

Studies of Gymnomyzinae (Diptera:
Ephydriidae), IV: A Revision
of the Shore-Fly Genus
Hecamede Haliday

WAYNE N. MATHIS

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Studies of Gymnomyzinae (Diptera:
Ephydridae), IV: A Revision of the Shore-Fly
Genus *Hecamede* Haliday

Wayne N. Mathis



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ABSTRACT

Mathis, Wayne N. Studies of Gymnomyzinae (Diptera: Ephydriidae), IV: A Revision of the Shore-Fly Genus *Hecamede* Haliday. *Smithsonian Contributions to Zoology*, number 541, 46 pages, 64 figures, 1 table, 1993.—Species of *Hecamede*, which now number 12, are revised. New synonyms are as follows (the junior synonym is listed first): *Hecamede grisescens* Becker is conspecific with *Notiphila albicans* Meigen, *Hecamede affinis* Canzoneri and Meneghini is conspecific with *Hecamede brasiliensis* Cresson, *Hecamede lacteipennis* Lamb is conspecific with *Notiphila granifera* Thomson, and *Hemicyclops maculipleuris* de Meijere is conspecific with *Hecamede planifrons* de Meijere. The following new species are described (type localities are noted in parentheses): *Hecamede (Hecamede) africana* (Kenya. 100 km N Mombasa), *H. (H.) australis* (Australia. New South Wales: Deewhy), *H. (H.) maritima* (Egypt. Sinai: Nabk), *H. (H.) socotra* (South Yemen. Socotra: Rás Shóab), *H. (Soikia) tomentosa* (Nigeria. Lagos), *H. (S.) bocki* (Australia. New South Wales: Deewhy). The monophyly of *Hecamede* within the tribe Hecamedini is demonstrated, and a hypothetical phylogeny of the included species is generated from a matrix of 23 characters. From this phylogeny, a classification of two subgenera (*Hecamede* and *Soikia*) is recognized, and in the subgenus *Hecamede*, two species groups (the *planifrons* group and the *albicans* group) are distinguished. All known species of *Hecamede* and its outgroups are found in the Old World, and the probable origin of the genus also occurred there, specifically within the basin of the Indian Ocean. The two species that occur in the New World appear to have arrived there as part of range expansion. No species occur along the Pacific coast of the New World. Maps, keys to subgenera and species, and illustrations (scanning electron micrographs and line drawings) are provided to assist in the identification of the species.

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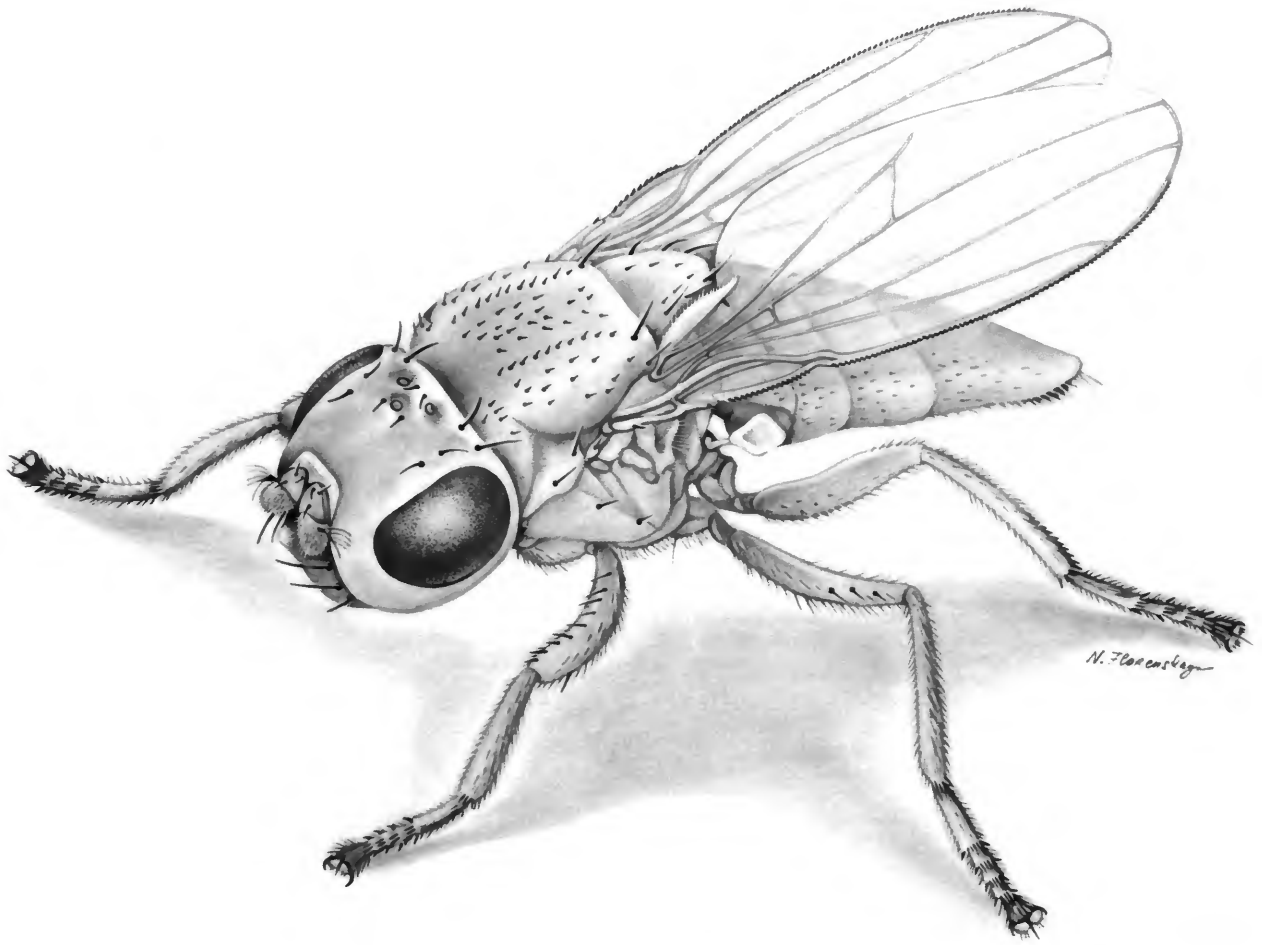


FIGURE 1.—Frontispiece, habitus of *Hecamede (Soikia) nuda* Wirth.

Studies of Gymnomyzinae (Diptera: Ephydriidae), IV: A Revision of the Shore-Fly Genus *Hecamede* Haliday

Wayne N. Mathis

Introduction

Among valid shore-fly genera, which now number more than 110, only 13 were named before *Hecamede* Haliday (1837), the subject of this revision. The initial naming of *Hecamede*, however, was not without controversy, and the early nomenclatural history that resulted is rather convoluted. Haliday (1837) first proposed the genus in an addendum to a book on British entomology that John Curtis, an English contemporary, published. Authorship of *Hecamede* is thus ambiguous, with the possibility that either Haliday or Curtis was the author. Contemporaries, including Curtis, all considered Haliday as the author, even though Curtis unquestionably published the book. Although valid arguments, including precedence, could be made for either author, Thompson and Mathis (1981) elected to follow the obvious intention of the two principals and have credited authorship to Haliday. That precedent is continued here.

Further compounding the nomenclatural status of *Hecamede* was its proposal in synonymy, a fact that was overlooked by most subsequent workers and which makes its availability and validation, and the dates of either, a consideration that is subject to a rule that is seldom used (ICZN, 1985, Article 11, Section e). Although *Hecamede* was initially listed without a diagnosis or description of any kind, which would normally make the name unavailable, its listing was as a synonym. According to the rules, a name first proposed as a synonym becomes available if prior to 1961 it had been adopted as the name of a taxon or treated as a senior homonym. Haliday (1839:221, 224) fulfilled these requirements two years after he first listed *Hecamede* as a synonym by including it in a paper on British Hydromyzidae (= Ephydriidae) where it was treated as a

valid subgeneric name under the genus *Notiphila* Fallén, included in a key, and also given a separate diagnosis. In this same paper, Haliday (1839:224) also cited *Notiphila albicans* Meigen as the only included species, and this species became the type species of *Hecamede* by monotypy. Even though *Hecamede* became available in 1839, the rules (Section e) further state that such a "name dates from its first publication as a synonym," or in this case 1837. Thus by an encumbered process *Hecamede* was given birth into the world of zoological nomenclature in 1837 and conferred retroactive legitimacy in 1839.

As an aside to the issues pertaining to publication of a name in synonymy is Haliday's listing of *Notiphila albicans* Meigen as an available species name under *Hecamede*. Most synonyms that Haliday introduced in the 1837 list did not include an available species, but where one was included, that species can serve as an indication (sense of the code, ICZN), and before 1931 would make the associated generic name available (ICZN, 1985, Article 12(b)(5)). Thus the inclusion of *N. albicans* further substantiates the validity of the *Hecamede* from the date when it was first listed in 1837.

Despite nomenclatural issues that are debated from time to time (Thompson and Mathis, 1981), the status of *Hecamede* as a zoological taxon has remained stable from its inception and has been universally recognized by subsequent workers. Although the generic concept of *Hecamede* has remained unchanged, the genus has never been revised on a world basis nor within the context of a phylogenetic framework at the specific, generic, or tribal levels. As part of this revision, the genus is recharacterized, its monophyly confirmed within the phylogenetic framework of the newly established tribe Hecamedini (Mathis, 1991), and the phylogenetic relationships among the included species are elaborated. The coverage of this revision is worldwide.

This revision is a continuation of studies on the tribe

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Hecamedini that are intended to better characterize the tribe and elucidate the relationships between the component lineages. Genus-group taxa of this tribe that have recently been revised are: *Eremotrichoma* Giordani Soika (as a subgenus of *Allotrichoma*; Mathis, 1986a), *Elephantinosoma* Becker (Mathis and Deeming, 1987), *Diphua* Cresson (Mathis, 1990), and the subgenus *Pseudohecamede* Hendel of the genus *Allotrichoma* Becker (Mathis, 1991). Only *Allotrichoma*, sensu stricto, the most speciose and widespread genus of the tribe, remains to be revised.

METHODS.—The methods used generally in this study were explained previously (Mathis, 1986a, 1990, 1991). Because specimens are small, all less than 4 mm, study and illustration of the male terminalia required use of a compound microscope. To better assure effective communication about structures of the male terminalia, the terminology of other workers in Ephyridae (see references in Mathis, 1986b) has been adopted. Usage of these terms, however, should not be taken as an endorsement of them from a theoretical or morphological view over alternatives that have been proposed (Griffiths, 1972; McAlpine, 1981). Rather, I am deferring to tradition until the morphological issues are better resolved. The terminology for structures of the male terminalia is provided directly on Figures 13 and 14 (*Hecamede albicans*) and is not repeated for comparable illustrations of other species.

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

1. Costal vein ratio: the straight line distance between the apices of R_{2+3} and R_{4+5} /distance between the apices of R_1 and R_{2+3} .

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

The phylogenetic analysis was performed with the assistance of Hennig86 (copyrighted), a computerized algorithm that produces cladograms on the basis of parsimony. Before performing the analysis, the character data were arranged in transformation series and then polarized primarily using outgroup procedures.

ACKNOWLEDGMENTS.—Although this study was based primarily on specimens in the National Museum of Natural History, numerous others were borrowed, particularly type specimens of the species previously described. To my colleagues and their institutions listed below who loaned specimens, I express my sincere thanks. Without their cooperation this study could not have been completed.

- AMNH American Museum of Natural History, New York, New York (Dr. David A. Grimaldi and Mr. Julian Stark)
 ANIC Australian National Insect Collection, CSIRO, Canberra, Australia (Dr. Donald Colless)
 ANSP Academy of Natural Sciences of Philadelphia,

- Pennsylvania (Drs. Jon K. Gelhaus and Donald Azuma)
 BBM Bernice P. Bishop Museum, Honolulu, Hawaii (Dr. Neal L. Evenhuis)
 BMNH British Museum (Natural History), London, England (Drs. Adrian Pont and Brian Pitkin)
 CNC Canadian National Collection, Ottawa, Canada (Dr. J.R. Vockeroth)
 MBP personal collection of M. Barták, Prague, Czech Republic (formerly Czechoslovakia)
 MNHN Muséum National d'Histoire Naturelle, Paris, France (Dr. Loïc Matile)
 MNRJ Museu Nacional, Rio de Janeiro, Brazil (Dra. Márcia S. Couri)
 NMW Naturhistorisches Museum, Vienna, Austria (Dr. Ruth Contreras Lichtenberg)
 NMWL National Museum of Wales, Cardiff, Wales, United Kingdom (Mr. John C. Deeming)
 NRS Naturhistoriska Riksmuseet, Stockholm, Sweden (Dr. Per Inge Persson)
 NZAC New Zealand Arthropod Collection, Auckland, New Zealand (Dr. Beverly A. Holloway)
 TAU Tel Aviv University (Zoology Department), Tel Aviv, Israel (Dr. Amnon Freidberg)
 USNM former United States National Museum, collections in the National Museum of Natural History, Smithsonian Institution, Washington, D.C.
 UZMC Universitetets Zoologiske Museet, Copenhagen, Denmark (Drs. Thomas Pape and Leif Lyneborg)
 WSU Washington State University, Pullman, Washington (Dr. Richard Zack)
 ZMA Instituut voor Taxonomische Zoologie, Zoologisch Museum, Universiteit van Amsterdam, Netherlands (Dr. Th. H. van Leeuwen)

Ms. Hollis B. Williams prepared the distribution maps, and the line illustrations were carefully rendered by Mrs. Elaine R.S. Hodges. The frontispiece was produced in carbon dust by Mrs. Natalia A. Florenskaya (St. Petersburg, Russia). Mrs. Susann Braden and Ms. Victoria Godwin assisted with the preparation of the scanning electron micrographs. Drs. F.C. Thompson and C.W. Sabrosky reviewed portions of the manuscript that deal with nomenclature. For reviewing a complete draft of this paper I thank Drs. G.W. Courtney, A.L. Norrbom, and R.V. Peterson. I am also grateful to Dr. David Challinor, former Assistant Secretary for Research, Smithsonian Institution, and Dr. Stanwyn G. Shetler, Deputy Director, National Museum of Natural History, for financial support to conduct field work through grants from the Research Opportunity Fund. Dr. J.W. Ismay made special effort to collect shore flies in Papua New Guinea; his efforts are gratefully appreciated. Dr. Curtis W. Sabrosky kindly hand

carried the holotypes of *H. affinis* and *Soikia argentata* from MNHN to Washington, D.C., and Dra. Márcia S. Couri sent me information on the holotype of *H. brasiliensis*.

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Tribe Hecamedini Mathis

Hecamedini Mathis, 1991:2. Type genus: *Hecamede* Haliday, 1837.

DIAGNOSIS.—*Head:* Arista with 3 to 5 dorsally branching rays, longer 2 or 3 rays subequal, inserted toward arista base; compound eye bare of microsetulae or the latter very sparse.

Thorax: Usually with a gray to silvery stripe on thorax from

postpronotum through ventral portion of notopleuron; anterior supra-alar seta lacking; posterior notopleural seta inserted at distinctly elevated position, especially as compared to anterior seta; anepisternum usually two toned, dorsal portion concolorous with mesonotum, ventral portion gray; anepisternum with 2 subequal setae inserted along posterior margin. *Wing:* venation of wing generally pale colored; vein R_{2+3} elongate, section III much shorter than section II; apical section of vein M longer than section between crossveins r-m and dm-cu; alula wide, width subequal to that of costal cell. *Abdomen:* Male terminalia: Pregonite either lacking or fused indistinguishably with postgonite; subepandrial sclerite lacking; postgonite generally elongate and bearing few setulae, usually only 2 are conspicuous.

Key to Genera of the Tribe Hecamedini

1. Oral opening large, gaping; only reclinate fronto-orbital seta present; anteroventral margin of face essentially flat, at same level with rest of oral margin; clypeus broad; katapisternal seta lacking *Elephantinosoma* Becker
 Oral opening narrow; usually both a reclinate and proclinate fronto-orbital seta present; anteroventral margin of face emarginate with narrow clypeus exposed within facial emargination; katapisternal seta usually present 2
2. Scutellum bearing 3 marginal setae; postgenal margin sharp; gena high, over 1/2 eye height *Hecamede* Haliday
 Scutellum bearing 2 marginal setae; postgenal margin rounded; gena short, less than 1/2 eye height 3
3. Palpus mostly yellow; prescutellar acrostichal setae greatly reduced or absent; 1 katapisternal seta; face with 1 large lateral seta *Eremotrichoma* Giordani Soika
 Palpus blackish; 1 pair of prescutellar acrostichal setae, well developed; 2 katapisternal setae, the 2nd seta smaller and inserted below larger seta; face with 2 or more large lateral setae 4
4. Color generally black; microtomentum sparse, subshiny to shiny *Diphuia* Cresson
 Color generally gray to brown; microtomentum dense, generally appearing dull (Genus *Allotrichoma* Becker) 5
5. Median facial carina above facial prominence distinct, high, acute; presutural seta lacking (except in *A. slossonae*); proboscis geniculate, labella lanceolate, elongate, nearly equal to length of mediproboscis; face carinate above medial prominence Subgenus *Pseudohecamede* Hendel
 Median facial carina above facial prominence shallow; presutural seta present; labella broad, fleshy, shorter than mediproboscis 6
6. Clypeus microtomentose, usually gray; 5th tergum of male long and tubular; cerci of male terminalia elongate and with irregular, species-specific shape Subgenus *Allotrichoma* Becker
 Clypeus bare, black; 5th tergum of male short, 1/2 length of 4th tergum; cerci normally developed, oval to lenticular "The *atrilabrae* Group"

[see Mathis (1991) for information regarding the recognition and naming of this species group]

Genus *Hecamede* Haliday

Hecamede Haliday in Curtis, 1837:281 [published in synonymy; first made available by use of Haliday, 1839:221, 224; type species: *Notiphila albicans* Meigen, by monotypy].—Loew, 1860:12–13 [review].—Schiner, 1863:245 [description].—Becker, 1896:119–121 [discussion, description]; 1926:18–19 [description, revision of palearctic species].—Cresson, 1925:228–229 [treated in subfamily Gymnopyinae (= Gymnomyzini), notes on species of Old World].—Malloch, 1933:11 [discussion].—Harrison, 1959:219 [description].—Wirth, 1965:737 [nearctic catalog]; 1968:5 [neotropical catalog].—Papp, 1975:25 [description].—Cogan and Wirth, 1977:325 [Oriental catalog].—Cogan, 1980:657 [Afrotropical catalog]; 1984:130–131 [palearctic catalog].—Canzoneri and Meneghini, 1983:231 [diagnosis].—Mathis, 1989a:641 [Australasian/Oceanian catalog].

Notiphila (*Hecamede*).—Walker, 1853:254 [review].

DESCRIPTION.—Small to medium-sized shore flies, length 1.30 to 3.50 mm, thinly to mostly densely microtomentose.

Head: Wider than high; frons wider than high, at least posterior portion (from anterior ocellus posteriad) densely microtomentose, usually gray, anterior $1/2$ frequently mostly red to mostly yellow and thinly microtomentose; ocellar setae lacking but usually setulae present; 1 to 3 intrafrontal setae, inserted laterad or in front of anterior ocellus; a reclinate fronto-orbital seta (sometimes with laterocline orientation); proclinate fronto-orbital seta variable; pseudopostocellar setae present, development variable; both inner and outer vertical setae present; ocelli arranged to form isosceles triangle, with distance between posterior pair slightly greater than between anterior ocellus and either posterior ocellus. Antenna exerted; pedicel with well-developed, proclinate, dorsal seta; arisal length subequal to combined length of pedicel and flagellomere 1, bearing 3 or 4 dorsal rays, with basal rays longer than apical 1–2. Face between antennae and antennal grooves shallowly but sharply carinate; antennal grooves moderately well developed; face becoming more prominent below level of facial grooves, distinctly conically protrudent; facial setae in 1 vertical series near parafacial; facial setae arising from small, shiny tubercles; anteroventral facial margin shallowly emarginate; clypeus protrudent through ventral facial emargination. Eye irregularly round to subovate; apparently bare of microsetulae (using a stereomicroscope). Gena high, at least $1/2$ eye height, usually bearing 1 to several genal seta; posterior margin of gena acutely angulate. Palpus pale; labella broad, fleshy, shorter than mediproboscis.

Thorax: Mesonotum usually darker than pleural region, usually tan to brown; chaetotaxy variable, setae usually dark colored, arranged in setal tracks as follows: rows of acrostichal setulae variable; dorsocentral track terminated posteriorly with larger seta; intra-alar setulae irregularly seriated; presutural seta variable; 1 postpronotal seta; 1 postalar seta; 3 scutellar setae well developed with sparse, scattered setulae on scutellar disc; 2 notopleural setae, insertion of posterior seta elevated above level of anterior seta; 2 anepisternal setae along posterior margin; katapisternal setae variable. Wing mostly hyaline to slightly milky white, veins mostly pale yellow; venation as

follows: vein R_{2+3} extended beyond level of crossvein dm-cu, 3rd costal section about $1/3$ length of 2nd section; alular marginal setulae short, less than $1/2$ alular height. Legs: tibiae pale, mostly yellow to yellowish orange, less densely microtomentose than femora.

