Van Horn, 14 Jun 1950, M.R. Wheeler (2♂, 4♀; USNM). Travis County: Austin, 14 Jun–27 Oct 1901, 1950, M.R. Wheeler (6♂, 15♀; ANSP, USNM). *Utah.* Emery County: Green River, 19 Jul 1988, D. and W.N. Mathis (1♀; USNM).

Neotropical. BARBADOS. *St. Andrew:* Long Pond (13°15.1'N, 59°33.3'W), 10–11 Sep 1996, W.N. Mathis (18♂, 4♀; USNM). *St. Peter:* Six Mens Bay (13°16.5'N, 59°38.8'W), 12 Sep 1996, W.N. Mathis (1♂; USNM).

BRAZIL. Natal, 5–24 Feb 1943, F.M. Snyder (1♀; AMNH).

DOMINICA. Layou River mouth, 9 Jan–24 Mar 1965, W.W. Wirth (74♂, 43♀; USNM).

DOMINICAN REPUBLIC. *La Vega:* Constanza (~16 km SE; 18°50.2'N, 70°40.7'W; 1550 m), 27 Mar 1999, W.N. Mathis (1♂; USNM); El Rio (9.5 km E; 19°0.9'N, 70°33.5'W; 980 m), 6 May 1995, W.N. Mathis (12♂, 8♀; USNM); Rio Camu (3.5 km NW La Vega; 19°13.7'N, 70°35.2'W; 100 m), 10 May 1995, W.N. Mathis (2♂, 2♀; USNM). *Puerto Plata:* Rio Camu (14 km E Puerto Plata; 19°11.9'N, 70°37.4'W), 17 May 1995, W.N. Mathis (2♂, 1♀; USNM).

ECUADOR. Balao Guayas, Dec 1955, J.R. Levi-Castillo (2♂, 1♀; USNM).

GUATEMALA. Escuintla, Grutas de San Pedro Martir, 10 Aug 1965, P.J. Spangler (1♂; USNM).

HONDURAS. Puerto Castilla, 28 May 1924, R.H. Painter (1♀; ANSP).

MEXICO. *Chiapas:* Boca de Cielo (17 km S Puerto Arista), 18 May 1985, A. Freidberg, W.N. Mathis (1♂, 3♀; USNM).

PERU. *Madre de Dios:* Manu, Rio Manu (near Romero), 8 Sep 1988, W.N. Mathis (6♂, 3♀; USNM).

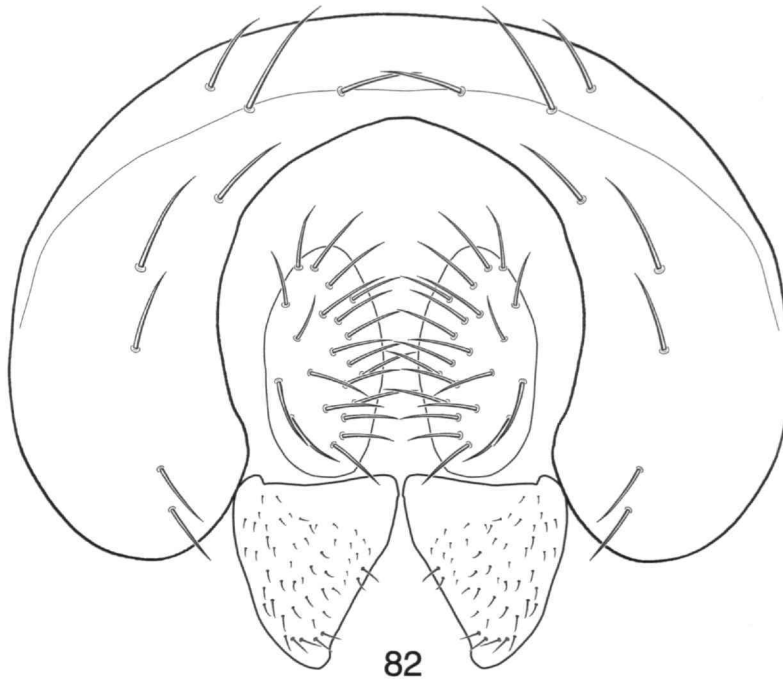
PUERTO RICO. Fajardo, Las Croabas (Seven Seas Beach; 18°23'N, 65°37'W), 17 Feb 1996, W.E. Steiner, J.M. Swearingen (1♀; USNM).

ST. VINCENT. *St. Andrew:* Buccament Bay (near beach; 13°11'N, 61°16'W), 8 Jun 1991, D. and W.N. Mathis (11♂, 10♀; USNM). *St. Patrick:* Wallilabou (beach; 13°15'N, 61°16'W), 27 Mar 1989, W.N. Mathis (1♀; USNM).

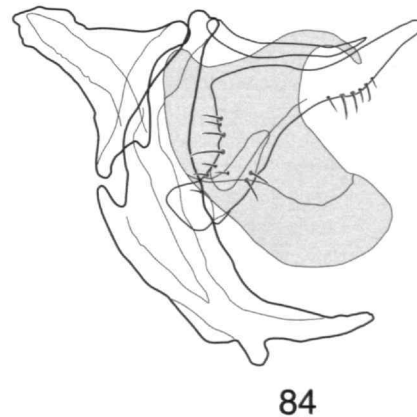
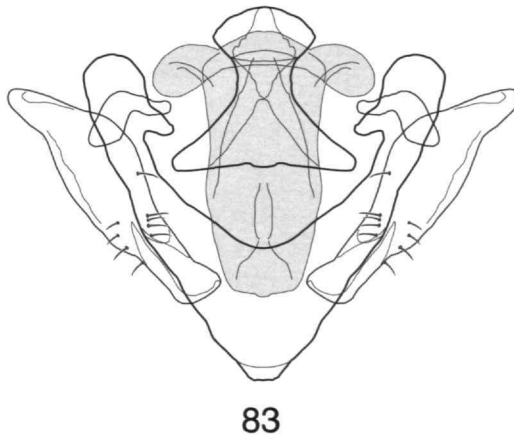
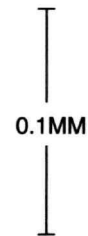
VENEZUELA. Guarico, Hato Masaguaral (45 km S Calabozo; 8.57°N, 67.58°W; 75 m; ultraviolet light), Gallery Forest #28, 3–5 Jun 1988, M. Epstein (1♂; USNM).

DISTRIBUTION.—Nearctic: USA (AK, AZ, CA, FL, IA, IL, MO, MS, OK, TN, TX, UT). Neotropical: Brazil, Ecuador, Guatemala, Honduras, Mexico (Chiapas, Tabasco), Peru, Venezuela, West Indies (Barbados, Dominica, Dominican Republic, Puerto Rico, St. Vincent).

NATURAL HISTORY.—This species, although primarily occurring in freshwater habitats, can apparently tolerate some brackish water. On Barbados, for example, the species was abundant along the sandy shore of a brackish-water pool at the base of secondary dunes on the beach with the Atlantic Ocean.



FIGURES 82–84.—Male terminalia of *Oedenops nudus* (Coquillett): 82, epanthrium, cerci, and presurstyli, posterior aspect; 83, internal male terminalia, ventral aspect; 84, same, lateral aspect.



The obvious common feature to all habitats, fresh water or marine, is a sandy substrate, often bare of conspicuous vegetation.

REMARKS.—This is the only species of *Oedenops* to occur in the New World, where the species is relatively widespread.

Genus *Paralimna* Loew

Paralimna Loew, 1862a:138 [type species: *Paralimna appendiculata* Loew, 1862 (= *Notiphila punctipennis* Wiedemann, 1830), monotypy]; 1862b:13 [review, Afrotropical species].—Osten Sacken, 1878:201 [Nearctic catalog].—Becker, 1896:114–115 [review, discussion of relationships].—Williston, 1908:308 [key to Nearctic genera].—Hendel, 1914:103–109 [review, Oriental species].—Cresson, 1916:101–124 [revision]; 1946:229 [key to Nearctic species]; 1947a:37, 46 [key, review of Neotropical species]; 1947b:106, 108–118

[key, review of Afrotropical species]; 1948:6–12 [review of Australasian species, key].—Malloch, 1933:11 [review]; 1934b:196–197 [generic key, Marquesas and Society Islands].—Curran, 1934:347 [key to Nearctic genera].—Wirth and Stone, 1956:465, 470 [generic key, review, California species].—Wirth, 1965:748 [Nearctic catalog]; 1968:14–16 [Neotropical catalog].—Cole, 1969:392, 396 [generic key, review of species from western United States].—Cogan and Wirth, 1977:333–335 [Oriental catalog].—Cogan, 1980:663–664 [Afrotropical catalog]; 1984:148 [Palearctic catalog].—Mathis and Zatwarnicki, 1995:118–127 [world catalog].

DIAGNOSIS.—This genus is distinguished from other genera of Dryxini by the following combination of characters: anterior proclinate fronto-orbital seta larger than posterior seta; arista bearing 8 or more dorsal hairs; facial seta usually 1, if more,

not well separated; notopleuron bearing 2 large setae; anepisternal and anterior dorsocentral (1+3) setae well developed; presutural supra-alar seta present (lacking in 1 species of *Oedenops*); katapisternal seta present; forefemur lacking row of short, somewhat blunt spines along anteroventral surface; and mid- and hindfemora normally developed, much shorter than length of abdomen.

DESCRIPTION.—Small to large shore flies, body length 1.85–7.80 mm.

Head: Frons wider than high, shallowly arched anteroventrally, not projected forward, sparsely setulose; ocelli in equilateral or isosceles triangle; pseudopostocellar setulae well developed, divergent; paraverticilar seta moderately well developed, less than ½ length of outer vertical seta; ocellar seta, inner and outer vertical setae, and reclinate fronto-orbital seta well developed; proclinate fronto-orbital setae 2, both shorter than reclinate seta, moderately well developed, anterior seta about twice length of posterior seta. First flagellomere broadly rounded; arista bearing 5 or more long rays along dorsal surface. Face with 2 or 3 long (subequal to length of large reclinate seta), inclinate (but not cruciate) facial setae on ventral ½ of face and with 3 or 4 smaller setulae interspersed along same vertical series as larger setae. Parafacial at anterior margin of eye narrow, width much less than length of 1st flagellomere. Gena high, height subequal to combined length of 1st flagellomere and pedicel; genal seta well developed.

Thorax: Mesonotum more or less uniformly setulose; acrostichal setulae in 6–8 irregular rows; 1 pair of large, prescutellar, acrostichal setae; dorsocentral setae 4 (1+3), well developed, posterior pair displaced laterally; acrostichal setulae well developed, conspicuous, in about 6 irregular rows; presutural seta well developed, subequal in length to anterior dorsocentral seta; supra-alar setae 2 (1+1), presutural seta inserted more mediad than postsutural seta; postpronotal seta well developed; notopleural setae 2, posterior seta shorter; anepisternum bearing 2 large setae along posterior margin, ventral seta greatly elongate; katapisternal seta well developed. Posterior margin of scutellum truncate, nearly flat. Veins lacking setulae; costa long, extended to vein M; crossvein dm-cu regularly developed, nearly straight, longer than apical section of vein CuA₁, and at distinct angle with posterior margin of wing. Mid- and hindfemora normally developed, not conspicuously elongate; foretibia of male lacking several long, slender setae at

apex on ventral surface; forebasitarsus lacking row of long, slender, pale setulae inserted along anterior surface; midtibia with 3 dorsal extensor setae (subapically, subbasally, and near basal ⅓); mid- and hindfemora normally developed, much shorter than abdomen.

Abdomen: Male terminalia: epandrium broadly and uniformly U-shaped in posterior view, lateral arms of similar width; cercus ovoid with rounded apices; presurstylus bar-like, wide and short with extero-lateral appendage directed antero-internal or antero-external; presurstyli usually separated, rarely fused to each other; postsurstylus in dorsal view about 5 times as long as wide, apex broadly bifurcate, internal lobe wide and directed ventrally; in lateral view postsurstylus distinctly sinuous, ventral margin bearing long setae, terminal bifurcation with 2 very long and 2 short setae inside; aedeagus elongate, shape in dorsal view triangular or rhomboidal, mostly with lateral appendices with length to ⅔ that of aedeagus; in lateral view aedeagus irregular in shape, mostly tapered anteriorly with sinuous margins, apex usually acutely pointed and projected; aedeagal apodeme in dorsal view with apex wide, in lateral view triangular; hypandrium in dorsal view broadly oval, posterior margin incised to about ⅓ length of hypandrium; in lateral view moderately deep to very deep (height equal to length).

DISTRIBUTION.—The genus *Paralimna* occurs pantropically, with a few species extending into temperate areas (Egypt, Japan, northern Australia, North America).

DISCUSSION.—*Paralimna*, with 85 species (Mathis and Zatzwarnicki, 1995), includes most of the species diversity of Dryxini, and we know that there are numerous undescribed species in collections and, undoubtedly, undescribed species that await collection. For example, in a faunistic work on the shore flies of the West Indies, Mathis (in prep.) is describing seven new species, which comprise over one-half of the known fauna of *Paralimna* from these islands.

The species diversity of *Paralimna* is matched by its structural diversity, and the genus is difficult to characterize. The only synapomorphy we have discovered that establishes the monophyly of the genus is the lateral aedeagal processes of the aedeagus.

Herein we revise at the species level only the subgenus *Phaiosterna*, but we also review the species of the *limbata* group.

Key to Subgenera of *Paralimna* Loew

1. Gena short, height about ¼ eye height; 1st flagellomere elongate, length more than twice width 2
 Gena high, height about ⅓ eye height or more; 1st flagellomere shorter than above, length at most 1.5 times width *Paralimna* Loew, in part
2. Mesonotum (brown medially and through dorsocentral track, yellowish to brownish gray between) and anepisternum (brown dorsally and ventrally, gray between) conspicuously vittate; crossvein dm-cu and sometimes adjacent veins with halo of brown (the *limbata* group) *Paralimna* Loew, in part
 Mesonotum and anepisternum mostly unicolorous and grayish brown to black; crossvein dm-cu and rest of wing essentially unicolorous *Phaiosterna* Cresson

Subgenus *Paralimna* Loew

Paralimna Loew, 1862a:138 [type species: *Paralimna appendiculata* Loew, 1862 (= *Notiphila punctipennis* Wiedemann, 1830), monotypy].—Cresson, 1947a:47–54 [diagnosis, review of Neotropical species]; 1947b:108–118 [review of Afrotropical species, key]; 1948:6–9, 11–12 [review of Afrotropical species, key].—Wirth, 1965:748 [Nearctic catalog]; 1968:14–15 [Neotropical catalog].—Cogan, 1980:663–664 [Afrotropical catalog].—Mathis and Zatwarnicki, 1995:118–126 [world catalog].

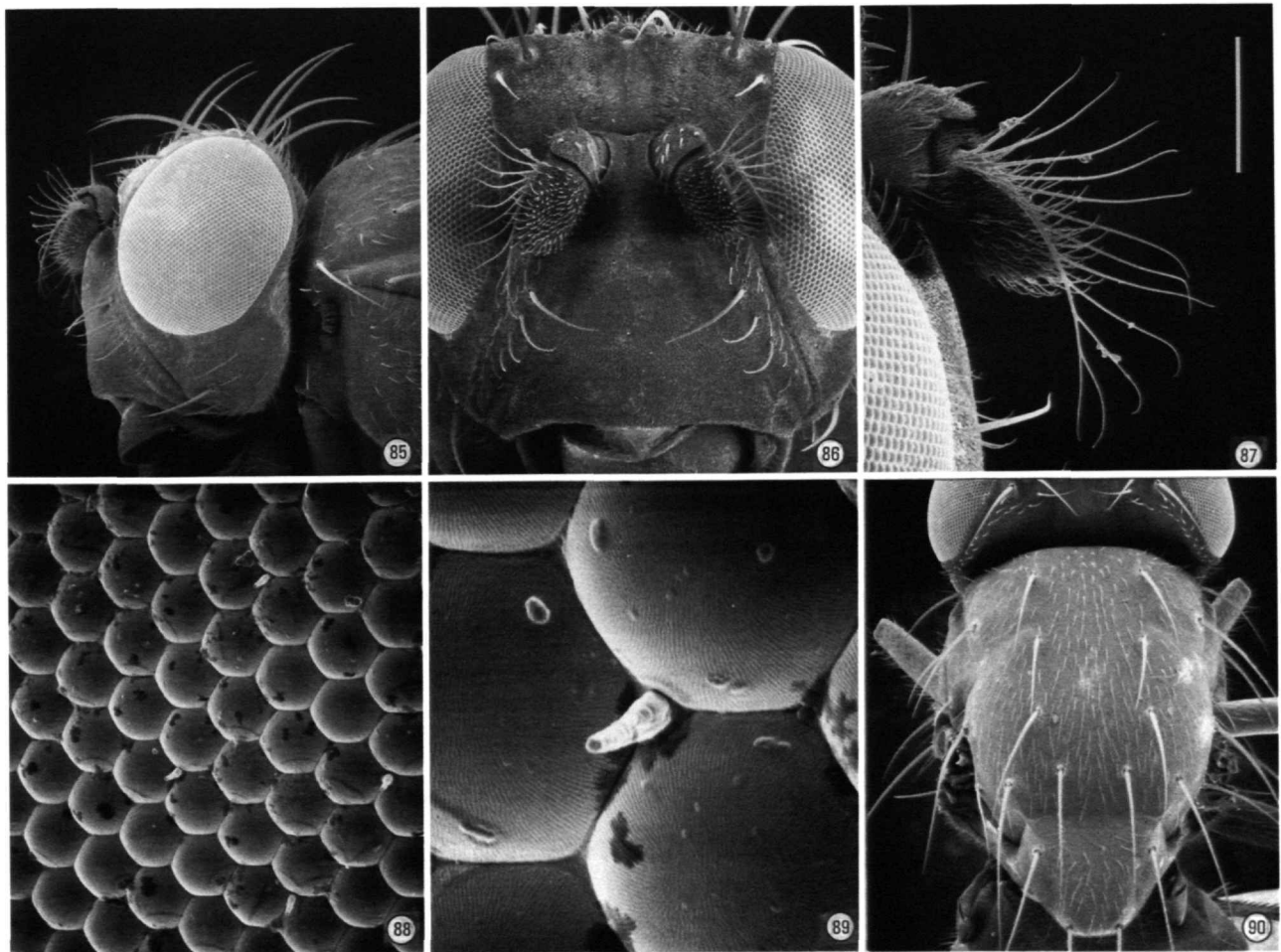
Poecilothorax Becker, 1922:73 [as a genus; type species: *Poecilothorax angustus* Becker, 1922 (= *Paralimna puncticollis* Becker, 1922), monotypy].—Cresson, 1947b:108 [synonymy].

DIAGNOSIS.—This subgenus is distinguished from other congeneric subgenera by the following combination of characters: gena short, height about $\frac{1}{4}$ eye height; 1st flagellomere elongate, length more than twice width; mesonotum (brown medi-

ally and through dorsocentral track, yellowish to brownish gray between) and anepisternum (brown dorsally and ventrally, gray between) conspicuously vittate; and crossvein dm-cu and sometimes adjacent veins with halo of brown (the *limbata* group).

DESCRIPTION.—Small to large shore flies, body length 1.85–6.30 mm.

Head (Figures 85–89): Ocelli in equilateral triangle; pseudopostocellar setulae well developed, divergent; paraverticlar seta well developed, subequal in length to anterior proclinate fronto-orbital seta; ocellar seta well developed, usually longer than anterior fronto-orbital seta and subequal to outer vertical seta, setae well separated, inserted anterolaterad of anterior ocellus. First flagellomere usually gradually narrowed toward apex; length about twice width; arista bearing 9–16 long hairs along dorsal surface. Face usually conspicuously convex,



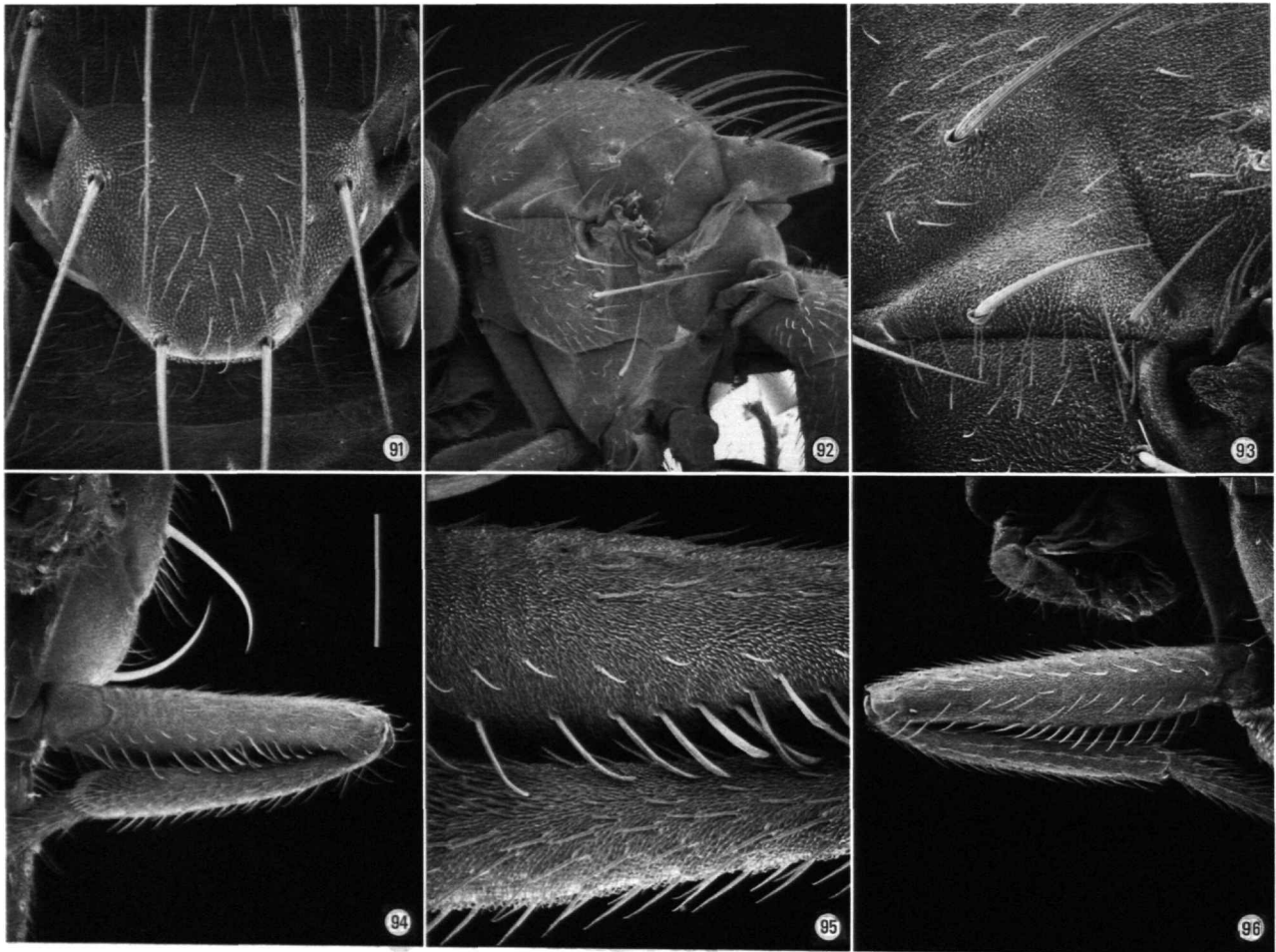
FIGURES 85–90.—Scanning electron micrographs of *Paralimna* (*Paralimna*) *fellerae* (Belize, Stann Creek District: Glover's Reef; scale length in parenthesis; scale for all photographs = Figure 87): 85, head, lateral aspect (0.43 mm); 86, face, anterior aspect (0.30 mm); 87, antenna, lateral aspect (150 μ m); 88, ommatidia and occasional interfacetal setae of compound eye, lateral aspect (30 μ m); 89, enlargement of same, lateral aspect (6.0 μ m); 90, mesonotum, dorsal aspect (0.50 mm).

comparatively well arched, usually bearing 1 (occasionally 2 or 3) long (subequal to length of large, reclinate seta), inclinate, but not cruciate facial seta on ventral $\frac{1}{2}$ of face, if more than 1, setae approximate; usually 3 or 4 smaller setulae interspersed along same vertical series as larger setae. Eye with oblique orientation. Gena comparatively high, height slightly more than $\frac{1}{3}$ eye height.

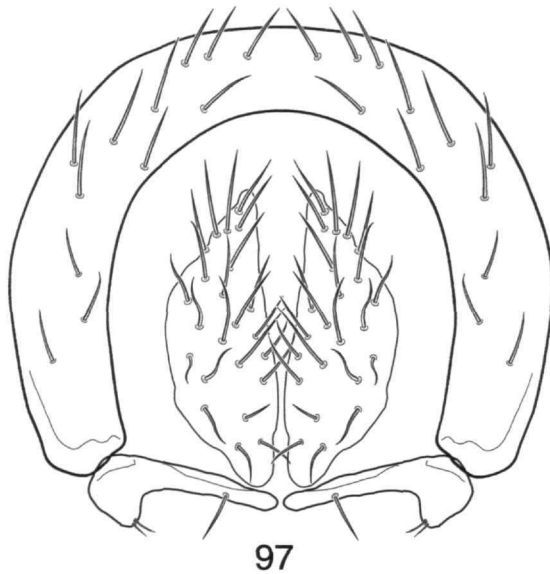
Thorax (Figures 90–96): Acrostichal setulae well developed, conspicuous, in about 6 irregular rows; presutural supraalar seta well developed, subequal in length to anterior dorso-central seta. Veins lacking setulae; crossvein dm-cu regularly developed, nearly straight, longer than apical section of vein CuA₁, and at distinct angle with posterior margin of wing. Forefemur of male lacking comb-like row of short, stout, slightly flattened setae along apical $\frac{1}{2}$ of anteroventral sur-

face; foretibia of male lacking several long, slender setae at apex on ventral surface; forebasitarsus lacking row of long, slender, pale setulae inserted along anterior surface; midtibia with 3 dorsal extensor setae (subapically, subbasally, and near basal $\frac{1}{3}$).

Abdomen (Figures 97–99): Frequently with fasciate pattern with darker band basally. Male abdominal sternites 3 and 4 rectangular, longer than wide; sternite 5 narrow basally, becoming wider posteriorly, posterior margin shallowly concave. Male terminalia (Figures 97–99): presurstyli L-shaped, medial arms from each side connected just below cerci, ventral arm reduced, shorter than cercus (Figures 97–99); lateral aedeagal process enlarged; aedeagal apodeme broad basally and apically; hypandrium forming a relatively deep, conically shaped pouch (Figures 98, 99).

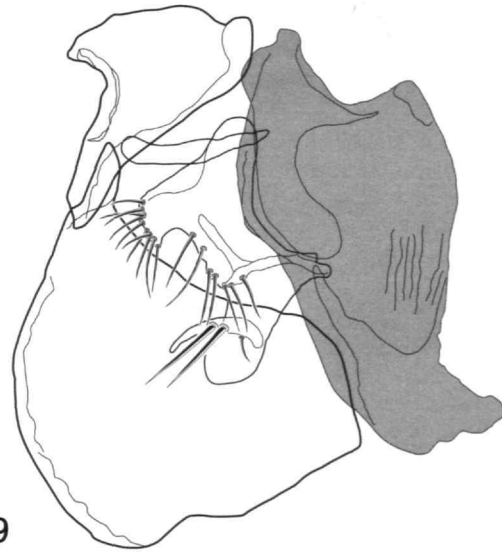
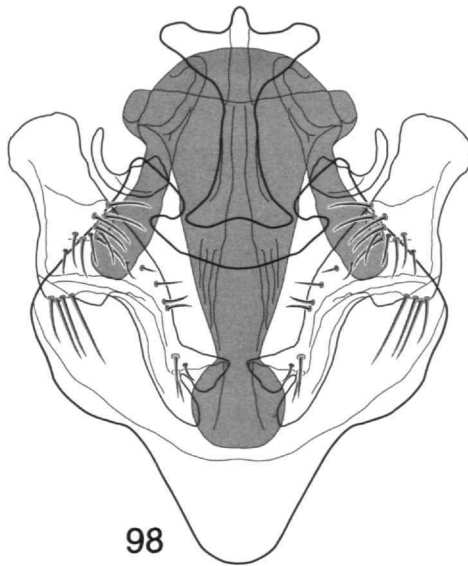


FIGURES 91–96.—Scanning electron micrographs of *Paralinna (Paralinna) fellerae* (Belize, Stann Creek District: Glover's Reef; scale length in parenthesis; scale for all photographs = Figure 94): 91, scutellum, dorsal aspect (231 μ m); 92, pleural sclerites, lateral aspects (0.50 mm); 93, notopleuron, lateral aspect (167 μ m); 94, left foreleg, anterior aspect (250 μ m); 95, enlargement of same, anterior aspect (86 μ m); 96, left foreleg, posterior aspect (0.27 mm).



FIGURES 97-99.—Male terminalia of *Paralomna* (*Paralomna*) *punctipennis* (Wiedemann): 97, epandrium, cerci, and presurstyli, posterior aspect; 98, internal male terminalia, ventral aspect; 99, same, lateral aspect.

0.1mm



98

99

DISTRIBUTION.—As for the genus.