Abdomen: Tergum 5 of male not generally visible from dorsal view, retracted within 4th; 4th tergum long, length subequal to combined length of 2nd and 3rd. Male terminalia as follows: symmetrical; epandrium and cerci well developed, separate; surstylus well developed, elongate, shape variable with species; gonite (= postgonite + fused pregonite ?) triangular to lunate; aedeagus simple, tubular, lightly sclerotized, no distinct basiphallus or distiphallus, apex usually membranous; ejaculatory apodeme lacking; aedeagal apodeme evenly curved to angulate, better developed toward attachment with hypandrium; hypandrium well developed, a lightly sclerotized plate that is a shallowly concave receptacle for the male genitalia.

DISTRIBUTION AND BIOGEOGRAPHIC CONSIDERATIONS.—Species of the genus *Hecamede* occur primarily on maritime coasts throughout most temperate and tropical regions of the world, sometimes in great abundance. A major departure from this generalization is the apparent absence of any species along the Pacific coast of the Western Hemisphere. Even that coastline may soon be invaded (see "Natural History" section of *H. brasiliensis*).

Although *Hecamede* was proposed early in the nomenclatural history of shore flies and its known species are geographically widespread, the genus has never included many species. Moreover, most species now included in the genus have widespread distributions, typical of many coast-inhabiting Ephydridae. One species occurs on both sides of the Atlantic Ocean and another throughout the Indian and much of the Pacific oceans. Even those species that are more localized are relatively widespread, such as the coasts of Australia or those of Madagascar and the southeastern coast of Africa, and except for *H. socotra* and possibly *H. africana*, none is known to be a narrow endemic. The former is known only from the island of Socotra, and the latter is described from specimens collected recently in East Africa, and although presently known from a single locality, sampling for this species along the east coast of Africa is woefully incomplete. Collecting was attempted at only two or three sites in Kenya.

NATURAL HISTORY.—All instars occur primarily on and/or in highly organic microhabitats that are associated with beaches and other maritime habitats. Ardö (1957:184) suggested that *H. albicans* is confined "wholly to the marine shore dune ecosystem." Apparently the larvae and adults are general scavengers, perhaps secondarily on bacteria that are associated with concentrated organic debris. Haliday (1839:224) appropriately described this medium as "marine rejectamenta." The debris frequently accumulates in the strand zone, where it often decays, providing a good habitat and food source for many beach and shore flies. Adults also feed on pollen and nectar

from various flowering plants that occur near or on beaches.

The number of generations per year is apparently determined by climate and is dependent upon availability of adequate food and habitat. Ardö (1957) suggested two generations for *H. albicans* in northern Europe, but several generations are possible in Connecticut (Steinly, 1992) and the tropics.

What little is known about the immature stages of *Hecamede* is reported in the following papers (further details are cited in the treatment of the appropriate species): Bohart and Gressitt (1951; description and discussion of the adult and figure of the puparium of *H. granifera* (as *H. persimilis*) from Guam, the Solomons, and Guadalcanal), Tenorio (1980; reared and described the adults, third-instar larvae, and puparia of *H. granifera* (as *H. persimilis*), which was found on all major islands of the Hawaiian Islands), Norrbom (1983; description and illustrations of the third-instar larva and the puparium of *H. albicans*; discussion of feeding habits as a scavenger on dead horseshoe crabs, *Limulus polyphemus* L.), and Steinly (1992; description and illustrations of the third-instar larva and puparium of *H. albicans*; discussion of feeding habits as a scavenger on decaying horseshoe crabs, putrefying blue

mussels (*Mytilus edulis* L.), and common spider crabs (*Libinia emarginata* Leach)). In addition to the papers just noted, A. Valdenberg (1985) completed a Master's thesis on the macrofauna of the Mediterranean beach at Ma'agan Michael, Israel, which includes information and illustrations on the natural history and immature stages of *H. albicans*.

DISCUSSION.—*Hecamede* is easily distinguished from other shore-fly genera of the tribe Hecamedini by the following synapomorphic characters: gena high, usually over one-half height of eye and in some species nearly equaling it; face conically protrudent, frequently pointed and with point bare of microtomentum; postgenal margin sharp; acrostichal setae arranged in four to six irregular rows; scutellum with 3, rarely 4, pairs of marginal setae, these not arising from tubercles; scutellar disc with numerous, scattered setulae; katapisternum with 1 large seta and numerous smaller setae anterior of larger seta; fore femur slightly to conspicuously swollen, especially when compared with femora of middle and hind legs; tibiae pale, although sometimes invested with white to gray microtomentum; wing membrane lacteous; and wing veins pale colored.

Key to Subgenera of *Hecamede*

- Facial prominence bare at apex, shiny; proclinate fronto-orbital seta present, well developed; intrafrontal seta present. Acrostichal setae in about 6 irregular rows; katapisternal seta well developed *Hecamede* Haliday
 Facial prominence microtomentose; proclinate fronto-orbital seta either weakly developed or lacking; intrafrontal setae lacking. Acrostichal setae in 4 more or less regular rows; katapisternal seta lacking *Soikia* Canzoneri and Meneghini

Subgenus *Hecamede* Haliday

Hecamede Haliday, 1837:281 [see generic synonymy].

Hemicyclops de Meijere, 1913:66 [type species: *Hemicyclops planifrons* de Meijere, 1913, by monotypy (preoccupied, Boeck, 1873, crustacea)].—Cogan and Wirth, 1977:325 [Oriental catalog].—Mathis, 1989a:641 [synonymy with *Hecamede*].

DESCRIPTION.—Small to medium-sized shore flies, length 1.15 to 3.10 mm; setae generally well developed and numerous.

Head: Area surrounding ocellar triangle and fronto-orbits densely microtomentose, anterior portion of frons more thinly microtomentose, frequently reddish; proclinate fronto-orbital seta 1 or 2; intrafrontal setae 1, inserted about midway between anterior ocellus and anterior margin of frons, insertions more approximate than ocellar setae. Antenna usually pale, yellow to yellowish orange, flagellomere 1 sometimes mostly black (*H. planifrons*) or slightly blackish anterodorsally near insertion of arista. Conical facial prominence bare at apex, shiny, size variable; clypeus microtomentose.

Thorax: Mesonotum either mostly light brown to faintly golden or bronzish or mostly gray; pleural areas mostly gray

but sometimes with a wide, faintly gold stripe through dorsum of anepisternum; chaetotaxy generally well developed; acrostichal setae arranged in about 6 irregular rows; prescutellar acrostichal setae usually longer than other acrostichal setae and more widely set apart; presutural and prescutellar acrostichal setae usually evident but variable; katapisternal seta well developed.

Abdomen: Male terminalia as follows: 5th tergum normally retracted within 4th, anterior $\frac{3}{4}$ to $\frac{7}{8}$ more lightly sclerotized than posterior portion, and covered with numerous, evenly scattered spicules, from dorsal view with anterior margin broadly bifid, posterior $\frac{1}{4}$ to $\frac{1}{8}$ a sclerotized band bearing 8 to 11 setae along posterolateral margin; epandrium a dorsolateral band, gradually enlarged posteriorly; surstylus long and usually narrow with apex slightly expanded and bearing setulae (shape, however, varies depending on species); cercus long and narrow, length subequal to or greater than that of surstylus, apex bearing a few long setulae; gonites with basal extension that connects over aedeagus, forming a gonial arch, usually pointed ventrally; aedeagus cylindrical, becoming smaller apically, curved basally, thereafter straight.

DISTRIBUTION.—Of the two subgenera of *Hecamede*, this is by far the most widespread, with species occurring along temperate and tropical beaches along the Indian, much of the Pacific, and both sides of the Atlantic oceans. Only the western coast of the Western Hemisphere is apparently uninhabited.

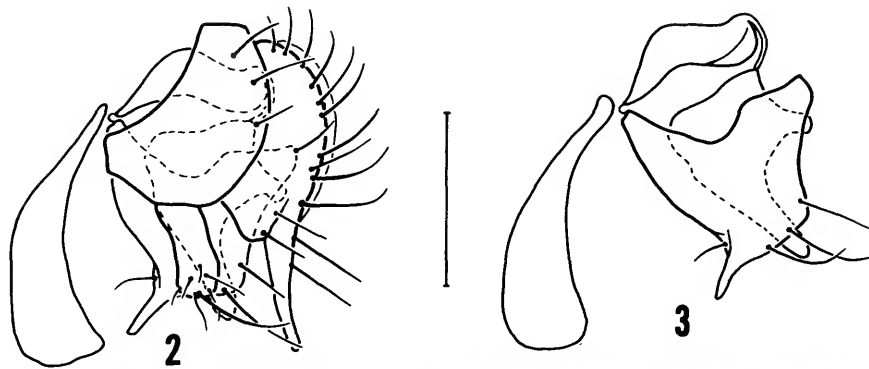
DISCUSSION.—*Hecamede*, sensu stricto, is apparently the relatively more derived subgenus and is characterized by several synapomorphies (see description above and "Phylogenetic Consideration" p. 39) that confirm its monophyly. It also has the most species (9), and these, for the most part, closely resemble each other and are fairly easily clustered into two monophyletic lineages, the *albicans* and *planifrons* species

groups.

When de Meijere (1913:66) proposed the genus *Hemicyclops* he was unaware that this name was preoccupied (Boeck, 1873; Crustacea) nor did he appreciate the interspecific variation within *Hecamede*, the genus with which *Hemicyclops* was compared for diagnostic purposes. This study, which included an examination of the features that de Meijere used to characterize *Hemicyclops*, has revealed that the characters he used reflect interspecific variation that is encompassed within the concept of *Hecamede* sensu stricto. Thus, I am treating *Hemicyclops* as a junior, preoccupied synonym of *Hecamede* that will not need a replacement, genus-group name.

Key to Species of the Subgenus *Hecamede*

1. Proclinate fronto-orbital setae 2; gena with 1 black seta near middle 2
 Proclinate fronto-orbital seta 1; gena either with a few to several black setae, scattered, or bare of setae 3
2. Clypeus dark colored; only apical tarsomere dark colored; posteriorproclinate fronto-orbital seta inserted distinctly anterior of reclinate seta (distance between subequal to width of median ocellus) *H. brasiliensis* Cresson
 Clypeus with anterior surface mostly yellow; apical 2 tarsomeres dark colored; posterior proclinate fronto-orbital seta aligned essentially with reclinate seta *H. africana*, new species
3. Fore femur bearing a distinct row of short, slightly stout setae along anteroventral margin 4
 Fore femur lacking a distinct row of setae along anteroventral margin 5
4. Gena conspicuously shorter than eye height and bearing scattered setae; 1 pair of large, intrafrontal setae inserted in front of ocellar setae; flagellomere 1 mostly yellow, at most faintly black dorsally, pedicel mostly yellowish orange, sometimes mostly black dorsally *H. granifera* (Thomson)
 Gena almost as high as eye height and lacking setae (a few pale, fine setulae are present, however); intrafrontal seta either lacking or greatly reduced; flagellomere 1 blackish orange laterally, more orangish medially, pedicel with dorsal surface blackish, otherwise reddish orange (The *planifrons* Group) *H. planifrons* de Meijere
5. Fore basitarsus with 2 or 3 black setae inserted toward base of posteroventral surface 6
 Fore basitarsus lacking black setae at base of posteroventral surface 7
6. Tibiae, especially the fore tibia, mostly grayish, only apices of fore tibia mostly yellow (Australia) *H. australis*, new species
 Tibiae mostly yellow, similar to basal tarsomeres (east and west coasts of the North Atlantic) *H. albicans* (Meigen)
7. Mesonotum darker, golden brown to brown; 5th tergum of ♂ appearing hirsute, invested with numerous, long, cuticular microtrichia (Australasian/Oceanian) *H. inermis* Malloch
 Mesonotum lighter, more grayish, frequently concolorous with pleural areas; 5th tergum of ♂ appearing bare or at most with sparse, inconspicuous cuticular microtrichia 8
8. Surstylus about $\frac{2}{3}$ length of cerci and bearing not more than 6 fine, long setulae at ventral margin; gonite irregularly triangular, posterior margin conspicuously sinuous (Red Sea) *H. maritima*, new species
 Surstylus as long as cerci, bearing about 12 stout setulae along anteroventral margin; gonite more regularly triangular (Socotra) *H. socotra*, new species



FIGURES 2, 3.—*Hecamede (Hecamede) africana*: 2, male terminalia, lateral aspect; 3, internal structures of the male genitalia, lateral aspect. (Bar = 0.1 mm.)

The albicans Group

SPECIES INCLUDED.—*Hecamede africana*, new species; *H. albicans* (Meigen); *H. australis*, new species; *H. brasiliensis* Cresson; *H. granifera* (Thomson); *H. inermis* Malloch; *H. maritima*, new species; *H. socotra*, new species.

DIAGNOSIS.—This species group is distinguished from other lineages of the subgenus *Hecamede* by the presence of intrafrontal setae (not to be confused with ocellar setae, which are inserted in front of the anterior ocellus); the presence of black genal setulae (pale setulae are also present sometimes, however); the shorter genal height, which is approximately one-half that of the eye; the lack of a posteroventral row of stout setae on the fore femur; and the mostly to entirely pale-colored flagellomere 1.

DISTRIBUTION.—Widespread, occurring on maritime beaches within the temperate and tropical zones of the Afrotropical, Australasian/Oceanian, Nearctic, Neotropical, and Palearctic regions.

DISCUSSION.—The seven species of this species group are very similar externally and are sometimes difficult to distinguish. Even the structures of the male terminalia are quite similar in some species, but the differences are consistent and are part of the suite of characters used to distinguish the species.

Hecamede (Hecamede) africana, new species

FIGURES 2-4

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

Head: Fronto-orbits, most of face, and gena silvery gray, densely microtomentose, microtomentum slightly less lustrous than that of pleura; ocellar triangle large, grayish tan to slightly golden, usually slightly darker laterally at vertex; mesofrons more thinly invested with microtomentum than fronto-orbits, light brown to grayish brown towards vertex, becoming mostly orange to reddish orange toward anterior margin; 1 reclinate and 2 proclinate fronto-orbital setae; reclinate seta aligned with

and inserted mesad to posterior proclinate seta; anterior proclinate seta inserted slightly anterior to alignment of anterior setae of ocellar triangle. Antenna mostly yellowish orange to orange; flagellomere 1 with some brown coloration toward base, near insertion of arista; arista bearing 3 dorsal branches. Face with 3 lateral setae, each arising from subshiny, bare, shallow tubercle; facial prominence bare at apex. Gena with pale, indistinct setulae except for 1 black seta inserted near middle slightly above midheight; eye-to-cheek ratio averaging 0.48. Clypeus yellow to grayish yellow, very thinly invested with microtomentum.

Thorax: Scutum and disc of scutellum mostly grayish tan; lateral margins of scutum, beginning slightly above level of notopleuron, becoming gray; prescutellar setae well developed, distinct; pleural sclerites gray and microtomentum with faint shiny luster; anepisternum bearing numerous setulae on dorsal $1/2$ toward posterodorsal angle. Coxae mostly grayish, with some yellow coloration ventrally; trochanters mostly yellow; apices of femora mostly yellow; fore femur mostly black anteriorly, gray posteriorly; middle and hind femora grayish anteriorly, posterior surface blackish; tibiae yellow with very thin investment of white microtomentum; tarsomeres mostly yellow except for apical 2, which are dark brown. Wing with costal vein ratio averaging 0.46; M vein ratio averaging 0.54; last section of vein M shallowly sinuous.

Abdomen: Male terminalia (Figures 2, 3) as follows: 5th tergum largely membranous, anterior margin with lateral, spherical apodemes; epandrium (Figure 2) a dorsal band, becoming broader ventrally; surstylus (Figure 2) in lateral view moderately long, digitiform, parallel-sided, bluntly rounded apically, apex bearing 4 to 6 setulae; cercus (Figure 2) moderately long, length of main portion subequal to height of epandrium in lateral view, bearing a very long, narrow process medially that extends ventrally; gonite more or less triangular in shape in lateral view, with an anteroventral, narrow process, bearing 3 or 4 setulae ventrally and a subapical seta anteriorly; aedeagal apodeme (Figure 3) sinuous, broader in lateral view toward middle; aedeagus (Figure 3) angulate, curved at a right

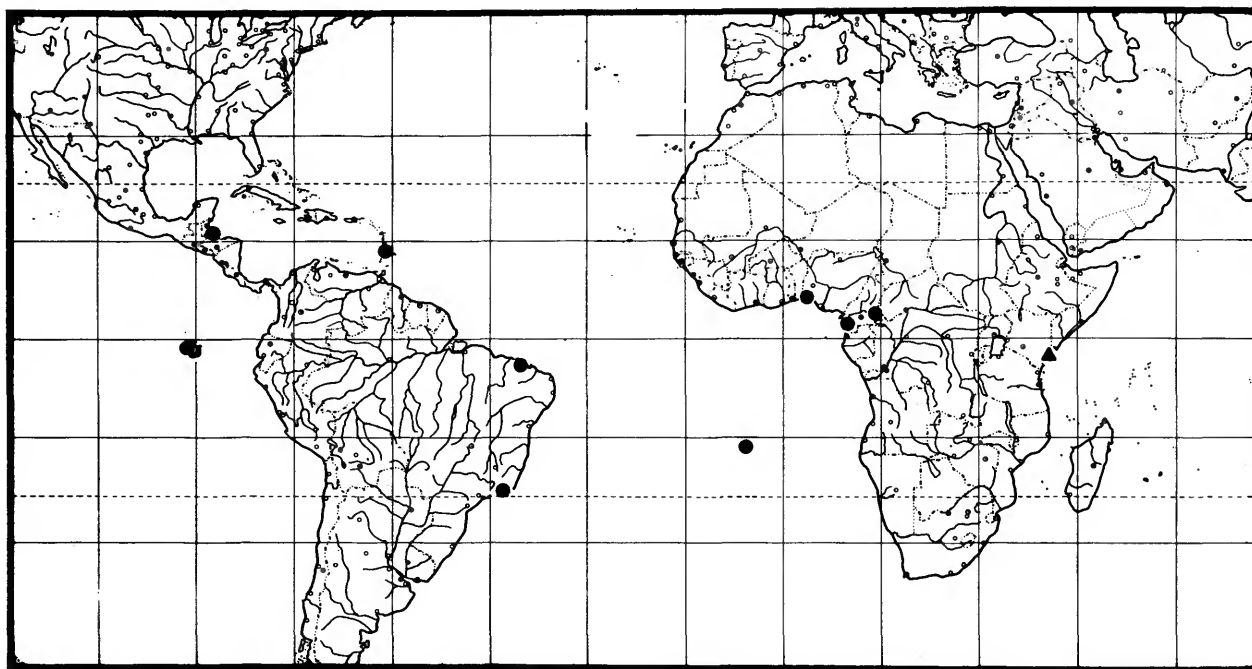


FIGURE 4.—Distribution map for *Hecamede (Hecamede) africana* (open triangle) and *H. brasiliensis* (dots and open diamond).

angle, broad basally, narrowed and tapered apically; hypantrium relatively narrow, shallowly rounded anteriorly.

TYPE MATERIAL.—The holotype male is labeled "KENYA 100Km North Mombasa[,] 4. XII. 1989 [4 Dec 1989] A. FREIDBERG & FINI KAPLAN." The allotype female and five paratypes (3 ♂, 2 ♀; TAU, USNM) bear the same locality label data as the holotype. The holotype is double mounted (minuten in a plastic elastomer block), is in excellent condition, and is deposited in the USNM.

DISTRIBUTION (Figure 4).—Afrotropical: This species is known only from the type locality near the Equator on the east coast of Africa.

ETYMOLOGY.—The species epithet, *africana*, alludes to the continent where this species was collected.

PHYLOGENETIC RELATIONSHIPS.—The monophyly of this species and its sister species, *H. brasiliensis*, is demonstrated by the following synapomorphies: 1. Proclinate fronto-orbital setae 2 (usually there is one proclinate seta); and 2. gena with 1 black seta near middle (usually these are a few to several setae).

DIAGNOSIS.—This species is distinguished from *H. brasiliensis* by the position of the proclinate setae, which are inserted more posteriad. This is especially evident in the posterior proclinate set, which in *H. africana* is nearly aligned with the reclinate seta.

The structures of the male terminalia of *H. africana* differ markedly from those of *H. brasiliensis*. In the former, the cercus bears a long, narrow process that extends ventrally from the ventromedial angle of the cercus, the surstylus is

comparatively narrower (Figure 3), the gonite has a finger-like process that is straight in lateral view (Figure 3), and the aedeagus in lateral view is angulate, with the basal portion 3–4 × wider than the apical portion (Figure 3).

Hecamede (Hecamede) brasiliensis Cresson

FIGURES 4–9

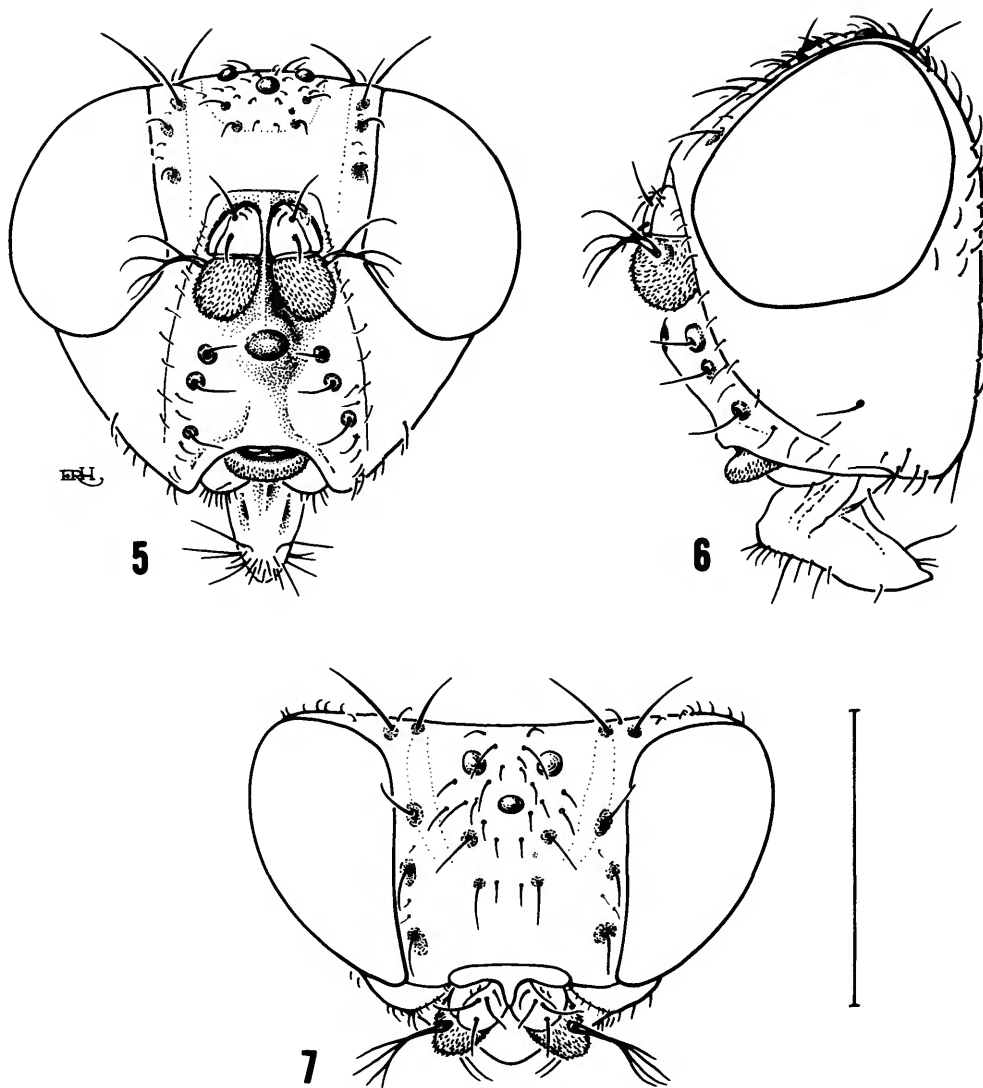
Hecamede brasiliensis Cresson, 1938:24; 1946a:137 [review].—Wirth, 1968:5 [neotropical catalog].—Cogan, 1976b:108 [discussion, list, St. Helena, Ascension Isles]; 1980:657 [Afrotropical catalog].

Hecamede afinis Canzoneri and Meneghini, 1969:1483.

Hecamede affinis.—Cogan, 1980:657 [Afrotropical catalog, corrected original spelling as first revisor].—Canzoneri, 1981:203 [list, Senegal]; 1982:58 [list, Sierra Leone]. [New synonym.]

DESCRIPTION.—Small to moderately small shore flies, length 1.60–2.65 mm.

Head (Figures 5–7): Fronto-orbits, most of face, and gena silvery gray, densely microtomentose, microtomentum slightly less lustrous than that of pleura; ocellar triangle large, gray to lightly orangish to golden gray, usually slightly darker laterally at vertex; mesofrons more thinly invested with microtomentum than fronto-orbits, light brown to grayish brown towards vertex, becoming mostly orange to reddish orange toward anterior margin; 1 reclinate and 2 proclinate fronto-orbital setae; both proclinate setae inserted well in front of alignment with and slightly laterad of reclinate seta; anterior proclinate seta inserted slightly anterior to alignment of anterior setae of ocellar triangle. Antenna yellow to yellowish orange; arista



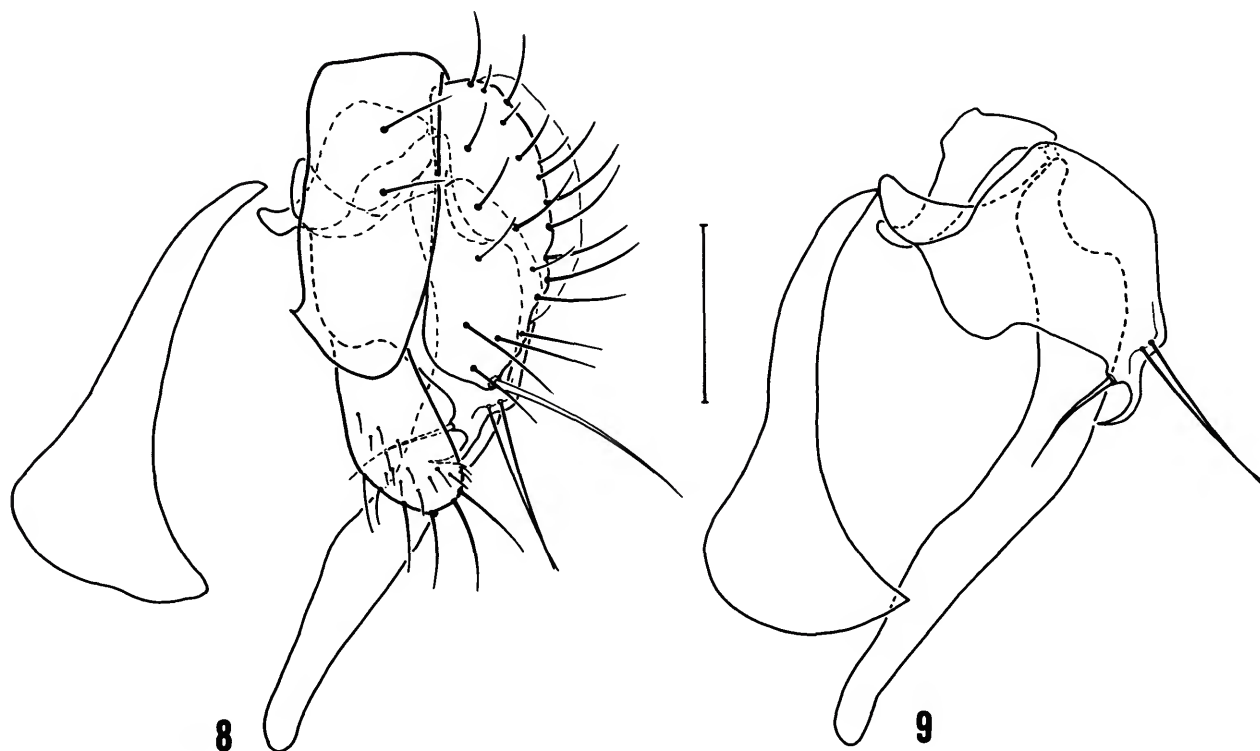
FIGURES 5-7.—*Hecamede (Hecamede) brasiliensis*: 5, head, anterior aspect; 6, head, lateral aspect; 7, head, dorsal aspect. (Bar = 0.5 mm.)

bearing 3 dorsal branches. Face with 3, rarely 4, lateral setae, each arising from a subshiny, bare, shallow tubercle; facial prominence bare to only partially bare at apex, amber colored. Gena with pale, indistinct setulae except for 1 black seta inserted near middle slightly above midheight; eye-to-cheek ratio averaging 0.60. Clypeus mostly black with moderately dense investment of microtomentum.

Thorax: Scutum and disc of scutellum completely gray to mostly tan; if tan, lateral margins of scutum, beginning slightly above level of notopleuron, gradually becoming gray; prescutellar acrostichal seta well developed; pleural sclerites gray and microtomentum with faint shiny luster; anepisternum bearing several setulae on dorsal $\frac{1}{2}$ towards posterodorsal angle. Coxae mostly grayish, with some yellow coloration ventrally; trochanters mostly yellow; apices of femora yellowish;

fore femur mostly black anteriorly, mostly gray posteriorly; middle and hind femora mostly gray anteriorly, posterior surface blackish; tibiae yellow with thin investment of mostly white microtomentum; tarsomeres mostly yellow except for apical 2, which are dark brown. Wing with costal vein ratio averaging 0.46; M vein ratio averaging 0.50, last section of vein M shallowly sinuous.

Abdomen: Male terminalia (Figures 8, 9) as follows: 5th tergum mostly membranous, 2 globular apodemes anterodorsally; epandrium (Figure 8) a dorsal band, more or less parallel sided laterally; surstylus (Figure 8) in lateral view irregularly spatulate, length about $1.5 \times$ width, bearing several longer setae along apical margin; cercus (Figure 8) moderately long, length subequal to height of epandrium in lateral view, bearing a conspicuously longer seta at posteroventral margin; gonite



FIGURES 8, 9.—*Hecamede (Hecamede) brasiliensis*: 8, male terminalia, lateral aspect; 9, internal structures of the male genitalia, lateral aspect. (Bar = 0.1 mm).

(Figure 9) with an apical, hook-like process and a larger, subapical seta; aedeagal apodeme (Figure 9) sinuous, broader in lateral view toward middle; aedeagus (Figure 9) long and narrow, tapered gradually to bluntly rounded apex, shaped like a slightly curved, simple tube; hypandrium nearly 3 times longer than wide, anterior portion only slightly wider than remainder, anterior margin mostly straight, at most very shallowly emarginate.

TYPE MATERIAL.—The holotype male of *H. brasiliensis* is labeled “[Brazil] Rio de Janeiro. Praia Gavea [handwritten] H.S[ouza]. Lopes [black submarginal border] 29.IV.36 [date handwritten on underside]/TYPE No. [no number] Hecamede BRASILIENSIS E. T. Cresson, Jr. [species name handwritten, red].” A paratype male is labeled “Rio de Janeiro. Praia Gavea [handwritten] H.S. Lopes 21 IV 36 [date handwritten on underside]/PARATYPE Hecamede BRASILIENSIS E.T. Cresson, Jr. [species name handwritten, blue].” The holotype was collected by H. Souza Lopes and is deposited in the MNRJ (Originally the holotype was deposited in the Instituto de Biologia Vegetal, Rio de Janeiro, Brazil. The insect collections that were housed at the Instituto have since been transferred to the Museu Nacional, also in Rio de Janeiro). I did not examine the holotype but studied a paratopotype male. The label data was transcribed and sent to me by Dra. Márcia Souto Couri (MNRJ).

The holotype male of *H. affinis* is labeled “plage SOMONE SENEGAL 4. X. 61 [4 Oct 1961, A. Villiers collector, handwritten]/dans detritus vegetaux [handwritten]/HOLOTYPUS ♂ Hecamede affinis [sic] sp.n. [red, handwritten except for “HOLOTYPUS”].” The holotype is double mounted (pin in a rectangular card), is in poor condition (right mid leg and hind legs missing, right wing crumpled; I removed the abdomen, macerated it in NaOH, and placed it in a microvial of glycerin that is attached to the specimen pin), and is deposited in the MNHN.

OTHER SPECIMENS EXAMINED.—Afrotropical: *CAME-ROON*. Kribi (beach), 28–29 Nov 1987, F. Kaplan (9♂; TAU, USNM); Kribi (beach), Rt. N7, 28–29 Nov 1987, A. Freidberg (8♂, 3♀; TAU, USNM); Limbe (shore), 14–15 Nov 1987, A. Freidberg (1♂; USNM).

NIGERIA. Lagos: Ikoyi, 12 May–9 Jun 1974, M.A. Cornes (4♂, 1♀; NMWL); Lagos, L.H. beach (driftwood), 5 Jan 1975, M.A. Cornes (1♂; NMWL); Lagos (shore), 15 Dec 1987, A. Freidberg (1♂; USNM); Tarkwa Lagos, 17 Feb 1974, M.A. Cornes (6♂; NMWL); Tarkwa Bay Lagos, 10 Mar 1974, M.A. Cornes (1♂, 1♀; NMWL); Victoria (shore), 15 Dec 1987, F. Kaplan (5♂; TAU, USNM).

SAINT HÉLENA (15°57'S, 5°42'W): Sud Sandy-Bay, 15 May 1967 (6♂, 3♀; BMNH).

Neotropical: *BELIZE*. Stann Creek District: Carrie Bow Cay,

18 Jun–30 Jul 1989, 1990, W.N. Mathis, H.B. Williams (51 ♂, 27 ♀; USNM); Coco Plum Cay, 31 Jul 1989, W.N. Mathis (1 ♀; USNM); Man of War Cay, 24 Jun 1990, H.B. Williams (1 ♂; USNM); Twin Cays (south end of East Island), 25 Jul 1989, W.N. Mathis (1 ♂, 2 ♀; USNM).

BRAZIL. Ceará: Retiro, Nov 1938, R.C. Shannon (1 ♂, 1 ♀; USNM).

GALÁPAGOS ISLANDS. Floreana: Puerto Cormorant (littoral, white sand beach), 26 Mar 1989, B.J. Sinclair (3 ♂, 7 ♀; CNC, USNM). Isabela: Puerto Villamil (littoral, sweeping sand beach), 7 Mar 1989, B.J. Sinclair (2 ♂; CNC, USNM).

WEST INDIES. St. Lucia. Soufrière (13°51'N, 16°54'W, beach, especially on dead fish), 11–12 Jun 1991, W.N. and D. Mathis (31 ♂, 3 ♀; USNM).

DISTRIBUTION (Figure 4).—Afrotropical: Cameroon, Nigeria, Saint Helena, Senegal, Sierra Leone. Neotropical: Brazil (Ceará, Rio de Janeiro), Belize (Stann Creek District), West Indies (St. Lucia), and Galápagos Islands.

NATURAL HISTORY.—All the specimens from the Belizean cays, except for the female from Coco Plum Cay, occurred on decaying leaves of cabbage or a discarded fish head that were laying at the high tide mark on sandy to sandy/rocky beaches. The female from Coco Plum was collected on a protected and bare sandy beach that was about 30 m from a cabin used by fishermen.

Despite careful sampling on Carrie Bow Cay (Belizean barrier reef) for every year between 1984 and 1990, this species was only recently collected (1989, 1990). Since its discovery, however, it has been found to be abundant on Carrie Bow Cay, as well as other Belizean cays in the Stann Creek District. Brad Sinclair (Ottawa, Ontario, Canada) found this species on two islands of the Galápagos Archipelago in 1989, whereas previous entomological expeditions to these islands (Linsley and Usinger, 1966; Wirth, 1969) did not collect this species. Its sudden and widespread occurrence, frequently in plentiful numbers, leads me to suspect that this species was recently introduced to Belize and possibly the Galápagos Islands, probably through human commerce on organic debris.

DIAGNOSIS.—This species is distinguished from congeners by having two proclinate fronto-orbitals (most species have one), both inserted in front and slightly laterad of the reclinate seta; facial setae three; conical facial prominence only partially bare, slightly pale colored, mostly yellow (concolorous with anterior margin of frons); genal seta one, inserted near middle of gena; gena high, subequal to eye height.

From specimens of *H. africana*, this species is distinguished by the more anterior placement of the proclinate fronto-orbital setae. Sometimes the distance between the reclinate seta and the posterior proclinate seta is nearly equal to that between the two proclinate setae. The structures of the male terminalia also differ, especially the aedeagus that is elongate, shallowly curved on the basal third and gradually tapered to the rounded apex (Figure 9), and the gonite that bears a conspicuously curved process distally (Figure 9).

Hecamede (Hecamede) albicans (Meigen)

FIGURES 10–15

Notiphila albicans Meigen, 1830:65.—Macquart, 1835:522 [review, list, France].

Hecamede albicans.—Haliday, 1839:224 [generic combination].—Walker, 1856:344 [list].—Rondani, 1856:131–132 [list, Italy].—Loew, 1860:13 [review, synonymy].—Schiner, 1863:245 [review].—Becker, 1896:121 [list]; 1905:189 [paleartic catalog]; 1926:18 [revision].—Jones, 1906:181 [list].—Ringdahl, 1921:70 [note]; 1941:17 [note].—Cresson, 1925:229 [lectotype designation, list]; 1942:107 [review]; 1946b:248 [review].—Wahlgren, 1927:329 [review].—Séguy, 1934:408 [review, list, France].—Duda, 1942:6 [note on distribution].—Caspers, 1951:156 [list, Bulgarian coast].—Ardö, 1957:132 [natural history, list, Sweden].—Frey, 1958a:53 [list, Canary Islands]; 1958b:38 [list, Cape Verde Islands].—Dahl, 1959:160 [review, list, Sweden].—Wirth, 1965:737 [nearctic catalog].—Papp, 1975:26 [review].—Cogan, 1976a:83 [list, England]; 1980:657 [Afrotropical catalog]; 1984:130 [paleartic catalog].—Norrbom, 1983:118 [natural history].—Canzoneri and Meneghini, 1983:231–235 [review, list, Italy].—Valdenberg, 1985:172–173 [natural history, immature stages].—Steinly, 1992:329–335 [natural history, immature stages].

Notiphila (Hecamede) albicans.—Walker, 1853:254 [review].

Psilopa (Clasiopa) globifera Boheman, 1853:204.—Walker, 1856:344 [synonymy with *H. albicans*].—Loew, 1860:13 [synonymy].

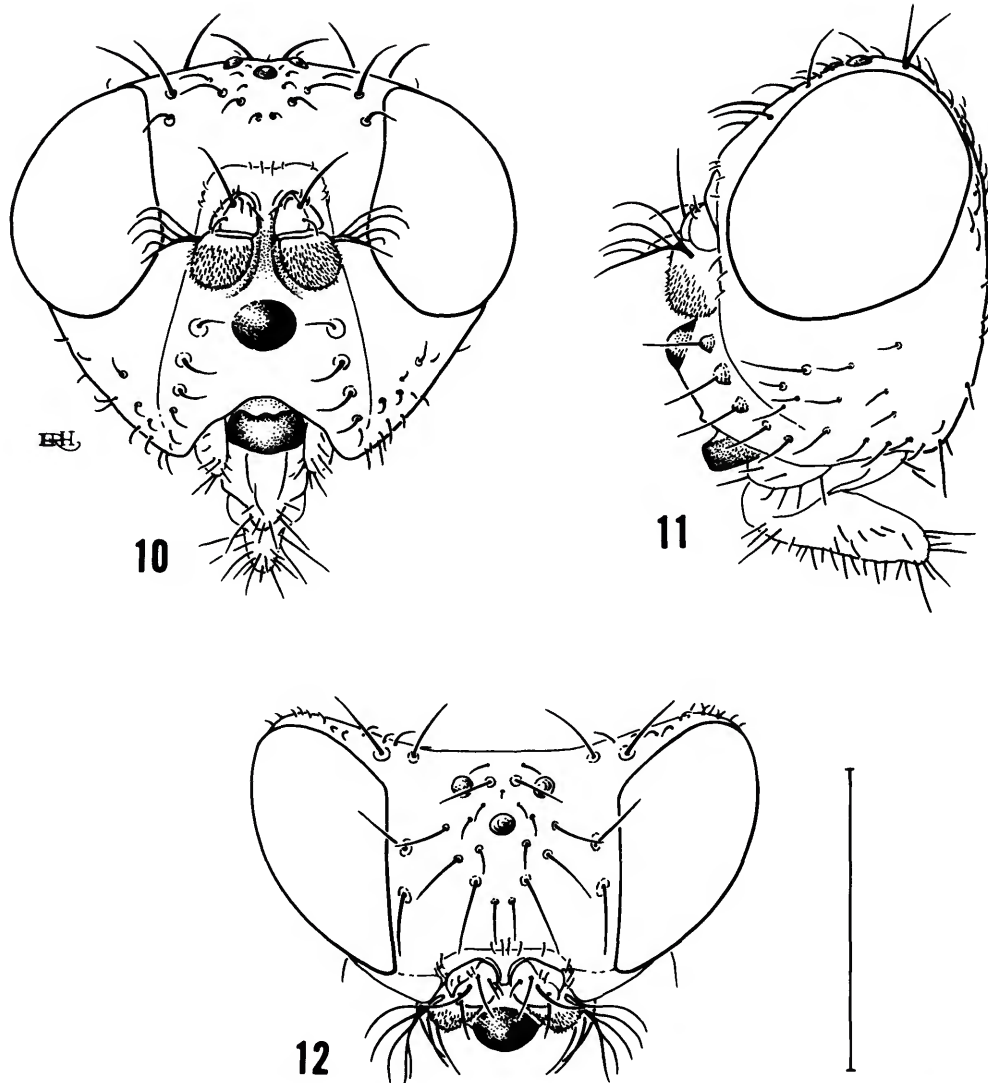
Notiphila globifera.—Zetterstedt, 1855:4760 [review]; 1860:6314–6315 [review].