DISCUSSION.—There are now nearly 80 species in this subgenus, and many additional species remain to be described, especially species from the New World. Except for the *limbata* group, which had been placed in the subgenus *Phaiosterna* (Mathis and Zatwarnicki, 1995), we have not characterized any of the sublineages within this subgenus. Mathis is now revising the New World species of *Paralomna*, and that revision will include phylogenetic and descriptive sections that will address these sublineages, as they are germane to that fauna.

The *limbata* Group

DIAGNOSIS.—The *limbata* group is distinguished from other species of *Paralomna*, especially species of the subgenus *Phaiosterna*, by the following combination of characters: gena short, height about $\frac{1}{4}$ eye height; 1st flagellomere elongate, length more than twice height, broadly rounded apically; arista bearing 12-14 long dorsal rays; mesonotum vittate, broad brown stripe medially and through dorsocentral track, yellowish to brownish gray between brown stripes; anepisternum brown dorsally and ventrally, gray between, conspicuously vit-

tate; wing with crossvein dm-cu and sometimes adjacent veins surrounded with halo of brown; forefemur bearing comb-like row of short, stout, spine-like setulae along apical ½ of anteroventral surface. Male terminalia: epandrium as wide as high; cercus well developed, bearing numerous setulae; presurstylus quite variable, depending on species; postsurstylus somewhat rectangular, deeply bifurcate apically, bearing somewhat vertical row of long setulae; aedeagal apodeme with prominent keel, irregularly rectangular to slightly rounded; aedeagus in lateral view with moderately deep notch dorsobasally, broadly developed over basal ¾, apex pointed; hypandrium wider than long, moderately to shallowly depressed.

DISTRIBUTION.—Afrotropical: Angola, Cameroon, Ethiopia, Gambia, Ghana, Kenya, Liberia, Madagascar, Malawi, Mozambique, Nigeria, Rwanda, Senegal, Sierra Leone, South Africa (Cape Province), Sudan, Tanzania, Uganda, Zaire, Zambia, Zimbabwe.

Key to Species of the *limbata* Group

1. Frons with dark brown medial and orbital stripes but lacking velvety black, microtomentose squarish area on fronto-orbit; frons lacking black spots adjacent to ocelli; pedicel and 1st flagellomere blackish brown. Wing lacking reticulate pattern in membrane, but crossvein dm-cu with dark brown halo 21. *P. limbata* Loew
- Frons with squarish spot at base of reclinate fronto-orbital seta densely microtomentose, appearing velvety black; frons with black spots (sometimes slightly shiny) anterior of anterior ocellus and laterad of posterior ocelli; pedicel tan to grayish yellow; 1st flagellomere with dorsal ½ dark brown, ventral ½ yellowish. Wing conspicuously reticulate 22. *P. reticulata* Cogan

21. *Paralimna (Paralimna) limbata* Loew

FIGURES 100–102

Paralimna limbata Loew, 1862b:13.—Becker, 1922:72 [list from Sudan (Renk, Tonga)].—Cresson, 1929:188 [discussion].—Giordani Soika, 1956b:495 [list, Zaire].—Cogan, 1968:326 [revision]; 1980:663 [Afrotropical catalog].—Canzoneri and Meneghini, 1969:150–151 [list, Zaire].—Canzoneri, 1982:57 [list, Sierra Leone]; 1986:68 [list, Sierra Leone]; 1987:83 [list, Sudan].—Canzoneri and Raffone, 1987:64 [list, Kenya].—Canzoneri and Rampini, 1990:109 [list, Sierra Leone]; 1994:248 [list, Sierra Leone].

Paralimna (Phaiosterna) limbata.—Cresson, 1947b:115–116 [review; list, Zaire].—Mathis and Zatwarnicki, 1995:126–127 [world catalog].

DIAGNOSIS.—This species is distinguished from congeners by the frons having a dark medial and orbital stripe but lacking a velvety black, microtomentose squarish area on the fronto-orbit and by the wing lacking a maculation pattern in the membrane.

DESCRIPTION.—*Head:* Frons with dark brown medial and orbital stripe but lacking black spots. Antenna with pedicel and 1st flagellomere blackish brown.

Thorax: Scutum with dark medial stripe. Wing with crossvein dm-cu surrounded by dark brown halo. Legs, including basitarsi, black.

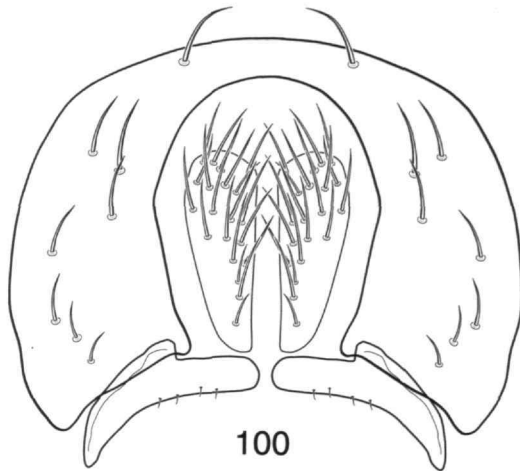
Abdomen: Male terminalia (Figures 100–102): epandrium about as wide or wider than high in posterior view, extended arms much wider than dorsum (Figure 100); cercus wider dorsally, 3–4 times higher than wide, bearing numerous

DISCUSSION.—We have reviewed this species group because Cogan (1968) recognized the included species to be related to if not included in the subgenus *Phaiosterna* (although Cogan did not recognize *Phaiosterna* as a subgenus of *Paralimna*, he identified the included species as a species group in which he placed the species of *Phaiosterna* as well as the two we review herein). Here we restrict the characterization of the species group to include only two Afrotropical species, *P. limbata* Loew and *P. reticulata* Cogan. Although both of these species superficially resemble species of *Phaiosterna*, the similarities probably arose through convergence.

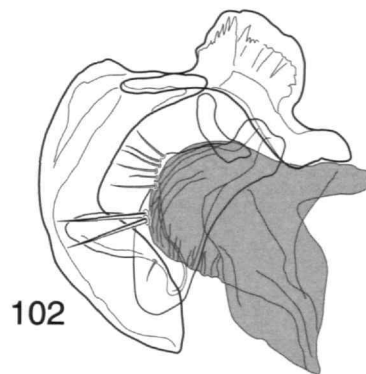
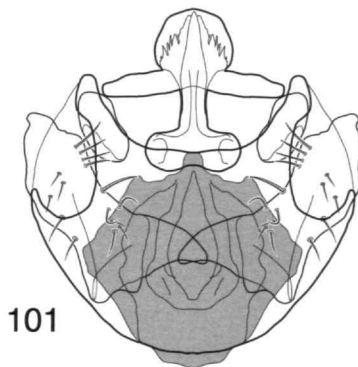
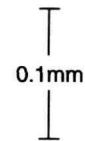
The adults of the *limbata* group are similar externally, particularly in overall shape, but some structures of the male terminalia are markedly different, especially the presurstylus (see species descriptions). Other structures of the male terminalia, however, such as the postsurstylus, aedeagal apodeme, aedeagus, and gonite, are very similar.

setulae, especially dorsomedially (Figure 100); presurstylus in posterior view a shallowly curved bar, much wider than high, bearing few tiny setulae along posterior margin (Figure 100); postsurstylus somewhat rectangular in lateral view (Figure 102), apex broadly bifurcate, bearing vertical row of setulae, apical setulae longer; aedeagus in lateral view (Figure 102) with moderately deep notch dorsobasally, broadly developed over basal ¾, apex pointed; aedeagal apodeme with wide, irregularly rounded, moderately deep keel, extended process to base of aedeagus wider; gonite in lateral view (Figure 102) a shallowly curved, small bar, slightly wider toward base of postsurstylus; hypandrium wider than long (Figure 101), shallowly depressed, in lateral view moderately curved (Figure 102).

TYPE MATERIAL.—The lectotype male, here designated to stabilize and make more universal the use of this name, is labeled “[South Africa] 450 [handwritten]/330 [handwritten]/Paralimna [sic] limbata/248 66 [pink label]/Riksmuseum Stockholm [light green label]/LECTOTYPE *Paralimna limbata* Loew ♂ By Mathis & Zatwarnicki [all except “LECTOTYPE” and “By” handwritten; label with black submarginal border].” The lectotype is pinned directly, is in poor condition (wings broken off, antennae and most setae missing), and is deposited in the NRS.



FIGURES 100–102.—Male terminalia of *Paralomna* (*Paralomna*) *limbata* Loew: 100, eandrium, cerci, and presurstyli, posterior aspect; 101, internal male terminalia, ventral aspect; 102, same, lateral aspect.



OTHER SPECIMENS EXAMINED.—Afrotropical. CAMEROON. Bambalang (off route N11; 35 km E Bamenda; 1200 m), 18 Nov 1987, A. Freidberg, F. Kaplan (3♂; USNM). Limbe (shore), 14–15 Nov 1987, A. Freidberg (1♂, 2♀; USNM).

ETHIOPIA. Gila River, Mission Station, Sep 1963, M.L. Schmidt (1♀; USNM).

KENYA. Lake Bugoria, 26 Aug 1983, A. Freidberg (3♂; USNM). Marmar Springs (S of Maralal), 28 Nov 1986, A. Freidberg (1♂; USNM). Masai Mara, Keekoro Lodge, 29–30 Aug 1983, A. Freidberg (1♂; USNM).

LIBERIA. *Grand Cape Mount*: Dia, 17 Feb 1953, O. Blickenstaff (2♂, 3♀; USNM).

MALAWI. Lake Malombe, Nkungulu, 25 Oct 1983, A. Freidberg (13♂, 27♀; USNM).

MOZAMBIQUE. Luabo, Jan 1956, P. Usher (1♀; USNM).

TANZANIA. Mount Wa Mbu (near Lake Manyara Swamp; 900 m), 6 Sep 1992, A. Freidberg (1♂, 3♀; USNM). Ngorongoro Reserve, Gate (1500 m), 6 Sep 1992, A. Freidberg (2♂; USNM).

DISTRIBUTION.—Afrotropical: Angola, Cameroon, Ethiopia, Gambia, Ghana, Kenya, Liberia, Malawi, Mozambique, Nigeria, Rwanda, Senegal, Sierra Leone, South Africa (Cape Province), Sudan, Tanzania, Uganda, Zaire, Zambia, Zimbabwe.

22. *Paralomna* (*Paralomna*) *reticulata* Cogan

FIGURES 103–105

Paralomna (*Paralomna*) *reticulata* Cogan, 1968:327; 1980:664 [Afrotropical catalog].

Paralomna (*Phaiosterna*) *reticulata*.—Mathis and Zatwarnicki, 1995:127 [world catalog].

DIAGNOSIS.—This species is distinguished from congeners by the frons having a dark medial and orbital stripe but lacking a velvety black, microtomentose squarish area on the fronto-orbital and by the wing lacking a maculation pattern in the membrane.

DESCRIPTION.—*Head*: Frons with dark brown medial and orbital stripe but lacking black spots. Antenna with pedicel and 1st flagellomere blackish brown.

Thorax: Scutum with dark medial stripe. Wing with cross-vein dm-cu surrounded by dark brown halo. Legs, including basitarsi, black.

Abdomen: Male terminalia (Figures 103–105): epandrium about as wide as high in posterior view, extended arms much wider than more narrowly rounded dorsum (Figure 103); cercus wide ventrally, 3 times higher than wide, bearing numerous long setulae, especially medially (Figure 103); presurstylus in posterior view (Figure 103) elongate, length 2–3 times width, pointed apically, medial margin more conspicuously curved, bearing few setulae along curvature; postsurstylus somewhat rectangular in

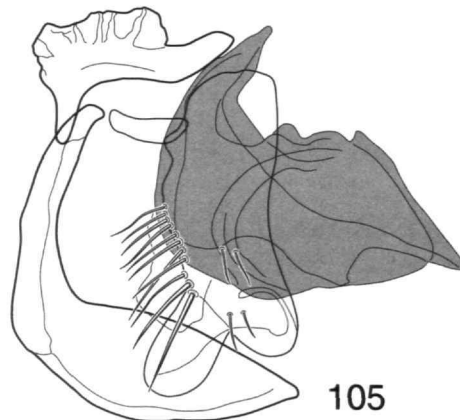
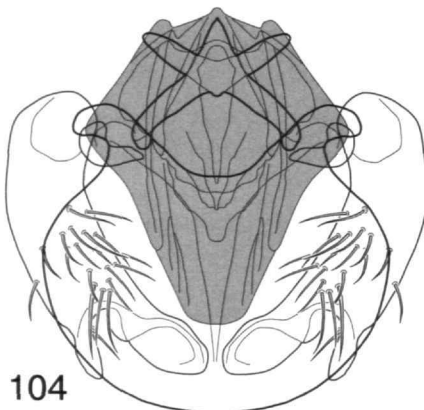
lateral view (Figure 105), apex broadly bifurcate, bearing vertical row of setulae, apical setulae longer; aedeagus in lateral view (Figure 105) with moderately deep notch dorsobasally, broadly developed over basal $\frac{3}{4}$, apex pointed; aedeagal apodeme with wide, irregularly rectangular, moderately deep keel, extended process to base of aedeagus wider and slightly longer; gonite in lateral view (Figure 105) a shallowly curved, small bar; hypandrium wider than long (Figure 104), shallowly to moderately depressed, in lateral view moderately curved (Figure 105).

TYPE MATERIAL.—The holotype male of *Paralimna reticulata* Cogan is labeled "holo- type [red margin]/Madagascar-



FIGURES 103–105.—Male terminalia of *Paralimna (Paralimna) reticulata* Cogan: 103, epandrium, cerci, and presurstyli, posterior aspect; 104, internal male terminalia, ventral aspect; 105, same, lateral aspect.

0.1mm



Ouest [Toliara:] Ranohira[,] 860m[,] 26.I-4.II.58 [26 Jan-4 Feb 1958][,] B.Stuckenberg/Paralimna reticulata sp. n. det. B.H.Cogan 1966 ["reticulata sp. n." and last number of year handwritten]." The holotype is double mounted (minutes in a block of plastic foam), is in excellent condition, and is deposited in the NMSA.

OTHER SPECIMENS EXAMINED.—Afrotropical. MADAGASCAR. *Antsiranana*: Sambava (30 km W), 13 Apr 1991, A. Freidberg, F. Kaplan (3♂, 2♀; USNM). *Toliara*: Fort Dauphin (50 km W), 22 Apr 1991, A. Freidberg, F. Kaplan (1♂; USNM).

DISTRIBUTION.—Afrotropical: Madagascar.

REMARKS.—The reticulate wing of this species is unmistakable and facilitates identification. Like the wing, the presurstylus is markedly different, being two to three times longer than wide. In *P. limbata*, the presurstylus is much wider than long and is bar-like.

Subgenus *Phaiosterna* Cresson

Phaiosterna Cresson, 1916:104 [type species: *Paralimna decipiens* Loew, 1878, original designation].—Cresson, 1947a:54–55 [review of Neotropical species]; 1947b:115–117 [review of Afrotropical species, key]; 1948:9–11 [review of Australasian species, key].—Wirth, 1965:748 [Nearctic catalog]; 1968:16 [Neotropical catalog].—Cogan and Wirth, 1977:334 [synonymy with *Paralimna*].—Cogan, 1980:663–664 [Afrotropical catalog, as the subgenus *Paralimna* in part].—Mathis and Zatwarnicki, 1995:126–127 [world catalog].

DIAGNOSIS.—This genus is distinguished from other congeneric subgenera by the following combination of characters: gena moderately high to high, gena-to-eye ratio 0.19–0.40; 1st flagellomere short, length at most 1.5 times width; mesonotum and anepisternum mostly unicolorous and grayish brown to black; and crossvein and veins and rest of wing essentially unicolorous.

DESCRIPTION.—Small to moderately sized shore flies, body length 1.85–3.85 mm; chaetotaxy generally well developed.

Head: Ocelli in equilateral triangle; pseudopostocellar setulae well developed, divergent; paraverticilar seta well developed, subequal in length to anterior proclinate fronto-orbital seta; ocellar seta well developed. Antenna black; 1st flagellomere broadly rounded, length about twice width; arista bearing 6–8 long hairs along dorsal surface. Face only slightly convex, comparatively flattened, bearing 2 or 3 long (subequal to length of large, reclinate seta), inclinate (but not cruciate) facial setae on ventral ½ of face, and 3 or 4 smaller setulae interspersed along same vertical series as larger setae. Eye with vertical orientation. Gena comparatively short, height slightly more than width of 1st flagellomere.

Thorax: Acrostichal setulae well developed, conspicuous, in about 6 irregular rows; presutural supra-alar seta well developed, subequal in length to anterior, dorsocentral seta. Veins lacking setulae; crossvein dm-cu regularly developed, nearly straight, longer than apical section of vein CuA₁, and at distinct angle with posterior margin of wing. Legs black; forefemur of male lacking comb-like row of short, stout, slightly flattened setae along apical ½ of anteroventral surface; foretibia of male

lacking several long, slender setae at apex on ventral surface; forebasitarsus lacking row of long, slender, pale setulae inserted along anterior surface; midtibia with 3 dorsal extensor setae (subapically, subbasally, and near basal ⅓).

Abdomen: Frequently with fasciate pattern with darker band basally. Male abdominal sternites 3 and 4 rectangular, longer than wide; sternite 5 narrow basally, becoming wider posteriorly, posterior margin shallowly concave. Male terminalia: presurstylus L-shaped, medial arms from each side connected just below cerci, ventral arm reduced, length less than cerci; lateral aedeagal process enlarged; aedeagus pointed apically (Figures 107–112); aedeagal apodeme broad basally and apically; hypandrium forming relatively deep, conically shaped pouch.

DISTRIBUTION (Figure 106).—Afrotropical: Aldabra, Burundi, Cameroon, Ethiopia, Gambia, Ghana, Kenya, Madagascar, Namibia, Nigeria, Seychelles (Cousin, La Digue, Mahé, Praslin), Sudan, Tanzania, Uganda, Yemen, Zaire. Australasian/Oceanian: American Samoa, Australia (Coral Sea Islands Territory, Northern Territory, Queensland, Western Australia), Christmas Island, Federated States of Micronesia, Fiji, Guam, Kiribati (Gilbert Islands, Phoenix Islands), Marquesas (Fatu Hiva, Nuku Hiva), Northern Marianas, Palau, Papua New Guinea, Society Islands (Moorea, Raiatea, Tahiti), Solomon Islands, Vanuatu, Western Samoa. Oriental: India (Andhra Pradesh, Assam, Kerala, Tamil Nadu, West Bengal), Indonesia (Java, Lesser Sunda Islands, Sumatra), Laos, Malaysia, Nepal, Pakistan, Philippines (Luzon, Panay, Visayan), Sri Lanka, Taiwan, Thailand, Vietnam. Nearctic: Bermuda, USA (AK, AZ, CA, FL, GA, LA, MS, NJ, TX). Neotropical: Argentina, Bahamas, Belize, Bolivia, Brazil (Mato Grosso, Rio de Janeiro), Colombia, Costa Rica, Ecuador, Guatemala, Guyana, Honduras, Mexico (Jalisco, San Luis Potosí, Sonora, Tamaulipas, Veracruz), Panama, Paraguay, Trinidad and Tobago, Venezuela, West Indies (Barbados, Cuba, Dominica, Dominican Republic, Grand Cayman, Grenada, Jamaica, Puerto Rico, St. Lucia, St. Thomas, St. Vincent, Virgin Islands). Palearctic: Egypt.

DISCUSSION.—Cresson described *Phaiosterna* as a subgenus of *Paralimna*, and we have continued to recognize this group as a subgenus. Certainly the group is monophyletic, as evidenced by numerous synapomorphies. The sister group of *Phaiosterna* is not as well established, although there is some external resemblance with species of the *limbata* group.

The species of *Phaiosterna* are very similar externally, and there is considerable variation and overlap in such features as the amount and pattern of microtomentum, for example. From localities where more than one species occurs, however, the differences between species seem to be accentuated, perhaps as a result of character displacement. Otherwise, especially in populations that are allopatric, the only reliable characters are those of the male terminalia. Exceptions to this generality are the two new species. For example, the new species from the Indian subcontinent has a shiny, mostly bare mesonotum that consistently differs from *P. lineata*, which is more densely mi-

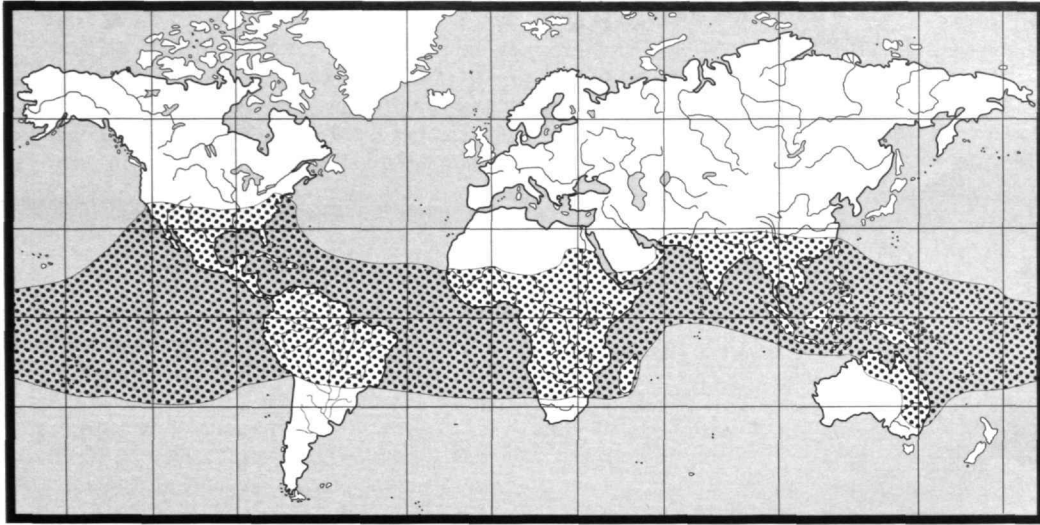


FIGURE 106.—Distribution map for *Paralomna* (*Phaiosterna*).

crotomentose. Males of the new species from tropical America, *P. longiseta*, bear long setulae on the foreleg, a character that consistently distinguished them from congeners. Otherwise, however, accurate identification will frequently require examination of structures from the male terminalia.

The synapomorphies that we have discovered that confirm the monophyly of *Phaiosterna* are as follows: (1) generally

more uniformly dark colored (there is still some distinctly bicolored areas, especially the scutum, but the differences are not as pronounced as in typical *Paralomna*); (2) gena secondarily shorter; (3) 1st flagellomere long, length about twice height; (4) presurstylus reduced; (5) lateral aedeagal process enlarged; and (6) hypandrium a relatively deep, conically shaped pocket or pouch.

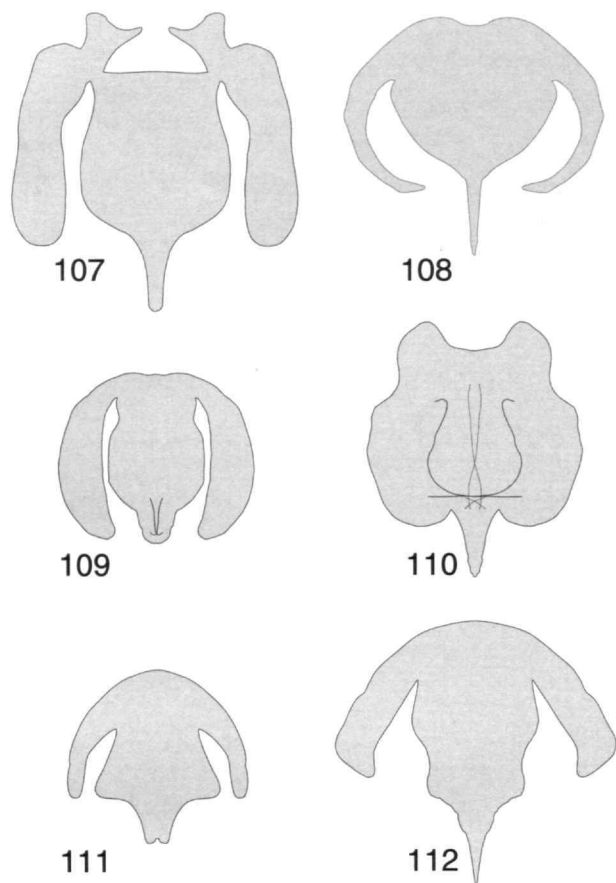
Key to Species of *Phaiosterna* Cresson

New World Species

1. Ventral apex of male foretibia bearing numerous long, slender setulae; male forebasitarsus bearing long setulae along posterior surface (Neotropical) 27. *P. longiseta*, new species
Foreleg of male lacking long, slender setulae 2
2. Abdomen subshiny to shiny, sparsely microtomentose; aedeagus in posterior view higher than wide, narrow (Nearctic, Neotropical) 28. *P. obscura* Williston
Abdomen appearing dull, microtomentose, tannish gray; aedeagus in posterior view wider than high; wide (Nearctic, Neotropical) 24. *P. decipiens* Loew

Old World Species

1. First flagellomere bearing long fringe of whitish setulae along dorsum and dorsal portion of apex, length of setulae greater than $\frac{1}{2}$ height of 1st flagellomere. Mesonotum unicolorous, blackish brown, sparsely microtomentose, subshiny to shiny (Australasian/Oceanian, Oriental) 25. *P. fusca* Bock
First flagellomere either lacking long fringe of setulae or setulae short, considerably less than $\frac{1}{2}$ height of flagellomere. Mesonotum usually with some evidence of stripes, varicolored, grayish tan to dark brown, densely microtomentose, at most slightly subshiny 2
2. Face grayish yellow, mostly uniform in color, generally lighter-colored species, gray to tan, but frequently with dark brown stripes between dorsocentral setae (Afrotropical, Australasian/Oceanian, Palearctic) 23. *P. bicolor* (Macquart)
Face generally dark brown with gray to yellowish gray areas; usually darker-colored species, pleural regions dark brown (Australasian/Oceanian, Oriental) 26. *P. lineata* de Meijere



FIGURES 107–112.—Ventral view of the aedeagus: 107, *Paralimna (Phaiosterna) lineata* de Meijere; 108, *P. (P.) longiseta*, new species; 109, *P. (P.) obscura* Williston; 110, *P. (P.) decipiens* Loew; 111, *P. (P.) fusca* Bock; 112, *P. (P.) bicolor* (Macquart).

23. *Paralimna (Phaiosterna) bicolor* (Macquart)

FIGURES 112–115

Ephydra bicolor Macquart, 1851:276.

Paralimna bicolor.—Wirth, 1975:40–41 [generic combination, lectotype designation].

Paralimna lineata of authors, not de Meijere [misidentification].—Lamb, 1912:317 [list, Seychelles].—Cresson, 1948:10 [in part; listed as a species incertae].—Cogan, 1980:663 [Afrotropical catalog].—Canzoneri, 1987:83 [list, Sudan].—Canzoneri and Raffone, 1987:64 [list, Kenya].—Canzoneri and Rampini, 1990:109 [list, Sierra Leone]; 1994:248 [list, Sierra Leone].

Paralimna (Phaiosterna) lineata in part of authors, not de Meijere [misidentification].—Mathis and Zatwarnicki, 1995:127 [world catalog].

Paralimna decipiens of authors, not Loew [misidentification].—Becker, 1903:168–169 [list, Egypt]; 1926:16 [list, Egypt].

Phaiosterna (Paralimna) aequalis of authors, not Cresson [misidentification].—Cogan, 1968:325 [revision, Afrotropical Region].

Paralimna (Phaiosterna) vidua Giordani Soika, 1956a:124.—Cogan, 1968:325 [synonymy with *P. aequalis* Cresson]; 1980:663 [synonymy with *P. lineata* de Meijere]. [New synonymy.]

Paralimna vidua.—Canzoneri and Meneghini, 1969:151–152 [list, Zaire].

DIAGNOSIS.—This species is distinguished from congeners, especially those of the subgenus *Phaiosterna*, by the following combination of characters: first flagellomere lacking fringe of long, whitish setulae along dorsum and dorsal portion of rounded apex; apex of 1st flagellomere evenly rounded; and mesonotum black, dull to subshiny, with moderately dense gray to brown microtomentum, frequently with conspicuous, longitudinal stripes medially.