Hecamede grisescens Becker, 1903:166; 1905:189 [paleartic catalog].—Cogan, 1984:131 [paleartic catalog]. [New synonym.]

DESCRIPTION.—Small to moderately small shore flies, length 1.60 to 2.70 mm.

Head (Figures 10–12): Fronto-orbits and ocellar triangle densely microtomentose, mostly tan but quite variable (gray to blackish gray); mesofrons, except for ocellar triangle, sparsely microtomentose, only anterior $\frac{1}{3}$ of mesofrons yellowish orange to slightly reddish orange; 1 proclinate fronto-orbital seta, inserted anterolaterad of reclinate seta. Antenna mostly yellowish orange to orange; flagellomere 1 usually with some brown coloration toward base, near insertion of arista; arista bearing 4 dorsal branches, rarely 3. Face whitish to silvery gray, bearing 3 large lateral setae and 1 or 2 smaller ones ventrad, each arising from subshiny, bare, shallow tubercle; facial prominence bare at apex, bare area usually large, subequal to width of pedicel. Gena bearing 1 large and several smaller black setae; gena high, eye-to-cheek ratio averaging 0.55. Clypeus black with light to dense investment of gray microtomentum.

Thorax: Scutum and disc of scutellum mostly grayish tan, frequently with some faint golden luster; lateral margins of scutum, beginning slightly above level of notopleuron or as far ventrad as dorsal portion of anepisternum, becoming grayer; prescutellar acrostichal setae and presutural seta usually well developed; microtomentum of pleural sclerites with faint shiny luster, anepisternum bearing several setulae on dorsal $\frac{1}{2}$ towards posterodorsal angle. Legs, except for tibiae and tarsi, mostly gray; fore femur mostly black anteriorly, mostly gray posteriorly; middle and hind femora mostly gray anteriorly, posterior surface blackish; fore femur lacking distinct row of



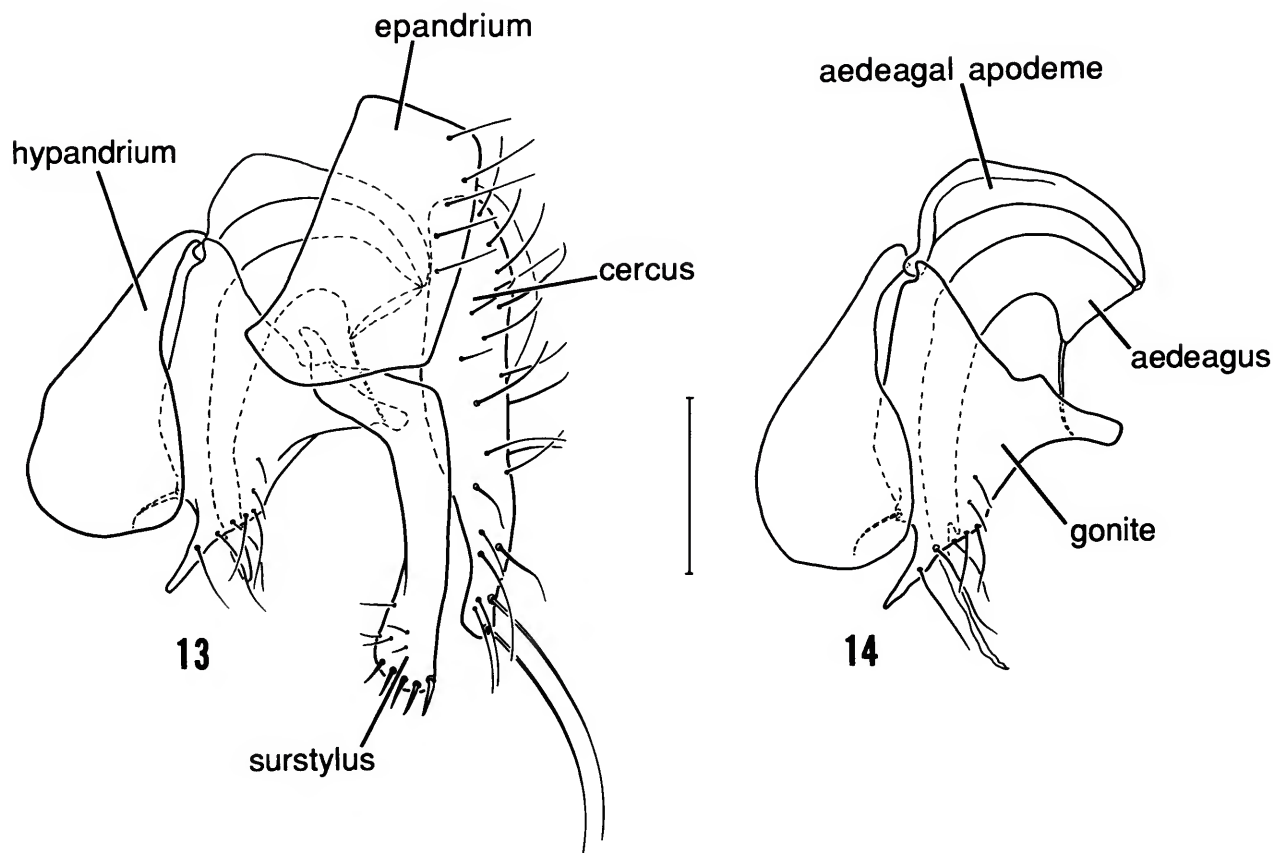
FIGURES 10-12.—*Hecamede (Hecamede) albicans*: 10, head, anterior aspect; 11, head, lateral aspect; 12, head, dorsal aspect. (Bar = 0.5 mm.)

setae along anteroventral surface; tibiae yellow, usually with thin investment of mostly white microtomentum; fore basitarsus with 2 or 3 black setae inserted toward base at posteroventral surface; tarsomeres mostly yellow except for apical 1-2, which are dark brown. Wing with costal vein ratio averaging 0.35; M vein ratio averaging 0.60; last section of vein M shallowly arched posteriorly.

Abdomen: Male terminalia (Figures 13, 14) as follows: 5th tergum with anterior $\frac{3}{4}$ to $\frac{7}{8}$ more lightly sclerotized and bearing numerous, evenly scattered spicules, from dorsal view with anterior margin broadly bifid, posterior $\frac{1}{4}$ to $\frac{1}{8}$ a sclerotized band bearing 8 to 11 setae along posterolateral margin; epandrium (Figure 13) a dorsal band, gradually enlarged posteriorly; surstylus (Figure 13) in lateral view L-shaped, longer arm extended ventrally, long and narrow,

parallel sided, posterior and anterior margins slightly curved, apex bluntly rounded, bearing 4 or 5 setulae; cercus (Figure 13) long and narrow, length almost twice that of epandrium, bearing conspicuously longer setae at posteroventral margin; gonite (Figure 14) roughly triangular in shape, with a narrow connection above aedeagus, ventral angle as a narrow, short, parallel-sided, blunt process; aedeagal apodeme (Figure 14) L-shaped, with arms curved, better developed toward angle; aedeagus (Figure 14) long and narrow, tapered gradually to apex, shaped like a pipe, with right angle curve at basal $\frac{1}{4}$ to $\frac{1}{3}$; hypandrium slightly emarginate anteriorly.

TYPE MATERIAL.—The lectotype male of *Notiphila albicans* (designated by Cresson, 1925:229) is labeled "TYPE [red]/Marseille [France; handwritten]/albicans [handwritten] Coll. Winth. [black border along both longer sides of label]." The



FIGURES 13, 14.—*Hecamede (Hecamede) albicans*: 13, male terminalia, lateral aspect; 14, internal structures of the male genitalia, lateral aspect. (Bar = 0.1 mm.)

specimen is double mounted (pin in a rectangular block of cork), is in good condition, and is deposited in the NMW. There are also five paralectotypes in the NMW.

The lectotype male of *Psilopa globifera*, designated herein, is labeled “[Sweden] Sc. [Skåne, handwritten]/Bhn [Bohemian, handwritten]/Notiph[ila]. globifera Boh.Scan. a Bohem. 52. [handwritten]/LECTOTYPE *Psilopa globifera* ♂ Boheman By W.N.Mathis [handwritten except for “LECTOTYPE” and “By”, a black submarginal border].” The lectotype is directly pinned, is in fair condition (considerable verdigris present), and is deposited in ZIL (Göteborg collection). There are also four paralectotypes (2♂, 2♀; ZIL) that bear the same first two labels as the lectotype.

The holotype male of *Hecamede grisescens* Becker is labeled “Alexandrien 44158 XI [handwritten]/*Hecamede* n.sp. [handwritten]/Holotypus [red]/Zool. Mus. Berlin.” The holotype is double mounted (minuten in a rectangular block of pith?), is in fair condition (the left wing is missing, the right wing is twisted), and is deposited in the ZMHU.

OTHER SPECIMENS EXAMINED.—OLD WORLD. Palearctic: **BULGARIA**. Achtopol (seashore, 42°09'N, 27°52'E), 7–10 May–Aug 1941, 1958, 1987, M. Barták, H. Caspers, B.

Pisarski (6♂, 8♀; BMNH, MBP, USNM); Aladza bei Varna, 16 Jul 1930, H. Zerny (12♂; NMW); Irakli (damp meadow, 42°47'N, 27°54'E), 16 Jul 1987, M. Barták (24♂, 10♀; MBP). Primorsko ad Burgas, 7 Jun 1959, R. Bielwawski (1♂; USNM).

CROATIA. Dalmatia, G. Strobl (1♂; UZMC); Korcula, Lombarda, 19 Apr 1930, H. Zerny (1♀; NMW); Split (on shore), 2 Sep 1986, F. Kaplan (3♂; USNM).

DENMARK. Hellebaek, (1♀; UZMC). Hornbaek, 31 May 1887 (2♂, 2♀; UZMC). Roenne, Jul 1883, H.J. Hansen, W. Lundbeck (4♂, 19♀; UZMC, WSU).

EGYPT. Fayoum, Lake Karun, 2–23 Nov 1945, R.L. Coe (25♂, 6♀; BMNH).

FRANCE. Marseille, Winth (1♀; ANSP).

GREAT BRITAIN. Cornwall: Lelant Towans, 27 May 1935 (4♂, 3♀; BMNH); Mayle, 22 Jul 1934, L. Parmenter (1♂, 1♀; BMNH); Padstow, 16 Mar–3 ct 1905, C.G. Lamb (2♂, 3♀; BMNH, USNM). Devon: Dartmoor, Wistman's Wood, 5 Oct 1959, A.C. Pont (1♂; BMNH). Dorset: Studland, 13 May–26 Oct 1912, 1961, Verbury (3♂, 2♀; BMNH). Kent: Deal, 3–18 Jul 1905, 1948, J.J.F.X. King (4♂, 1♀; BMNH); Sandwich Bay, 23 Jul 1957, E.A. Fonseca (9♂, 6♀; ZIL).

GREECE. Crete: Chania, 11 Jul 1981, A. Freidberg (5♂, 1♀; USNM); Längs vägen Malia-Hersonissos, 19 May 1979, R. Danielsson (1♂, 3♀; ZIL); Paleochora, 9 Jul 1981, A. Freidberg (4♂, 11♀; USNM).

ISRAEL. Akhziv, 19 Aug 1982, A. Aadka (1♂; TAU); Akko, 16 May 1980, W.N. Mathis (3♂, 2♀; USNM); Haifa, 18 May–25 Nov 1971, 1980, J. Kugler, W.N. Mathis (6♂, 2♀; TAU, USNM); Herzliyya, 26 May–19 Nov 1980, 1981, A. Freidberg (1♂, 2♀; TAU); Kefar Rosh HaNiqra, 2 Jun 1981, A. Freidberg, W.N. Mathis (2♂, 4♀; TAU, USNM); Ma'agan Michael (beach), 17 May–22 Aug 1980, 1984, F. Kaplan, W.N. Mathis (24♂, 39♀; TAU, USNM); Michmoret, 3 Aug 1983, A. Freidberg (1♂; TAU); Nahariyya (beach), 8 Aug 1986, W.N. Mathis (11♂, 1♀; USNM); Taba, 27 Apr 1974, A. Freidberg (1♂, 1♀; TAU); Tel Aviv (dunes), 8 Apr 1981, A. Freidberg (1♀; TAU); Zaharani spill, 19 Jun 1982, I. Yarom (1♂; TAU); Ziqim, 29 Feb 1984, A. Freidberg (1♂, 1♀; TAU).

ITALY. Friuli-Venezia Giulia: Trieste, 24 Jul 1886, A. Handlirsch (2♂, 2♀; ANSP). Marches: Porto Civitanova, 10 Aug 1897, M. Bezzi (2♂, 2♀; USNM); San Benedetto (10 km N, damp valley, 42°58'N, 13°53'E), 3 Aug 1988, M. Barták (1♀; MBP). Sicily: Capo San Vito, 29 Aug 1982, A. Freidberg (3♂, 4♀; USNM); Schioedte (2♂; UZMC). Veneto: Venezia (seashore, 45°27'N, 12°18'E), 7 Aug 1988, M. Barták (2♂, 1♀; MBP).

LIBYA. Tripoli, Wheelers Field, 26 Apr 1951, R.W. Brown (1♂, 2♀; USNM).

PORTUGAL. Estrema Dura, So Martinho do Porto, 16 Sep 1964, O.W. Richards (1♀; BMNH); Lisbon (on dead fish), 21 Jul 1962, L. Horacsek (1♂; BMNH); Porto, 5 Aug 1962, J. Abraham, L. Horacsek (2♂, 1♀; BMNH); Porto, Leca da Palmeira (low vegetation near seashore), 7 Aug 1962, J.A. and L.H. (19♂, 8♀; BMNH); Porto, Boa Nova, Jun 1960, N.L.H. Krauss (1♀; USNM). Azores: So Miguel, So Populo, Ponta Delgada (7.5 km E), 12 Mar 1957, P. Brinck, R. Dahl (2♂, 2♀; ZIL).

ROMANIA. Lake Sinoe (edge, low salinity maritime flats near Histria), 18–20 Jun 1969, B.H. and M.C. Cogan, R. Vane-Wright (3♂, 3♀; BMNH); Olimp (near Constanta) 20 Aug 1975, A.N. Clements (5♂; BMNH).

SPAIN. Provence. Fréjus (Var), 9 Jun 1924, H. Zerny (♂, ♀; NMW). Andalusia, Algeciras, 12–20 May 1925, H. Zerny (3♂, 3♀; NMW). Almeria, Albufera, 23 Mar 1966, L. Lyneborg (2♀, 2 [sex ?]; UZMC). Granada, Torrehuerva (E Motril), 14 Apr 1966, L. Lyneborg (1♂; UZMC). CANARY ISLANDS. Lanzarote, El Golfo, 4 Sep 1976, M. Baez (1♀; USNM).

SWEDEN. Halland: Laxvik, Jul 1985, P. Ardö (2♂; ZIL); Laxvik, Trönninge, Jun–Jul 1954, 1955, P. Ardö, R. Dahl (6♂, 7♀; ZIL); Eldsberga, Tönnersa, 1 Jul 1954, R. Dahl (1♂; ZIL). Skåne: Ängelholm, 5 Sep 1915 (1♂; ZIL); Bjärred (strand), 4 Oct 1973, H. Andersson (2♂; ZIL); Hallands Väderö, 18 Jul 1924 (1♂; ZIL); Kullaberg, 24 Aug 1983, H. Andersson (1♀; ZIL); Lerberget (strand), 13 Aug 1969, H. Andersson (4♂, 1♀; ZIL); Lomma, 11 Aug 1974, H. An-

dersson (8♂, 2♀; ZIL); Mölle, 24 Jun–8 Aug 1926, 1969, H. Andersson (12♂, 9♀; ZIL); Strandbaden, Tallbacken, 4 Aug 1975, H. Andersson (1♂; ZIL); Torekov, Jul 1860, C.D.E. Roth (5♀; ZIL).

TURKEY. Istanbul, 30 Aug 1965, B.H. Cogan (1♀; BMNH); Silivri, 3 Nov 1965, B.H. Cogan (2♂, 2♀; BMNH).

NEW WORLD. Nearctic: *BERMUDA*. Devonshire Parish: Devonshire Bay (32°18'N, 64°44'W), 29 May 1991, W.N. Mathis (16♂, 4♀; USNM). Hamilton Parish: Shelly Bay Beach (32°19'N, 64°44'W), 31 May 1991, W.N. Mathis (2♂, 5♀; USNM). Paget Parish: Hungry Bay (beach, 32°17'N, 64°45'W), 2 Jun 1991, W.N. Mathis (3♂, 2♀; USNM). Pembroke Parish: Spanish Point (beach, 32°18'N, 64°49'W), 2 Jun 1991, W.N. Mathis (1♂, 1♀; USNM). Warwick Parish: Long Bay Beach (32°15'N, 64°48'W), 30 May 1991, W.N. Mathis (2♂, 1♀; USNM); Warwick Long Bay, 18 Nov 1987, D.J. Hilburn, N.E. Woodley (4♂, 3♀; USNM).

UNITED STATES. Connecticut: Fairfield Co., Westport, 14 Aug 1939, A.L. Melander (1♂, 5♀; USNM). New Haven Co., Anchor Beach, Milford-West Haven, 5–15 Aug 1978, B.A. Steinley (about 1000♂ and ♀; USNM); Branford, 30 Jun 1952, A.H. Sturtevant (1♂, 2♀; USNM). Delaware: Sussex Co., Rehoboth, 25 Jun–4 Aug 1939, 1941, A.L. Melander (4♂, 4♀; ANSP, USNM). Maine: Cumberland Co., Chebeague Island, 3 Sep 1952, A.H. Sturtevant (5♂; USNM). Maryland: Calvert Co., Lusby, G.C. Steyskal (1♀; USNM); Port Republic, 26 Apr 1971, R.J. Gagné (2♂, 5♀; USNM). Massachusetts: Barnstable Co., Falmouth, 11 Aug 1979, A. Freidberg (2♂; USNM); Cape Cod (end), 6 Jun–3 Aug 1939, 1970, A.L. Melander, H. Weems (5♂, 16♀; USNM); Woods Hole, 28 Jun–24 Aug 1950, 1952, A.H. Sturtevant (4♂, 4♀; USNM). Dukes Co. Pasque Island, 15 Aug 1952, A.H. Sturtevant (1♂, 3♀; USNM); Vineyard Haven, 17 Aug 1954, A.H. Sturtevant (2♂; USNM). North Beach (reared from seaweed), 3 Sep 1955, M. Williams (1♂, 2♀; USNM). New Hampshire: Rockingham Co., Rye Beach, 31 Jul 1950, A.H. Sturtevant (1♂, 2♀; USNM). New Jersey: Cape May Co., Town Bank (ex. flowering *Prunus serotina*), 31 May 1983, A.L. Norrbom (1♂, 2♀; USNM). New York: Queens Co., New York City, Douglaston, 2 Sep 1954, A.H. Sturtevant (1♂, 1♀; USNM). Suffolk Co., East Quogue, 10 Aug 1957, L. Wilcox (1♀; USNM); Montauk, 23 Jul 1932, A.L. Melander (5♂, 4♀; ANSP, USNM); Orient, 30 Apr 1953, R. Latham (1♂; USNM); Riverhead, Baiting Hollow (north shore), 9 Sep 1961, P.H. Arnaud, Jr. (10♂, 12♀; AMNH). Rhode Island: Newport Co., Tiverton, 13 Aug 1952, A.H. Sturtevant (2♀; USNM). Virginia: Accomack Co., Assateague Island, 19 Aug 1969, G.C. Steyskal (1♀; USNM). Westmoreland Co., Westmoreland State Park, 9 Jun 1988, D. and W.N. Mathis (3♂, 3♀; USNM). Norfolk, 14 Aug 1969, G.C. Steyskal (7♂, 4♀; USNM).