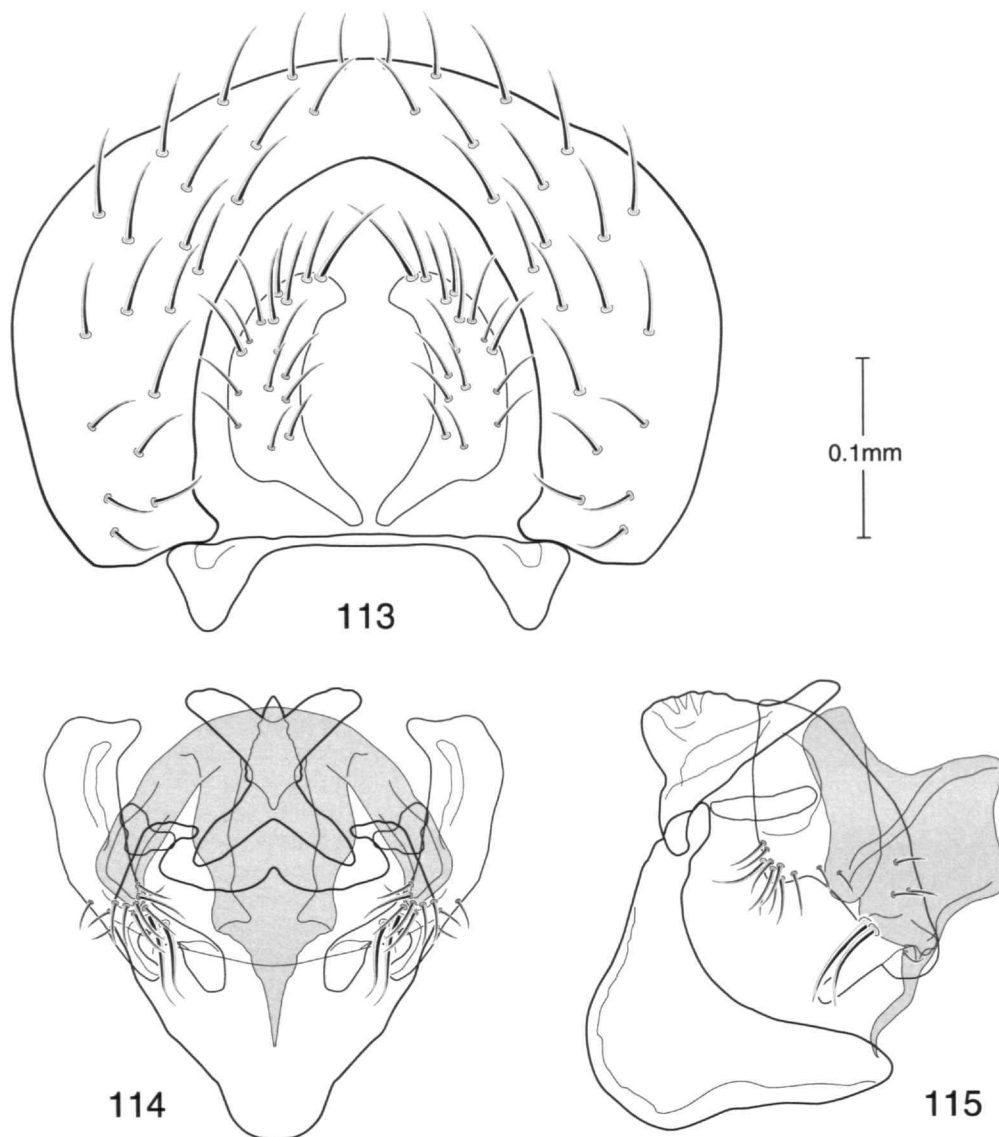
DESCRIPTION.—Small to moderately small shore flies, body length 1.95–2.90 mm; generally dark, whitish gray to brown species, moderately densely to densely microtomentose, dorsum appearing dull to slightly subshiny, especially mesonotum.

Head: Generally grayish brown. First flagellomere bearing long fringe of whitish setulae along dorsum and dorsal portion of apex, setulae longer than ½ height of 1st flagellomere. Face uniformly colored, grayish yellow, subdued, lacking lighter colored areas on darker background. Gena-to-eye ratio 0.21–0.25.

Thorax: Generally whitish gray to brown; mesonotum moderately densely gray to brown microtomentose, appearing dull to very slightly subshiny, usually with conspicuous, darker brown, longitudinal stripes medially, between dorsocentral setae. Costal-vein ratio 0.48–0.50; M-vein ratio 0.82–0.89. Foreleg of male lacking long, slender setulae.

Abdomen: Slightly lighter in color than mesonotum, mostly gray; anterior portion of tergites fasciate, darker gray to brown, less microtomentose. Male terminalia (Figures 112–115): epandrium in posterior view inverted U-shaped (Figure 113), moderately wide, dorsally slightly narrower than width of lateral arms and with dorsal margin of cercal cavity narrowly projected and pointed ventromedially, medial margin concave in posterior view (Figure 113); presurstyli narrowly connected medially, forming nearly straight, long band at ventral margin of cerci, produced ventrolaterally as wide, triangular-shaped projections; postsurstylus in lateral view (Figure 115) with anterior margin wider and swollen medially, bearing several setulae medially, bifurcate apically, anterior lobe longer and only slightly narrower, posterior lobe in lateral view broadly rounded, truncate apically; aedeagal apodeme with keel asymmetrical, more angulate toward hypandrium; aedeagus in posterior view with base subrectangular, apex broadly rounded to truncate medially, in lateral view (Figure 115) narrowly triangular and with pointed lobe near middle along posterior surface, becoming wider subapically, thereafter narrowed to narrow extension, acutely pointed apically; lateral aedeagal processes robust (Figure 114), parallel sided throughout length, narrowly rounded apically; hypandrium deeply invaginated, pocket-like (Figures 114, 115).

TYPE MATERIAL.—The lectotype male (not a female as stated by Wirth) of *Ephydra bicolor* Macquart (designated by Wirth, 1975:40) is labeled “Holo-type [round label with red border]/*Ephydra bicolor*. P. Macq. n. sp. [handwritten]/*E. bicolor* EX COLL. BIGOT/LECTOTYPE ♂ *Ephydra bicolor* Macquart By W. W. Wirth 1975 [handwritten except for “LEC-



FIGURES 113–115.—Male terminalia of *Paralimna (Phaiosterna) bicolor* (Macquart): 113, epandrium, cerci, and presurstyli, posterior aspect; 114, internal male terminalia, ventral aspect; 115, same, lateral aspect.

TOTYPE” and “By”; label with black submarginal border].” The lectotype is directly pinned, is in poor condition (right wing mostly missing, several setae missing or misoriented, and covered by hyphae), and is deposited in the UMO. In Macquart’s paper, the type locality is stated to be “Egypte.”

The holotype female of *Paralimna vidua* Giordani Soika is labeled “HOLOTYPUS [light orange label with black submarginal border]/vois autres ex. en alcool [handwritten]/MUSÉE DU CONGO [Zaire] Banana-6-X-1934 [6 Oct 1934] (D.M. Wanson) n. 2 {pris de trous de Crabes} [all except “MUSÉE

DU CONGO” handwritten]/HOLOTYPUS *Paralimna vidua* A. G[iordani]. Soika [red label; handwritten]/*Paralimna aequalis* Cress. det. B.H.Cogan 1967 [“aequalis Cress.” and “7” handwritten].” The holotype is double mounted (minuten in a paper card), is in poor condition (both wings torn, part of right wing missing, generally appearing “rubbed”), and is deposited in the MRAC. We have also studied a female paratype (MRAC) that bears the same locality data as the holotype.

OTHER SPECIMENS EXAMINED.—Afrotropical. ALDABRA. *Grande Terre*: Cinq Cases, fresh water pool, 23–29 Jan 1968,

B.H. Cogan, A.M. Hutson (4♂, 3♀; BMNH); Dune Jean-Louis, at light, 13–20 Mar 1968, B.H. Cogan, A.M. Hutson (1♀; BMNH).

BURUNDI. Usumbura (780 m), 10 Apr 1953, F. Francois (1♀; IRSN).

CAMEROON. Kribi (beach), route N7, 28–29 Nov 1987, A. Freidberg (2♂, 6♀; TZ, USNM). Kumba, 6 Oct 1949, H. Oldroyd (1♀; BMNH). Limbe (shore), 14–15 Nov 1987, A. Freidberg, F. Kaplan (6♂, 9♀; USNM).

ETHIOPIA. Lake Shala (7°21'N, 39°11'E), 1 Jul 1973, R. Baker (2♀; BMNH).

GAMBIA. Bakau (kotu stream, 3 km SW), 23 Feb 1977 (1♂; BMNH). Gunjur (5 km SSW; near beach in oil palm and mangrove vegetation), 22 Feb 1977 (1♀; BMNH).

GHANA. Neawani, 29 Sep 1921, J.W.S. Macfie (3♂, 3♀; BMNH). Ashanti, Obuasi, 3 Apr 1906, W.H. Graham (1♀; BMNH).

KENYA. Gazi (60 km S Mombasa), 5 May 1991, A. Freidberg, F. Kaplan (2♂; USNM). Lake Victoria, Kisumu (10 km S), 19 Nov 1986, A. Freidberg (4♂, 6♀; USNM). Mombasa (45 km S), 5 May 1991, A. Freidberg, F. Kaplan (1♀; USNM).

MADAGASCAR. *Antsiranana*: Diégo Suarez (30 m), 4–9 Dec 1957, B.R. Stuckenberg (2♂, 2♀; BMNH, NMSA); Nosy Bé Beach, Ambatoloaka, 4–7 Apr 1992, A. Freidberg, F. Kaplan (2♂; USNM); Nosy Tanikely, 6 Apr 1996, A. Freidberg, F. Kaplan (1♀; USNM). *Toamasina*: Est Ivontaka, Mananara (15 m), 10–14 Mar 1958, B.R. Stuckenberg (2♀; BMNH, NMSA). *Toliara*: Saint Augustin (6 m), 11–13 Feb 1953, B.R. Stuckenberg (1♂, 2♀; BMNH, NMSA); South Berenty Reserve, 20 Apr 1991, A. Freidberg, F. Kaplan (1♂, 1♀; USNM).

NAMIBIA. Skeleton Coast Park, Möwe Bay (19°21.51'S, 12°42.29'E), 22 Mar 1998, A.H. Kirk-Spriggs (1♂; NNIC).

NIGERIA. Lake Chad, Mallam Fatori, 13 Apr 1967, J.C. Deeming (2♀; BMNH).

SEYCHELLES. *Cousin*: 30 Mar 1952, E.S. Brown (4♀; BMNH). *La Digue*: Grand Anse (4°22.4'S, 55°50.6'E), 12 May 1997, V. Hollmann, W.N. Mathis (19♂, 17♀; USNM, ZMHU); La Passe (4°20.8'S, 55°49.8'E), 14 May 1997, V. Hollmann, W.N. Mathis (5♂, 2♀; USNM, ZMHU); Petite Anse (4°22.4'S, 55°50.6'E), 12 May 1997, V. Hollmann, W.N. Mathis (13♂, 6♀; USNM, ZMHU). *Mahé*: Airport, 7–8 Apr 1986, W.N. Mathis (6♂, 2♀; USNM); Anse Boileau (4°42.5'S, 55°28.7'E), 4 May 1997, V. Hollmann (3♂; ZMHU); Anse Forbans (4°46.7'S, 55°31.5'E), 4–19 May 1997, V. Hollmann, W.N. Mathis (9♂, 11♀; USNM, ZMHU); Anse Royale Bay, 6–9 Apr 1986, W.N. Mathis (17♂, 18♀; USNM); Auberge D'Anse Boileau (4°42.3'S, 55°28.6'E), 7–18 May 1997, V. Hollmann, W.N. Mathis (28♂, 18♀; USNM, ZMHU); Baie de La Mouche (4°44.3'S, 55°29.5'E), 19 May 1997, V. Hollmann, W.N. Mathis (2♂, 6♀; USNM, ZMHU); Beau Vallon, 20 Feb–10, 11 May 1965, W.T. Tams, I.B. Nye (5♂; BMNH); Bel Ombre (4°37'S, 55°24.9'E), 3 May 1997, W.N. Mathis (9♂, 2♀; USNM); Bel Ombre, Corsaire (4°37.1'S, 55°24.6'E), 3–18

May 1997, V. Hollmann, W.N. Mathis (15♂, 2♀; USNM, ZMHU); Intendance (4°47.1'S, 55°30.1'E), 16 May 1997, W.N. Mathis (1♂; USNM); La Retraite (4°35.1'S, 55°27.7'E), 18–21 May 1997, V. Hollmann, W.N. Mathis (7♂, 2♀; USNM, ZMHU); Machabee, 5–6 Apr 1986, W.N. Mathis (31♂, 28♀; USNM); Point Nord D'est (4°34.5'S, 55°27.7'E), 5 May 1997, W.N. Mathis (3♂; USNM); Police Bay (4°48.0'S, 55°31.3'E), 16 May 1997, W.N. Mathis (4♂; USNM); Roche Caiman Bird Sanctuary (4°38.3'S, 55°28.1'E), 7 May 1997, V. Hollmann, W.N. Mathis (12♂, 9♀; USNM, ZMHU). *Praslin*: Anse Kerlan Farm (4°18.5'S, 55°41.2'E), 13 May 1997, V. Hollmann, W.N. Mathis (8♂, 4♀; USNM, ZMHU); Anse Lazio (4°17.6'S, 55°42.1'E), 8–13 May 1997, W.N. Mathis (6♂, 2♀; USNM); Anse Volbert (4°18.9'S, 55°44.7'E), 8 May 1997, W.N. Mathis (1♂; USNM); Baie Ste. Anne, Anse Takamaka (4°19.6'S, 55°46.3'E), 10–13 May 1997, W.N. Mathis (3♂; USNM); Cote D'Or (4°17.6'S, 55°42.1'E), 9 May 1997, W.N. Mathis (7♂; USNM).

Lamb (1912:317) reported this species from Seychelles, Mahé, Port Glaud (beach), 5 Nov 1908, and Cascade (marshy ground near sea level), 20 Feb 1909.

SUDAN. Yirol, 28 Mar 1954, E.T.M. Reid (1♂, 2♀; BMNH).

TANZANIA. Mto Wa Mbu, near Lake Manyara Swamp (900 m), 6 Sep 1992, A. Freidberg (1♀; USNM).

UGANDA. Katwe, Lac cratere salin, 20 Feb 1954 (1♀; IRSN).

YEMEN. Kirsh (914 m; on camels near waterholes; 14°37'N, 46°45'E), P.W.R. Petrie (3♂, 3♀; BMNH).

ZAIRE. *Kivu*: Kayimvira (Uvira; at light), Feb–Mar 1955, G. Marlier (1♀; MRAC); Rutshuru (river Kanzarue; 1200 m), 15 Jul 1935, G.F. de Witte (1♀; MRAC). *Without Further Locality*: Albert National Park (=Virunga National Park), S.L. Edouard: Bitshumbi (925 m), 20–22 Apr 1936, L. Lippens (5♂, 7♀; MRAC); Kamande (925 m), 1 Oct 1935, L. Lippens (1♂; MRAC); Kitembo (925 m), 3–4 Apr 1936, L. Lippens (2♂, 1♀; MRAC); May ya Moto (950 m), 15–16 Nov 1934, G.F. de Witte (39♂, 55♀; MRAC); Rwindi (river; 1000 m), 9 Feb–17 Apr 1936, L. Lippens (12♂, 20♀; MRAC); Talia (925 m), 7 Apr 1936, L. Lippens (3♀; MRAC). Ituri Kasenyi (Lac Albert), 5 Jul 1953, J. Verbeke (1♂, 1♀; IRSN).

Australasian/Oceanian. PAPUA NEW GUINEA. *Central*: Moreguina, near Cape Rodney (stone river bank), 23 Jul 1982, J.W. Ismay (1♂; USNM).

Palaearctic. EGYPT. Birket Qârûn, near El Faiyûm, Mar (2♀; ZMHU). Cairo, Mar (2♀; ZMHU). Cairo, El Marg (orange orchard), 22 Mar 1996, M. Bartak (3♂, 3♀; BAR).

DISTRIBUTION.—Afrotropical: Aldabra, Burundi, Cameroon, Ethiopia, Gambia, Ghana, Kenya, Madagascar, Namibia, Nigeria, Seychelles (Cousin, La Digue, Mahé, Praslin), Sudan, Tanzania, Uganda, Yemen, Zaire. Australasian/Oceanian: Papua New Guinea. Palaearctic: Egypt.

REMARKS.—Our study of specimens of *Phaiosterna* from the Afrotropical Region indicates a single species, *P. bicolor*, occurring there. The other four names that have been used for this region (Cogan, 1980) are synonyms or represent misidenti-

fications (see species synonymy). One available name, *P. vidua*, was originally determined to be conspecific with *P. lineata*, a valid species that occurs in the Oriental and Australasian/Oceanian Regions, not the Afrotropical Region. Our conclusions are based on dissection and study of structures of the male terminalia of numerous Afrotropical specimens (Madagascar, Seychelles, and Cameroon).

24. *Paralimna (Phaiosterna) decipiens* Loew

FIGURES 110, 116–121

Paralimna decipiens Loew, 1878:195.—Osten Sacken, 1878:201 [Nearctic catalog].—Becker, 1896:270 [list, Texas].—Coquillett, 1900:259 [list, Puerto Rico].—Aldrich, 1905:624 [Nearctic catalog].—Jones, 1906:178–179 [key, catalog].—Thaxter, 1917:672–675 [parasites: *Stigmatomyces rostratus* Thaxter, *S. paralimnae* Thaxter]; 1931:145–146 [parasite: *S. gracilior* Thaxter].—Wirth and Stone, 1956:470 [list, California].

Paralimna (Phaiosterna) decipiens.—Cresson, 1916:105 [subgeneric combination], 108 [revision, figure of head]; 1946:230 [review, Nearctic Region]; 1947a:54–55 [review].—Wirth, 1965:748 [Nearctic catalog]; 1968:16 [Neotropical catalog].—Cole, 1969:396 [list, western United States].—Mathis and Zatwarnicki, 1995:126 [world catalog].—Mathis, 1995:633–635 [list, Galápagos Islands]; 1997:59–60 [list, Belize, figures of male genitalia].

DIAGNOSIS.—This species is distinguished from congeners, especially those of the subgenus *Phaiosterna*, by the following combination of characters: coloration variable but tending to be tan to grayish brown, moderately microtomentose, at most subshiny; 1st flagellomere lacking fringe, or fringe of long, whitish setulae along dorsum and dorsal portion of rounded apex much shorter than ½ height of 1st flagellomere; apex of 1st flagellomere with dorsoapical corner more angulate than posteroapical corner; mesonotum mostly uniform, gray to dark brown, dull to subshiny, with moderately dense gray to brown microtomentum, consistently darker medially, between dorsocentral setae; ventral apex of male foretibia lacking numerous long, slender setulae; posterior surface of forebasitarsus lacking scattered long, slender setulae; and aedeagus wider than long in dorsal view, somewhat rectangular with distal angles rounded, and in lateral view with distal aspect of sclerotized portion slightly concave and actual apex of aedeagus as a pointed process projecting in an anteroventral angle.

DESCRIPTION.—Small to medium-sized shore flies, body length 1.85–3.60 mm; generally dark gray brown to black species, moderately densely microtomentose, dorsum appearing more or less uniform in color, dull to subshiny, especially mesonotum.

Head (Figures 116, 117): Generally gray brown to black. First flagellomere bearing short, generally inconspicuous fringe of whitish setulae along dorsum and dorsal portion of apex, length of setulae far less than ½ height of 1st flagellomere. Face gray to grayish brown, microtomentose, appearing dull, subdued. Gena-to-eye ratio 0.23–0.29.

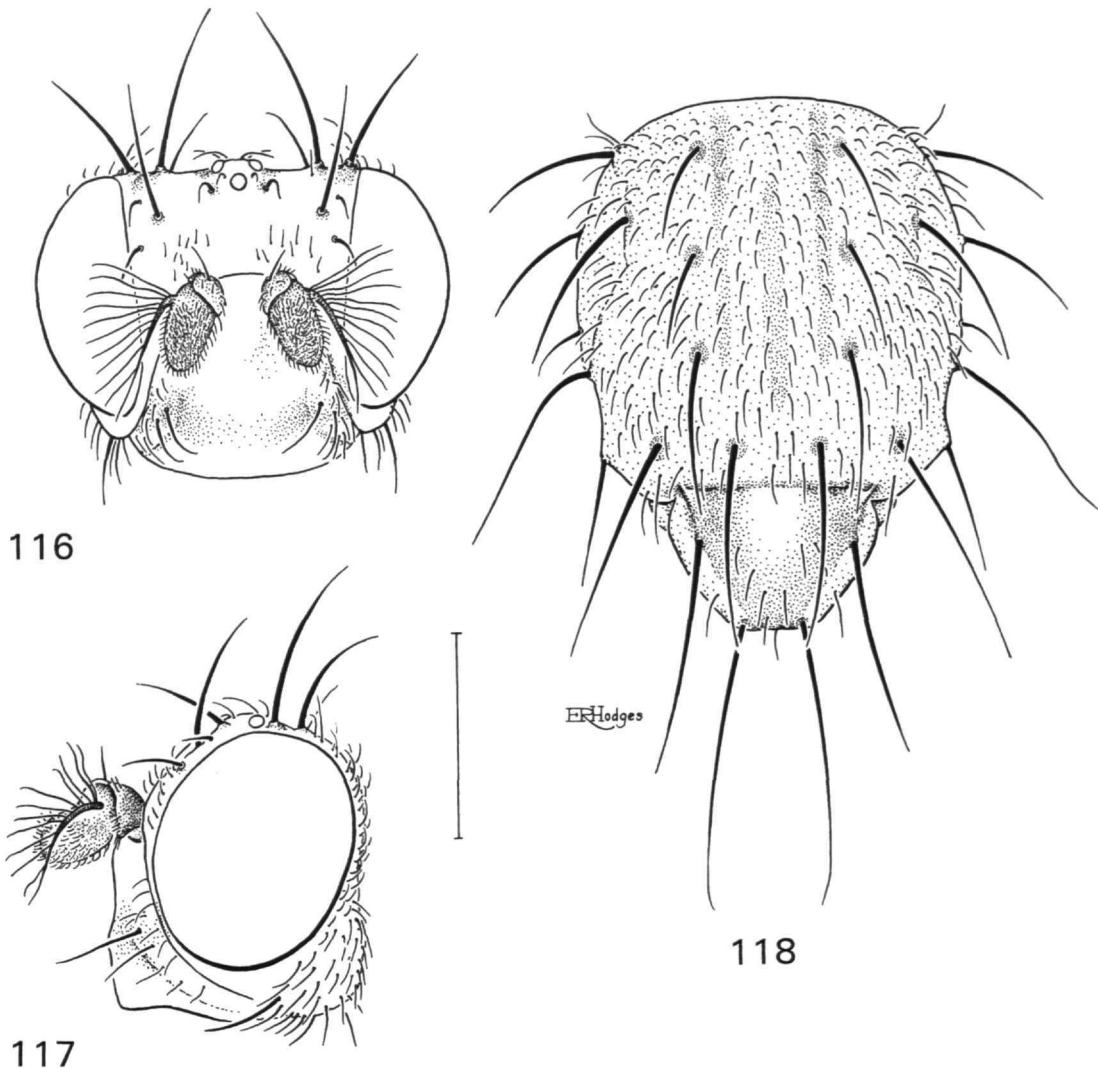
Thorax (Figure 118): Generally gray brown to black, legs darker, black with some grayish microtomentum; mesonotum moderately densely gray to grayish brown microtomentose, appearing dull to subshiny, frequently with brown, short to long

stripes between dorsocentral setae, especially anteriorly. Costal-vein ratio 0.41–0.50; M-vein ratio 0.94–0.97. Ventral apex of foretibia lacking numerous, long, slender setulae; posterior surface of forebasitarsus lacking scattered long, slender setulae.

Abdomen: Slightly to distinctly lighter in color than mesonotum, mostly brownish gray to brownish black; tergites usually fasciate, with anterior portion of tergites darker gray to brownish black, less microtomentose, posterior portion more densely microtomentose, grayer. Male terminalia (Figures 110, 119–121): epandrium in posterior view inverted U-shaped (Figure 119), width about equal throughout length with dorsal margin of cercal cavity broadly rounded; cercus acutely pointed dorsomedially and ventrally, medial margin nearly straight; presurstyli in posterior view (Figure 119) connected medially, forming shallowly arched and medially narrowed band at ventral margin of cercus, produced ventrolaterally as narrow, triangular-shaped projections; postsurstylus in lateral view (Figure 121) with anterior margin bifurcate apically, anterior lobe narrower and shorter than apically expanded posterior lobe, bearing several setulae medially and 2 longer setulae just above bifurcation; gonite short, ovate; aedeagal apodeme with keel symmetrical (Figure 121), attachment with base of aedeagus recurved in direction of keel, attachment with hypandrium curved slightly ventrally; aedeagus broadly rounded apically, thereafter forming a short, narrow point (Figure 120); lateral aedeagal processes wide throughout length, broadly rounded apically, held close to lateral margins of aedeagus; hypandrium deeply invaginated, pocket-like (Figures 120, 121).

TYPE MATERIAL.—The lectotype male of *Paralimna decipiens* Loew (designated by Mathis, 1995:633) is labeled “[yellow square]/Loew Coll./decipiens m[ihi]. [handwritten]/Type 11136 [number handwritten, red label]/LECTOTYPE *Paralimna decipiens* Loew ♂ By W.N.Mathis [handwritten except for “LECTOTYPE” and “By,” label with black submarginal border].” Loew noted that the type series was from Texas, although a locality label bearing this information does not accompany the lectotype. The lectotype is pinned directly, is in good condition (some setae are missing on the dorsum of the head and thorax; part of the abdomen has been removed and dissected, and the parts are in an attached microvial), and is deposited in the MCZ. A female paralectotype (label data similar, head missing) is designated here.

OTHER SPECIMENS EXAMINED.—Nearctic. UNITED STATES. *Arizona.* Coconino County: Bill Williams Fork, F.H. Snow (6♂, 6♀; ANSP). Pima County: Kits Peak (near; 32°N, 111°32′W; 1097 m), Baboquivari Mountains, 7–9 Aug 1916 (2♀; AMNH). *Arkansas.* Garland County: Hot Springs, 24 Jun, H.S. Barber (1♂, 1♀; ANSP). *California.* Del Norte County: Crescent City, 19 Apr 1908, M.C. Van Duzee (1♀; AMNH). Imperial County: Calipatria, 13 Nov 1921, E.R. Kalmbach (1♂, 2♀; ANSP); Salton Sea, 24 Nov 1921, E.R. Kalmbach (1♂, 1♀; ANSP). Riverside County: Palm Canyon, 7 Nov 1934, A.L. Melander (2♂, 1♀; ANSP). *Florida.* Dade County: Biscayne Bay, A.T. Slosson (1♀; AMNH); Miami,

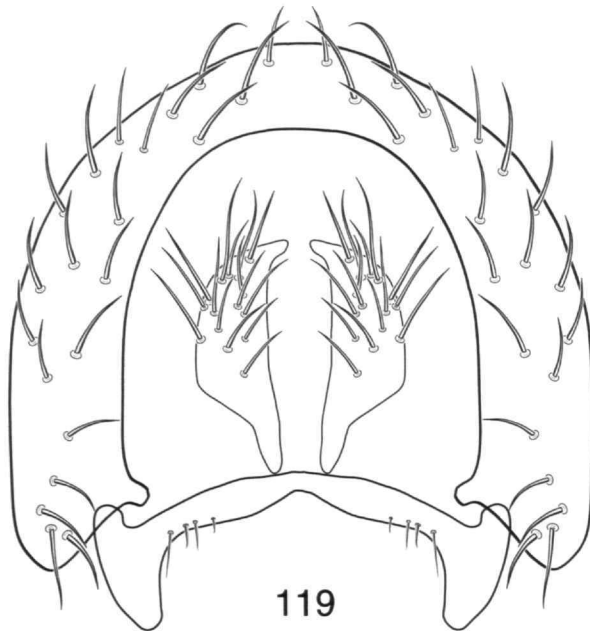


FIGURES 116–118.—*Paralimna (Phaiosterna) decipiens* Loew: 116, head, anterior aspect; 117, same, lateral aspect; 118, mesonotum, dorsal aspect. Scale = 0.5 mm.

23 Feb 1912, F. Knab (1♂; ANSP); Royal Palm Park, 28–29 Jan 1933, 1939, A.L. Melander (1♂, 2♀; ANSP). Henry County: Clewiston, 20 Jan 1938, A.L. Melander (1♂; ANSP). Manatee County: Bradenton, Mar, M.C. Van Duzee (1♂; ANSP). Marion County: Silver Springs, 2 Apr 1932, A.L. Melander (1♂; ANSP). Monroe County: Everglades, 25 Jan 1932, A.L. Melander (1♂, 1♀; ANSP); Flamingo, 25 Jan 1939, A.L. Melander (3♂, 5♀; ANSP). Orange County: Orlando, 2 Feb 1932, A.L. Melander (2♂, 2♀; ANSP). Palm Beach County: Lake Worth, A.T. Slosson (1♂, 1♀; AMNH). Pinellas County: Saint Petersburg, 15 Feb 1924, E.T. Cresson, Jr. (3♀; ANSP). Polk County: Lakeland, 10 Nov 1911 (1♀; AMNH). Georgia. Charlton County: Bill's Island, Okefenokee Swamp, Jun 1912 (1♀; ANSP). Louisiana. St. Charles

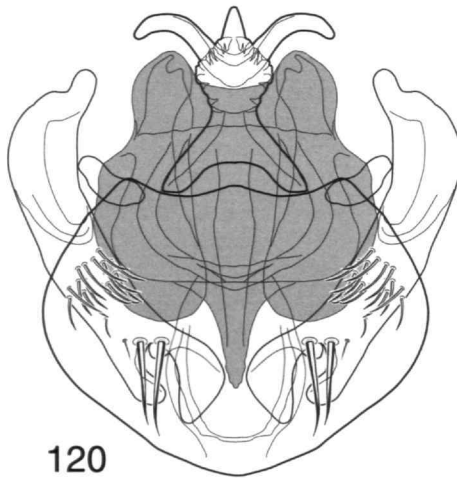
County: New Orleans, 1 Jan 1932, A.L. Melander (1♂; ANSP). Mississippi. Harrison County: Pass Christian, 6 Jul 1917; J.M. Aldrich (1♂, 1♀; ANSP). Oktibbeha County: Mississippi State, 30 Oct 1925 (1♂; ANSP). New Jersey. Cape May County: Cape May, 9 Sep 1932, W. Stone (1♀; ANSP). Texas. Cameron County: Brownsville, 2–13 Jan 1928 (1♀; AMNH); Brownsville (pond shore), 29 Nov 1910 (1♀; ANSP); Brownsville (9.7 km N), 20 Jul 1933, C.W. Sabrosky (1♂, 1♀; ANSP). Galveston County: Dickinson, Jun 1929 (2♂, 2♀; ANSP). Travis County: Austin, 7–20 Oct 1899, 1901 (1♂, 4♀; AMNH, ANSP).