DISTRIBUTION (Figure 15).—Holarctic along coasts of the northern Atlantic Ocean, including the Mediterranean Sea. Palearctic: Azores, Bulgaria, Canary Islands, Croatia, Den-

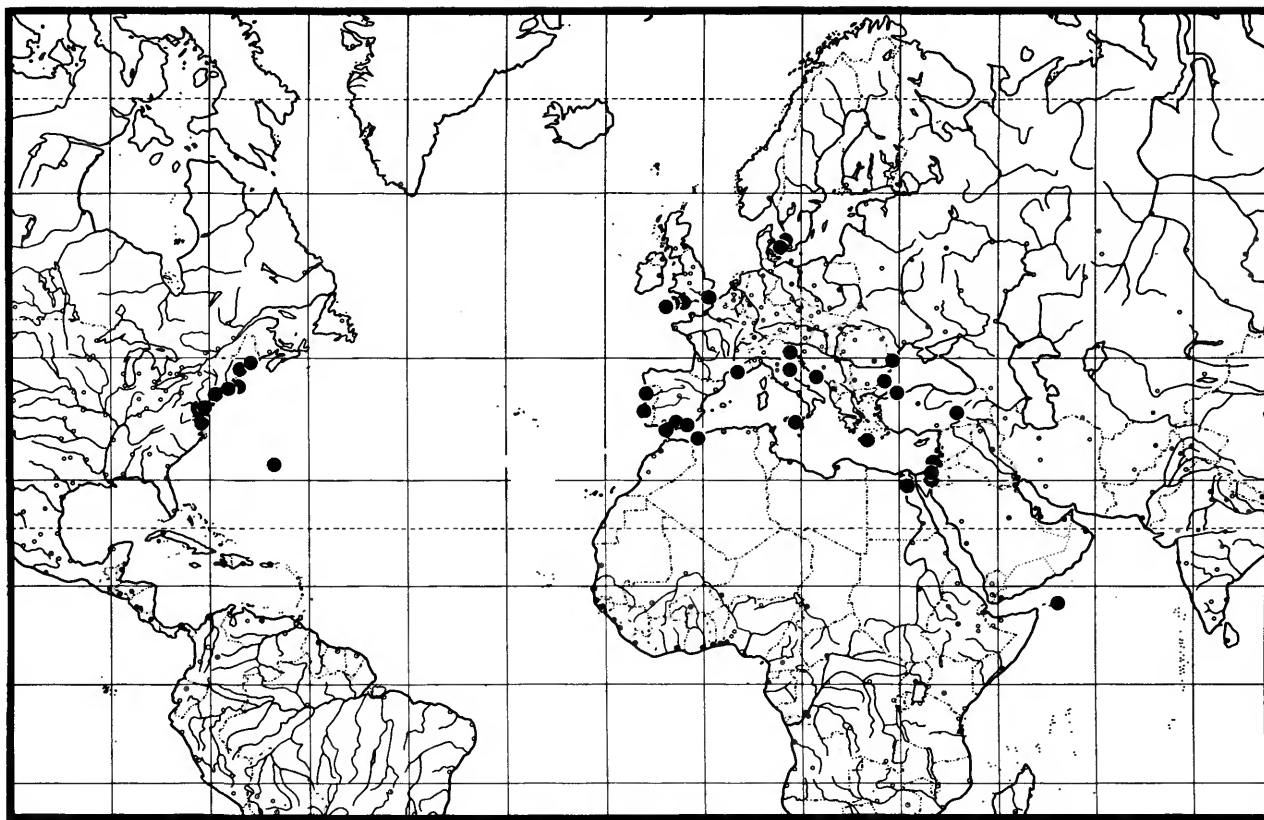


FIGURE 15.—Distribution map for *Hecamede (Hecamede) albicans*.

mark, Egypt, France (type locality of senior synonym), Great Britain, Greece, Ireland, Israel, Italy, Libya, Portugal, Romania, Spain, Sweden, Turkey, (also reported from Cape Verde Island, Madeira). Nearctic: Bermuda, United States (CT, DE, MA, ME, MD, NH, NJ, NY, RI, VA).

NATURAL HISTORY.—In Ireland, Haliday (1839:224) first noted that this species occurs “On sandy coasts, especially on fresh marine rejectamenta; runs fast and does not fly readily.” Ardö (1957:184) found this species wholly in the “marine shore dune ecosystem” where it was baited to and trapped on decaying herring. Ardö reported two generations at higher latitudes, such as in Sweden, but on beaches of the eastern Mediterranean (Israel), adults are fairly common throughout the year (February to November), suggesting several generations per year. Dahl (1959:160), from studies also done in Sweden, suggested that this species prefers halophilous habitats but also has xerophilous tendencies and a preference for habitats that have soil substrates with microflora.

In addition to summarizing past work on the natural history of this species, Norrbom (1983:118) succeeded in rearing over 200 adults from larvae that were feeding on dead horseshoe crabs that had washed ashore in Delaware Bay near Town

Bank, New Jersey (USA). He observed larvae mostly between the gills and on other moist membranous surfaces but found that pupariation occurred in the sand and on the sides of the rearing jar as well as within the crab. Norrbom also described and illustrated the third-instar larva and the puparium and noted that one puparium was parasitized by the pteromalid, *Urolepsis rufipes* (Ashmead).

Steinly (1992) recently confirmed Norrbom’s work and added many details about the life cycle, especially how quality and quantity of nutrient resources affect size, from both field and in vitro rearings. His field work was conducted in Connecticut, where the species is multivoltine and can complete a life cycle in less than two weeks.

DIAGNOSIS.—This species is distinguished from similar congeners by the following combination of characters: proclinate fronto-orbital setae 1; gena with several black setae; fore femur lacking a distinct row of setae along anteroventral surface; tibiae mostly yellow, investment of mostly white microtomentum thin; fore basitarsus with 2 or 3 black setae inserted toward base of posteroventral surface; and structures of the male terminalia (see description and Figures 13, 14), especially the shape of the surstylus and gonite.

Hecamede (Hecamede) australis, new species

FIGURES 16-18

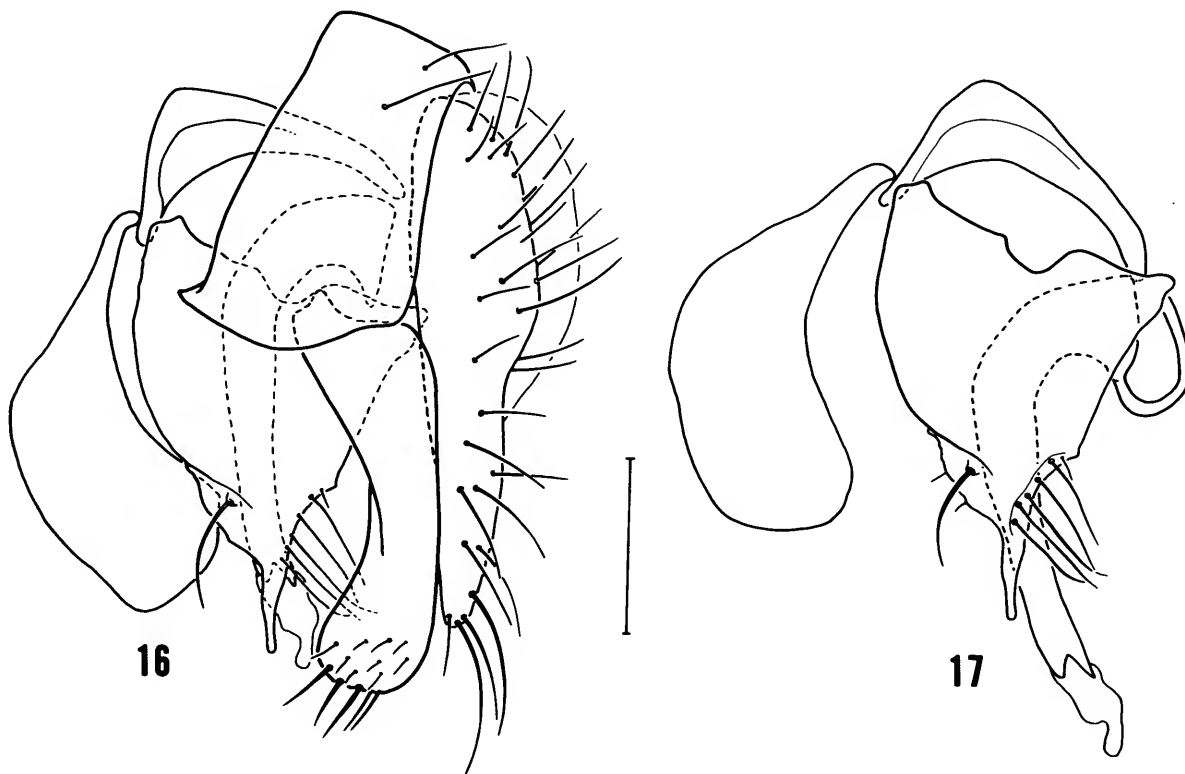
DESCRIPTION.—Small to medium-sized shore flies, length 1.85 to 3.00 mm.

Head: Fronto-orbits and ocellar triangle golden gray to mostly whitish gray, densely microtomentose; proclinate fronto-orbital seta 1, inserted anteriorad and laterad of reclinate seta; mesofrons distinctly less densely microtomentose than ocellar triangle or fronto-orbits, posterior angles dark colored, brownish, becoming orangish to yellowish orange anteriorly. Antenna yellowish orange, pedicel with sparse microtomentum, flagellomere 1 with slightly dark coloration dorsobasally, near insertion of arista; arista with 5 dorsal branches. Face mostly whitish gray, densely microtomentose; conical facial prominence with apex large and bare; face 3 large lateral setae and 1 or 2 smaller ones ventrad, larger setae arising from bare, slightly raised tubercles; parafacial a gradual transition color between fronto-orbit and whitish gray gena; gena usually with 1 larger seta and several smaller black setae; eye-to-cheek ratio averaging 0.55. Clypeus black with dense investment of gray microtomentum.

Thorax: Mesonotum tan to gray, usually darker than pleural areas, if tan, lateral margins becoming grayer, espe-

cially ventrad through notopleuron and dorsal half of anepisternum; presutural seta and prescutellar acrostichal setae well developed; pleural sclerites mostly gray to whitish gray, dorsal portion of anepisternum sometimes faintly tan to golden gray; anepisternum bearing several setulae on dorsal $\frac{1}{2}$ towards posterodorsal angle. Coxae and trochanters blackish gray to gray; middle and hind femora gray anteriorly, posterior surface blackish; fore femur lacking a distinct row of setae along anteroventral surface, anterior surface mostly blackish, mostly gray posteriorly; tibiae, especially fore tibia, mostly yellow but moderately densely invested with whitish gray microtomentum, appearing white to grayish white, only femoral/tibial articulation mostly yellow; fore basitarsus with 2 or 3 black setae, these inserted toward base of posteroventral surface; apical 2 tarsomeres blackish brown. Wing with costal vein ratio averaging 0.40; M vein ratio averaging 0.66; last section of vein M shallowly arched posteriorly.

Abdomen: Male terminalia (Figures 16, 17) as follows: 5th tergum with anterior $\frac{3}{4}$ to $\frac{7}{8}$ more lightly sclerotized and bearing numerous, evenly scattered spicules, from dorsal view with anterior margin broadly bifid, posterior $\frac{1}{4}$ to $\frac{1}{8}$ a sclerotized band bearing 8 to 11 setae along posterolateral margin, with 2 globular apodemes anterobasally; epandrium (Figure 16) a dorsal band, gradually enlarged posteriorly;



FIGURES 16, 17.—*Hecamede (Hecamede) australis*: 16, male terminalia, lateral aspect; 17, internal structures of the male genitalia, lateral aspect. (Bar = 0.1 mm.)

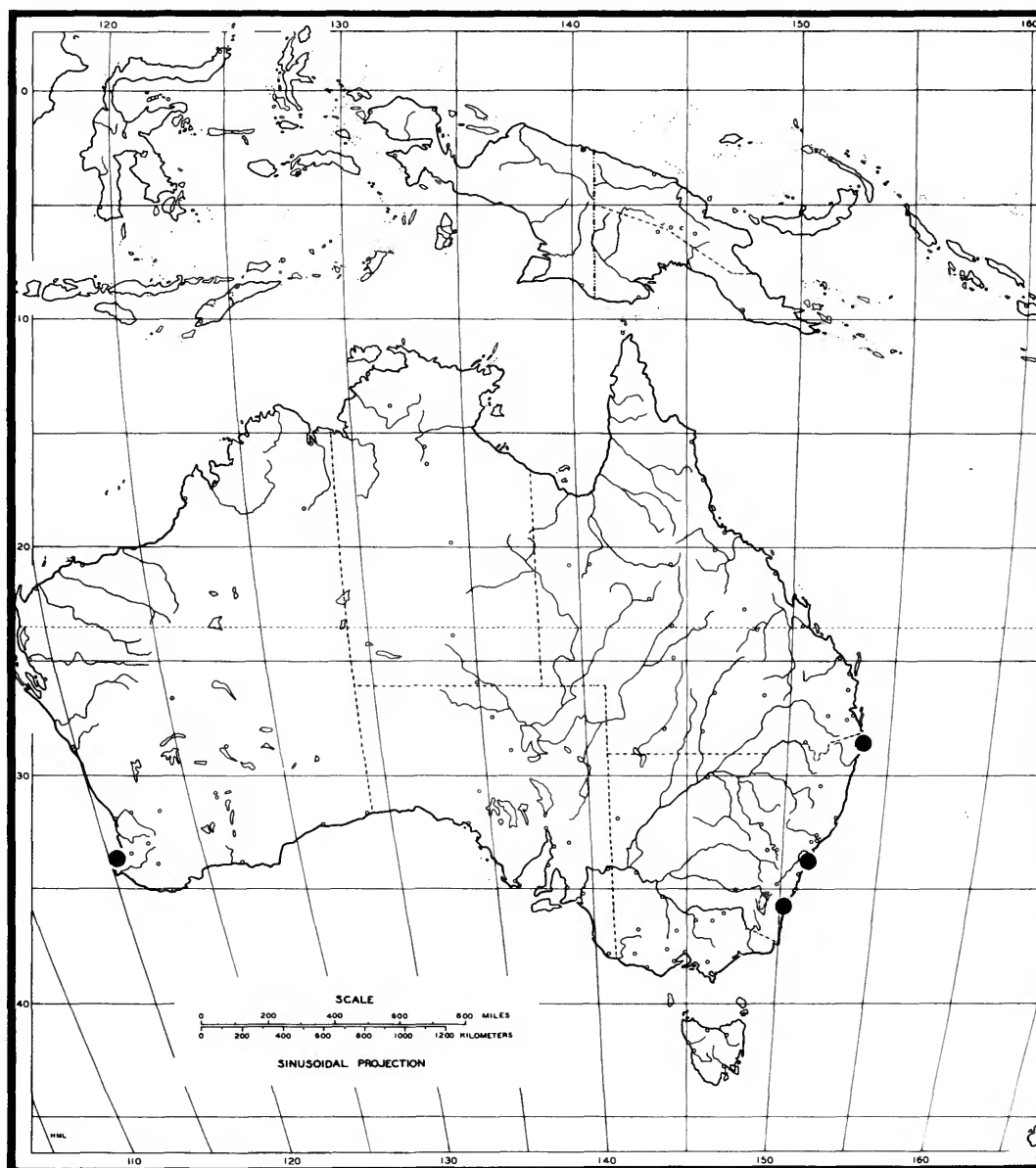


FIGURE 18.—Distribution map for *Hecamede (Hecamede) australis*.

surstylus (Figure 16) in lateral view long and relatively broad, slightly narrowed toward middle, ventral margin bluntly rounded and bearing 5 or 6 acutely pointed setae and several setulae; cercus (Figure 16) long and narrow, extended nearly to apex of surstylus, bearing a conspicuously longer seta at posteroventral margin; gonite (Figure 17) roughly triangular in shape, with a narrow connection above aedeagus, ventral angle a narrowed, short, parallel-sided, blunt process; aedeagal apodeme (Figure 17) L-shaped in lateral view, slightly broader toward attachment with hypandrium; aedeagus (Figure 17) long and narrow, tapered gradually to apex, shaped like a pipe,

with a right angle curve at basal $\frac{1}{4}$ to $\frac{1}{3}$; hypandrium slightly emarginate anteriorly.

TYPE MATERIAL.—The holotype male is labeled "Deewhy, New South Wales[,] 24 Feb. 1957 beachdunes/W.W. Wirth collector/HOLOTYPE *Hecamede australis* ♂ W.N.Mathis [species name and gender symbol handwritten, red]." The holotype is double mounted (minuten in a polyporus block), is in excellent condition, and is deposited in the ANIC. The allotype female and 12 paratypes (8♂, 4♀; USNM) bear the same locality label as the holotype (dates vary from 15 Jan to 24 Feb 1957). Other paratypes are as follows: AUSTRALIA.

New South Wales: Cape Byron, Jan 1961, K.R. Norris (2♂; ANIC); Durras, 15 Sep 1955, S.J. Paramonov (4♂; ANIC, USNM). Queensland: Broadbeach (puparia collected 25 May 1966, adult emerged 11 Jun 1966, Z. Liepa (4♂, 2♀, 2 puparia; ANIC). Western Australia: Dunsborough, Eagle Bay, 18 Nov 1959, M.M.H. Wallace (2♀; ANIC).

DISTRIBUTION (Figure 18).—Australasian/Oceanian: Australia. (NSW, QLD, WA).

ETYMOLOGY.—The species epithet, *australis*, alludes to the continent where this species was collected.

DIAGNOSIS.—This species is distinguished from similar congeners by the following combination of characters: proclinate fronto-orbital setae 1; gena with several black setae; fore femur lacking a distinct row of setae along anteroventral surface; tibiae, especially the fore tibia, mostly grayish, only apex of fore tibia mostly yellow; fore basitarsus with 2 or 3 black setae inserted toward base of posteroventral surface; and structure of the male terminalia (see description and Figures 16, 17), especially the shape of the surstylus and gonite.

Hecamede (Hecamede) granifera (Thomson)

FIGURES 19–33

Notiphila granifera Thomson, 1869:594.—Becker, 1896:271 [list].—Jones, 1906:176 [list].—Cresson, 1945:56 [footnote, as *grandifera* (sic)]; 1948:18 [suggested to be in the genus *Hecamede*].

Hecamede granifera.—Cogan and Wirth, 1977:325 [synonymy with *H. persimilis*, generic combination].—Mathis, 1989a:641 [Australasian/Oceanian catalog].

Hecamede lacteipennis Lamb, 1912:318.—Bezzi and Lamb, 1926:561.—Cresson, 1946b:248 [review].—Canzoneri and Meneghini, 1969:1483 [list, Senegal].—Cogan, 1980:657 [Afrotropical catalog]. [New synonym.]

Hecamede persimilis Hendel, 1913:99.—Cresson, 1925:229 [discussion]; 1945:56 [list, Indoaustralian]; 1948:23 [note on synonymy].—Bohart and Gressitt, 1951:84–85 [review, natural history].—Adachi, 1952:353 [synonymy].—Hardy, 1952:468 [synonymy].—Cogan and Wirth, 1977:325 [Oriental catalog].—Tenorio, 1980:275–276 [review, list, Hawaii, notes on natural history], 318–319 [figures of larva and puparium], 339 [description of larva and puparium].

Hecamede nivea de Meijere, 1916:61.—Cresson, 1948:23 [synonymy with *H. persimilis*].

Hecamede femoralis Malloch, 1930:245.—Wirth, 1947:21 [list, Hawaii].—Cresson, 1948:23 [synonymy with *H. persimilis*].—Miller, 1950:111 [New Zealand catalog].—Adachi, 1952:353 [synonymy].—Harrison, 1959:219–220 [description, list, New Zealand].

Hecamede albicans.—Of authors [misidentification].—Bryan, 1934:433 [list, Kahoolawe].—Miyagi, 1977:7–8 [probably *H. granifera*].

DESCRIPTION.—Small to medium-sized shore flies, length 1.60 to 3.20 mm.

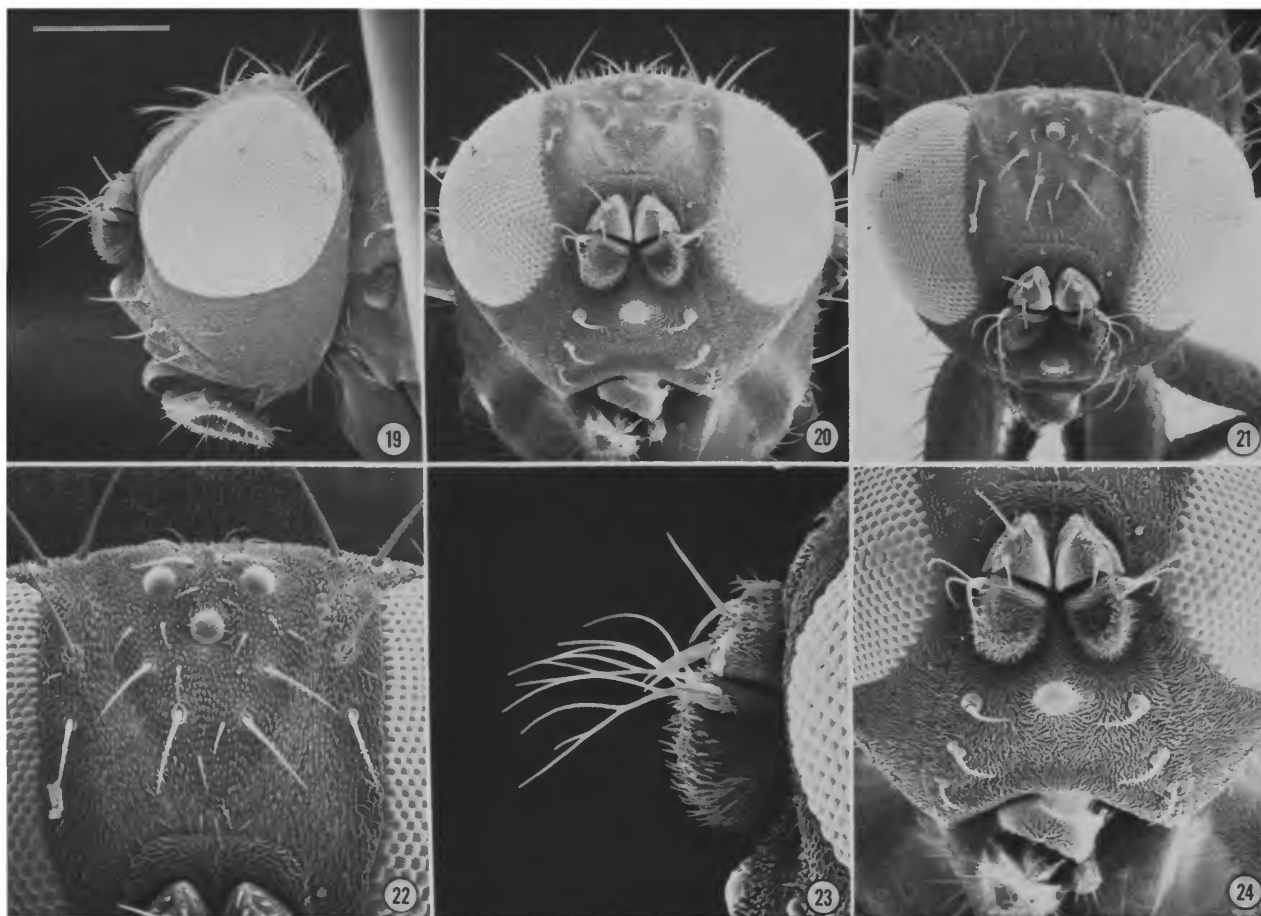
Head (Figures 19–24): Fronto-orbits and ocellar triangle densely microtomentose, silvery gray to tan with some golden coloration; mesofrons less densely microtomentose, coloration darker posteriorly with some mostly brown to black coloration, becoming yellowish orange to orange anteriorly; proclinate fronto-orbital setae 1, inserted anterolaterad of reclinate seta. Antenna mostly yellow; flagellomere 1 slightly darker, especially dorsobasally near insertion of arista; arista with 4 dorsal branches. Facial setae 3 or 4; facial prominence bare, not

much larger than shiny area at base of facial setae. Gena bearing 1 large and several smaller black setae, these scattered; gena high, eye-to-cheek ratio averaging 0.45. Clypeus black with an investment of gray microtomentum.

Thorax (Figures 25–28): Mesonotum golden tan to whitish gray, usually darker than pleural areas, if tan, lateral margins becoming grayer, whitish to silvery gray, especially ventral through notopleuron and dorsal half of anepisternum; presutural seta and prescutellar acrostichal setae well developed; posterior notopleural seta inserted distinctly above level of anterior seta; pleural sclerites mostly gray to whitish gray, dorsal portion of anepisternum sometimes faintly tan; anepisternal setulae mostly on dorsal $\frac{1}{3}$, occupying an area that is more or less triangular, with a line of setulae to ventral portion of pleuron where several more setulae are inserted. Coxae and trochanters lightly blackish gray to gray; middle and hind femora gray anteriorly, posterior surface blackish; fore femur bearing distinct row of setae along anteroventral margin, anterior surface mostly blackish, mostly gray posteriorly; tibiae, especially the fore tibia, mostly yellow but moderately densely invested with whitish gray microtomentum, appearing whitish gray, only femoral/tibial articulation mostly yellow; fore basitarsus with 2 or 3 black setae, these inserted toward base of posteroventral surface; apical 2 tarsomeres blackish brown. Wing with costal vein ratio averaging 0.38; M vein ratio averaging 0.55; last section of vein M shallowly arched posteriorly.

Abdomen: Male terminalia (Figures 29–32) as follows: 5th tergum with anterior $\frac{3}{4}$ to $\frac{7}{8}$ more lightly sclerotized and bearing numerous, evenly scattered spicules, from dorsal view with anterior margin broadly bifid, posterior $\frac{1}{4}$ to $\frac{1}{8}$ a sclerotized band bearing 8 to 11 setae along posterolateral margin, with 2 globular apodemes anterobasally; epandrium (Figure 29) a dorsal band, gradually enlarged posteriorly; surstylus (Figures 29–31) in lateral view long and narrow, posterior margin more or less straight, anterior margin sinuous, anteroapical margin curved, apex bearing approximately 6–7 moderately long, broad setulae; cercus (Figure 29) long and narrow, length extended nearly to apex of surstylus, bearing a conspicuously longer seta at posteroventral margin; gonite (Figure 32) roughly triangular in shape, with a narrow connection above aedeagus, ventral angle a narrowed, short, parallel-sided, blunt process; aedeagal apodeme (Figure 32) allantoid in lateral view, slightly broader toward attachment with hypandrium; aedeagus (Figure 32) long and narrow, tapered gradually to apex, shaped like a pipe, with right angle curve at basal $\frac{1}{4}$ to $\frac{1}{3}$; hypandrium slightly emarginate anteriorly.

TYPE MATERIAL. The holotype female of *Notiphila granifera* is labeled “Ins. Ross. [Insulae Rossii (Cocos or Keeling Islands), as noted by Cogan and Wirth (1977)]/Kinb./Iypus/472 73 [“73” handwritten, pink]/Hecamede granifera (Thom.) det. B.H.Cogan 1976. [handwritten except for “det. B.H. Cogan 19”]/HOLOTYPE ♀ *Notiphila granifera* Thomson det. B.H. Cogan 1976. [handwritten except for “det. B.H. Cogan 19”, red



FIGURES 19–24.—Scanning electron micrographs of *Hecamede (Hecamede) granifera* (scale length in parenthesis; bar scale for all photographs = Figure 19): 19, head, lateral aspect (231 μm); 20, head, anterior aspect (231 μm); 21, head, dorsal aspect (231 μm); 22, frons, dorsal aspect (120 μm); 23, antenna, lateral aspect (86 μm); 24, face, anterior aspect (150 μm).

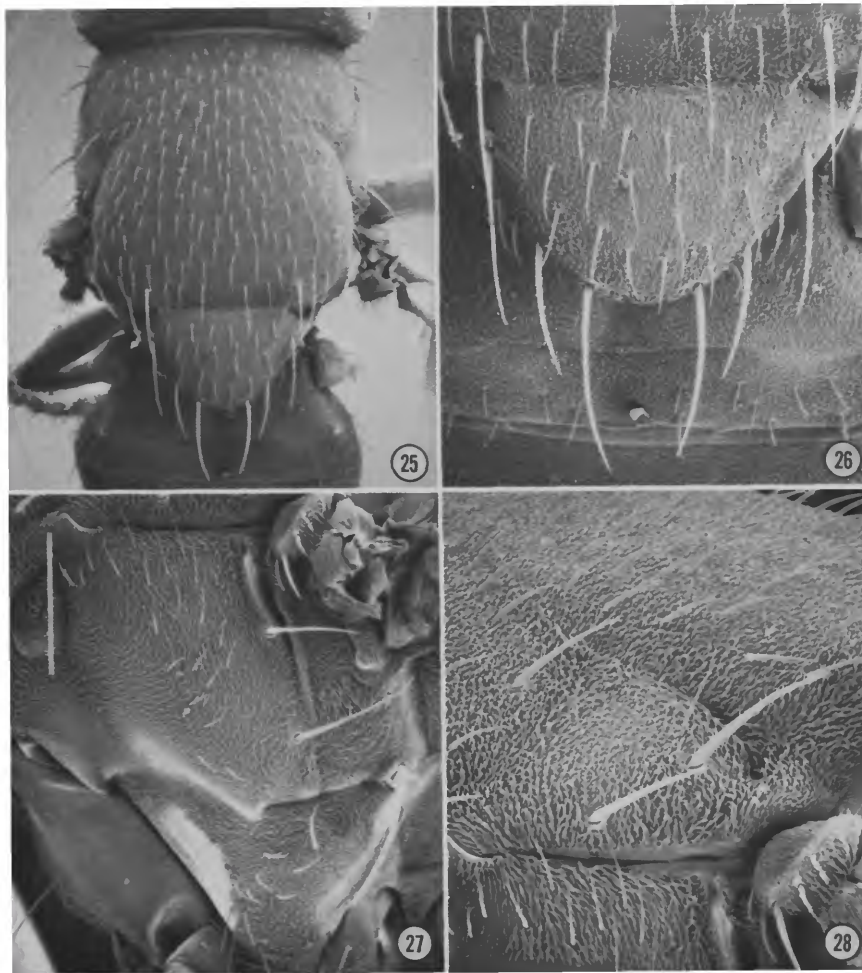
border]/Naturhistoriska Riksmuseet Stockholm Loan no 523/91 [light green.]” The holotype is pinned directly, is in poor condition (wings, right legs, most dorsal setae, and antennae except for scapes missing), and is deposited in the NRS.

The three syntype females of *H. lacteipennis* are labeled “Type [round label with a red border]/Mahe [Long Island (seaweed on beach), Jul 1908], ’08–9. Seychelles Exp [glued to a rectangular, larger label, the underside of which has “Seaweed” handwritten in pencil]/Seychelles Is. Prof. J.S. Gardiner. 1914-537/TYPE [blue label glued to the larger determination label] *S. Hecamede lacteipennis* n. sp. CGL [except for the “TYPE” label, handwritten]. The syntypes are double mounted on a single block of cork (pin mounted in a paper-covered, rectangular block of cork with the number “107” handwritten on top), are in good condition, and are in the BMNH. ASTOVE. 1907, H.P. Thomasset (4♀; BMNH). Lamb (1912:319) also reported syntypes of this species from Astove Island, 1907, H.P. Thomasset and from Coetivy, 24 Sep 1905.

The lectotype male of *H. nivea*, designated herein, is labeled

“Edw. Jacobson Pulu Bahi. Sim Sum.4, 1913 [black submargin]/*Hecamede nivea* det de Meijere. Type [black submargin, species name and “type” handwritten]/Lectotype [red]/Lectotype ♂ *Hecamede nivea* de Meij. det. B.H. Cogan 1971 [all but “det. B.H. Cogan 1971” handwritten].” The lectotype is double mounted (minuten in foam rectangular block), is in good condition (the abdomen has been removed and dissected; the parts are in an attached microvial), and is deposited in the ZMA. My study of this specimen reconfirms the synonymy of this species with *H. granifera*. Although this specimen bears Cogan’s lectotype label, it was never so designated in the literature. Data on the lectotype are as follows: 3.17 mm in length (before the abdomen was removed), the M vein ratio is 0.62, and the costal vein ratio is 0.35.

The lectotype male of *H. persimilis* Hendel, designated herein, is labeled “Tainan Formosa H. Sauter 11.09 [Nov 1909]/*Hecamede persimilis* H[endel]. det. Hendel [species name and “H.” handwritten]/Coll. Hendel/LECTOTYPE *Hecamede persimilis* Hendel ♂ By W.N. Mathis 1991 [“LECTO-



FIGURES 25–28.—Scanning electron micrographs of *Hecemede (Hecemede) granifera* (scale length in parenthesis; bar scale for all photographs = Figure 27): 25, thorax, dorsal aspect (30 mm); 26, scutellum, dorsal aspect (136 μm); 27, pleural area, lateral aspect (150 μm); 28, notopleuron, lateral aspect (100 μm).

TYPE” and “By” in red, name, designator, and year handwritten, black sub-border].“ Mounted with the lectotype is a paralectotype female. Other paralectotypes are as follows: the type locality (2♀); Anping (2♀). The lectotype is double mounted (minuten in a plastic foam block), is in poor condition (the left wing and most of the forelegs are missing, the abdomen is greasy), and is deposited in the NMW. I selected this specimen as the lectotype as it is the only male that remains from the original syntype series in NMW.

The holotype female of *H. femoralis* is labeled “Nelson N[ew].Z[ealand]. 20.II.24 [20 Feb 1924, not Nov as stated in the original description] A.Tonnoir Beach [date and “Beach” handwritten]/*Hecemede femoralis* Type Det. J.R. Malloch [species name and “Type” handwritten, black submargin].” The holotype is double mounted (minuten wired to main pin), is in good condition (head partially greasy), and is deposited in the NZAC. Although originally deposited in the Cawthorn Institute

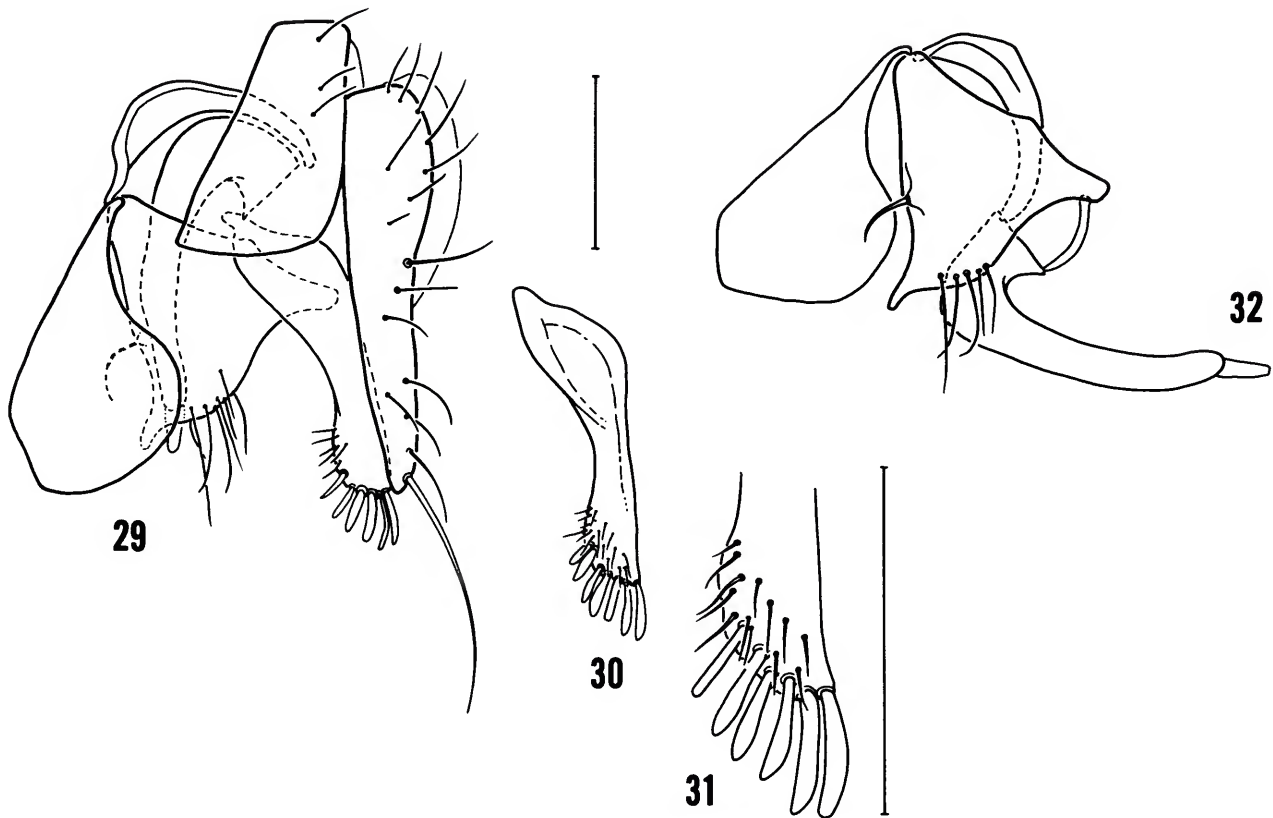
(Nelson, New Zealand), it is now at the NZAC.

OTHER SPECIMENS EXAMINED.—Afrotropical: **ALDABRA**. Grande Terre: Anse Mais, 17 Mar 1986, W.N. Mathis (6♂, 14♀; USNM); Anse Takamaka, 7 Apr 1986, W.N. Mathis (11♂, 11♀; USNM); Cinq Cases, 12–13 Mar 1986, W.N. Mathis (8♂, 21♀; USNM). Malabar: Passe Houareau, 14–18 Mar 1986, W.N. Mathis (27♂, 21♀; USNM). Picard: La Gigi, 19–24 Mar 1986, W.N. Mathis (28♂, 9♀; USNM); Settlement, 15–21 Mar 1986, W.N. Mathis (44♂, 15♀; USNM).

ASTOVE. Around coconut plantation, 5 Mar 1968, B.H. Cogan, A.M. Hutson (♂ undetermined number, 2♀; BMNH).

COSMOLEDO. Menai Island: Station, 26 Mar 1986, W.N. Mathis (18♂, 9♀; USNM).

KENYA. Gazi (60 km S Mombasa, Rt. A14), 5 May 1991, A. Freidberg, F. Kaplan (18♂, 14♀; USNM). Mombasa, Yadini Beach, 15 Jan 1983, A. Valdenberg (4♂, 1♀; TAU, USNM). Mombasa (45 km S), 5 May 1991, A. Freidberg, F. Kaplan (1♀;



FIGURES 29–32.—*Hecamede (Hecamede) granifera*: 29, male terminalia, lateral aspect; 30, apex of surstylus, lateral aspect (?); 31, same, enlarged; 32, internal structures of the male genitalia, lateral aspect. (Bar = 0.1 mm.)

USNM). Ngomeni (150 km N Mombasa), 4 Dec 1989, A. Freidberg, F. Kaplan (14♂, 8♀; USNM).

MADAGASCAR. Antseranana: Nosy Be, Ambatoloaka (beach), 4–7 Apr 1991, A. Freidberg, F. Kaplan (20♂, 14♀, TAU, USNM); Nosy Komba, 6 Apr 1991, A. Freidberg, F. Kaplan (6♂, 3♀; TAU, USNM); Nosy Tanikely, 6 Apr 1991, A. Freidberg, F. Kaplan (5♂, 4♀; TAU, USNM); Ramena, 10 Apr 1991, A. Freidberg, F. Kaplan (7♂, 3♀; TAU, USNM); Sambava (beach), 14 Apr 1991, A. Freidberg, F. Kaplan (5♂, 3♀; Tau, USNM). Toliara: Fort Dauphin (beach), 18 Apr 1991, A. Freidberg, F. Kaplan (11♂, 13♀; TAU, USNM); Fort Dauphin, Taolanaro (beach), 18–23 Apr 1991, A. Freidberg, F. Kaplan (1♂, 2♀; TAU, USNM); Fort Dauphin, Libanona (beach), 20 Apr 1991, A. Freidberg, F. Kaplan (4♂, 2♀; TAU, USNM); Morondava, 28–31 Mar 1990, W.E. Steiner, C. Kremen, V. Razafimahatratra (120♂, 9♀; TAU, USNM).

MOZAMBIQUE. Laureco Marques, Polana Beach, Jan 1956, B. Stuckenberg (3♂, 1♀; USNM).

SEYCHELLES. Mahé: Anse aux Pins, 2 Apr 1986, W.N. Mathis (1♂; USNM); Anse Takamaka, 7 Apr 1986, W.N. Mathis (10♂, 10♀; USNM); Beau Vallon Beach, 20 Feb–4 Apr 1965, 1986, W.N. Mathis, I.B. Nye, W.T. Tams (9♂, 20♀; BMNH, USNM); Bel Ombre, 5 Apr 1986, W.N. Mathis (8♂, 2♀; USNM); Port Launay, 8 Apr 1986, W.N. Mathis (1♂, 2♀;

USNM).

Australasian/Oceanian: AUSTRALIA. Queensland: Cairns, 19–25 Apr 1957, W.W. Wirth (3♂, 2♀; USNM); Cairns, Ellis Beach, 28 Apr 1957, W.W. Wirth (7♂, 2♀; USNM); Green Island (on decaying organism on beach), 17 Apr 1980, G.F. Hevel, J.A. Fortin (18♂, 6♀; USNM); Port Douglas (sand beach), 24 Apr 1957, W.W. Wirth (8♂, 12♀; USNM).

BONIN ISLANDS. Chichi Jima: Omura (camp beach), 2–25 Apr 1958, F.M. Snyder (3♂, 2♀; USNM); Takayama Bay, 22 Apr 1958, F.M. Snyder (1♂; USNM). Haha Jima: Okimura, 26 May–9 Jun 1958, F.M. Snyder (4♂; USNM).

COOK ISLANDS. Aitutaki Island, 27 Oct 1945, D.G. Hall (1♀; USNM).

FEDERATED STATES OF MICRONESIA. Kusie: Mutunlik (22 m), 1 Apr 1953, J.F.G. Clarke (2♂; USNM); Yeta Cave, 9 Apr 1953, J.F.G. Clarke (1♀; USNM). Pingalep Atoll, 22 Jul 1949, R.P. Owen (1♂; USNM). Ponape Island, Kolonia, Aug 1956, M.R. Wheeler (1♂; USNM). Yap Islands: Gagil, Gachapar, 19 Jun 1957, C.W. Sabrosky (3♂, 2♀; USNM); Weloy, 19 Jun 1957, C.W. Sabrosky (2♂; USNM).