Neotropical. BAHAMAS. Andros: Andros Town, 27–28 Feb 1966, O.L. Cartwright (1♂, 2♀; USNM); Mangrove Cay, 26 Apr 1953, E.B. Hayden (1♂, 1♀; AMNH). Exuma Cays:



FIGURES 119–121.—Male terminalia of *Paralimna* (*Phaiosterna*) *decipiens* Loew: 119, epandrium, cerci, and presurstyli, posterior aspect; 120, internal male terminalia, ventral aspect; 121, same, lateral aspect.

0.1mm



Stainaard Cay, 13 Jan 1953, E.B. Hayden (1♂, 3♀; AMNH). *Rum Cay*: near Port Nelson, 16 Mar 1953, E.B. Hayden, L. Giovannoli (1♂, 2♀; AMNH). *San Salvador*: near Cockburn Town, 18 Mar 1953, L. Giovannoli (2♀; AMNH). *Turks and Caicos Islands*: South Caicos Island, 11 Feb 1953, E.B. Hayden (2♂; AMNH).

BELIZE. *Stann Creek District*: Man of War Cay, Nov 1987, W.N. and D. Mathis (1♂; USNM); Stewart Cay, Mar 1988, W.N. Mathis (1♀; USNM); Wee Wee Cay, Mar 1988, W.N. Mathis (5♂, 3♀; USNM).

BOLIVIA. *La Paz*: Yolosa (16°14'S, 67°44.4'W; 1185 m), 18 Mar 2001, W.N. Mathis (3♂; USNM).

BRAZIL. *Rio de Janeiro*: Rio de Janeiro, S.W. Williston (1♂, 1♀; AMNH).

COSTA RICA. Cartago, 25 May 1909, P.P. Calvert (4♂, 5♀; ANSP). Philadelphia, 18 Jan 1910, P.P. Calvert (1♂; ANSP). Santa Cruz, 30 Jan 1910, P.P. Calvert (1♂, 5♀; ANSP).

CUBA. *Havana*: Havana (beach; 23°5.8'N, 82°27.7'W), 2–14 Dec 1994, W.N. Mathis (14♂; USNM); Ojo de Agua (23°54.6'N, 82°29.1'W), 8 Dec 1994, W.N. Mathis (1♂, 1♀;

USNM); Palmarejo (67 km E Havana), 26 Apr 1983, W.N. Mathis (8♂, 1♀; USNM); Puerto Escondido, 26 Apr 1983, W.N. Mathis (1♂, 2♀; USNM). *Matanzas*: Palpite (2 km NE), 30 Apr 1983, W.N. Mathis (1♀; USNM); Playa Larga (1 km E), 2 May 1983, W.N. Mathis (1♀; USNM). *Pinar del Rio*: Soroa (22°47.7'N, 83°W), 4–6 Dec 1994, W.N. Mathis (9♂, 1♀; USNM); Soroa (2 km E), 29 Apr 1983, W.N. Mathis (9♂, 4♀; USNM). *Sancti Spiritus*: Playa Ancón (21°44.1'N, 79°59.9'W), 12 Dec 1994, W.N. Mathis (6♂, 3♀; USNM); Topes de Collantes (21°54.4'N, 80°01.4'W; 670 m), 9–11 Dec 1994, W.N. Mathis (7♂, 4♀; USNM).

DOMINICA. Coulibistri, 21 Mar 1989, W.N. Mathis (1♂; USNM). Soufrière Bay, 24 Mar 1989, A. Freidberg, W.N. Mathis (7♂, 1♀; USNM).

DOMINICAN REPUBLIC. *Azuá*: near Pueblo Viejo (18°24.8'N, 70°44.7'W), 19 May 1998, D. and W.N. Mathis (5♂; USNM); Puerto Viejo (18°20.9'N, 70°50.4'W), 14 May 1995, W.N. Mathis (11♂; USNM). *Barahona*: Barahona (18°12'N, 71°5.3'W), 20 May 1998, D. and W.N. Mathis (5♂; USNM); Los Patos (17°57.6'N, 71°10.9'W), 15 May 1995, W.N. Mathis (3♂; USNM). *El Seibo*: Pedro Sánchez (18°51.4'N, 69°6.5'W), 26 May 1998, D. and W.N. Mathis (3♂; USNM); Rincón (near; 18°45.3'N, 68°55.7'W), 12 May 1995, W.N. Mathis (1♂; USNM). *Hato Mayor*: Hato Mayor (5.5 km E; 18°46.4'N, 69°12.5'W), 26 May 1998, D. and W.N. Mathis (1♂; USNM). *Independencia*: Mella (canal W; 18°21.5'N, 71°25.7'W), 20 May 1998, D. and W.N. Mathis (6♂; USNM); near Jimani (18°32.6'N, 71°50.3'W), 20 May 1998, D. and W.N. Mathis (2♂; USNM). *La Romana*: Isla Saona, Mano Juan (18°08.1'N, 68°44.5'W), 13 May 1995, W.N. Mathis (2♂, 1♀; USNM). *La Vega*: Jarabacoa (1–2 km S; 19°06.9'N, 70°37'W; 520 m), 8–21 May 1995, 1998, D. and W.N. Mathis (3♂; USNM); Rio Camu (3.5 km NW La Vega; 19°13.7'N, 70°35.2'W; 100 m), 10 May 1995, W.N. Mathis (1♂; USNM); Rio Camu (3.5 km NW La Vega; 19°13.8'N, 70°35.2'W; 100 m), 18 May 1998, D. and W.N. Mathis (7♂, 1♀; USNM). *Pedernales*: Lago Oviedo (N shore; 17°47'N, 71°22.5'W), 15 May 1995, W.N. Mathis (1♂, 1♀; USNM). *Peravia*: Rio Ocoa (San José Ocoa; 18°31.7'N, 70°30.4'W), 21 May 1998, D. and W.N. Mathis (3♂; USNM). *Puerto Plata*: Rio Camu (14 km E Puerto Plata; 19°11.9'N, 70°37.4'W), 17 May 1995, W.N. Mathis (4♂; USNM). *San Cristobal*: Nigua (18°22.4'N, 70°03'W), 27 May 1998, D. and W.N. Mathis (5♂; USNM); Rio Haina (18°25.9'N, 70°00.4'W), 27 May 1998, D. and W.N. Mathis (1♂; USNM).

ECUADOR. *Galápagos*. Isabela: Puerto Villamil (Flamingo lagoon, arid zone), 5 Mar 1989, Bradley J. Sinclair (1♂, 4♀; CNC); Puerto Villamil (arid zone, 5 m), 5 Mar 1989, Bradley J. Sinclair (1♂, 1♀; CNC). Santa Cruz: Academy Bay (arid zone, thorn scrub, Malaise-FT trap, 30 m), 10 May–14 Jun 1985, Stewart and J. Peck (1♀; CNC); Charles Darwin Research Station (arid zone), 2 Apr 1989, Bradley J. Sinclair (1♀; CNC); Charles Darwin Research Station, Tortoise Pool (arid zone, 5 m), 21 Jan 1989, Bradley J. Sinclair (1♂, 2♀; CNC);

Los Gemelos (*Scalesia* forest, 600 m), 1–9 Apr 1989, Stewart B. Peck, Bradley J. Sinclair (1♂, 6♀; CNC); Puntudo (1 km N, *Scalesia* forest, 650 m), 1–30 Mar 1989, S.B. Peck, Bradley J. Sinclair (3♀; CNC).

GRAND CAYMAN. Airport (W end; 19°17.4'N, 81°22.2'W), 26 Apr 1994, W.N. Mathis (5♂, 2♀; USNM). Airport (2 km E; 19°17.1'N, 81°21'W), 26 Apr 1994, W.N. Mathis (6♂; USNM). Frank Sound Road (19°18.9'N, 81°10.9'W), 28 Apr 1994, W.N. Mathis (8♂; USNM). Governor Gore Bird Sanctuary (19°16.7'N, 81°18.5'W), 25 Apr 1994, W.N. Mathis (10♂; USNM). Spotts (19°16.5'N, 81°19.1'W), 25 Apr 1994, W.N. Mathis (5♂, 3♀; USNM).

GRENADA. *St. Patrick*: Bathway Beach (12°12.6'N, 61°36.7'W), 13 Sep 1997, W.N. Mathis (1♂, 4♀; USNM).

GUATEMALA. Gualan, 15 Feb 1905 (3♂, 5♀; ANSP).

GUYANA. Dubulay Ranch, Berbice River (5°40.9'N, 57°51.5'W), 9–11 Apr 1994, W.N. Mathis (3♂, 2♀; USNM); Lethem, Takatu River (3°22.6'N, 59°48.2'W), 4 Apr 1994, W.N. Mathis (5♂, 1♀; USNM); Lodge Village (on dung at cow byre), Demerara River, 19 Oct 1933, C. Williams (1♂, 1♀; ANSP); Mahaica (3 km W; 6°43.5'N, 57°56.6'W), 14 Apr 1994, W.N. Mathis (1♂; USNM).

HONDURAS. *Colón*: Puerto Castilla, 28 May 1926, R.H. Painter (3♀; ANSP). *Cortés*: Omoa (15°47.8'N, 87°58.4'W), 26 Sep 1995, D. and W.N. Mathis (1♂; USNM); Puerto Coreés/Omoa (15°49'N, 87°56.2'W), 26 Sep 1995, D. and W.N. Mathis (3♂; USNM); San Pedro Sula (8 km S; 15°25.7'N, 88°01.4'W), 25–26 Sep 1995, D. and W.N. Mathis (3♂; USNM). *Francisco Morazán*: Valle de Angeles (14°09.4'N, 87°02.4'W), 29 Sep 1995, D. and W.N. Mathis (12♂; USNM).

JAMAICA. *Manchester*: Alligator Pond (17°52.1'N, 77°33.9'W), 8 May 1996, D. and W.N. Mathis, H. Williams (5♂; USNM); near Clandon (18°09'N, 77°28.3'W), 8 May 1996, D. and W.N. Mathis, H. Williams (1♂; USNM); Hanoover, The Great River, 2 Jun 1920 (1♂; AMNH); near Warwick (17°54.1'N, 77°25.5'W), 7 May 1996, D. and W.N. Mathis, H. Williams (1♂; USNM). *Portland*: Reach (4 km N; 18°03.6'N, 76°20.4'W), 15 May 1996, D. and W.N. Mathis, H. Williams (1♀; USNM). *St. Andrew*: Hope Botanical Garden (198 m), 4–5 Dec 1919 (1♂; AMNH); Irishtown (8 km SW), 7 Dec 1975, G.F. Hevel (1♂; USNM). *St. Elizabeth*: Brae River (2 km S; 18°04.2'N, 77°39.5'W), 10 May 1996, D. and W.N. Mathis, H. Williams (5♂; USNM); Elim (18°07.1'N, 77°40.6'W), 10 May 1996, D. and W.N. Mathis, H. Williams (1♂; USNM); near Port Kaiser (17°52.3'N, 77°34.9'W), 8 May 1996, D. and W.N. Mathis, H. Williams (1♂; USNM). *St. Thomas*: Bath Fountain Spring (17°57.6'N, 76°21.3'W), 15 May 1996, D. and W.N. Mathis, H. Williams (1♂; USNM); Mt. Lebanon (17°58.2'N, 76°32.7'W), 16 May 1996, D. and W.N. Mathis, H. Williams (2♂; USNM). *Without Further Locality*: Apr 1891 (2♂, 2♀; ANSP).

PUERTO RICO. Adjuntas (18°09.8'N, 66°43.2'W), 22 Sep 1995, D. and W.N. Mathis (2♂; USNM). Arecibo (beach; 18°28.7'N, 66°42'W), 23 Sep 1995, D. and W.N. Mathis (5♂,

1♀; USNM). Playa de Guayanilla (18°0.4'N, 66°46.1'W), 19 Sep 1995, D. and W.N. Mathis (5♂; USNM). Punta Jacinto (near Guanica; 17°57'N, 66°52.6'W), 20 Sep 1995, D. and W.N. Mathis (1♂; USNM).

MEXICO. *Jalisco*: Guadalajara, 8 Aug 1903 (1♂; ANSP). *Sonora*: Imuris, 2 Jul 1952, C. and P. Vaurie (3♂, 2♀; AMNH). *Tamaulipas*: Tampico, 27 Jul–28 Dec 1908, 1933, C.W. Sabrosky (2♀; ANSP). *Veracruz*: Tamos, 28 Jul 1933, C.W. Sabrosky (1♂; ANSP).

PANAMA. *Canal Zone*: Ancon, 4 Dec 1909, S.T. Darling (2♂, 2♀; ANSP).

ST. LUCIA. Dauphin Boguis (1.6 km S Marquis; 14°01'N, 60°55'W), 17 Jun 1991, D. and W.N. Mathis (4♂; USNM). Micoud (13°49'N, 60°54'W), 15 Jun 1991, D. and W.N. Mathis (3♂; USNM). Soufrière (beach; 13°51'N, 16°54'W), 11–12 Jun 1991, D. and W.N. Mathis (5♂, 1♀; USNM). Sulphur Spring (13°50'N, 61°03'W), 14 Jun 1991, D. and W.N. Mathis (4♂, 3♀; USNM).

ST. VINCENT. *Charlotte*: Owia Salt Pond (13°22.5'N, 61°08.5'W), 6 Sep 1997, W.N. Mathis (1♂, 1♀; USNM); Peruvian Vale (13°10.7'N, 61°08.7'W), 6–8 Sep 1997, W.N. Mathis (6♂; USNM). *St. Andrew*: Camden Park (13°10.2'N, 61°14.7'W), 25 Mar–4 Sep 1989, 1997, W.N. Mathis (20♂, 5♀; USNM); Layou (13°12'N, 61°17'W), 8 Jun 1991, D. and W.N. Mathis (10♂, 3♀; USNM). *St. Patrick*: Cumberland Bay (13°16'N, 61°16'W), 28 Mar 1989, A. Freidberg, W.N. Mathis (1♂; USNM); Wallilabou (beach; 13°15'N, 61°16'W), 27 Mar–8 Jun 1989, 1991, D. and W.N. Mathis (3♂, 1♀; USNM).

TOBAGO. *St. John*: Charlotteville (beach; 11°19.5'N, 60°32.9'W), 16–18 Apr–10–16 Jun 1993, 1994, D. and W.N. Mathis (20♂, 3♀; USNM). *St. Patrick*: Pigeon Point (beach; 11°9.7'N, 60°50'W), 19 Apr 1994, D. and W.N. Mathis (1♂; USNM).

TRINIDAD. *St. George*: Arima (8 km N; 10°41'N, 61°18'W), Verdant Vale, 19 Jun 1993, W.N. Mathis (7♂, 3♀; USNM); Mount St. Benedict (10°39'N, 61°24'W; creek near base), 19 Jun 1993, W.N. Mathis (5♂, 3♀; USNM).

VENEZUELA. Caripito, 16 Jun 1942 (1♂, 10♀; AMNH).

DISTRIBUTION.—Nearctic: Bermuda, USA (AK, AZ, CA, FL, GA, LA, MS, NJ, TX). Neotropical: Argentina, Bahamas, Belize, Bolivia, Brazil, Colombia, Costa Rica, Ecuador, Guatemala, Guyana, Honduras, Mexico (Jalisco, Sonora, Tamaulipas, Veracruz), Panama, Paraguay, Trinidad and Tobago, Venezuela, West Indies (Barbados, Cuba, Dominica, Dominican Republic, Grand Cayman, Grenada, Jamaica, Puerto Rico, St. Lucia, St. Vincent, Virgin Islands).

REMARKS.—This species and *Paralimna obscura* are closely related and are very similar in appearance. Externally we have difficulty in distinguishing between them due to variation in coloration and microtomentum. Both species can be somewhat dark or light colored, with the darker specimens usually shinier as a result of having less microtomentum. There is a tendency for specimens of *P. decipiens* to be lighter and duller (more microtomentose) but with considerable variation, sometimes over-

lapping with *P. obscura*. Accurate identification may require examination of the aedeagus and lateral aedeagal processes.

Because specimens of *P. decipiens* are similar to and frequently occur sympatrically with those of *P. obscura*, Mathis (1995) had previously designated a lectotype for the former to keep nomenclatural issues at the same level of resolution as our understanding of the zoology.

25. *Paralimna (Phaiosterna) fusca* Bock

FIGURES 111, 122–124

Paralimna fusca Bock, 1988:896.—Mathis and Zatwarnicki, 1995:120 [world catalog].

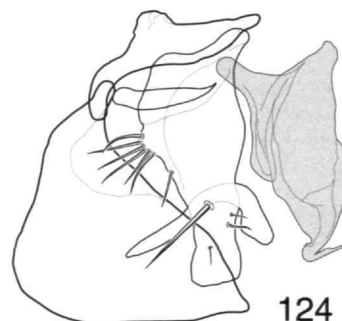
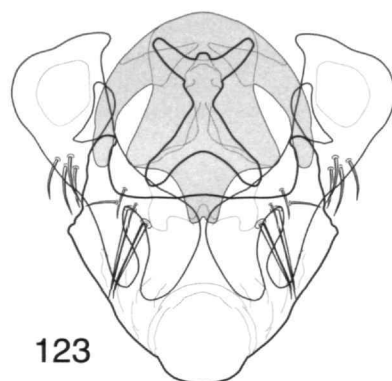
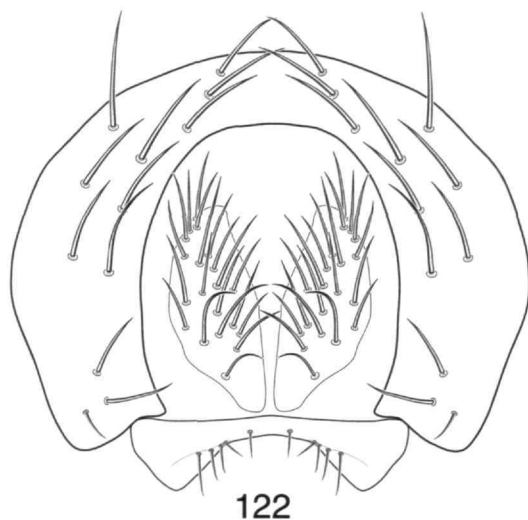
DIAGNOSIS.—This species is distinguished from congeners by the following combination of characters: first flagellomere bearing fringe of long, whitish setulae along dorsum and dorsal portion of rounded apex, setulae longer than ½ height of 1st flagellomere; apex of 1st flagellomere evenly rounded; and mesonotum black, subshiny to shiny, with sparse brown microtomentum, lacking conspicuous, longitudinal stripes.

DESCRIPTION.—Moderately small to medium-sized shore flies, body length 2.0–3.10 mm; generally dark, blackish brown to brownish black species, sparsely to moderately microtomentose, dorsum appearing subshiny to shiny, especially mesonotum.

Head: Generally blackish brown. First flagellomere bearing long fringe of whitish setulae along dorsum and dorsal portion of apex, setulae longer than ½ height of 1st flagellomere. Face uniformly brown to brownish black, subshiny, lacking lighter-colored areas on darker background. Gena-to-eye ratio 0.19–0.20.

Thorax: Generally blackish brown to black; mesonotum black with sparse brown microtomentum, appearing subshiny to shiny, lacking conspicuous, longitudinal stripes. Costal-vein ratio 0.46–0.50; M-vein ratio 0.83–0.86. Foreleg of male lacking long, slender setulae.

Abdomen: Slightly lighter in color than mesonotum; posterior portion of tergites fasciate, grayish microtomentose. Male terminalia (Figures 111, 122–124): epandrium in posterior view inverted U-shaped (Figure 122), moderately wide, width dorsally slightly less than that of lateral arms, with dorsal margin of cercal cavity broadly rounded; cercus broadly pointed dorsally and ventrally, medial margin shallowly convex in posterior view (Figure 122); presurstyli connected medially, forming a nearly straight, short band at ventral margin of cerci, produced ventrolaterally as wide, triangular-shaped projections; postsurstylus in lateral view (Figure 124) with anterior margin swollen medially, bearing several setulae medially, bifurcate apically, anterior lobe long and narrow, posterior lobe in lateral view broadly rounded, truncate apically; aedeagal apodeme with keel slightly asymmetrical, weakly developed; aedeagus in lateral view (Figure 124) narrowly triangular, in posterior view becoming wider subapically, thereafter narrowed to narrow, shallowly bifurcate extension (Figure 123); lateral



FIGURES 122–124.—Male terminalia of *Parolimna* (*Phaiosterna*) *fusca* Bock: 122, epandrium, cerci, and presurstyli, posterior aspect; 123, internal male terminalia, ventral aspect; 124, same, lateral aspect.

0.1mm

aedeagal processes narrow throughout length, narrowly rounded apically (Figure 123); hypandrium deeply invaginated, pocket-like (Figures 123, 124).

TYPE MATERIAL.—The holotype male is labeled “On beach[,] Lloyd Bay, 3 mi. N. Claudie R[iver]. mouth, Qld. [Australia] 25 Dec. 1971/DMcAlpine & GHolloway coll/HO-LOTYPE [florescent red label]/Australian Museum Collection Loan No. 1461 [pink label].” The holotype is double mounted (glued to a large paper triangle), is in excellent condition, and is deposited in the AM.

OTHER SPECIMENS EXAMINED.—Australasian/Oceanian. **AUSTRALIA.** *Coral Sea Islands Territory:* Willis Islets (at light), Jan–Feb 1978, R. Farrow (2♀; ANIC). *Northern Territory:* Wessel Islands, Rimbija Island, 3–4 Feb 1977, T.A. Weir (1♀; ANIC). *Queensland:* Broadbeach, 3 May 1970, Z. Liepa (1♀; ANIC).

CHRISTMAS ISLAND. Canyon, 21 Oct 1934, E.C. Zimmerman (3♂, 3♀; BMNH).

GUAM. Feb 1958, N.L.H. Krauss (14♂, 6♀; BMNH).

PAPUA NEW GUINEA. *Central:* Yule Island (rocky shore), 1 Jan 1983, J.W. Ismay (1♂; USNM). *North:* Gira River near Popodetta, 30 Jun 1982, J.W. Ismay (1♀; USNM).

VANUATU. Malekula: Malua Bay, Jun 1929, L.E. Cheesman (3♂, 6♀; BMNH).

ORIENTAL INDIA. *West Bengal:* Barrackpore, 20 May 1944, D.E. Hardy (1♂; BMNH).

INDONESIA. *Sumatra:* Belawan (at light), Apr 1954, H.S. Evans (1♂; BMNH).

MALAYSIA. *East Malaysia:* Sabah, Kundasang (1 km S; 1530 m), 6 Aug 1983, G.F. Hevel, W.E. Steiner (1♂; USNM); Tenjung Aru (beach), 3–4 Aug 1983, G.F. Hevel, W.E. Steiner (8♂, 12♀; USNM). *West Malaysia:* Kuala Lumpur, 1–3 Oct 1976, P.S. Cranston (1♀; BMNH); Negri Sembilan, 29 Nov 1926, P. Dickson, T. Kemang (1♀; BMNH).

SRI LANKA. *Eastern Province.* Amparai: Maha Oya, 1 May 1980, L. Jayawickrema, W.N. Mathis, T. Wijesinhe (1♀; USNM). *Southern Province.* Hambantota: Bundala, 25 Apr 1980, L. Jayawickrema, W.N. Mathis, T. Wijesinhe (3♂, 1♀;

USNM); Kirinda, 25 Apr 1980, L. Jayawickrema, W.N. Mathis, T. Wijesinhe (17♂, 37♀; USNM). *Western Province*. Colombo: Colombo, Kalutaluwewa (light trap), 19 Feb 1958, (1♂, 1♀; BMNH); Negombo, 7 May 1980, L. Jayawickrema, W.N. Mathis, T. Wijesinhe (5♂, 3♀; USNM).

THAILAND. Bangkok: Pratomvan (at light), Aug–Sep 1962, J.E. Scanlon (1♀; BMNH).

DISTRIBUTION.—Australasian/Oceanian: Australia (Coral Sea Islands Territory, Northern Territory, Queensland), Christmas Island, Guam, Papua New Guinea, Vanuatu. Oriental: India (West Bengal), Indonesia (Sumatra), Malaysia, Sri Lanka, Thailand.

REMARKS.—Although this species was described and until now was known only from Queensland, Australia, we have discovered it to occur widely throughout the Australasian/Oceanian and Oriental Regions.

This is the only species of the subgenus *Phaiosterna* from the Old World that has a subshiny to shiny dorsum, especially the mesonotum, and lacks any evidence of longitudinal stripes.

26. *Paralimna (Phaiosterna) lineata* de Meijere

FIGURES 107, 125–127

Paralimna lineata de Meijere, 1908:165.—Bezzi, 1928:154 [list, Fiji].—Malloch, 1933:11 [list, Marquesas]; 1934a:313 [list, Samoa].—Cresson, 1948:10 [in part; listed as a species incertae].—Cogan and Wirth, 1977:334 [Oriental catalog].—Bock, 1988:893–894 [revision].—Mathis, 1989:644 [Australasian/Oceanian catalog].

Phaiosterna aequalis Cresson, 1929:193 [list, Philippines, Taiwan, Vietnam].—Cogan and Wirth, 1977:334 [synonymy].—Cogan, 1980:663 [synonymy].

Paralimna (Phaiosterna) aequalis.—Cresson, 1948:10 [generic combination; list, India, Philippines, Taiwan].—Mathis and Zatwarnicki, 1995:127 [world catalog].

DIAGNOSIS.—This species is distinguished from congeners, especially those of the subgenus *Phaiosterna*, by the following combination of characters: first flagellomere lacking fringe or fringe of long, whitish setulae along dorsum and dorsal portion of rounded apex far shorter than ½ height of 1st flagellomere; apex of 1st flagellomere with dorsoapical corner more angulate than posteroapical corner; and mesonotum mottled, gray to dark brown, dull to subshiny, with moderately dense gray to brown microtomentum, consistently darker medially, between dorsocentral setae.

DESCRIPTION.—Small to medium-sized shore flies, body length 2.15–3.0 mm; generally dark, whitish gray to brown species, moderately densely to densely microtomentose, dorsum appearing mottled, dull to slightly subshiny, especially mesonotum.

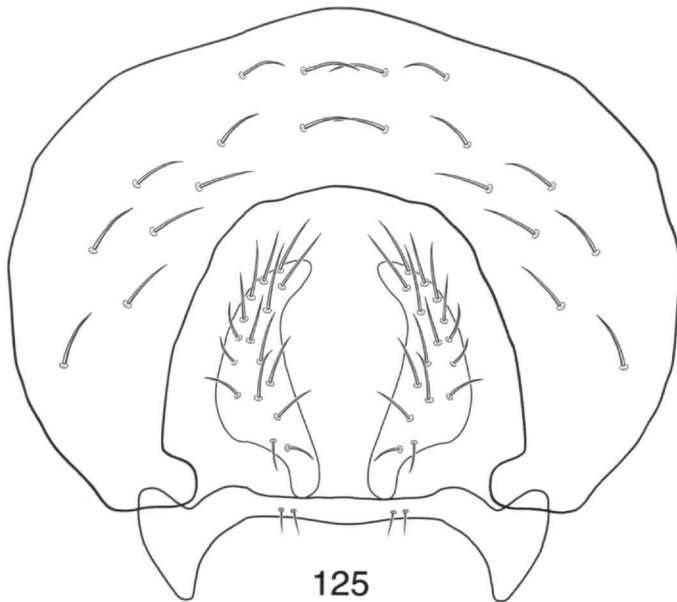
Head: Generally grayish brown to dark brown. First flagellomere bearing short, generally inconspicuous fringe of whitish setulae along dorsum and dorsal portion of apex, setulae far less than ½ height of 1st flagellomere. Face mottled, gray to dark brown, moderately densely microtomentose, appearing dull, subdued. Gena-to-eye ratio 0.23–0.24.

Thorax: Generally gray to dark brown, legs darker; mesonotum mottled, moderately densely gray to dark brown microtomentose, appearing dull to very slightly subshiny, infrequently with darker brown, longitudinal stripes medially, between dorsocentral setae, although consistently darker there. Costal-vein ratio 0.51–0.52; M-vein ratio 0.85–0.94. Foreleg of male lacking long, slender setulae.