GUAM. Point Oca, 6–14 Jun 1945, G.E. Bohart, J.L. Gressitt (1♂, 1♀; ANSP); Point Ritidian, 16 Apr–Jun 1936, 1945, E.H. Bryan, Jr., G.E. Bohart, J.L. Gressitt (4♂, 2♀; ANSP, USNM).

HAWAIIAN ISLANDS. Kaua'i: Anini Beach (about 4 mi [6.4 km] NE Hanalei), 7 Jul 1985, R.S. and V.L. Zack (6♂; WSU). Maui: Hana, 10 Jan 1973, J.R. Vockeroth (1♂; USNM); Kihei (rocky beach), 30 Jun 1985, R.S. and V.L. Zack (1♂, 2♀; WSU). Oahu: Bellows Field, 8 Jul 1952, A.L. Melander (8♂, 1♀; USNM); Hanauma Bay (crab hole), 28 Jun-3 Jul 1936, 1952, A.L. Melander (4♂, 2♀; ANSP, USNM); Kailua Beach, 26 Mar 1968, J.A. Tenorio (2♂, 5♀; USNM, WSU); Moanalua (salt lake), 7 Mar 1945, Y. Tahada (2♀; USNM); Mokuleia, 16 May 1952, A.L. Melander (1♂, 2♀; USNM); Waiamae (resting on crab holes on sandy beach), 8 Nov 1946, W.W. Wirth (1♂, 3♀; USNM); Waimanalo Beach (crab hole), 8 May-2 Oct 1936, 1946, 1952, 1966, A.L. Melander, J.R. Vockeroth, W.W. Wirth (9♂, 5♀; ANSP, USNM); Sep 9-10 1955, M.R. Wheeler (1♂; USNM). Johnston Island, 10 Jul 1958, H.I. Rainwater (1♂; USNM).

KIRIBATI. Gilbert Islands. Aronuka Atoll: 20 Nov 1964, B.D. Perkins (1♀; USNM). Butaritari Atoll: Butaritari Island, Jul 1957, N.L.H. Krauss (1♂, 1♀; USNM). Makin Atoll: B.D. Perkins (2♂, 1♀; USNM). Tarawa Atoll: Bairiki Island, Nov 1957, N.L.H. Krauss (1♂, 1♀; USNM); Banraeaba, Jul 1957, N.L.H. Krauss (1♀; USNM); 23-27 Jul 1945, D.G. Hall (2♂; USNM). Phoenix Islands: Kanton Island, 25 Apr 1940, D.B. Langford (1♂; BBM). Line Islands: Palmyra Atoll, Feb-Jul 1948, 1962, N.L.H. Krauss, M.R. Wheeler (1♂, 2♀; USNM).

MARSHALL ISLANDS. Enewetak Atoll: Enewetak Island, 13 May 1946, H. Townes (1♂, 3♀; USNM). Jaluit Atoll: Jabor Island, 27 Apr 1958, J.L. Gressitt (1♂; USNM). Japtan Island, Aug-Sep 1955, M.R. Wheeler (1♀; USNM). Kwajalein Atoll: 8 Aug 1944, D.G. Hall (2♂, 1♀; USNM). Kwajalein Atoll: Kwajalein Island, 17 Aug 1946 (1♀; USNM); Loi Island, 3 Sep 1944, H.S. Wallace (1♂; WSU). Likiep Atoll: Likiep Islet, 30 Aug 1946 (1♂; USNM). Majuro Atoll: Uliga Island, Aug-Sep 1955, M.R. Wheeler (1♂; USNM). Parry Island, Aug-Sep 1955, M.R. Wheeler (2♂, 1♀; USNM); 24 Dec 1950, Y. Oshiro (1♂; USNM).

MOLUCCAS. Bacan: Labuha (sweeping shoreline debris), 26 Sep 1985, A.H. Kirk-Spriggs (10♂, 14♀; NMWL).

NEW ZEALAND. North Island. Auckland: Cape Reinga Beach, 20 Jan 1966, J.M. Riches (1♀; NZAC); Clarks Beach (weeds on beach), 2 Feb 1953, K.A.J. Wise (1♀; NZAC); Green Bay (on Asteraceae), 6 Apr 1975, B.Z. Holloway (1♀; NZAC); Kare Kare (kelp on beach), 28 May-6 Apr 1975, B.A. Holloway, G.Kuschel (5♂, 3♀; 4 adults reared from puparia; NZAC); Ruapuke (beach W of Hamilton, mussels on rocks), 27 Feb 1971, J. Gillespie (1♂, 1♀; NZAC); Wattle Bay (plants on mud flats or on dead stingray), 23-24 Feb 1977, B.A. Holloway, G. Kuschel (1♂, 2♀; NZAC). South Island. Canterbury: Napenape Scenic Reserve (near mouth of Hurunui River, freshwater pond near ocean), 17 Nov 1977, E. Schlinger (1♀; NZAC). North Chatham Island: Ocean Mail point (on flowers of *Sonchus grandifolius* Kirk), 20 Jan 1976, R.P. Macfarlane (1♂; NZAC); Wharekauri (on beach, 1♀ on flower of *Cotula coronopifolia* L.), 16 Jan 1976, R.P. Macfarlane

(1♂, 2♀; NZAC). Whale Bay Road, 9 Dec 1970, J. Gillespie (1♂; NZAC).

NORTHERN MARIANA ISLANDS. Pagan: Songsofig, 27 May 1940, Yasu. et Yosi. (1♀; USNM).

PALAU. Babelthup Island: Melekeiok (beach), 23 May 1957, C.W. Sabrosky (5♂, 3♀; USNM); Ngerehelong, 6 May 1957, C.W. Sabrosky (5♂, 2♀; USNM); Ngial (beach), 9 May 1957, C.W. Sabrosky (1♂; USNM). Ngaiangl Atoll, 9 May 1957, C.W. Sabrosky (1♀; USNM). Nguruukdabel Island, Ngaremediu, 24 May 1957, C.W. Sabrosky (14♂, 3♀; USNM). Ulebsehel Island, 21 May 1957, C.W. Sabrosky (4♂, 2♀; USNM).

PAPUA NEW GUINEA. Admiralty Islands: Los Negros, 27 Mar 1945, D.G. Hall (21♂, 25♀; USNM). Bismark Archipelago: Hermit Island, 26 Jun 1962 (13♂, 8♀; USNM, UZMC); Lavongai, Banatam, 24 Mar 1962 (1♂; USNM). Manus Lorengau, 14 Jun 1962 (8♂; UZMC). Papua New Guinea. Central Province: Boerg (seashore), 29 Nov 1982, J.W. Ismay (1♂, 1♀; USNM); Gabagaba (W Kwikila), 1 Jan 1983, J.W. Ismay (8♂, 4♀; USNM); LeaLea (saltpan margin), 6 Oct 1985, J.W. Ismay (1♂; USNM); Loloata Island (seashore), 31 Mar 1985, J.W. Ismay (2♂, 1♀; USNM); Yule Island (rocky shore, strandline), 1 Jan 1983, J.W. Ismay (2♂, 3♀; USNM). West New Britain Province: Dami (beach, near Kimbe), 29 Feb 1983, J.W. Ismay (6♂, 2♀; USNM). West Sepik Province: Wutung (seashore), 12 Nov 1985, J.W. Ismay (3♂, 3♀; USNM).

SOLOMON ISLANDS. Guadalcanal: Koli Point, Oct 1944, J. Laffoon (2♂, 3♀; USNM). Guadalcanal and Florida Islands, 1 Mar 1945, J.R. Stuntz (1♂, 1♀ USNM).

WAKE ISLAND. Peale Island, Nov 1957, N.L.H. Krauss (1♂, 1♀; USNM). Oriental: CHAGOS ARCHIPELAGO. Diego Garcia: Baracholis Section (on dead fish), 25 Apr 1971, A. Hutson (1♂, 2♀; BMNH); East Point, 7 May 1971, A. Hutson (10♂, 6♀; BMNH).

Oriental: CHINA. Hong Kong: Lantau Island, Trappist Monastery to Silver Mine Bay (over hills), 24 Jul 1964, W.J. Woss (1♀; BBM).

INDIA. Maharashtra: Bombay, Juhu Beach, 7 Mar 1985, K.A. Spencer (1♀; NMWL).

MALAYSIA. Penang: Georgetown (dirty sand ocean beach and wave swept rocks), 2-17 Jan 1990, J.R. Vockeroth (27♂, 11♀; CNC). Sabah: Kota Kinabalu (17 km S), 9 Aug 1983, G.F. Hevel, W.E. Steiner (5♂, 12♀; USNM).

PHILIPPINES. Balabac Dalawan Bay, 12 Oct 1961 (1♀; UZMC). Calicoan, 27 Jul 1945, F.F. Bibby (11♂, 1♀; USNM). Jul 1945, F.F. Bibby (12♂, 13♀; USNM).

RYUKYU ISLANDS (JAPAN). Okinawa: Chizuka, Jul-Sep, G.E. Bohart (13♂, 3♀; USNM); Okinawa (rotting fish on shore), 17-20 Aug-23 Sep 1945, 1980, P.S. Cranston, W.D. Field (7♂, 10♀; BMNH, USNM).

SRI LANKA. West Province: Ratmalana, Colombo (9 mi S), 7-13 Jan 1962, H. Andersson, P. Brinck, L. Cederholm (5♂, 2♀; ZIL). Northwest Province: Kadaimparu, Negombo (15 mi [24 km] N), 31 Jan 1962, H. Andersson, P. Brinck, L.

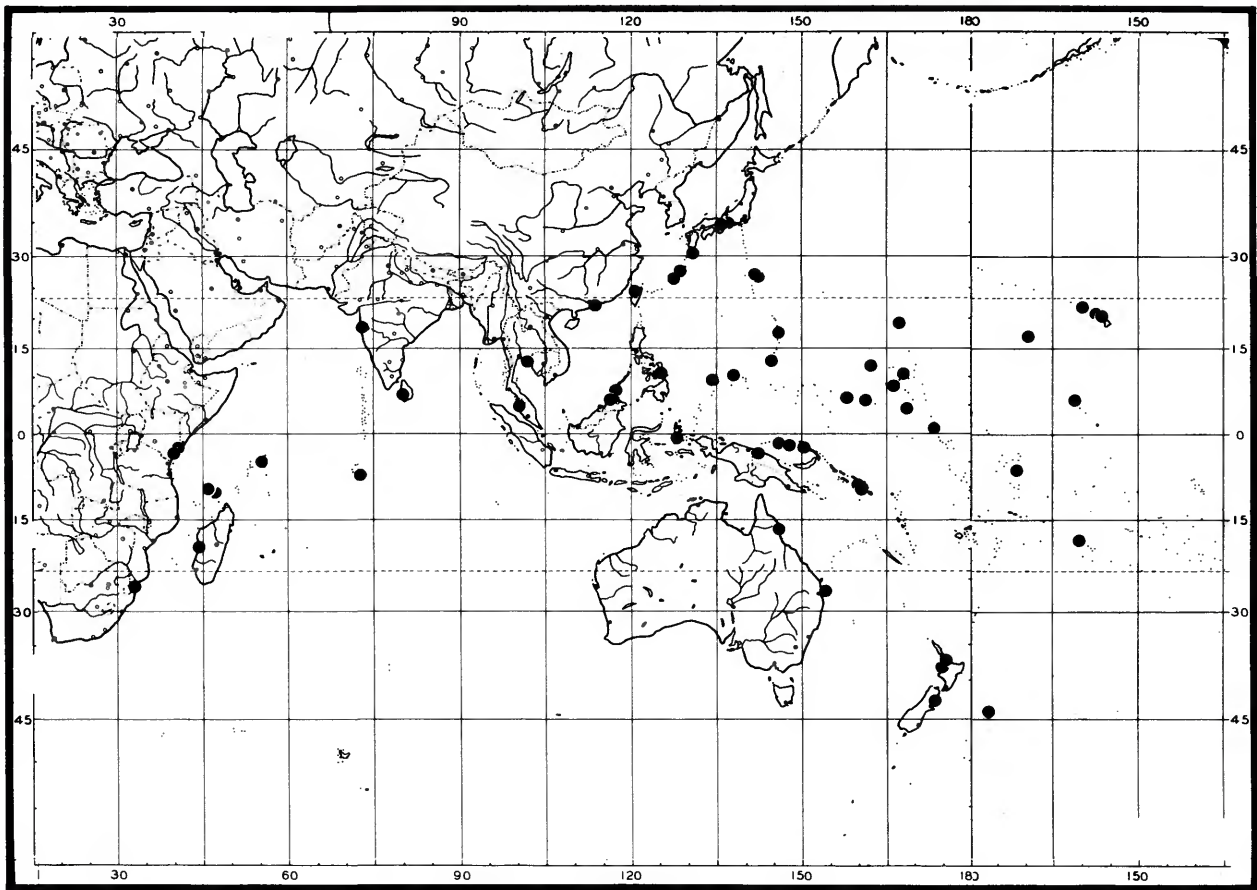


FIGURE 33.—Distribution map for *Hecamede (Hecamede) granifera*.

Cederholm (1♂; ZIL).

TAIWAN. Takao, 3 May 1907, H. Sauter (5♂, 1♀; ANSP, USNM).

THAILAND. Bangphra, Cholburi (light trap), Oct 1962, J.E. Scanlon (1♀; USNM).

Palaearctic: JAPAN. Honshu: Osaka, Hamadera Koen, 29 Aug 1954, P.H. Arnaud, Jr. (56♂, 31♀; CAS, USNM, WSU). Okitsu, Jun 1913, F. Muir (1♀; BBM); Okitsu (in cage), 27 Oct 1914, F. Muir (1♀; BBM); Noma Tanegashima, Jun 1958, N.L.H. Krauss (1♂; BBM). Amami Group: Tokuno Shima, Hetono, 23 Jul 1963, C.M. Yoshimoto (20♂, 1♀, 1 abdomen missing; BBM).

DISTRIBUTION (Figure 33).—Old World along coasts of the Indian and Pacific oceans. Afrotropical: Kenya, Madagascar, Mozambique, islands in the Indian Ocean (Aldabra, Astove, Cosmoledo, Seychelles). Australasian/Oceanian: Australia (QLD), Belau, Bonin Islands, Cook Islands, Federated States of Micronesia, Hawaiian Islands (Maui, Oahu), Kiribati, Marshall Islands, Moluccas, New Zealand, Northern Mariana Islands, Papua New Guinea (Admiralty Islands, Bismark Archipelago, Papua New Guinea), Solomon Islands, Wake Island. Oriental: Chagos Archipelago (Diego Garcia), China, India, Indonesia

(Irian Jaya), Malaysia, Philippines, Ryukyu Islands, Sri Lanka, Taiwan, Thailand. Palearctic: Japan (Honshu).

NATURAL HISTORY.—Bohart and Gressitt (1952) found adults of this species (as *H. persimilis*) to be abundant on beaches of the island of Guam. Specimens occurred on moist sand, low-growing beach vegetation, and dead fish. They also discovered large numbers of maggots in damp, foul-smelling sand beneath a human carcass. Only rarely did they find adults on vegetation in a coconut grove, about a mile from sea.

Tenorio (1980:276), working on Hawaii, successfully reared this species (as *H. persimilis*) from larvae and puparia that had been collected and maintained on a medium of moist seaweed. He also reported an abundance of adults on rotting fish and crabs on the sand.

DIAGNOSIS.—This species is distinguished from all others of the *albicans* group by the distinct row of short and slightly stout setae along the anteroventral margin of the fore femur.

NOTES ON VARIATION.—Some variation in the coloration of this species appears to have a geographic component. In the Pacific, especially the north Pacific (Japan), the dorsum of the thorax is light brown, distinctly contrasted with the gray pleural areas. In the Indian Ocean (Madagascar, the Seychelles, India),

the dorsal and pleural areas are essentially concolorous, gray to silvery gray. Setae also seem to be more robust in the Japanese specimens, perhaps best seen in the comblike row of setae along the anteroventral surface of the fore femur. Otherwise, however, the specimens are very similar, and the structures of the male genitalia are virtually identical. Because the variation is gradual, apparently clinal, I have interpreted it to be intraspecific.

***Hecamede (Hecamede) inermis* Malloch**

FIGURES 34–37

Hecamede inermis Malloch, 1933:12.—Cresson, 1948:23 [note].

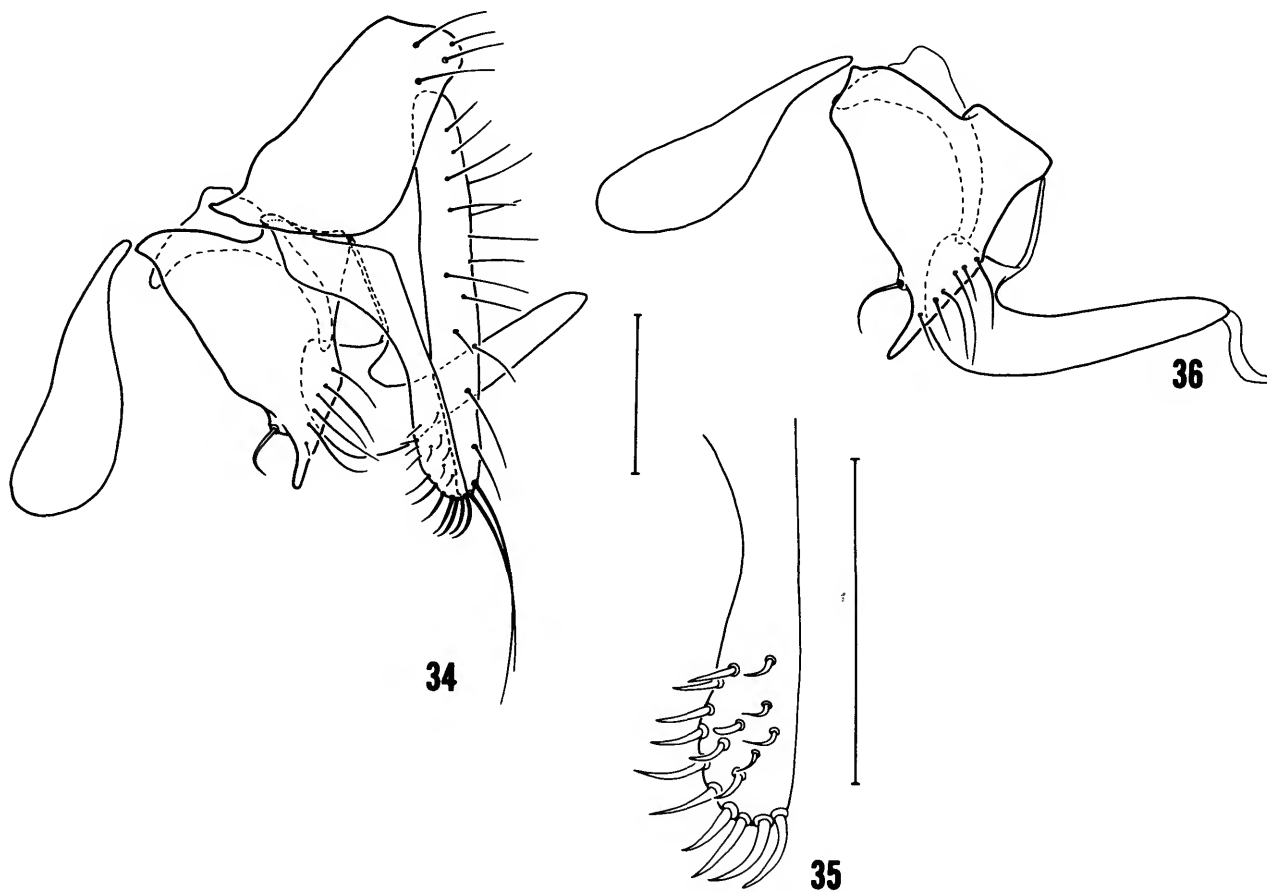
Hecamede granifera.—Of authors [misidentification].—Mathis, 1989a:641 [Australasian/Oceanian catalog]; 1989b:8 [list of Diptera from the Pitcairn Group].

DESCRIPTION.—Small to medium-sized shore flies, length 1.30 to 3.00 mm.

Head: Fronto-orbits narrow, gray, or indistinct, with similar coloration as mesofrons; ocellar triangle densely

microtomentose, mostly tan, occasionally mostly gray; mesofrons less densely microtomentose than ocellar triangle, coloration darker posteriorly with some mostly brown to black coloration, becoming yellowish orange to reddish orange anteriorly; proclinate fronto-orbital setae 1, inserted anterolaterad of reclinate seta. Antenna usually mostly yellow; flagellomere 1 usually darker, sometimes extensively so, especially dorsobasally near insertion of arista; arista with 4 dorsal branches. Face mostly whitish gray, frequently with some yellowish coloration, especially at sutures; facial setae 3 or 4, arising from bare, slightly elevated spots within densely microtomentose face; facial prominence bare, not much larger than shiny area at base of facial setae; gena mostly concolorous with face, bearing 1 larger seta and a few other black setae, these scattered; gena high, eye-to-cheek ratio averaging 0.50. Clypeus black, densely invested with gray microtomentum.