Abdomen: Slightly lighter in color than mesonotum, mostly grayish brown; anterior portion of tergites fasciate, darker gray to brown, less microtomentose. Male terminalia (Figures 107, 125–127): epandrium inverted U-shaped in posterior view (Figure 125), wide, width about equal throughout length, with dorsal margin of cercal cavity broadly rounded; cercus pointed dorsomedially and ventrally, medial margin sinuous; presurstyli in posterior view (Figure 125) connected medially, forming shallowly arched band at ventral margin of cerci, produced ventrolaterally as narrow, triangular-shaped projections; postsurstylus in lateral view (Figure 127) with anterior margin swollen medially, bearing several setulae medially, bifurcate apically, anterior lobe narrower and shorter than posterior lobe in lateral view, posterior lobe broadly rounded apically; aedeagal apodeme with keel asymmetrical, more angulate toward hypandrium and more rounded toward base of aedeagus, attachment with base of aedeagus shallowly recurved, attachment with hypandrium curved slightly ventrally; aedeagus in lateral view (Figure 127) narrowly triangular, subrectangular in ventral view (Figures 107, 126), slightly narrowed basally, otherwise mostly parallel sided, apex broadly rounded to truncate thereafter, forming short, narrow point; lateral aedeagal process wide throughout length, broadly rounded apically, spatulate (Figure 126); hypandrium deeply invaginated, pocket-like (Figures 126, 127).

TYPE MATERIAL.—The lectotype male of *Paralimna lineata* de Meijere (designated by Bock, 1988:894) is labeled “[Indonesia.] Java[:] I.’ 08 [Jan 1908] Semarang. Jacobson./Paralimna lineata de Meijere Type. [handwritten]/ Lectotype [red label]/LECTOTYPE *Paralimna lineata* ♂ de Meij. det B.H. Cogan 1971. [all except “det B.H. Cogan” handwritten]/LECTOTYPE *Paralimna lineata* de Meijere ♂ By I.R. Bock, 1988 [“LECTOTYPE” and “By” in red type; all else handwritten; label with black submargin].” The lectotype is double mounted (minuten into venter of specimen and in rectangular block of pith), is in fair condition (setae on right side largely missing), and is deposited in the ZMA. Three female paralectotypes bear the same locality label data as the lectotype.

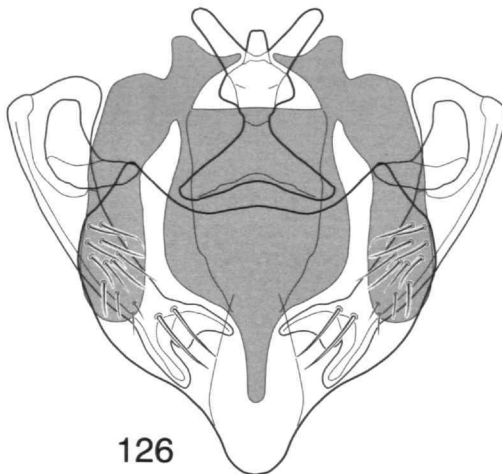
The holotype male of *Phaiosterna aequalis* Cresson is labeled “Fruhstorfer Mittel-Annam [Vietnam]/♂/Phaiosterna AEQUALIS E.T.Cresson, Jr. [red label; species name handwritten]/Collection of the Academy of Natural Sciences of Philadelphia (ANSP).” The holotype is double mounted (minuten in a rectangular block of foam-like plastic, is in good condition (right foreleg missing; some setae, especially on left side of head, displaced or missing), and is deposited in ANSP



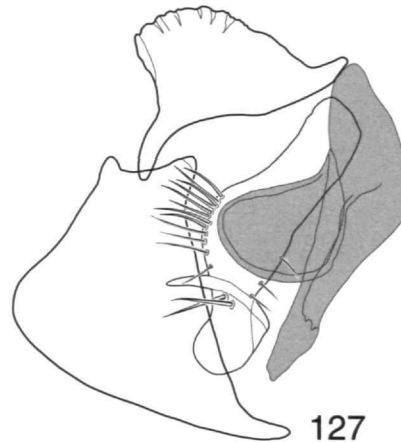
125

FIGURES 125-127.—Male terminalia of *Paraimna* (*Phaiosterna*) *lineata* de Meijere: 125, epandrium, cerci, and presurstyli, posterior aspect; 126, internal male terminalia, ventral aspect; 127, same, lateral aspect.

0.1mm



126



127

(6340). There are also four paratypes (1♂, 3♀; ANSP, NMW) that bear the same locality data as the holotype.

OTHER SPECIMENS EXAMINED.—Australasian/Oceanian. AMERICAN SAMOA. *Tutuila*: Aunuu Island, 10 Dec 1953, C. Hoyt (1♂; BMNH); Malae'imiV'ey, 7 Jul 1953, C. Hoyt (1♂, 1♀; BMNH); Pago Pago, 14 Dec 1925, G.H. Hopkins (1♂; BMNH).

AUSTRALIA. *Queensland*: Cairns (bay shore and puddles), 19-25 Apr 1957, W.W. Wirth (3♂, 5♀; BMNH). *Western Australia*: Millstream (at light), 7 Apr 1971, D.H. Colless (2♀; ANIC).

FEDERATED STATES OF MICRONESIA. *Yap*: Giliman, 11 Jun 1957, C.W. Sabrosky (1♀; BMNH); Ruul, near Kolonia, 13 Jun 1957, C.W. Sabrosky (2♀; BMNH). *Ifalik*: Ifalik Atoll, 6 Sep 1953 (1♂; BMNH). *Kosrae* (=Kusaie): Mutunlik, 18 Mar 1953, J.F.C. Clarke (1♂; BMNH). *Ponape*: Not, Paliej, Jan 1948, N.S. Hurlbut (1♂; BMNH). *Truk Islands*: Moen, South Valley, Mt. Tonaachau, 25 Apr 1949, R.W.L. Potts (1♀; BMNH).

FIJI. *Viti Levu*: Lautoka, 28 Feb 1919, H. Greenwood (2♂, 1♀; BMNH); Lautoka (0.5 m), Mar 1976, N.L. Krauss (1♂, 1♀;

USNM); Nandi (0–100 m), 5 May 1973, N.L.H. Krauss (2♂, 3♀; USNM).

GUAM. Agana (muddy stream), 25 May 1936, R.L. Usinger (1♀; BMNH). Agat (grass), 20 May 1936, O.H. Sweezy (1♀; BMNH). Inarajan (on rice), 25 Jul 1936, O.H. Sweezy (1♀; BMNH).

KIRIBATI. *Gilbert Islands*: Marakei Atoll, Dec 1957, N.L.H. Krauss (1♀; BMNH).

MARQUESAS. *Fatu Hiva*: Oomoa Valley, 21 Aug 1930, Le Bronnec (1♂; BMNH). *Nuku Hiva*: Haaotupa, 14 Jun 1987, W.N. Mathis (6♂, 1♀; USNM); Taiohae, 9–15 Jun 1987, W.N. Mathis (8♂, 2♀; USNM); Toovii (800 m), 10–12 Jun 1987, W.N. Mathis (34♂, 12♀; USNM).

NORTHERN MARIANAS. *Saipan*: Tsutsuuran, 31 Aug 1944, D.G. Hall (1♂; USNM).

PALAU. *Babelthuap*: Babelthuap (along streams and cacao), 16 Apr–21 May 1957, C.W. Sabrosky (5♂, 2♀; BMNH); Ulimang, 14 Dec 1947, H.S. Dybas (1♀; BMNH).

PAPUA NEW GUINEA. *Central*: Aieme River (river side), 31 Oct 1982, J.W. Ismay (1♀; USNM); Brown River Bridge (12 km NW), 18 May 1986, J.W. Ismay (4♂, 7♀; USNM); Iomari Creek (stream), 23 May 1986, J.W. Ismay (1♀; USNM); Kwikila (muddy stream), 23 Jul 1982, J.W. Ismay (1♂, 1♀; USNM); Laloki (river margin, mud under tree, marsh), 2 Feb–13 Dec 1982, 1986, J.W. Ismay (6♂, 8♀; USNM); Rubberlands (near), 22 Mar 1986, J.W. Ismay (7♂, 3♀; USNM); Woitope (river margin), 9 Jun 1986, J.W. Ismay (3♀; USNM). *Morobe*: Bubia (marsh), 10 Apr 1986, J.W. Ismay (1♂, 7♀; USNM). *Western*: Sapoka, 4 Mar 1981, J.W. Ismay (1♂; BMNH).

SOCIETY ISLANDS. *Moorea*: Opunohu Bay, 16 Oct 1958, D.E. Puleston (3♂, 1♀; BMNH). *Raiatea*: 26 Feb 1921, J.W. Moore (1♂; BMNH). *Tahiti*: 13 Mar 1925, L.E. Cheesman (1♂, 2♀; BMNH); near Papeete, Mar–Apr 1925, L.E. Cheesman (1♂; BMNH).

SOLOMON ISLANDS. *New Georgia Islands*: Gizo, Dec 1980, N.L.H. Krauss (9♂, 4♀; BMNH); Kolombangara (8°05'S, 156°47'E), Jan 1974, N.L.H. Krauss (2♂, 2♀; BMNH). *Guadalcanal*: Tenaru River, Apr 1945, G.E. Bohart (2♂; BMNH); Umasami River, Oct 1944, J. Laffoon (2♀; BMNH); Guadalcanal and Florida Islands, Jan–Mar 1945, J.R. Stuntz (3♀; BMNH).

VANUATU. *Malekula*: Malua Bay, Jun 1929, L.E. Cheesman (1♀; BMNH); Oonua, Apr–May 1929, L.E. Cheesman (1♂; BMNH); Malekula (NE), Jun 1929, L.E. Cheesman (1♂, 1♀; BMNH).

WESTERN SAMOA. Upolu (610 m), 1 May 1924, P.A. Buxton (1ex; BMNH).

Oriental. INDIA. *Andhra Pradesh*: Hyderabad (17°23'N, 78°28'E), 26–30 Oct 1971, A.C. Pont (100♂, 100♀; BMNH). *Assam*: Rupsi (24 km NW Dhubri), 3 Nov 1943, D.E. Hardy (1♂; BMNH). *Dehli*: Dehli (at light), 26 Aug 1962, P.W. Oman (1♂; BMNH). *Kerala*: Calicut, 7 Feb 1976 (1♂; USNM). *Tamil Nadu*: Coimbatore, Oct 1955, P.S. Nathan

(1♂, 1♀; BMNH); Madras, Tondiarpet (over open sewage), 13 Aug, Fletcher (1♂, 1♀; ANSP, BMNH); Kurumbagaram (associated with stagnant water), Nov 1951, P.S. Nathan (4♂, 2♀; BMNH). *West Bengal*: Calcutta, Tollygunge, 29 Sep 1904, Brunetti (2♂, 6♀; BMNH). Calcutta, Edengard, 22 Dec 1956, A.P. Kapur (2♀; BMNH). Diamond Harbour, 1 Dec 1927, R. Hoogly (1♀; BMNH).

INDONESIA. *Java*: Djakarta, Aug 1908, Jacobson (1♂; ZMA); Wonosobo, May 1909, Jacobson (1♀; ZMA). (Although Cogan labeled these two specimens as paralectotypes, the localities are not mentioned in the original description, nor do the collection dates correspond.) *Lesser Sunda Islands*. West Sumbawa: Semongkat (8°35'S, 117°20'E), 10–15 May 1927, Sunda-Expedition, Rensch (3♂, 1♀; BMNH); Dompoe (8°32'S, 118°28'E), 24–25 May 1927, Sunda-Expedition, Rensch (2♂, 2♀; BMNH); Soembawa-Besár (8°30'S, 117°26'E), 24 Apr–2 May 1927, Sunda-Expedition, Rensch (1♂; BMNH).

LAOS. Ban Theuong (18 km NW Xieng Khouang; 1035 m; at light), 2–6 Aug 1960, R.E. Leech (2♂; BPBM, TZ). Bolouens Plateau (16 km S Thateng; 1020 m; at light), 22–24 Jul 1960, R.E. Leech (1♂; BPBM).

MALAYSIA. *Sabah*: Beaufort (6 km N), 11 Aug 1983, G.F. Hevel, W.E. Steiner (1♀; USNM); Kota Kinabalu (17 km S), 19 Aug 1983, G.F. Hevel, W.E. Steiner (1♂; USNM); Kundasang (1 km S; 1530 m), 6 Aug 1983, G.F. Hevel, W.E. Steiner (3♀; USNM); Paal, 1 Sep 1983, G.F. Hevel, W.E. Steiner (1♂; USNM); Tambunan (10 km S), 30 Aug 1983, G.F. Hevel, W.E. Steiner (1♂; USNM); Tenjung Aru (beach), 3–20 Aug 1983, G.F. Hevel, W.E. Steiner (4♂, 3♀; USNM). *Sarawak*: 1st Division, Kuching, 6–7 Oct 1976, P.S. Cranston (7♂, 4♀; BMNH); 4th Division, Miri beach, 23 Oct 1976, P.S. Cranston (1♂; BMNH); Paloh (or Palch?) 1st Division, G.H. Voon (1♀; BMNH). *Selangor*: Kuala (3°21'N, 101°15'E), Klang (Nipa Swamp), 24–26 Dec 1958, T.C. Maa (2♂; BPBM); Klang Rantau Panjang (8 km N; at light), Sep–Dec 1959, H.E. McClure (1♂; BMNH); Port Kelang (salt marsh), 4 Mar 1982, C.E. Dyte (1♂, 2♀; BMNH).

NEPAL. Chitwan: Sauraha (Smithsonian Institution Camp), 31 Oct 1985, W.N. Mathis (5♂, 2♀; USNM); Sauraha (Smithsonian Institution Camp), Dhungari Khola (2 km E), 1 Nov 1985, W.N. Mathis (2♀; USNM).

PAKISTAN. Lahore (at light), Jun–Nov 1957, J. Maldonado (6♂, 4♀; BMNH).

PHILIPPINES. *Luzon*. Pangasinan: Manaoag (4 km NE; 16°4'N, 120°31'E; mungbean field), 31 Jan 1978, A.T. Barrion (1♂; TZ). Bulacon: near Bulacon (rice field), 1 Jun 1985, C.E. Dyte, J. van S. Graver (2♀; BMNH). Mt. Makiling, C.F. Baker (2♂, 1♀; ANSP, BMNH). Manila, 7 Jul 1930, R.C. McGregor (1♂, 1♀; ANSP). *Panay*. Iloilo: Oton (8 km N; 10°46'N, 122°27'E; rice field), 29 Oct 1976, M.D. Lumaban (1♀; TZ). *Visayan*. Siquijor: Leyte, Baybay ("Visca" grounds), 15–22 Aug 1980, R.I. Vane-Wright (1♀; BMNH).

SRI LANKA. *Central Province*. Kandy: Kandy (1600 m), 12 Sep 1967, P.B. Karunaratne (1♀; BMNH); Kohowala (Kohu-

wala; 07°09'N, 80°31'E), 7 Nov 1967, P.B. Karunaratne (5♂, 5♀; BMNH). Nuwara Eliya: Nuwara Eliya, Horton Plains, 23 Apr 1980, L. Jayawickrema, W.N. Mathis, T. Wijesinhe (1♂, 2♀; USNM); Nuwara Eliya, 22–23 Apr 1980, L. Jayawickrema, W.N. Mathis, T. Wijesinhe (1♀; USNM). *Eastern Province*. Amparai: Maha Oya, 1 May 1980, L. Jayawickrema, W.N. Mathis, T. Wijesinhe (11♂, 16♀; USNM). *North Central Province*. Anuradhapura: Anuradhapura (8°21'N, 80°23'E), 19 Feb 1974, P.J. Chandler, A.E. Stubbs (1♀; BMNH). *North-eastern Province*. Mannar: Murunkan (08°50'N, 80°02'E), 12 Feb 1938, J.C. Hutson (1♀; BMNH). *Southern Province*. Hambantota: Bundala, 25 Apr 1980, L. Jayawickrema, W.N. Mathis, T. Wijesinhe (9♂, 13♀; USNM); Kirinda, 25 Apr 1980, L. Jayawickrema, W.N. Mathis, T. Wijesinhe (33♂, 22♀; USNM). *Western Province*. Colombo: Bellanwila, 8 May 1980, L. Jayawickrema, W.N. Mathis, T. Wijesinhe (3♂, 4♀; USNM); Boralesgomuwa (06°50'N, 79°54'E), 17 Feb 1974, A.E. Stubbs, P.J. Chandler (1♀; BMNH); Gampaha Botanical Garden, 16 Apr 1980, L. Jayawickrema, W.N. Mathis, T. Wijesinhe (1♂; USNM); Kalutaluwewa (light trap), 19 Feb 1958, A.E. Stubbs (2♂, 1♀; BMNH); Negombo, 10–11 Feb–7 May 1974, 1980, P.J. Chandler, L. Jayawickrema, W.N. Mathis, T. Wijesinhe (39♂, 50♀; BMNH, USNM); Nugegoda (06°52'N, 79°53'E), 20 Oct 1967, P.B. Karunaratne (11♂, 13♀; BMNH); Siduwa (Seeduwa; 07°08'N, 79°53'E), 13 Feb 1974, P.J. Chandler, A.E. Stubbs (1♀; BMNH).

TAIWAN. Tainan, Oct 1908, Sauter (1♂, 3♀; ANSP). Hualien, 7 Oct 1993, A. Freidberg, F. Kaplan (2♂, 5♀; USNM).

THAILAND. Bangkok: Huaykwang (light trap), Aug–Sep 1962, J.E. Scanlon (1♀; BMNH); Bangpo (light trap), Aug–Sep 1962, J.E. Scanlon (1♀; BMNH); Thonglo, Aug–Sep 1962, J.E. Scanlon, light trap (2♂, 2♀; BMNH); Bangkok (at light), Plukchit, Aug–Sep 1962, J.E. Scanlon (2♂, 1♀; BMNH); Pratomvan (at light), Aug–Sep 1962, J.E. Scanlon (1♀; BMNH). Chiangmai: Chiangmai (at light), Apr–May 1958, V. Notonanda (1♂; BMNH). Cholburi: Bangphra (at light), Oct 1962, J.E. Scanlon (1♂, 2♀; BMNH). Loei: Loei (at light), 1–5 Jun 1959, Manop Rattarithikun (2♀; BMNH). Nakhonrajsima: (at light), 5–7 Jul 1959, Manop Rattarithikun (1♂; BMNH). Khon Kaen: Khon Kaen (at light), 20–24 May 1959, Manop Rattarithikun (1♂, 1♀; BMNH). Thon Buri: Bangkoknoi, 5–7 May 1959, Manop Rattarithikun (at light) (2♂, 4♀; BMNH). Udon Thani: Ampur Muang (at light), Sep 1962, J.E. Scanlon (1♂; BMNH).

VIETNAM. Fruhstorfer (2♀; ANSP). Saigon (at light), 30 May 1960, N.R. Spencer (1♀; BMNH).

DISTRIBUTION.—Australasian/Oceanian: American Samoa, Australia (Queensland, Western Australia), Federated States of Micronesia, Fiji, Guam, Kiribati (Gilbert Islands, Phoenix Island), Marquesas (Fatu Hiva, Nuku Hiva), Northern Marianas, Palau, Papua New Guinea, Society Islands (Moorea, Raiatea, Tahiti), Solomon Islands, Vanuatu, Western Samoa. Oriental: India (Andhra Pradesh, Assam, Dehli, Kerala, Tamil Nadu, West Bengal), Indonesia (Java, Lesser Sunda Islands), Laos,

Malaysia, Nepal, Pakistan, Philippines (Luzon, Panay, Visayan), Sri Lanka, Taiwan, Thailand, Vietnam.

REMARKS.—This is a very widespread species that exhibits considerable variation in color throughout its range, especially in the expression of stripes on the scutum. The only species within its range that could be confused with it is *Paralimna fusca*, which is distinguished by the sparse microtomentum, especially on the subshiny to shiny mesonotum.

27. *Paralimna (Phaiosterna) longiseta*, new species

FIGURES 108, 128–130

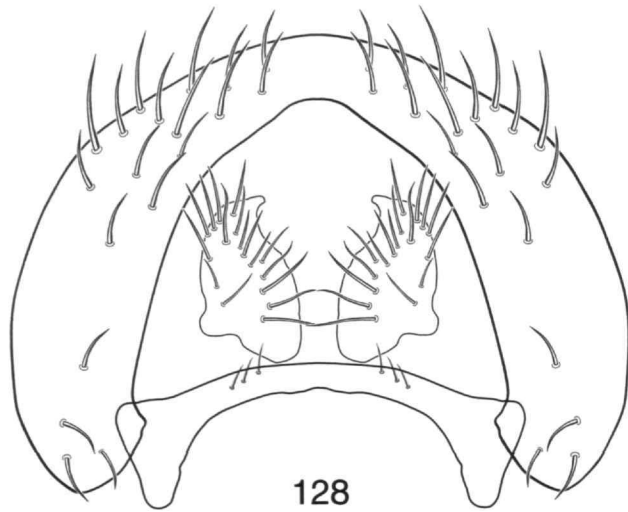
DIAGNOSIS.—This species is distinguished from congeners, especially those of the subgenus *Phaiosterna*, by the following combination of characters: first flagellomere lacking fringe or fringe of long, whitish setulae along dorsum and dorsal portion of rounded apex far shorter than ½ height of 1st flagellomere; apex of 1st flagellomere with dorsoapical corner more angulate than posteroapical corner; mesonotum mostly uniformly colored, gray to dark brown, dull to subshiny, with moderately dense gray to brown microtomentum, consistently darker medially, between dorsocentral setae; ventral apex of male foretibia bearing numerous long, slender setulae; and posterior surface of forebasitarsus bearing scattered long, slender setulae.

DESCRIPTION.—Moderately small to medium-sized shore flies, body length 2.35–3.85 mm; generally dark, yellowish gray to brown species, moderately densely to densely microtomentose, dorsum appearing relatively uniform in color, dull to slightly subshiny, especially mesonotum.

Head: Generally grayish brown to golden brown. First flagellomere bearing short, generally inconspicuous fringe of whitish setulae along dorsum and dorsal portion of apex, setulae far shorter than ½ height of 1st flagellomere. Face yellowish gray to golden brown, microtomentose, appearing dull, subdued. Gena-to-eye ratio 0.39–0.40.

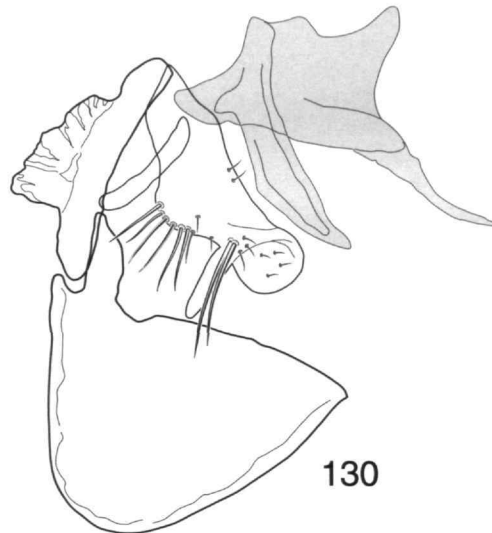
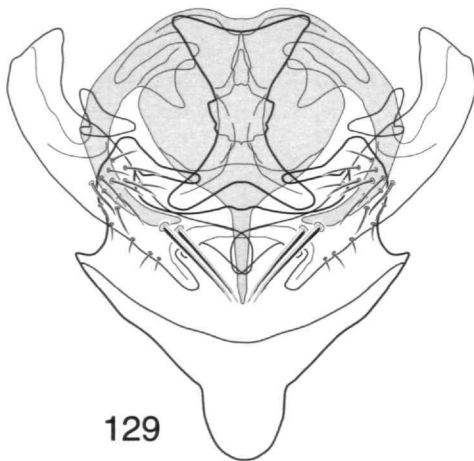
Thorax: Generally grayish yellow to golden brown, legs darker, black with some grayish microtomentum; mesonotum moderately densely grayish yellow to golden brown microtomentose, appearing dull to very slightly subshiny, infrequently with darker brown, short to long stripes between dorsocentral setae. Costal-vein ratio 0.40–0.43; M-vein ratio 0.86–0.96. Ventral apex of foretibia bearing numerous, long, slender setulae; posterior surface of forebasitarsus bearing scattered long, slender setulae.

Abdomen: Slightly lighter in color than mesonotum, mostly grayish to yellowish brown; tergites uniformly colored or anterior portion of tergites very fasciate, dark gray to brown, less microtomentose. Male terminalia (Figures 108, 128–130): epandrium in posterior view inverted U-shaped (Figure 128), narrower dorsally, with dorsal margin of cercal cavity narrowly rounded, arms of epandrium wider; cercus acutely pointed dorsomedially, medial margin sinuous, ventral margin with shallow, narrow indentation, slightly produced ventrolaterally; presurstyli in posterior view (Figure 128) connected medially,



FIGURES 128–130.—Male terminalia of *Parolimna* (*Phaiosterna*) *longiseta*, new species: 128, epandrium, cerci, and presurstyli, posterior aspect; 129, internal male terminalia, ventral aspect; 130, same, lateral aspect.

0.1mm



forming shallowly arched band at ventral margin of cerci, produced ventrolaterally as triangular-shaped projections; postsurstylus in lateral view (Figure 130) with anterior margin swollen medially, bearing several setulae, bifurcate apically, anterior lobe narrow, parallel sided in lateral view, posterior lobe broadly rounded in lateral view; gonite rod-like, very slightly arched; aedeagal apodeme with keel asymmetrical (Figure 130), extended outward more on ventral portion; aedeagus rounded basally in posterior view, thereafter forming a narrow point; lateral aedeagal process narrow, curved medially, acutely pointed apically (Figure 129); hypandrium deeply invaginated, pocket-like (Figures 129, 130).

TYPE MATERIAL.—The holotype male is labeled “**DOMINICAN RP.** Azua: near Pueblo Viejo 18°24.8'N, 70°44.7'W 19May1998, WNMathis/USNM ENT 00087712 [plastic bar code label]/HOLOTYPE ♂ *Parolimna longiseta* W.N.Mathis and Zatwarnicki USNM [red label; gender symbol, species name, and “Zatwarnicki” handwritten].” The holotype is double mounted (minuten in a block of plastic), is in excellent condition, and is deposited in the NMNH. The allotype female and 20 other paratypes (13♂, 7♀; USNM) bear the same label data as the holotype but with different bar code numbers. Other paratypes are as follows: **DOMINICAN REPUBLIC.** *La Vega:* El Rio (9.5 km E; 19°0.9'N, 70°33.5'W; 980 m), 6 May 1995,

W.N. Mathis (2♂; USNM); El Rio (9.5 km E; 19°0.7'N, 70°33.6'W; 980 m), 24 May 1998, D. and W.N. Mathis (6♂; USNM); Rio Camu (3.5 km NW La Vega; 19°13.7'N, 70°35.2'W; 100 m), 10 May 1995, W.N. Mathis (6♂, 1♀; USNM); Rio Camu (3.5 km NW La Vega; 19°13.8'N, 70°35.2'W; 100 m), 18 May 1998, D. and W.N. Mathis (6♂, 4♀; USNM). *Peravia*: Rio Ocoa (San José Ocoa; 18°31.7'N, 70°30.4'W), 21 May 1998, D. and W.N. Mathis (5♂, 1♀; USNM). *Puerto Plata*: Rio Camu (14 km E Puerto Plata; 19°41.9'N, 70°37.5'W), 23 May 1998, D. and W.N. Mathis (6♂; USNM); Rio Pérez (near Imbert; 19°44.1'N, 70°50.2'W), 24 May 1998, D. and W.N. Mathis (6♂; USNM).

OTHER SPECIMENS EXAMINED.—Neotropical. BRAZIL. *Mato Grosso*: Capitaio Vasconcelos, Rio Tuatuari, Upper Xingu Basin, 31 Jul 1957, B. Malkin (18♂, 28♀; CAS, USNM).

HONDURAS. *Cortés*: Omoa (15°47.8'N, 87°58.4'W), 26 Sep 1995, D. and W.N. Mathis (3♂, 1♀; USNM); San Pedro Sula (8 km S; 15°25.7'N, 88°01.4'W), 25–26 Sep 1995, D. and W.N. Mathis (2♂; USNM).

JAMAICA. *St. Andrew*: Wag Water River, 25 Feb 1969, W.W. Wirth (1♂; USNM). *St. Thomas*: Yallahs River (mouth; 17°53'N, 76°35.6'W), 14 May 1996, D. and W.N. Mathis, H. Williams (8♂, 1♀; MCV, USNM).

MEXICO. *San Luis Potosí*: Tamazunchale, 23 Nov 1946, R.E. Skinner (9♂; CAS, USNM).

PUERTO RICO. Rio Hoconuco (18°7.6'N, 67°2.6'W), 20 Sep 1995, D. and W.N. Mathis (1♂; USNM).

DISTRIBUTION.—Neotropical: Brazil (Mato Grosso), Honduras, Mexico, West Indies (Dominican Republic, Jamaica, Puerto Rico).

ETYMOLOGY.—The specific epithet, *longiseta*, alludes to the long, fine setae on the foreleg of males.

REMARKS.—Older specimens tend to be darker, more rusty colored and have more setae missing or broken.

We have frequently collected this species sympatrically with the other two species of the subgenus *Phaiosterna* that occur in the New World.

28. *Paralimna (Phaiosterna) obscura* Williston

FIGURES 109, 131–142

Paralimna obscura Williston, 1896:391.—Coquillett, 1900:259 [list, Puerto Rico].—Aldrich, 1905:624 [Nearctic catalog].—Jones, 1906:178–179 [key, catalog].

Paralimna (Phaiosterna) obscura.—Cresson, 1916:105 [subgeneric combination], 109–110 [revision]; 1946:230 [review, Nearctic Region]; 1947a:54–55 [review].—Wirth, 1965:748 [Nearctic catalog]; 1968:16 [Neotropical catalog].—Mathis and Edmiston, 1991:832–834 [discussion, designation of a lectotype].—Mathis and Zatwarnicki, 1995:127 [world catalog].—Mathis, 1997:56–59 [list, Belize, scanning electron micrographs, figures of male genitalia].

DIAGNOSIS.—This species is distinguished from congeners, especially those of the subgenus *Phaiosterna*, by the following combination of characters: specimens tending to be dark brown to black, shiny, sparsely microtomentose; 1st flagellomere

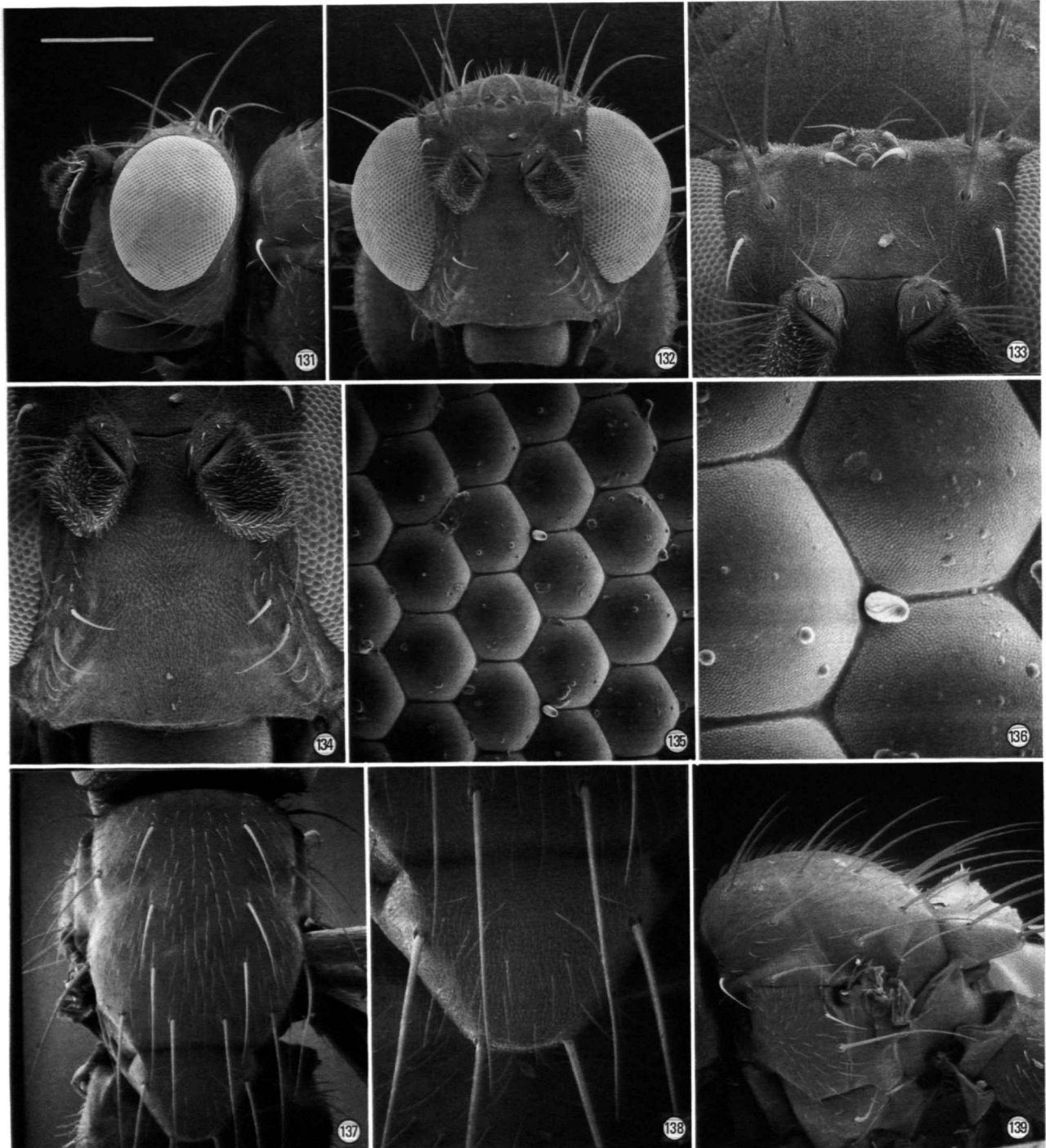
lacking fringe or fringe of long, whitish setulae along dorsum and dorsal portion of rounded apex far shorter than ½ height of 1st flagellomere; apex of 1st flagellomere with dorsoapical corner more angulate than posteroapical corner; mesonotum mostly uniform, gray to dark brown, dull to subshiny, with moderately dense gray to brown microtomentum, consistently darker medially, between dorsocentral setae; ventral apex of male foretibia not bearing numerous long, slender setulae; posterior surface of forebasitarsus not bearing scattered long, slender setulae; aedeagus narrow in dorsal view, slightly longer than wide, apical part of sclerotized portion distinctly pointed, especially evident in lateral view.

DESCRIPTION.—Moderately small to medium-sized shore flies, body length 2.25–3.50 mm; generally dark, gray brown to black species, moderately densely microtomentose, dorsum appearing relatively uniform in color, dull to subshiny, especially mesonotum.

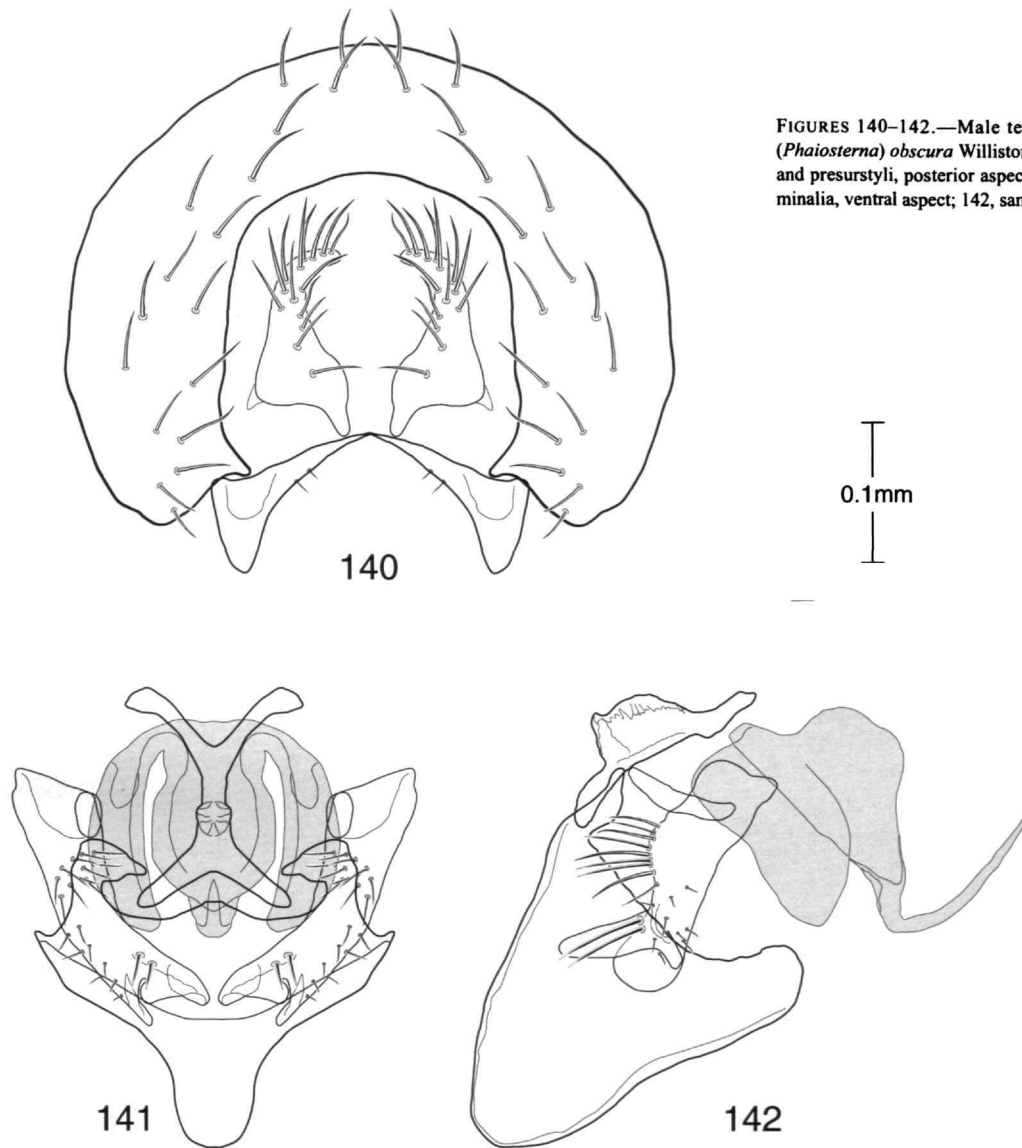
Head (Figures 131–136): Generally gray brown to black. First flagellomere bearing short, generally inconspicuous fringe of whitish setulae along dorsum and dorsal portion of apex, setulae far shorter than ½ height of 1st flagellomere. Face gray to grayish brown, microtomentose, appearing dull, subdued. Gena-to-eye ratio 0.24–0.27.

Thorax (Figures 137–139): Generally gray brown to black, legs darker, black with some grayish microtomentum; mesonotum moderately densely gray brown to brownish black, microtomentose, appearing dull to subshiny, frequently with lighter brown, short to long stripes between dorsocentral setae, especially anteriorly. Costal-vein ratio 0.48–0.53; M-vein ratio 0.95–1.0. Ventral apex of foretibia lacking numerous long, slender setulae; posterior surface of forebasitarsus lacking scattered long, slender setulae.

Abdomen: Slightly to distinctly lighter in color than mesonotum, mostly brownish gray to brownish black; tergites usually fasciate, with anterior portion of tergites darker gray to brownish black, less microtomentose than posterior, more densely microtomentose and grayer portion. Male terminalia (Figures 109, 140–142): epandrium in posterior view inverted U-shaped (Figure 140), wide, width about equal throughout length, with dorsal margin of cercal cavity narrowly rounded; cercus with medial margins deeply sinuous, concave dorsally, acutely pointed dorsomedially, ventral margin produced ventromedially in posterior view; presurstyli in posterior view (Figure 140) at most very narrowly connected medially or not touching, produced ventrolaterally as triangular-shaped projections; postsurstylus in lateral view (Figure 142) with anterior margin swollen medially, bearing several setulae, bifurcate apically, with anterior lobe short and narrow, posterior lobe broadly rounded in lateral view; gonite rod-like, very slightly arched; aedeagal apodeme with keel asymmetrical (Figure 142) and only moderately produced, with shallow indentation toward ventral margin; aedeagus somewhat triangular in lateral view (Figure 142), with long, narrow, medial process apically; lateral aedeagal processes robust (Figure 141), at apex very



FIGURES 131–139.—Scanning electron micrographs of *Paralimna (Phaiosterna) obscura* Williston (Belize. Stann Creek District: Wee Wee Cay; scale length in parenthesis; scale for all photographs = Figure 131): 131, head, lateral aspect (0.33 mm); 132, head, anterior aspect (0.30 mm); 133, frons, anterodorsal aspect (176 μ m); 134, face, anterior aspect (176 μ m); 135, ommatidia of compound eye, lateral aspect (17.6 μ m); 136, enlargement of interfacetal seta, lateral aspect (6.0 μ m); 137, mesonotum, dorsal aspect (0.38 mm); 138, scutellum, dorsal aspect (176 μ m); 139, thorax, lateral aspect (0.38 mm).



FIGURES 140–142.—Male terminalia of *Parolimna (Phaiosterna) obscura* Williston: 140, epandrium, cerci, and presurstyli, posterior aspect; 141, internal male terminalia, ventral aspect; 142, same, lateral aspect.

slightly oriented medially; hypandrium very deeply invaginated, pocket-like (Figures 141, 142).

TYPE MATERIAL.—The lectotype male of *Parolimna obscura* Williston (designated by Mathis and Edmiston, 1991:832) is labeled “Co-type [circular label with yellow border]/Leeward side St. Vincent, W.I. H. H. Smith./W.Indies. 1907-66./Parolimna brunnea [lined out] obscura Will. [handwritten, label with two red submarginal borders]/LECTOTYPE Parolimna obscura Will. ♂ By W.N.Mathis [handwritten except for “LECTOTYPE” and “By,” label with black submarginal border].” The lectotype is double mounted (pin in a rectangular

piece of cardboard), is in good condition, and is deposited in BMNH. There are also 15 paralectotypes as follows: BMNH (4♂, 3♀), KU (3♂, “35” and “21”), AMNH (1♂, 4♂, 20326). Williston, in the original description, indicated that there were “Numerous specimens.”

OTHER SPECIMENS EXAMINED.—Nearctic. BERMUDA. 29 Jul 1905, T. Kincaid (1♀; ANSP).

Neotropical. BAHAMAS. *San Salvador*: near Cockburn Town, 18 Mar 1953, E.B. Hayden (1♂; ANSP).

BARBADOS. *Christ Church*: Graeme Hall Swamp (13°04.2'N, 59°34.7'W), 21–22 May–12 Sep 1996, 1997, D.

and W.N. Mathis, H. Williams (22♂; USNM); Oistins (13°03.9'N, 59°32.7'W), 22 May 1996, D. and W.N. Mathis, H. Williams (4♂; USNM); Rockley Beach (13°04.3'N, 59°35.2'W), 21 May–11 Sep 1996, 1997, D. and W.N. Mathis, H. Williams (15♂, 1♀; USNM). *St. Andrew*: Bawdens Ponds (13°14.8'N, 59°34.9'W), 2 Sep 1997, W.N. Mathis (1♂; USNM); Baxters (13°13.2'N, 59°34.1'W), 21 May–11 Sep 1996, D. and W.N. Mathis, H. Williams (10♂, 1♀; USNM); Belleplaine (13°14.8'N, 59°33.6'W), 21 May 1996, D. and W.N. Mathis, H. Williams (6♂; USNM); Long Pond (13°15.1'N, 59°33.3'W), 21 May–11 Sep 1996, 1997, D. and W.N. Mathis, H. Williams (22♂; USNM). *St. Joseph*: Joes River (13°12.8'N, 59°32.3'W), 1–10 Sep 1996, 1997, W.N. Mathis (5♂, 1♀; USNM). *St. Peter*: Six Mens Bay (13°16.5'N, 59°38.8'W), 22 May–12 Sep 1996, D. and W.N. Mathis, H. Williams (7♂; USNM). *St. Philip*: Gemswick (13°05'N, 59°28.5'W), 31 Aug 1997, W.N. Mathis (8♂; USNM). *St. Thomas*: Farmers (13°12.8'N, 59°35.5'W), 2 Sep 1997, W.N. Mathis (4♂; USNM).

BELIZE. *Stann Creek District*: Bread and Butter Cay, Mar 1988, W.N. Mathis (1♀; USNM); Man of War Cay, Nov 1987, W.N. and D. Mathis (10♂, 1♀; USNM); Stewart Cay, Mar 1988, W.N. Mathis (1♂, 1♀; USNM); Twin Cays (Aanderaa Flats), Mar 1988, W.N. Mathis (3♂, 6♀; USNM); Wee Wee Cay, Jan–Nov 1987–1988, W.N. and D. Mathis, C. Feller (9♂, 1♀; USNM). *Belize District*: Lighthouse Reef, Half Moon Cay (17°12'N, 87°31'W), Apr 1993, W.N. Mathis (1♂, 3♀; USNM).

BOLIVIA. Rosario, Lake Rogagua, 28 Oct–9 Nov 1921, W.H. Mann (1♀; ANSP).

BRAZIL. *Guanabara*: Rio de Janeiro (1♀; ANSP).

COSTA RICA. Filadelfia, 18 Jan 1910, P.P. Calvert (1♂; ANSP). Santa Cruz, 30 Jan 1910, P.P. Calvert (2♂; ANSP).

CUBA. *Havana*: Havana, Baker (2♀; ANSP); San Antonio de los Baños (22°54.9'N, 82°29.3'W), 8 Dec 1994, W.N. Mathis (1♂; USNM); Ojo de Agua (23°54.6'N, 82°29.1'W), 8 Dec 1994, W.N. Mathis (8♂, 3♀; USNM); Palmarejo (67 km E Havana), 26 Apr 1983, W.N. Mathis (5♂, 4♀; USNM); Puerto Escondido, 26 Apr 1983, W.N. Mathis (1♂, 1♀; USNM). *Matanzas*: Buena Ventura (7 km N), 1 May 1983, W.N. Mathis (8♂, 3♀; USNM); Palpite (1 km NE), 2 May 1983, W.N. Mathis (24♂, 3♀; USNM); Palpite (2 km NE), 30 Apr 1983, W.N. Mathis (13♂, 7♀; USNM). *Pinar del Rio*: Pinar del Rio (S), 12–23 Sep 1913 (3♂, 2♀; AMNH, ANSP); San Diego de los Baños, Aug (1♀; ANSP); Soroa (22°47.7'N, 83°W), 27 Apr–6 Dec 1983, 1994, W.N. Mathis (13♂, 3♀; USNM); Soroa (2 km NW; 22°48.6'N, 83°1.0'W), 4–5 Dec 1994, W.N. Mathis (2♀; USNM); Soroa (2 km E), 29 Apr 1983, W.N. Mathis (3♂, 2♀; USNM). *Cienfuegos*: Soledad, Jardin Botánico (22°7.5'N, 80°19.2'W), Jan–Feb 1927, B.B. and C.T. Brues (1♂, 1♀; ANSP).

DOMINICA. Cabrits Swamp (15°35'N, 61°29'W), 22 Mar 1989, W.N. Mathis (1♂; USNM). Layou River mouth, 9

Jan–24 Mar 1965, W.W. Wirth (1♂, 3♀; TZ). Soufrière Bay, 24 Mar 1989, A. Freidberg, W.N. Mathis (1♀; USNM).

DOMINICAN REPUBLIC. *Azua*: near Pueblo Viejo (18°24.8'N, 70°44.7'W), 19 May 1998, D. and W.N. Mathis (6♂, 4♀; USNM). *Barahona*: Cabral (canals E of Cabral; 18°15.2'N, 71°13.4'W), 16 May 1995, W.N. Mathis (2♂, 2♀; USNM). *El Seibo*: El Seibo (5 km E; 18°44.73'N, 68°59.2'W; 120 m), 12 May 1995, W.N. Mathis (2♂; USNM); Pedro Sánchez (18°51.4'N, 69°6.5'W), 26 May 1998, D. and W.N. Mathis (2♂; USNM); Rincón (near; 18°45.3'N, 68°55.7'W), 12 May 1995, W.N. Mathis (6♂, 1♀; USNM). *Hato Mayor*: Hato Mayor (5.5 km E; 18°46.4'N, 69°12.5'W), 26 May 1998, D. and W.N. Mathis (5♂, 2♀; USNM). *La Vega*: El Rio (9.5 km E; 19°0.7'N, 70°33.6'W; 980 m), 24 May 1998, D. and W.N. Mathis (1♂; USNM); Jarabacoa (1–2 km S; 19°06.9'N, 70°37'W; 520 m), 8–21 May 1995, W.N. Mathis (1♀; USNM); Rio Camu (3.5 km NW La Vega; 19°13.7'N, 70°35.2'W; 100 m), 10 May 1995, W.N. Mathis (5♂, 1♀; USNM); Rio Camu (3.5 km NW La Vega; 19°13.8'N, 70°35.2'W; 100 m), 18 May 1998, D. and W.N. Mathis (2♂, 1♀; USNM). *Pedernales*: Lago Oviedo (N shore; 17°47'N, 71°22.5'W), 15 May 1995, W.N. Mathis (1♂; USNM). *Peravia*: Rio Ocoa (San José Ocoa; 18°31.7'N, 70°30.4'W), 21 May 1998, D. and W.N. Mathis (2♂; USNM). *Puerto Plata*: Rio Camu (14 km E Puerto Plata; 19°11.9'N, 70°37.4'W), 17 May 1995, W.N. Mathis (1♂; USNM). *San Cristobal*: Nigua (18°22.4'N, 70°03'W), 27 May 1998, D. and W.N. Mathis (5♂; USNM).

ECUADOR. *Orellana*: Rio Tiputini Biodiversity Station (0°38.2'S, 76°8.9'W), 12–26 Aug 1999, A. Baptista, M. Kotrba, W.N. Mathis (16♂, 4♀; USNM).

GRENADA. *St. Andrew*: Balthazar (12°07.7'N, 61°39.3'W), 19 Sep 1996, W.N. Mathis (1♂; USNM); Grand Étang (lake; 12°05.6'N, 61°41.7'W), 14–20 Sep 1996, 1997, W.N. Mathis (8♂; USNM); Pearls Airport (12°08.7'N, 61°36.6'W), 15–17 Sep 1996, 1997, W.N. Mathis (12♂, 1♀; USNM). *St. George*: Airport (Point Salines; 11°59.9'N, 61°46.1'W), 15 Sep 1996, W.N. Mathis (5♂, 2♀; USNM); Beauséjour Bay (12°05.5'N, 61°44.9'W), 21 Sep 1996, W.N. Mathis (1♂; USNM); Grand Anse (12°01.3'N, 61°45.6'W), 15 Sep 1996, W.N. Mathis (7♂; USNM); Point Salines Airport (W end; 12°0.3'N, 61°47.7'W), 12–19 Sep 1996, 1997, W.N. Mathis (7♂; USNM); Airport (Point Salines; 12°05'N, 61°46.9'W), 11–12 Sep 1997, W.N. Mathis (5♂; USNM); True Blue Beach (11°59.9'N, 61°46.1'W), 15 Sep 1996, W.N. Mathis (7♂; USNM). *St. John*: Palmiste (12°08.7'N, 61°44.4'W), 21 Sep 1996, W.N. Mathis (4♂; USNM); Palmiste Lake (12°08.3'N, 61°44'W), 19 Sep 1996, W.N. Mathis (9♂; USNM). *St. Patrick*: Bathway Beach (12°12.6'N, 61°36.7'W), 13–20 Sep 1996, 1997, W.N. Mathis (19♂; USNM); Levera Bay (12°13.6'N, 61°36.6'W), 18 Sep 1996, W.N. Mathis (6♂; USNM).

GUYANA. CEIBA (~40 km S Georgetown; 6°29.9'N, 58°13.1'W), 13 Apr 1994, W.N. Mathis (4♂; USNM). Dubu-

lay Ranch, Aramatani Creek (5°40.9'N, 57°51.5'W), 9–11 Apr 1994, W.N. Mathis (5♂, 4♀; USNM); Dubulay Ranch, Berbice River (5°40.9'N, 57°51.5'W), 9–11 Apr 1994, W.N. Mathis (2♂, 1♀; USNM). Hope Beach (6°44.7'N, 57°57.3'W), 14–22 Apr 1994, 1995, W.N. Mathis (9♂, 2♀; USNM). Karanambo (3°45.1'N, 59°18.6'W), 31 Mar 1994, W.N. Mathis (12♂, 3♀; USNM); Karanambo, Maricuba (pond; 3°45.1'N, 59°18.6'W), 31 Mar–2 Apr 1994, W.N. Mathis (8♂, 1♀; USNM); Karanambo, Rupununi River (ox bow; 3°45.1'N, 59°18.6'W), 2 Apr 1994, W.N. Mathis (2♂, 2♀; USNM). Kumo Pond (~20 km S Lethem; 3°16.7'N, 59°43.5'W), 30 Apr 1995, W.N. Mathis (4♂, 3♀; USNM); Kumo River and falls (25 km SE Lethem in Kanuku Mountains; 3°15.9'N, 59°43.6'W), 4–30 Apr 1994, 1995, W.N. Mathis (1♀; USNM). Mahaica (3 km W; 6°43.5'N, 57°56.6'W), 14 Apr 1994, W.N. Mathis (4♂, 1♀; USNM). Moco-Moco (30 km E Lethem in Kanuku Mountains; 3°18.2'N, 59°39.0'W), 29 Apr 1995, W.N. Mathis (1♂; USNM). Moreru (marsh near; 03°54.8'N, 59°32.7'W), 26 Apr 1995, W.N. Mathis (2♂, 1♀; USNM). Pirara Ranch, Cashew Creek (3°37.3'N, 59°44.2'W), 23 Apr 1995, W.N. Mathis (7♂, 1♀; USNM); Pirara Ranch, Cashew Lake (3°36.7'N, 59°40.5'W), 23–27 Apr 1995, W.N. Mathis (13♂, 1♀; USNM); Pirara Ranch and River (03°32.1'N, 59°40.5'W), 24–25 Apr 1995, W.N. Mathis (10♂, 2♀; USNM). Wiruni River (5°46.6'N, 58°01'W), 11 Apr 1994, W.N. Mathis (1♂; USNM).

HONDURAS. *Cortés*: Omoa (15°47.8'N, 87°58.4'W), 26 Sep 1995, D. and W.N. Mathis (2♂; USNM); San Pedro Sula (8 km S; 15°25.7'N, 88°01.4'W), 25–26 Sep 1995, D. and W.N. Mathis (5♂; USNM).

JAMAICA. *Clarendon*: Portland Cottage (17°45.4'N, 77°11'W), 13 May 1996, D. and W.N. Mathis, H. Williams (3♂; USNM); Rest (3.5 km N; 17°54.1'N, 77°21.1'W), 9 May 1996, D. and W.N. Mathis, H. Williams (2♂, 1♀; USNM); Salt River (4 km N; 17°52.1'N, 77°09.5'W), 13 May 1996, D. and W.N. Mathis, H. Williams (1♂; USNM); Toll Gate (7.7 km S; 17°58'N, 77°22.3'W), 9 May 1996, D. and W.N. Mathis, H. Williams (7♂; USNM). *Manchester*: Alligator Pond (17°52.1'N, 77°33.9'W), 8 May 1996, D. and W.N. Mathis, H. Williams (7♂; USNM); Battersea, Feb 1910, R. Thaxter (2♀; ANSP); near Warwick (17°54.1'N, 77°25.5'W), 7 May 1996, D. and W.N. Mathis, H. Williams (7♂, 1♀; USNM). *St. Elizabeth*: Brae River (18°05.2'N, 77°39.3'W), 10 May 1996, D. and W.N. Mathis, H. Williams (3♂, 2♀; USNM); Brae River (2 km S; 18°04.2'N, 77°39.5'W), 10 May 1996, D. and W.N. Mathis, H. Williams (3♂; USNM); Elim (18°07.1'N, 77°40.6'W), 10 May 1996, D. and W.N. Mathis, H. Williams (1♂, 1♀; USNM); near Port Kaiser (17°52.3'N, 77°34.9'W), 8 May 1996, D. and W.N. Mathis, H. Williams (2♂; USNM). *St. Thomas*: Bath River, Bath (17°56.8'N, 76°21.6'W), 16 May 1996, D. and W.N. Mathis, H. Williams (2♂; USNM); Yallahs River (mouth; 17°53'N, 76°35.6'W), 14 May 1996, D. and W.N. Mathis, H. Williams (5♂; USNM). *Westmoreland*: Negril Beach (mangrove, rocky shore), 12

Mar 1970, W.W. Wirth (4♂, 1♀; USNM); Negril (8 km E; freshwater marsh), 13 Mar 1970, W.W. Wirth (5♂, 5♀; USNM); Savanna-La-Mar, 13 Mar 1970, W.W. Wirth (7♂, 2♀; USNM).

MEXICO. *San Luis Potosí*: Guerrero, 3 Aug 1933, C.W. Sabrosky (1♂, 1♀; ANSP).

PUERTO RICO. Arecibo (beach; 18°28.7'N, 66°42'W), 23 Sep 1995, D. and W.N. Mathis (1♂; USNM). Fajardo, Las Croabas (Seven Seas Beach; 18°23'N, 65°37'W), 17 Feb 1996, W.E. Steiner, J.M. Swearingen (8♂, 6♀; USNM). Maricao (4 km WNW; 18°10.7'N, 66°59.6'W), 21 Sep 1995, D. and W.N. Mathis (5♂, 1♀; USNM). Playa de Guayanilla (18°0.4'N, 66°46.1'W), 19 Sep 1995, D. and W.N. Mathis (6♂; USNM). Punta Jacinto (near Guanica; 17°57'N, 66°52.6'W), 20 Sep 1995, D. and W.N. Mathis (2♂, 1♀; USNM). Toa-Baja, 17 Jan 1915, G. Garb (1♀; ANSP).

ST. LUCIA. Castries (5 km S; 13°59'N, 60°00'W), 16 Jun 1991, D. and W.N. Mathis (3♂; USNM). Dauphin Boguis (1.6 km S Marquis; 14°01'N, 60°55'W), 17 Jun 1991, D. and W.N. Mathis (5♂; USNM). Soufrière (beach; 13°51'N, 16°54'W), 11–12 Jun 1991, D. and W.N. Mathis (3♂; USNM). Sulphur Spring (13°50'N, 61°03'W), 14 Jun 1991, D. and W.N. Mathis (6♂; USNM).

ST. VINCENT. St. Vincent (2♂; CU; "Lot. 662 Sub. 75"; 1 male lacks head. Handwritten determination label reads "Paralimna brunnea Will. [cursive] mss. may be obscura"). *Charlotte*: Montreal (13°12'N, 61°11'W), 26 Mar 1989, A. Freidberg (1♂, 1♀; USNM); Peruvian Vale (13°10.7'N, 61°08.7'W), 6–8 Sep 1997, W.N. Mathis (1♂; USNM); Spring (13°11.1'N, 61°08.5'W), 6 Sep 1997, W.N. Mathis (5♂; USNM); Yambou River (13°09.8'N, 61°08.7'W), 8–10 Sep 1997, W.N. Mathis (7♂; USNM). *St. Andrew*: Buccament Bay (near beach; 13°11'N, 61°16'W), 25–28 Mar–8 Jun 1989, 1991, D. and W.N. Mathis (10♂, 6♀; USNM); Camden Park (13°10.2'N, 61°14.7'W), 25 Mar–4 Sep 1989, 1997, W.N. Mathis (11♂, 4♀; USNM); Layou (13°12'N, 61°17'W), 8 Jun 1991, D. and W.N. Mathis (4♂; USNM). *St. David*: Richmond Beach, 28 Mar 1989, W.N. Mathis (2♂; USNM). *St. George*: Yambou Head, 27 Mar 1989, W.N. Mathis (5♂, 2♀; USNM). *St. Patrick*: Cumberland Bay (13°16'N, 61°16'W), 8–10 Jun–15 Sep 1991, 1997, D. and W.N. Mathis (14♂; USNM); Hermitage (13°15'N, 61°12.9'W), 9 Sep 1997, W.N. Mathis (2♂; USNM); Palmiste Park (13°12.7'N, 61°14.9'W), 5 Sep 1997, W.N. Mathis (3♂; USNM); Wallilabou (beach; 13°15'N, 61°16'W), 8 Jun 1991, D. and W.N. Mathis (6♂, 1♀; USNM).

TOBAGO. *St. John*: Bloody Bay River (11°18'N, 60°38'W), 14 Jun 1993, W.N. Mathis (2♂; USNM); Charlotteville (beach; 11°19.5'N, 60°32.9'W), 16–18 Apr–10–16 Jun 1993, 1994, D. and W.N. Mathis (18♂; USNM); Charlotteville (5 km S; 11°18.9'N, 60°34.5'W), Hermitage River and beach, 10–11 Jun 1993, W.N. Mathis (10♂, 1♀; USNM); Parlatuvier (creek; 11°17.9'N, 60°35'W), 14 Jun 1993, W.N. Mathis (3♂; USNM); Speyside (11°18'N, 60°32'W), 13–15 Jun 1993, W.N.

Mathis (5♂; USNM); Speyside (Doctor River; 11°18.2'N, 60°31'W), 19 Apr 1994, D. and W.N. Mathis (7♂, 1♀; USNM); Speyside (Doctor River; 1 km NW; 11°18'N, 60°32'W), 12–13 Jun 1993, W.N. Mathis (5♂; USNM). *St. Patrick*: Pigeon Point (beach; 11°9.7'N, 60°50'W), 19 Apr 1994, D. and W.N. Mathis (8♂; USNM). *St. Paul*: Delaford, Kings Bay (11°16'N, 60°32.8'W), 13 Jun 1993, W.N. Mathis (5♂; USNM); Kendall (11°14.3'N, 60°35.7'W), 21 Apr 1994, W.N. Mathis (3♂; USNM).

TRINIDAD. *St. Andrew*: Lower Manzanilla (5 km S; 10°28'N, 61°03'W), 20 Jun 1993, W.N. Mathis (9♂; USNM); Lower Manzanilla (16 km S; 10°22'N, 61°01'W), 20 Jun 1993, W.N. Mathis (6♂, 1♀; USNM). *St. George*: Chacachacare Island (10°41'N, 61°46'W), saline pond margin, 29 Jun 1993, W.N. Mathis (4♀; USNM); Filette (1 km SE; 10°47'N, 61°21'W), Yarra River, 25 Jun 1993, W.N. Mathis (1♂; USNM). *St. Patrick*: Pitch Lake (10°14'N, 61°38'W), 24 Jun 1993, W.N. Mathis (2♀; USNM). *St. Thomas*: 2 Aug, A. Busck (1♀; ANSP).

DISTRIBUTION.—Nearctic: Bermuda, USA (CA, FL, TX). Neotropical: Argentina, Bahamas, Belize, Bolivia, Brazil, Colombia, Costa Rica, Ecuador, Guyana, Honduras, Mexico (San Luis Potosí), Panama, Paraguay, Trinidad and Tobago, West Indies (Barbados, Cuba, Dominica, Dominican Republic, Grenada, Jamaica, Puerto Rico, St. Lucia, St. Thomas, St. Vincent, Virgin Islands).

NATURAL HISTORY.—*Paralimna decipiens* and *P. obscura* often occur sympatrically. We first noted their sympatry on Belizian Cays in the western Caribbean and have since found them together on most of the West Indies. We often collected both species in the same swing of an aerial net. How these species partition the habitat would be an interesting study.

REMARKS.—This species and *P. decipiens* are closely related and are very similar in appearance. Externally we have difficulty in distinguishing between them due to variation in coloration and microtomentum. Both species can be somewhat dark or light colored, with the darker specimens usually shinier as a result of less microtomentum. There is a tendency for *P. obscura* to be darker and shinier and for *P. decipiens* to be lighter and duller, but there is considerable variation between the two species.

The shapes of the aedeagus and gonites, however, are very distinctive, and they readily provide characters to separate the two species. The aedeagus in *P. obscura* (Figure 109) is narrower in ventral view than that of *P. decipiens*, is slightly longer than wide, and the distal end of the sclerotized portion, especially in lateral view, is distinctly pointed. The aedeagus in *P. decipiens* (Figure 110) is much broader than long in ventral view, and it is somewhat rectangular with the distal angles rounded. In lateral view, the distal aspect of the sclerotized portion is slightly concave, and the actual apex of the aedeagus is a pointed process that extends from an anteroventral angle.

Papuama, new genus

TYPE SPECIES.—*Papuama ismayi* Mathis and Zatwarnicki, by present designation.

DIAGNOSIS.—This genus is distinguished from others of Dryxini by the following combination of characters: ocellar seta present, well developed; proclinate fronto-orbital setae greatly reduced, at most setula-like; reclinate fronto-orbital seta present, well developed; arisal hairs 8 or more; notopleuron bearing 2 setae (anterior seta greatly reduced, hair-like, pale in *P. ismayi*; posterior seta weaker in *P. calva* (Bock)); katapisternal seta absent or very weakly developed, at most a pale setula; stem vein lacking setulae; crossvein dm-cu normally developed, nearly straight, forming nearly right angle with vein M; forefemur bearing anteroventral row of very short, stout, tooth-like setae on apical ½; and mid- and hindfemora normally developed, length much shorter than abdomen.

DESCRIPTION.—Small to moderately small shore flies, body length 1.65–2.60 mm.

Head: Ocelli in equilateral or isosceles triangle, if latter, distance between posterior pair slightly longer than between anterior ocellus and either posterior ocellus; ocellar seta, inner and outer vertical setae, and reclinate fronto-orbital seta well developed; proclinate fronto-orbital setulae greatly reduced or lacking; paraverticilar seta greatly reduced or lacking. First flagellomere broadly rounded; arista bearing 8–11 long hairs along length of dorsal surface. Face with 1 primary vertical series of setae or setulae, comprising 3–5 short, hair-like, inclinate (but not cruciate) setae; some short, generally inconspicuous setulae immediately adjacent to parafacial. Parafacial at anterior margin of eye much narrower than length of 1st flagellomere. Gena high, height subequal to combined length of 1st flagellomere and pedicel.

Thorax: Chaetotaxy quite variable, depending on species, either greatly reduced or lacking (dorsocentral setae 0+1, pre- and postsutural supra-alar setae lacking) or normally developed (dorsocentral setae 1+3, pre- and postsutural supra-alar setae present); acrostichal setulae very weakly developed, almost completely inconspicuous, but with prescutellar pair well developed; postpronotal seta moderately well developed; notopleural setae 2 (anterior seta greatly reduced, hair-like, pale, sometimes lacking in *P. ismayi*); anepisternum bearing 3 or 4 poorly developed, short, thin, setula-like setae along posterior margin, 1 seta better developed; katapisternal seta either reduced, short, thin, setula-like, and sometimes pale, or lacking; posterior margin of scutellum truncate, nearly flat. Veins lacking setulae; crossvein dm-cu regularly developed, nearly straight, longer than apical section of vein CuA₁, at distinct angle with posterior margin of wing. Forefemur with apex on medial surface produced as a rounded, flange-like process; apical ⅓ of forefemur with anteroventral surface shallowly concave just before flange-like process; forefemur of males and females bearing anteroventral row of

very short, stout, tooth-like setae on apical 1/2; foretibia of male lacking several long, slender setae at apex on ventral surface; forebasitarsus lacking row of long, slender, pale setulae inserted along anterior surface; midtibia with 3 dorsal extensor setae (subapically, subbasally, and near middle); mid- and hindfemora normally developed, much shorter than abdomen.

Abdomen: Tergites lacking fasciate pattern. Male terminalia: epandrium broadly and uniformly U-shaped in posterior view, lateral arms slightly wider than dorsal bridge; cercus moderately broad to broad ventrally, rounded dorsally; presurstylus very well developed, elongate, wider basally than apically but only slightly narrowed to broadly rounded apex; post-surstylus in lateral view nearly linear, anterior margin sinuous,

only slightly wider basally than apically, apex knob-like, broadly rounded and very shallowly bifurcate; aedeagal apodeme with irregularly rounded, prominent keel; aedeagus wide basally, trifurcate from a dorsal view, with lateral arms well developed although not as long as medial arm, lateral arms perhaps homologous with lateral aedeagal process; hypandrium irregularly rounded, shallowly pouch-like.

DISTRIBUTION (Figure 143).—Australasian/Oceanian: Australia (New South Wales, Queensland), Irian Jaya, Papua New Guinea. Oriental: Indonesia (Sumatra), Nepal, Thailand.

DISCUSSION.—The thoracic chaetotaxy of this genus is variable depending on the species, with a general reduction being evident in specimens of *Papuama ismayi*.

Key to Species of *Papuama*

1. Thoracic setae normally developed, dorsocentral setae 1+3, pre- and postsutural supralar setae and anterior notopleural seta generally well developed; scutum and scutellum mostly concolorous, yellowish tan to gray (Australia) 29. *P. calva* (Bock)
- Thoracic setae weakly developed, dorsocentral setae 0+1, pre- and postsutural supralar setae and anterior notopleural seta greatly reduced or lacking; scutum mostly dark brown, contrasting with grayish scutellum (Australasian/Oceanian, Oriental) 30. *P. ismayi*, new species

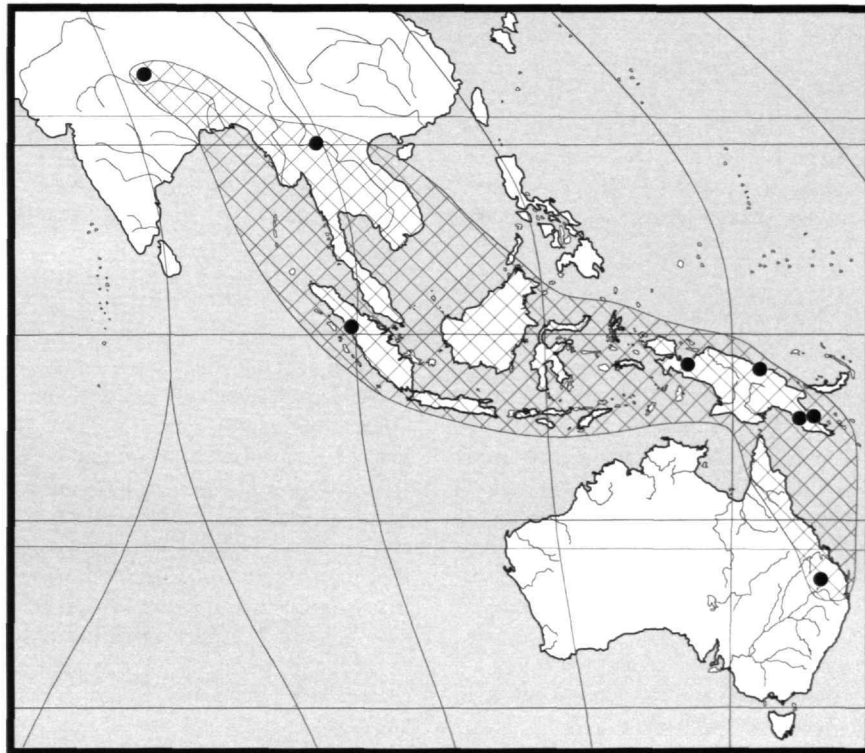


FIGURE 143.—Distribution map for *Papuama* (hatched and dots).

29. *Papuama calva* (Bock), new combination

FIGURES 144–146

Paralimna calva Bock, 1988:895.—Mathis and Zatwarnicki, 1995:119 [world catalog].

DIAGNOSIS.—This species is similar to *P. ismayi* but is distinguished from it and other taxa of Dryxini by the following combination of characters: ocellar seta present, well developed; proclinate fronto-orbital setae greatly reduced, at most setulae-like; reclinate fronto-orbital seta present, well developed; arista hairs 6–8; notopleuron with 2 setae, posterior seta more weakly developed; dorsocentral setae well developed (1+3); anepisternal setae along posterior margin weakly developed; katepisternal seta present but weakly developed, pale, setulae-like or occasionally absent. Forefemur lacking row of closely set, short, tooth-like setulae along anteroventral margin. Male terminalia as figured (Figures 144–146).

TYPE MATERIAL.—The holotype male is labeled “Castlereagh R[iver]. Mendooran, N.S.W. 24 March 1971 D.K. McAlpine/HOLOTYPIC [bright red label].” The holotype is double mounted (glued to a relatively large paper triangle), is in excellent condition, and is deposited in the AM.

OTHER SPECIMENS EXAMINED.—Australasian/Oceanian. AUSTRALIA. *New South Wales*: Mendooran, Castlereagh River, 24 Mar 1971, D.K. McAlpine (3♂, 2♀; AM).

DISTRIBUTION.—Australasian/Oceanian: Australia (New South Wales, Queensland).

REMARKS.—We have determined that this species, although not demonstrating some of the autapomorphies of *Papuama ismayi*, is similar and related to the latter species. This determination is primarily based on characters of the male terminalia. We suspect that this species is more like, if not the same species as, the basal taxon that gave rise to this genus and that *P. ismayi* is a more derived species, as evidenced by the reduction in chaetotaxy.

30. *Papuama ismayi*, new species

FIGURES 147–153

DIAGNOSIS.—This species is similar to *Papuama calva* but is distinguished by the following combination of characters: ocellar seta present, well developed; proclinate fronto-orbital setae greatly reduced, at most setulae-like; reclinate fronto-orbital seta present, well developed; arista hairs 8–10; notopleuron bearing 1 well-developed seta, anterior seta very weakly developed or lacking; dorsocentral setae weakly developed or absent (0+1); anepisternal setae along posterior margin weakly developed; katepisternal seta present but weakly developed, pale, setulae-like; scutum mostly dark brown, contrasting with grayish scutellum; and forefemur bearing row of closely set, short, tooth-like setulae along anteroventral margin.

DESCRIPTION.—Small to moderately small shore flies, body length 1.65–2.60 mm; generally densely microtomentose, dark

brown dorsally and gray to silvery white on the face and pleural areas; legs dark brown; chaetotaxy as in generic description.

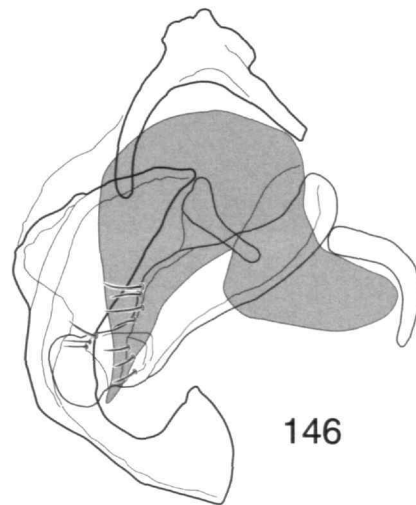
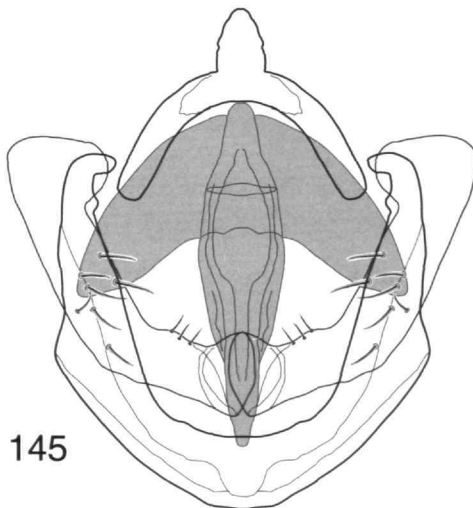
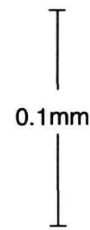
Head (Figures 147, 148): Frons with vertex dark brown, becoming golden brown anteriorly to about level of anterior ocellus, thereafter anteriorly gray to silvery white. Antenna brownish black to black; 1st flagellomere broadly rounded apically; arista with 8–10 dorsal rays. Face projected anteriorly, forming sloping, narrow shelf between and ventrad of antennal bases, color entirely gray to silvery white, appearing blackish gray from some angles; bearing 3 or 4 long, slender setae in a vertical row laterally and with several shorter setulae between row of longer setae and parafacial. Gena-to-eye ratio 0.30–0.33.

Thorax (Figure 149): Mesonotum mostly dark brown with some marginal areas gray to silvery white; scutellum usually considerably lighter, more silvery gray, than scutum; anterior notopleural seta very weakly developed or lacking; dorsocentral setae (0+1) weakly developed or absent, with only posterior seta well developed; anepisternal setae along posterior margin moderately weakly developed but evident; katepisternal seta weakly developed, setula-like, pale. Wing hyaline; costal-vein ratio 0.27–0.32; M-vein ratio 0.68–1.0. Coxae, femora, and tibiae mostly blackish gray to silvery gray, usually darker dorsally and on posterior surface; forefemur bearing row of closely set, short, tooth-like setulae along anteroventral margin; tarsi yellowish orange to blackish orange, darker dorsally, apical tarsomere blackish brown.

Abdomen: Male terminalia (Figures 150–153): epandrium in posterior view (Figure 150) thick-walled, inverted U-shaped, in lateral view pointed anterodorsally, sloping down posteriorly to dorsal $\frac{1}{3}$, thereafter ventrally nearly parallel sided, becoming very slightly wider only ventrally, ventral margin with shallow, broadly based point near middle; cercus in posterior view (Figure 150) irregularly oval; presurstylus longer than wide, in posterior view finger-like, curved medially, broadly rounded apically, in lateral view curved posteriorly on ventral $\frac{1}{3}$, apex pointed, bearing 3 or 4 long setulae medially from basal $\frac{1}{2}$; postsurstylus (Figures 152, 153) 3–4 times longer than wide, with medial, short process just before midheight dorsally, apex shallowly bifurcate, each process of bifurcation broadly rounded in lateral view, lateral process longer and spatulate, bearing 3 setulae on ventral $\frac{1}{3}$ along posterior margin and 2 setulae at dorsal $\frac{1}{3}$ along anterior margin, inner process of bifurcation with apex foot-like, posterior portion produced; aedeagus in lateral view (Figure 153) broadly foot-like, anteroventral portion broadly projected for short length, projection bearing several short papillae, in ventral view (Figure 152) like 3-pronged fork, medial prong nearly twice length of lateral prongs; aedeagal apodeme angulate (Figure 153) with posterior crest dorsomedially, attachment to aedeagus broader and shorter than attachment with hypandrium; hypandrium broadly and shallowly concave, anterior margin broadly rounded (Figures 152, 153).

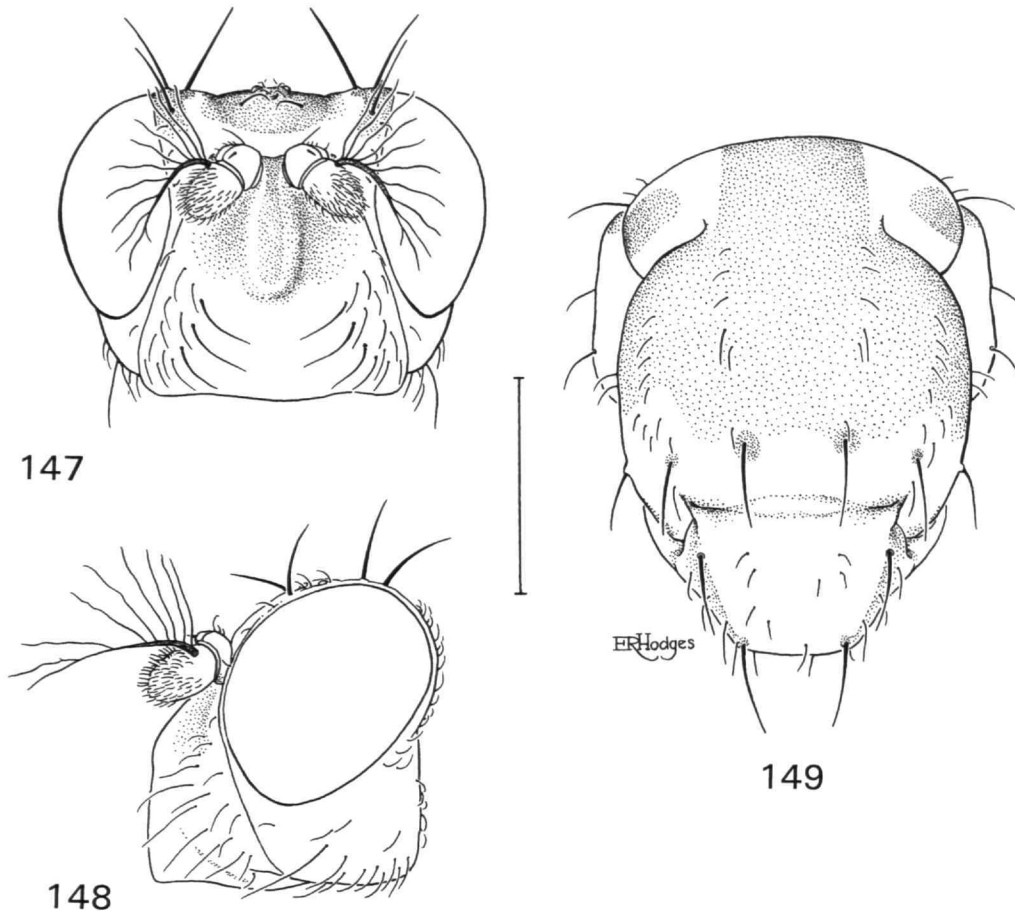


FIGURES 144–146.—Male terminalia of *Papuama calva* (Bock): 144, epandrium, cerci, and presurstyli, posterior aspect; 145, internal male terminalia, ventral aspect; 146, same, lateral aspect.



TYPE MATERIAL.—The holotype male is labeled “PAPUA NEW GUINEA Cen.Prov., Daramouka Vill. 19 Sept 1982 JW Ismay (riverside).” The holotype is double mounted (minute in

block of plastic), is in excellent condition, and is deposited in the NMNH. The allotype female and seven other paratypes (3♂, 4♀; USNM) bear the same locality label as the holotype.



FIGURES 147–149.—*Papuama ismayi*, new species: 147, head, anterior aspect; 148, same, lateral aspect; 149, mesonotum, dorsal aspect. Scale=0.5 mm.

Other paratypes are as follows: PAPUA NEW GUINEA. *Central*: LaLoki (river margin), 2 Feb 1986, J.W. Ismay (3♂, 6♀; USNM); Woitope (river margin), 9 Jun 1986, J.W. Ismay (1♀; USNM); Dauramouku Village (river side), 19 Sep 1982, J.W. Ismay (2♂, 4♀; USNM). *North*: Gira River near Popondetta (8°45'S, 148°15'E; bank fast river), 30 Jun 1982, J.W. Ismay (17♂, 8♀; MCV, USNM).

OTHER SPECIMENS EXAMINED.—Australasian/Oceanian. IRIAN JAYA. Siritwini River (Nabire; medium-sized river with gravel and mud banks), 21 Apr 1997, P. Grootaert (2♂, 3♀; IRSN). Sanoba (small river with sand and mud banks), 21 Apr 1997, P. Grootaert (30♂, 78♀; IRSN). Nabire (km 74; on road to Unipo, banks of a large river; rocks, pools, mud flats), 26 Apr 1997, P. Grootaert (16♂, 33♀; IRSN). Nabire (80 km from; on road to Unipo; 3°33'S, 135°46'E; banks of a large river), 25 Apr 1997, P. Grootaert (10♂, 14♀; IRSN). Idojaga River (km 80; banks of river), 26 Apr 1997, P. Grootaert (5♂, 16♀; IRSN).

PAPUA NEW GUINEA. Bainyik, 14 Dec 1963, D.K. McAlpine (5♂, 7♀; BMNH). Imbia, near Maprik, 19 Dec 1963, D.K. McAlpine (1♂, 1♀; BMNH).

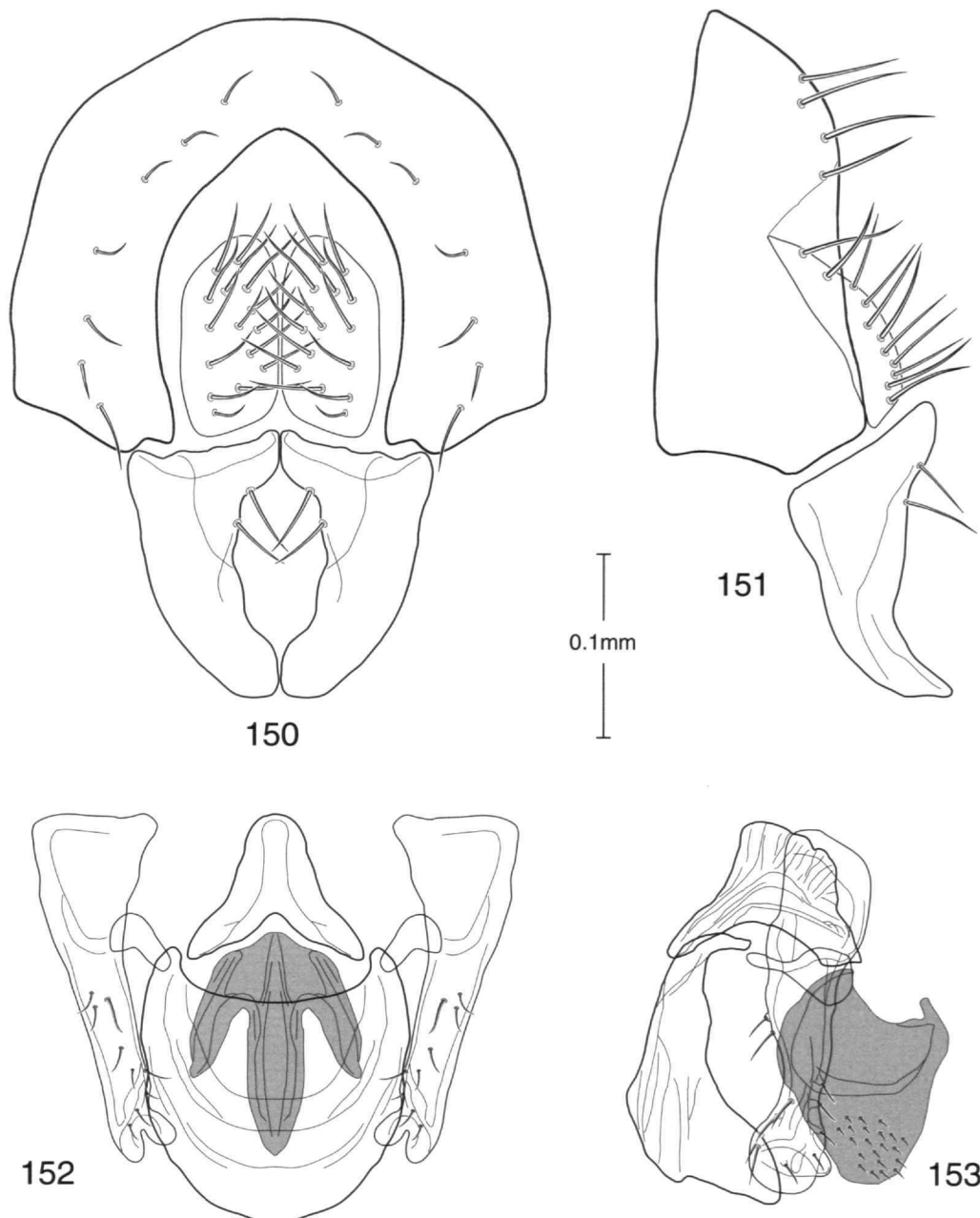
Oriental. INDONESIA. *Sumatra*: Fort de Kock (920 m), 1925, E. Jacobson (2♂, 3♀; BMNH).

NEPAL. *Chitwan*: Sauraha, Dhungari Khola (2 km E; Smithsonian Institution Camp; rocky bank), 1 Nov 1985, W.N. Mathis (1♂; USNM).

THAILAND. Loei: Na Haeo, 12 Feb 1999, P. Grootaert (1♂, 1♀; IRSN).

DISTRIBUTION.—Australasian/Oceanian: Irian Jaya, Papua New Guinea. Oriental: Indonesia (Sumatra), Nepal, Thailand.

ETYMOLOGY.—The specific epithet, *ismayi*, is a genitive patronym to recognize the collecting efforts of John W. Ismay, who collected the type series of this species in addition to several hundred other shore-flies while he and his wife were stationed in Papua New Guinea.



FIGURES 150–153.—Male terminalia of *Papuama ismayi*, new species: 150, epandrium, cerci, and presurstyli, posterior aspect; 151, same, lateral aspect; 152, internal male terminalia, ventral aspect; 153, same, lateral aspect.

REMARKS.—This species exhibits many apomorphies, especially reduction of setae, that obscures and makes determination of phylogenetic relationships difficult. The structures of the male terminalia, however, not only clearly differentiate this species but also demonstrate a close relationship with *P. calva*

Bock. The shape of the presurstylus, in particular, demonstrates this relationship. Assuming this relationship to be accurate, it is apparent that this species then underwent considerable anagenesis, resulting in the autapomorphies, such as the reduced chaetotaxy, that characterize this species.

Phylogenetic Considerations

The tribe Dryxini, which is one of five tribes now placed in the subfamily Hydrelliinae (Mathis and Zatwarnicki, 1995), appears to be most closely related to the tribe Notiphilini (Zatwarnicki, 1992). We have identified five synapomorphies (including Zatwarnicki's (1992) characters 20 and 21) that corroborate Dryxini's sister-group relationship with Notiphilini: (1) ventral anepisternal seta elongate, twice length of dorsal seta (secondarily reduced in a few taxa); (2) midtibia with prominent, erect, extensor setae along dorsal surface (Zatwarnicki's character 20); (3) only reclinate fronto-orbital seta well developed, proclinate seta(e) reduced or lacking; (4) abdominal tergites fasciate (secondarily reduced in some taxa); and (5) subepandrial plate reduced (Zatwarnicki's character 21).

The following characters distinguish Dryxini from Notiphilini and confirm the tribe's monophyly (synapomorphies are noted by an "*"): (*1) gena high (secondarily short in some species); (*2) face wide, transversely arched, and generally projected anteriorly (the face in *Notiphila* is comparatively narrower and much flatter); (3) dorsocentral setae 4 (1+3; sec-

ondarily reduced in some genera of Dryxini, whereas in Notiphilini there are 3 setae (1+2), a synapomorphy for Notiphilini); (4) costa elongate, extended to vein M (the costa is short, extended only to vein R₄₊₅, in Notiphilini, a synapomorphy for Notiphilini); (5) male terminalia with surstylus divided into a presurstylus (surstylus) and a postsurstylus (clasper) (postsurstylus reduced or fused with epandrium with only presurstylus present in Notiphilini, a synapomorphy for Notiphilini); (*6) presurstylus with apex angulate and bifurcate; (*7) pre- and postgonite reduced and/or lacking (the structure remaining may represent a fused and/or reduced pre- and postgonite); and (*8) hypandrium connected basally with postsurstylus, not with epandrium.

In the presentation on genus-level relationships that follows, the characters used in the analysis are noted first. Each character is immediately followed by a discussion to explain its states and to provide perspective and any qualifying comments about that character. After presentation of the information on character evidence, a hypothesis of the cladistic relationships is presented and briefly discussed. The cladogram (Figure 154) is the primary mode to convey relationships; the discussion is to sup-

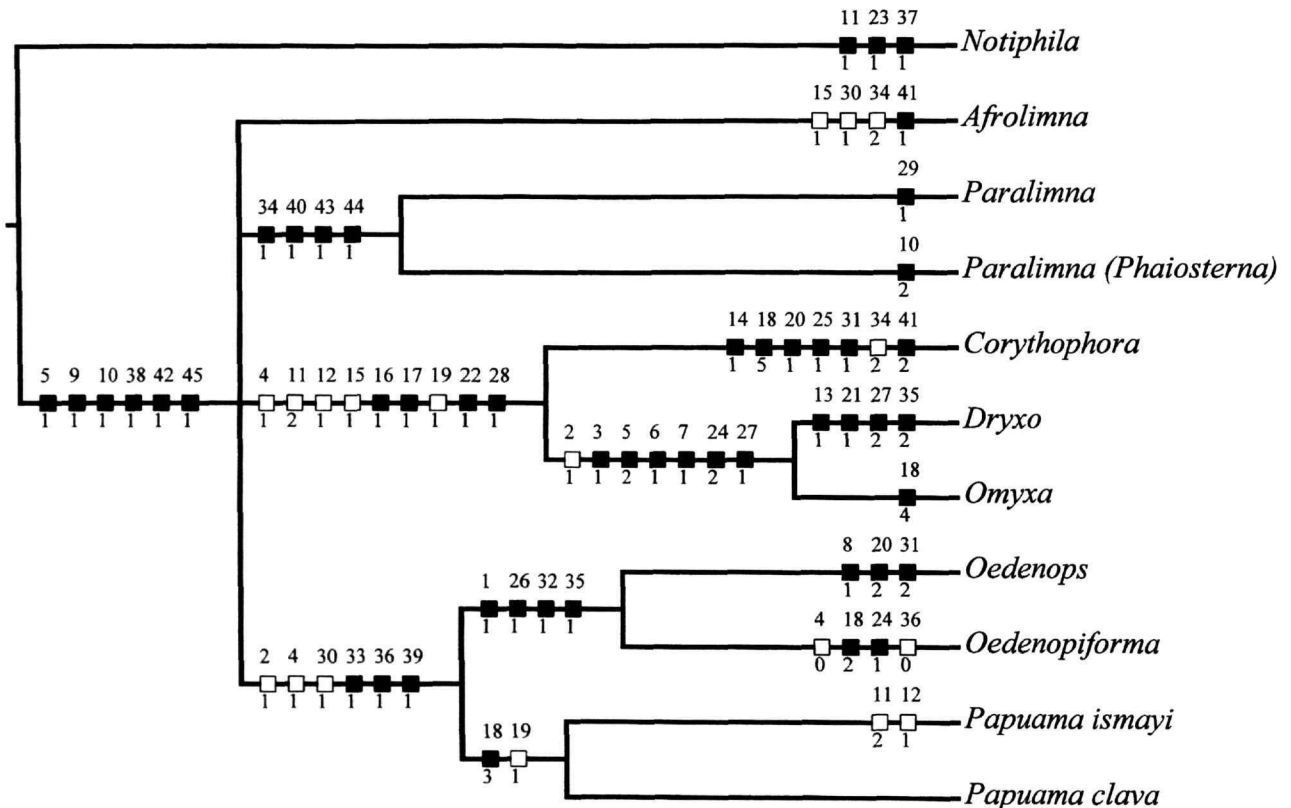


FIGURE 154.—Cladogram depicting hypothetical cladistic relationships among genera of Dryxini (55 steps, consistency index 0.92, retention index 0.92) (open squares=ambiguous synapomorphies and/or autapomorphies; solid squares=unambiguous synapomorphies and/or autapomorphies).

plement the cladogram and is intended only to complement the latter. In the discussion of character data, a "0" indicates the state of the outgroup; a "1" or "2" indicates the derived states. All multistate characters (5, 10, 11, 18, 20, 24, 27, 31, 34, 35, and 41) were treated as nonadditive (–), and characters 8, 9, 13, 14, 21, 23, 29, 32, 37, 38, and 42, which are autapomorphies for various genera or tribes, were made inactive (J) for the analysis and do not figure into the calculation of the consistency index. The numbers used for characters in the presentation are the same as those on the cladogram, and the sequence is the same as noted in the character matrix (Table 1). The genus *Notiphila*, which is the only genus included in the tribe Notiphilini, was the outgroup in our phylogenetic analysis.

CHARACTERS USED IN THE PHYLOGENETIC ANALYSIS

(character number in parenthesis)

General

- 1 (1). Color of head and thorax: (0) similar in both sexes; (1) distinctly sexually dimorphic (synapomorphy for *Oedenops* and *Oedenopiforma*).

Head

- 1 (2). Development of proclinate fronto-orbital setae: (0) present, well developed, anterior seta usually larger than posterior seta; (1) absent or weakly developed (synapomorphy for *Dryxo*, *Omyxa*, *Oedenops*, *Oedenopiforma*, and *Papuama*).
- 2 (3). Ocellar seta: (0) present (sometimes reduced); (1) absent (synapomorphy for *Dryxo* and *Omyxa*).
- 3 (4). Paravertical setae: (0) well developed, conspicuously evident although sometimes not long; (1) indistinguishable from other setulae or lacking (synapomorphy for *Dryxo*, *Omyxa*, *Corythophora*, *Oedenops*, and *Papuama*).
- 4 (5). Fronto-orbital setae: (0) both proclinate and reclinate fronto-orbital setae well developed, although reclinate seta usually better developed; (1) only reclinate seta well developed, proclinate setae reduced or lacking (an autapomorphy for the tribe Dryxini); (2) fronto-orbital setae absent (synapomorphy for *Dryxo* and *Omyxa*).
- 5 (6). Width of parafacial: (0) narrow, width much less than length of 1st flagellomere; (1) wide, width greater than length of 1st flagellomere (synapomorphy for *Dryxo* and *Omyxa*).
- 6 (7). Shape of frons: (0) shallowly arched anteroventrally, not projected forward, sparsely setulose; (1) projected forward as a densely setulose, shield-like plate (synapomorphy for *Dryxo* and *Omyxa*).

- 7 (8). Number of arisal hairs: (0) arista bearing 7–14 dorsal hairs; (1) arista bearing 3–6 dorsal hairs (autapomorphy for *Oedenops*).
- 8 (9). Shape of face: (0) face relatively narrow and flat; (1) face wide and transversely arched (autapomorphy for tribe Dryxini).
- 9(10). Height of gena (at ventral margin of eye): (0) relatively short; (1) relatively high (autapomorphy for tribe Dryxini); (2) secondarily short in *Paralimna* (*Phaiosterna*) and in the *limbata* group of *Paralimna*.

Thorax

- 1(11). Number of dorsocentral setae: (0) 4 (1+3; the generalized condition in Dryxini); (1) 3 (1+2) (autapomorphy for tribe Notiphilini); (2) 1 (0+1; only posterior-most dorsocentral seta, which is displaced laterally, is present) (apparently homoplasious: synapomorphy for *Dryxo*, *Omyxa*, and *Corythophora*; autapomorphy for *Papuama ismayi*).
- 2(12). Presutural supra-alar seta: (0) present; (1) absent (apparently homoplasious: synapomorphy for *Dryxo*, *Omyxa*, and *Corythophora*; autapomorphy for *Papuama ismayi*).
- 3(13). Prescutellar acrostichal setae: (0) 1 pair present, distinct; (1) absent (autapomorphy for *Dryxo*).
- 4(14). Shape of posterior margin of scutellum: (0) flat or nearly so; (1) broadly rounded (autapomorphy for *Corythophora*).
- 5(15). Setulae on venter of scutellum: (0) absent; (1) present (synapomorphy for *Dryxo*, *Omyxa*, and *Corythophora*).
- 6(16). Number and position of notopleural setae: (0) 2, one inserted toward anterior angle, the other inserted toward the posterior angle; (1) 1 seta, inserted centrally (synapomorphy for *Dryxo*, *Omyxa*, and *Corythophora*).
- 7(17). Dorsally curved setula (sometimes weakly developed) near posterodorsal angle of anepisternum: (0) present; (1) absent.
- 8(18). Number of anepisternal setae: (0) 2, both subequal in size (most Ephydridae); (1) 2, with ventral seta much longer than dorsal seta (synapomorphy for tribes Dryxini and Notiphilini); (2) 1, with dorsal seta greatly reduced (autapomorphy for *Oedenopiforma*); (3) bearing 2 or 3 long, thin, hair-like setae along posterior margin (autapomorphy for *Papuama*); (4) all setae along posterior margin weakly developed (autapomorphy for *Omyxa*); (5) 1, with dorsal seta lacking (autapomorphy for *Corythophora*).
- 9(19). Proepisternal seta (stigmatal): (0) present; (1) very weakly developed or absent (synapomorphy for *Dryxo*, *Omyxa*, *Corythophora*, and *Papuama*).

TABLE 1.—Matrix of characters and taxa used in the cladistic analysis of Dryxini (numbers for characters and character states correspond with those used in the text).

| Taxon | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 3 | 3 | 3 | 3 | 3 | 3 | 3 | 3 | 3 | 4 | 4 | 4 | 4 | 4 | 4 | | | | | | |
|-------------------------|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| <i>Notiphila</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | | |
| <i>Dryxo</i> | 0 | 1 | 1 | 1 | 2 | 1 | 1 | 0 | 1 | 1 | 2 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 2 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | | |
| <i>Omyxa</i> | 0 | 1 | 1 | 1 | 2 | 1 | 1 | 0 | 1 | 1 | 2 | 1 | 0 | 0 | 1 | 1 | 1 | 4 | 1 | 0 | 0 | 1 | 0 | 2 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | | | |
| <i>Corythophora</i> | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 2 | 1 | 0 | 1 | 1 | 1 | 1 | 5 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 2 | 0 | 0 | 0 | 1 | 0 | 0 | 2 | 1 | 0 | 0 | 1 | | | |
| <i>Papuama ismayi</i> | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 3 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | | |
| <i>Papuama clava</i> | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | | | |
| <i>Oedenops</i> | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 2 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | | | |
| <i>Oedenopiforma</i> | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | |
| <i>Afrolimna</i> | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | |
| <i>Paralimna</i> | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | |
| <i>P. (Phaiosterna)</i> | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 1 |

- 10(20). Katepisternal seta: (0) well developed; (1) reduced (autapomorphy for *Corythophora*); (2) absent (autapomorphy for *Oedenops*).
- 11(21). Vestiture of katepisternum: (0) lacking row of 6–10 setae posterodorsad of katepisternal seta; (1) bearing row of 6–10 hair-like to large setae posterodorsad of large katepisternal seta (autapomorphy for *Dryxo*).
- 12(22). Costal setae at apex of subcostal break: (0) present, prominent; (1) rudimentary, very short (synapomorphy for *Dryxo*, *Omyxa*, and *Corythophora*).
- 13(23). Costal vein: (0) long, extended to vein M; (1) short, extended to vein R₄₊₅ (autapomorphy for tribe Notiphilini).
- 14(24). R stem vein: (0) bare of setulae; (1) bearing 1–3 (usually 2) fine setulae along dorsum (autapomorphy for *Oedenopiforma*); (2) bearing several fine setulae on dorsum (synapomorphy for *Dryxo* and *Omyxa*).
- 15(25). Vein R node: (0) bare of setulae; (1) bearing 2 or 3 long setulae on dorsum (autapomorphy for *Corythophora*).
- 16(26). Color of wing membrane: (0) hyaline to faintly infuscate, sometimes with distinct pattern; (1) lightly milky white, especially toward base and alula (synapomorphy for *Oedenops* and *Oedenopiforma*).
- 17(27). Length and shape of crossvein dm-cu: (0) nearly straight, relatively short; (1) shallowly sinuous, moderately long (autapomorphy for *Omyxa*); (2) conspicuously sinuous, long (autapomorphy for *Dryxo*).
- 18(28). Leg length and width: (0) normally developed; (1) long and slender (synapomorphy for *Dryxo*, *Omyxa*, and *Corythophora*).
- 19(29). Vestiture of male forefemur: (0) lacking distinctive setal adornment; (1) bearing row of distinctive, frequently flattened and curved setae along anteroventral surface (autapomorphy for *Paralimna (Paralimna)*).
- 20(30). Vestiture of forefemur: (0) lacking comb-like row of short, stout, spine-like setulae; (1) bearing comb-like row of short, stout, tooth-like setulae in males and fe-

males (synapomorphy for *Papuama*, *Oedenops*, *Oedenopiforma*, and *Afrolimna*).

- 21(31). Erect setae along dorsum of midtibia (a synapomorphy for the tribes Notiphilini and Dryxini): (0) 3 setae; (1) 4 setae (autapomorphy for *Corythophora*); (2) 2 setae (autapomorphy for *Oedenops*).
- 22(32). Setae of tarsomeres: (0) not bearing long setae; (1) bearing long, anteroapical and posteroapical setae, length of setae subequal to width of tarsomere at apex (synapomorphy for *Oedenops* and *Oedenopiforma*).

Abdomen

- 1(33). Color pattern on abdomen: (0) fasciate; (1) unicolorous, lacking fasciate pattern (synapomorphy for *Papuama*, *Oedenops*, and *Oedenopiforma*).
- 2(34). Appendages of aedeagus: (0) lacking a lateral aedeagal process; (1) with lateral aedeagal processes fused with aedeagus (an autapomorphy for the genus *Paralimna*); (2) with lateral aedeagal processes adjacent to but separate from aedeagus (synapomorphy for *Afrolimna* and apparently for *Corythophora*).
- 3(35). Shape of apex of aedeagus: (0) with medial projection; (1) lacking medial projection (synapomorphy for *Oedenops* and *Oedenopiforma*); (2) projections reduced (autapomorphy for *Dryxo*).
- 4(36). Shape of aedeagus: (0) simple, oval in outline in posterior view, lacking appendages; (1) bearing posterodorsal fold (synapomorphy for *Oedenops* and *Papuama*).
- 5(37). Condition of pre- and postsurstylus: (0) male terminalia with surstylus divided into a presurstylus (surstylus) and postsurstylus (clasper); (1) postsurstylus reduced or fused with epandrium with only presurstylus present (autapomorphy for tribe Notiphilini).
- 6(38). Shape of apex of presurstylus: (0) presurstylus a simple to complex structure at ventral margin of epandrium, apex not angulate and bifurcate; (1) presurstylar apex angulate and bifurcate (autapomorphy for tribe Dryxini).

- 7(39). Shape of presurstylus: (0) robust and well sclerotized; (1) lobate and weakly sclerotized (synapomorphy for *Oedenops*, *Oedenopiforma*, and *Papuama*).
- 8(40). Postsurstylus: (0) lacking setae; (1) bearing 2 setae near apex (synapomorphy for *Paralimna sensu stricto* and *Paralimna (Phaiosterna)*).
- 9(41). Shape of aedeagal apodeme: (0) lacking an anteromedial projection; (1) with a long, medial, apically blunt projection (autapomorphy for *Afrolimna*); (2) with long projection extended from near articulation with hypandrium (autapomorphy for *Corythophora*).
- 10(42). Condition of gonite: (0) pre- and postgonites distinct and separate (pregonite usually smaller and bearing 2 apical setulae); (1) pre- and postgonite reduced and/or lacking (structure remaining may represent fused and/or reduced pre- and postgonite; autapomorphy for tribe Dryxini).
- 11(43). Position of gonite relative to postsurstylus: (0) gonite positioned at apical 1/4–1/3 of postsurstylus; (1) gonite positioned at apex of postsurstylus (synapomorphy for *Paralimna sensu stricto* and *Paralimna (Phaiosterna)*).
- 12(44). Shape of ventral margin of postsurstylus: (0) straight or shallowly curved; (1) conspicuously sinuous (synapomorphy for *Paralimna sensu stricto* and *Paralimna (Phaiosterna)*).
- 13(45). Connection of hypandrium posteriorly (basally): (0) hypandrium connected posteriorly with epandrium and aedeagal apodeme; (1) hypandrium connected basally with postsurstylus, not with epandrium (autapomorphy for tribe Dryxini).

Analysis, Results, and Conclusions

Using the implicit enumeration (ie*) option of Hennig86, which is an exhaustive search, nine most parsimonious trees were generated from the analysis of the 45 characters. The cladograms have a length of 55 steps and consistency and retention indices of 0.83 and 0.83, respectively. A strict consensus tree (nelsen) was then derived from the nine trees. The consensus tree has a polytomy of four lineages arising at the base of the tribe Dryxini, with *Notiphila* as the sister group. The matrix was then subjected iteratively to successive weighing (xs w, ie*, cc) to determine a character's contribution, or weight, and to find cladograms supported by the most consistent characters (Carpenter, 1988; Dietrich and McKamey, 1995). The successive weighing stabilized at 426 steps and reduced the number of trees from nine to six. A consensus of these six trees resulted in a tree that is identical to the consensus tree from the nine initial trees. The consensus tree (Figure 154), although with unresolved lineages (polytomies), is our cladogram of choice. The analysis of the characters for this cladogram and the weights of the various characters are given in Table 2. Given these charac-

TABLE 2.—Analysis of characters based on the cladogram (figure 154) and weights (varying between 1 and 10) and status of characters after successive weighing (+ = additive; - = nonadditive; [= active;] = inactive).

| Character | Steps | Consistency index | Retention index | Weight | Status |
|-----------|-------|-------------------|-----------------|--------|--------|
| 1 | 1 | 100 | 100 | 10 | +[|
| 2 | 2 | 50 | 75 | 3 | +[|
| 3 | 1 | 100 | 100 | 10 | +[|
| 4 | 2 | 50 | 75 | 1 | +[|
| 5 | 2 | 100 | 100 | 10 | -[|
| 6 | 1 | 100 | 100 | 10 | +[|
| 7 | 1 | 100 | 100 | 10 | +[|
| 8 | 1 | 100 | 100 | 10 | +[|
| 9 | 1 | 100 | 100 | 10 | +[|
| 10 | 2 | 100 | 100 | 10 | -[|
| 11 | 2 | 66 | 66 | 4 | -[|
| 12 | 2 | 50 | 66 | 3 | +[|
| 13 | 1 | 100 | 100 | 10 | +[|
| 14 | 1 | 100 | 100 | 10 | +[|
| 15 | 2 | 50 | 66 | 10 | +[|
| 16 | 1 | 100 | 100 | 10 | +[|
| 17 | 1 | 100 | 100 | 10 | +[|
| 18 | 3 | 100 | 100 | 10 | -[|
| 19 | 2 | 50 | 75 | 3 | +[|
| 20 | 2 | 100 | 100 | 10 | -[|
| 21 | 1 | 100 | 100 | 10 | +[|
| 22 | 1 | 100 | 100 | 10 | +[|
| 23 | 1 | 100 | 100 | 10 | +[|
| 24 | 2 | 100 | 100 | 10 | -[|
| 25 | 1 | 100 | 100 | 10 | +[|
| 26 | 1 | 100 | 100 | 10 | +[|
| 27 | 2 | 100 | 100 | 10 | -[|
| 28 | 1 | 100 | 100 | 10 | +[|
| 29 | 1 | 100 | 100 | 10 | +[|
| 30 | 2 | 50 | 75 | 10 | +[|
| 31 | 2 | 100 | 100 | 10 | -[|
| 32 | 1 | 100 | 100 | 10 | +[|
| 33 | 1 | 100 | 100 | 10 | +[|
| 34 | 3 | 66 | 50 | 3 | -[|
| 35 | 2 | 100 | 100 | 10 | -[|
| 36 | 2 | 50 | 50 | 2 | +[|
| 37 | 1 | 100 | 100 | 10 | +[|
| 38 | 1 | 100 | 100 | 10 | +[|
| 39 | 1 | 100 | 100 | 10 | +[|
| 40 | 1 | 100 | 100 | 10 | +[|
| 41 | 2 | 100 | 100 | 10 | -[|
| 42 | 1 | 100 | 100 | 10 | +[|
| 43 | 1 | 100 | 100 | 10 | +[|
| 44 | 1 | 100 | 100 | 10 | +[|
| 45 | 1 | 100 | 100 | 10 | +[|

ter weights, the analysis of the resultant cladogram resulted in consistency and retention indices of 0.92 and 0.92, respectively.

As indicated on the consensus cladogram (Figure 154), the tribe Dryxini is divided into four basal sublineages that form an unresolved quadritomy. The first basal sublineage is the genus *Afrolimna*, and as would be expected from a basal lineage that comprises a single genus, its relationship to other genera or groups of genera within Dryxini was the most unstable. *Afrolimna*, in the initial nine trees, varied from being the sister group to each of the other lineages to being the sister group to com-

bined lineages, such as the genera related to *Dryxo* (*Corythophora*, *Dryxo*, and *Omyxa*) or the genera related to *Oedenops* (*Oedenops*, *Oedenopiforma*, and *Papuama*). *Afrolimna*, which was described and has been treated as a subgenus within *Paralimna*, is accorded generic status. Although somewhat subjective, our preferred relationship for *Afrolimna* is as the sister group of the genera related to *Dryxo*, but the only evidence to support this relationship is character 15, which is not compelling. As alluded by its name, *Afrolimna* is known only from the Afrotropical Region, and only two species are presently known. The monophyly of *Afrolimna* is corroborated by characters 15, 30, 34, and 41.

The second basal sublineage comprises *Paralimna*, including the subgenus *Phaiosterna*. Unlike *Afrolimna*, *Paralimna* varied little in its relationship to the other genera. In six of the nine trees, *Paralimna* remained a separate and distinct lineage that was not closely related to other lineages within Dryxini with two exceptions: (1) as the sister group to *Afrolimna* or, (2) as the sister group to a combined lineage of *Afrolimna* and the genera related to *Dryxo*. *Paralimna* occurs pantropically in the Old and New Worlds with considerable species diversity (85 described species), including numerous undescribed species in both areas. In our review of *Paralimna*, we recognized only two subgenera despite the exceptional species diversity that exists in this genus. Our study of *Paralimna* is very preliminary, however, and with description of the numerous undescribed species and investigation of the phylogenetic relationships among these species, a much more elaborated classification for *Paralimna* will undoubtedly emerge. The monophyly of *Paralimna* is corroborated by characters 34, 40, 43, and 44.

The third basal sublineage is *Dryxo* and related genera (*Corythophora* and *Omyxa*). This sublineage is corroborated by several synapomorphies and autapomorphies (characters 4, 11, 12, 15, 16, 17, 19, 22, and 28), as are the relationships among these three genera. The three genera of this group include only 12 described species: *Corythophora* (2 species), *Dryxo* (9 species), and *Omyxa* (1 species). *Corythophora* is at the base of this sublineage and is the sister group to the lineage comprising *Dryxo* and *Omyxa*. *Corythophora* occurs exclusively in the Afrotropical Region, and the monophyly of the genus is established by six unambiguous autapomorphies (characters 14, 18, 20, 25, 31, and 41); both *Dryxo* and *Omyxa* are known only from the Old World. The species of *Dryxo* are relatively more widespread, occurring primarily in tropical to subtropical zones within the Afrotropical, Oriental, and Australasian Regions. An exception is *D. nudicarpus*, which occurs in temperate areas of China, Japan, and eastern Russia. *Omyxa*, which is monotypic,

is known thus far from the Oriental (India) and southeastern Palearctic (Iran, Oman) Regions. The taxa of this sublineage include some of the largest shore flies known, and by their size alone they are attractive material to collect and study. Unfortunately, nothing is known about their immature stages.

The fourth basal sublineage within Dryxini includes three genera: *Papuama* (2 species), *Oedenops* (3 species), and *Oedenopiforma* (3 species). Like *Paralimna*, *Oedenops* occurs in both the Old and New Worlds. The three known species are quite widespread, with *O. isis* occurring in the Afrotropical, Australasian/Oceanian, Oriental, and Palearctic Regions, *O. afrus* being found only in Africa, and *O. nudus* occurring only in the New World. *Oedenops* occurs primarily in tropical and subtropical regions but has range extensions into temperate Japan and North America.

Our review of *Oedenopiforma* provides a basis for a more substantive revision, including description of new taxa, as noted previously. *Oedenopiforma* is known only from the Old World, and there, primarily from Africa and Australia. The Australian species, *O. uniseta*, has a disjunct distribution from the other species in *Oedenopiforma*, but a specimen from Sri Lanka represents a link to African species. The Sri Lankan specimen, however, may represent a new species or is a major range extension for *O. argentea*. Specimens of this genus are relatively scarce in collections, and the species are represented by very few specimens. Like most taxa of Dryxini, the immature stages are unknown.

Within Dryxini, most lineages at the generic level or higher, including all basal lineages, occur exclusively or mostly in the Old World tropics and subtropics. We are thus of the opinion that the tribe probably had its origins there, perhaps in Africa. From the Old World, there were independent extensions into the New World by species of the genera *Paralimna* and *Oedenops*. In the New World, only *Paralimna* radiated and speciated to any extent, and there are now numerous species, described and undescribed, that occur exclusively there. Although our evidence is meager (there is no cladogram of lineages within *Paralimna*), there is some indication that more than one included lineage, such as species of the subgenera *Phaiosterna* and *Paralimna*, expanded into the New World and did so independently.

Numerous shore-fly taxa remain to be collected, described, and analyzed. Within Dryxini, we note that *Paralimna*, in particular, is in need of species-level revision. Even though this genus already includes most of the tribe's species diversity, almost 80%, there are numerous undescribed species that have already been segregated in existing collections.

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