Thorax: Mesonotum usually mostly light to moderately brown, frequently with some faint mostly red or golden coloration, sometimes mostly gray, nearly always darker than pleural areas, if dark, becoming grayer, whitish to silvery gray, especially ventrad through notopleuron and dorsal half of



FIGURES 34–36.—*Hecamede (Hecamede) inermis*: 34, male terminalia, lateral aspect; 35, apex of surstylus, lateral aspect; 36, internal structures of the male genitalia, lateral aspect. (Bar = 0.1 mm.)

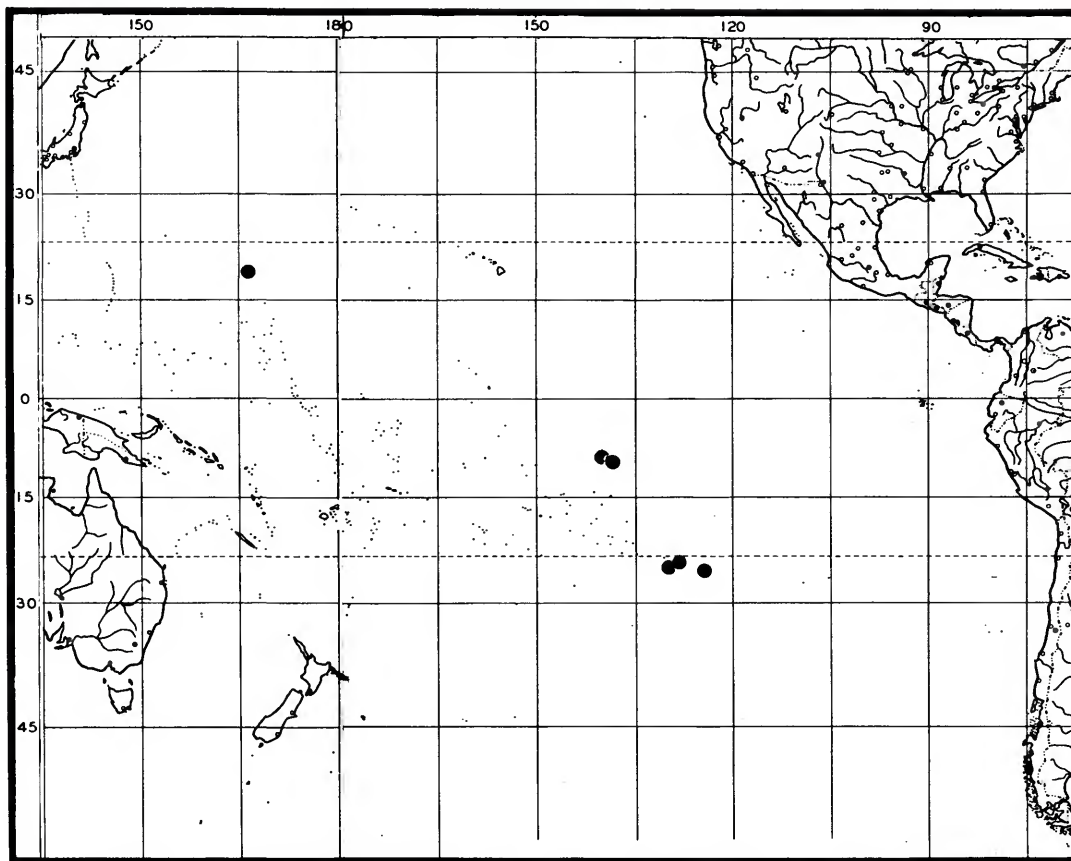


FIGURE 37.—Distribution map for *Hecamede (Hecamede) inermis*.

anepisternum; presutural seta and usually prescutellar acrostichal setae well developed, some specimens with indistinct prescutellar setae; posterior notopleural seta inserted distinctly above level of anterior seta; pleural sclerites mostly gray to whitish gray, dorsal portion of anepisternum sometimes faintly to conspicuously tan; anepisternal setulae mostly on dorsal $1/3$, occupying an area that is more or less triangular, with a line of setulae to ventral portion of pleuron where several more setulae are inserted. Coxae and trochanters lightly blackish gray to gray; middle and hind femora gray anteriorly, posterior surface blackish; fore femur lacking a row of setae along anteroventral margin, anterior surface mostly blackish, mostly gray posteriorly; tibiae mostly yellow, lightly invested with whitish gray microtomentum; fore basitarsus lacking black setae toward base of posteroventral surface; apical tarsomeres usually yellow, occasionally with apical tarsomere lightly brown. Wing with costal vein ratio averaging 0.35; M vein ratio averaging 0.60; last section of vein M shallowly arched posteriorly.

Abdomen: Male terminalia (Figures 34–36) as follows: 5th tergum with anterior $3/4$ to $7/8$ more lightly sclerotized and bearing numerous, evenly scattered spicules, from dorsal view with anterior margin broadly bifid, posterior $1/4$ to $1/8$ a sclerotized band bearing 8 to 11 setae along posterolateral

margin, with 2 globular apodemes anterobasally; epandrium (Figure 34) a dorsal band, gradually enlarged posteriorly; surstylus (Figures 34, 35) in lateral view long and narrow, posterior margin more or less straight, anterior margin sinuous, anteroapical margin curved, apex bearing approximately 6–7 moderately longer, sharply pointed setulae; cercus (Figure 34) long and narrow, length extended nearly to apex of surstylus, bearing a conspicuously longer seta at posteroventral margin; gonite (Figure 36) roughly triangular in shape, with a narrow connection above aedeagus, ventral angle as a narrowed, short, parallel-sided, blunt process; aedeagal apodeme (Figure 36) allantoid in lateral view, slightly broader toward attachment with hypandrium; aedeagus (Figure 36) long and narrow, tapered gradually to apex, shaped like a pipe, with right angle curve at basal $1/4$ to $1/3$; hypandrium slightly emarginate anteriorly.

TYPE MATERIAL.—The holotype male of *Hecamede inermis* is labeled “Tahauku, HivaOa VII-10-[19]29 X[~~crossing out a letter~~]/sea shore/Marquesas Islands/Mumford & Adamson/Pacific Entomological Survey/*Hecamede inermis* 1226 [number in red ink] Type det. JRMALLOCH [species name and number handwritten, black submargin].” The holotype is pointed, is in good condition, and is deposited in the BBM.

OTHER SPECIMENS EXAMINED.—Australasian/Oceanian: *MARQUESAS*. Hiva Oa: Tahauku, 10 Dec 1929, E.P. Mumford, A.M. Adamson (2♂, paratypes; BBM, USNM). Nuku Hiva: Taiohae, 9–15 Jun 1987, W.N. Mathis (1♂, 3♀; USNM).

PITCAIRN GROUP. Henderson Island: Northwest Beach, 12–20 May 1987, W.N. Mathis (88♂, 11♀; USNM); North Beach, 17–20 May 1987, W.N. Mathis (56♂, 10♀; USNM). Oeno Atoll, 28 May 1987, W.N. Mathis (34♂, 9♀; USNM). Pitcairn Island: Adamstown, 22–26 May 1987, W.N. Mathis (7♂, 3♀; USNM); Down Rope, 25 May 1987, W.N. Mathis (9♂, 6♀; USNM).

WAKE ISLAND. 8 Jan 1923, E.H. Bryan, Jr. (1♂, 1♀; ANSP).

DISTRIBUTION (Figure 37).—Australasian/Oceanian: South Pacific from Wake Island and the Marquesas south to the Pitcairn Group (Henderson, Pitcairn, and Oeno islands).

NATURAL HISTORY.—On islands of the Pitcairn Group, this species was abundant on the beach, especially where debris had accumulated at the high tide mark (Mathis, 1989b). Adults were also attracted in large numbers to specimens of corals and study skins of birds that had been set out to dry on exposed rocks.

DIAGNOSIS.—This species is distinguished from congeners by the following combination of characters: proclinate fronto-orbital seta 1, inserted anterolaterad of reclinate seta; gena with 1 larger seta and several smaller black setae; fore femur lacking a distinct row of setae along anteroventral margin; fore basitarsus lacking black setae at base of posteroventral surface; mesonotum golden brown to brown; 5th tergum of male appearing hirsute, invested with numerous, long, microtrichia; and the structure of the male terminalia (Figures 34–36), especially the shape of the surstylus and its setulae.

NOTES ON NOMENCLATURE.—Previously (Mathis, 1989b:8), I commented that “The genus *Hecamede* needs revision before many of the available names can be validly applied. For the present, I am using *H. granifera* for this species in accordance with the recent catalog of Australasian and Oceanian Diptera (Mathis, 1989a). A junior synonym, *H. inermis* Malloch, was used previously for the common species of *Hecamede* that occurs in the South Pacific.”

Hecamede (Hecamede) maritima, new species

FIGURES 38–40

DESCRIPTION.—Small to moderately small shore flies, length 1.50 to 2.90 mm.

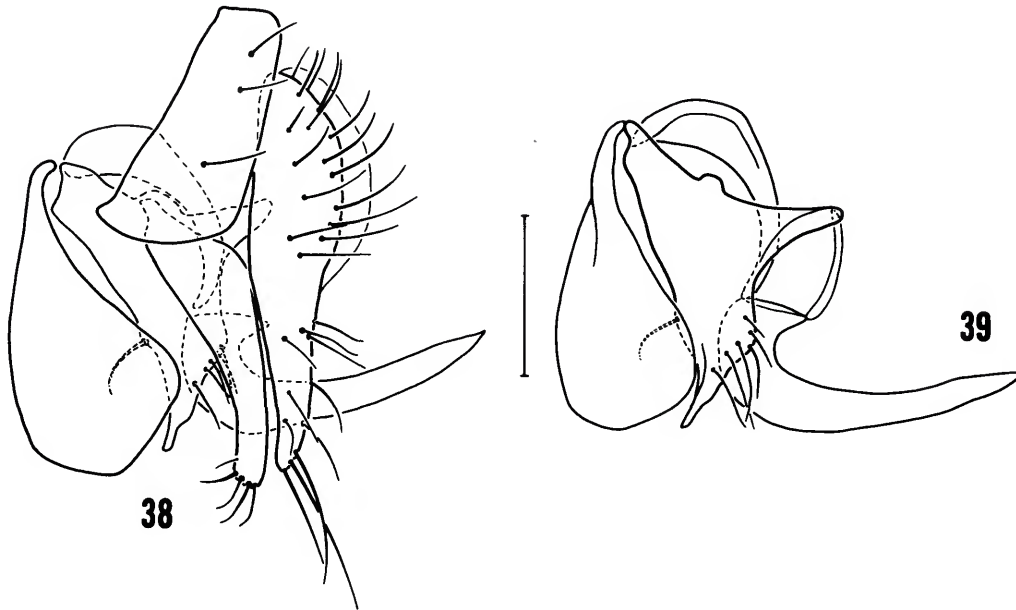
Head: Fronto-orbits and ocellar triangle densely microtomentose, gray; mesofrons, except for ocellar triangle, sparsely microtomentose, anterior portion mostly yellow to reddish orange; 1 proclinate fronto-orbital seta inserted anterolaterad of reclinate seta. Antenna mostly yellowish

orange to orange; flagellomere 1 mostly yellow but with some brownish coloration toward base on dorsal surface, near insertion of arista; arista bearing 3 or 4 dorsal branches. Face densely microtomentose, whitish gray to silvery gray, bearing 3 lateral setae, each arising from subshiny, bare, shallow tubercle, sometimes with a smaller 4th seta ventrad to other setae; facial prominence bare at apex, bare area relatively small, usually less in diameter than width of pedicel. Gena high, eye-to-cheek ratio averaging 0.40; densely microtomentose, concolorous with face, bearing 1 larger and a few to several smaller black setae. Clypeus black with moderate to dense investment of gray microtomentum.

Thorax: Scutum and disc of scutellum mostly grayish tan with some faint golden luster; lateral margins of mesonotum slightly grayer, becoming progressively more so ventrad through notopleural area or farther onto the dorsum of the anepisternum; pleural sclerites gray and microtomentum with faint shiny luster; anepisternal setulae mostly on dorsal $\frac{1}{3}$, occupying an area that is more or less triangular, with a line of setulae to ventral portion of pleuron where several more setulae are inserted. Legs with coxae, trochanters, and femora mostly gray; fore femur lacking row of setae on anteroventral surface, mostly black on anterior surface, mostly gray posteriorly; middle and hind femora mostly gray anteriorly, posterior surface blackish; tibiae yellow with thin investment of mostly white microtomentum; fore basitarsomere lacking black setae to base of posteroventral surface; tarsomeres mostly yellow except for apical 1–2, these dark brown. Wing with costal vein ratio averaging 0.35; M vein ratio averaging 0.50; last section of vein M shallowly sinuous.

Abdomen: Male terminalia (Figures 38, 39) as follows: 5th tergum with anterior $\frac{3}{4}$ to $\frac{7}{8}$ more lightly sclerotized and bearing numerous, evenly scattered spicules, from dorsal view with anterior margin broadly bifid, posterior $\frac{1}{4}$ to $\frac{1}{8}$ a sclerotized band bearing 8 to 11 setae along posterolateral margin, with 2 globular apodemes anterobasally; epandrium (Figure 38) a dorsal band, gradually enlarged posteriorly; surstylus (Figure 38) in lateral view long and narrow, tapered toward ventral apex, posterior and anterior margins slightly curved, apex bearing 4 or 5 setulae; cercus (Figure 38) long and narrow, length almost twice that of epandrium, bearing a conspicuously longer seta at posteroventral margin; gonite (Figure 39) roughly triangular in shape, with a narrow connection above aedeagus, ventral angle as a narrowed, short, parallel-sided, blunt process; aedeagal apodeme (Figure 39) L-shaped, with arms curved, better developed toward angle; aedeagus (Figure 39) long and narrow, tapered gradually to apex, shaped like a pipe, with right angle curve at basal $\frac{1}{4}$ to $\frac{1}{3}$; hypandrium slightly emarginate anteriorly.

TYPE MATERIAL.—The holotype male is labeled “ISRAEL [EGYPT]: Sinai: Nabek [Nabk] 21 May 1981 W. Mathis/ HOLOTYPE *Hecamede maritima* ♂ W.N. Mathis USNM



FIGURES 38, 39.—*Hecamede (Hecamede) maritima*: 38, male terminalia, lateral aspect; 39, internal structures of the male genitalia, lateral aspect. (Bar = 0.1 mm.)

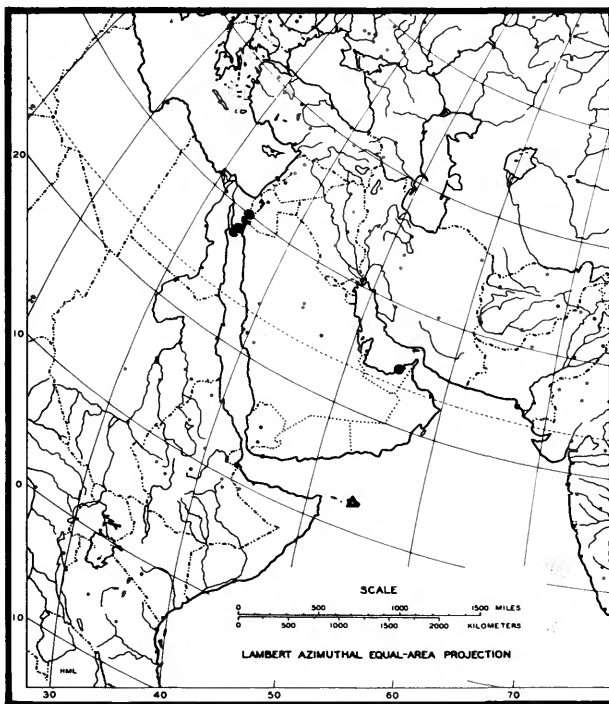


FIGURE 40.—Distribution map for *Hecamede (Hecamede) maritima* (dots) and *Hecamede (Hecamede) socotra* (open triangle).

[species name and gender handwritten, red.]” The holotype is double mounted (minuten in a plastic block), is in excellent condition, and is deposited in the USNM. The allotype female and 17 paratypes (5♂, 12♀; USNM) bear the same locality label data as the holotype. Other paratypes are as follows: *EGYPT*. Sinai: Dahab, 23 May 1981, A. Freidberg, W.N. Mathis (4♂, 8♀; TAU, USNM); Elat (15 km S), 15 Mar 1982, A. Freidberg (2♀; TAU); Na’ama, 22 May 1981, W.N. Mathis (10♂, 7♀; TAU, USNM); Nabk, 23 Mar–30 May 1980, 1981, A. Freidberg, A. Valdenberg (8♂, 6♀; TAU); Ofira, 22 Mar 1981, A. Freidberg (2♂; TAU); Rás Burqá, 23 May–8 Aug 1981, A. Freidberg, W.N. Mathis (5♂; TAU, USNM). *ISRAEL*. Elat, 23 May–4 Apr 1981, 1986, A. Freidberg, F. Kaplan, W.N. Mathis (6♂, 3♀; TAU, USNM).

OTHER SPECIMENS EXAMINED.—Old World. Palearctic: *OMAN*. Barka (beach), 8 Apr 1985, P. Ardö (1♀; ZIL). Dhofar: Mughsail beach (in burrow of turret-building crab, *Ocypode rotundata* Miers), 11 Oct 1990, M. Ebejer, J.C. Deeming (1♂; NMWL). Muscat: Al Khuwair, Oct 1990, J.C. Deeming (1♀; NMWL); Seeb beach (on stranded jelly fish), 16 Oct 1990, J.C. Deeming (15♂, 8♀; NMWL). Qurm (hotel garden), 5 Apr 1985, P. Ardö (2♂, 4♀; ZIL).

DISTRIBUTION (Figure 40).—Old World. Palearctic: Egypt (Sinai), Israel, and Oman.

ETYMOLOGY.—The species epithet, *maritima*, is of Latin derivation and refers to the maritime habitat of this species.

DIAGNOSIS.—This species is distinguished from congeners

by the following combination of characters: proclinate, fronto-orbital seta 1, inserted anterolaterad of reclinate seta; gena with 1 larger and several smaller black setae; fore femur lacking a row of setae along anteroventral surface; fore basitarsus lacking black setae at base of posteroventral surface; 5th tergum of male appearing bare or at most with sparse, inconspicuous microtrichia, and the structure of the male terminalia (Figures 38, 39), especially the surstylus and gonite.

Hecamede (Hecamede) socotra, new species

FIGURE 40-42

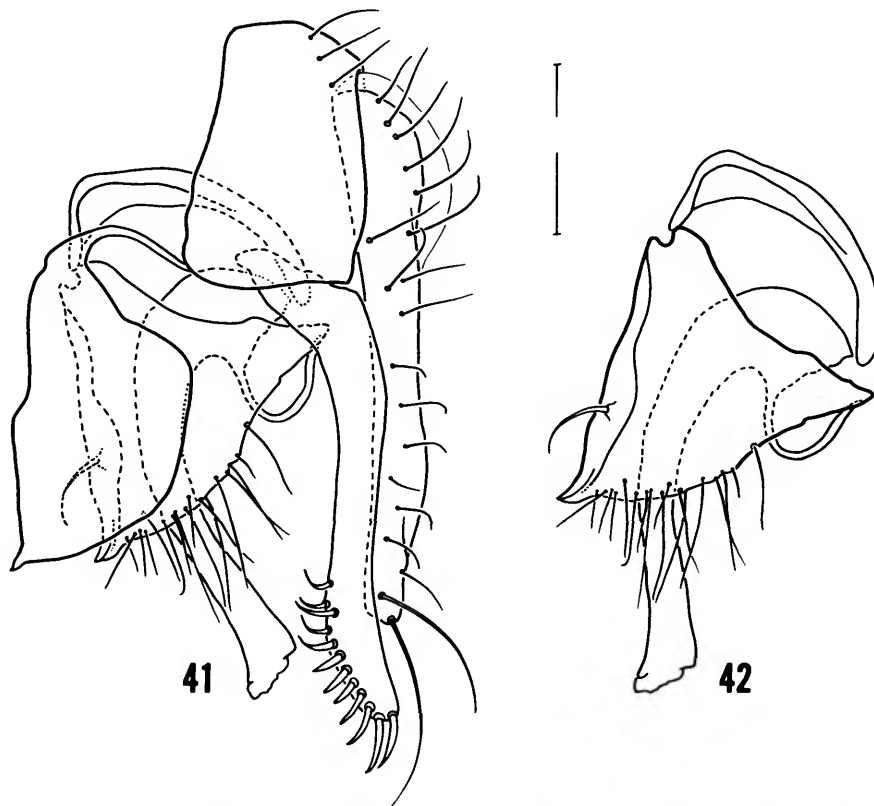
Hecamede albicans.—Of authors [misidentification].—Becker, 1910:154 [list, Socotra].

DESCRIPTION.—Moderately small shore flies, length 2.30 to 2.50 mm.

Head: Fronto-orbits and ocellar triangle densely microtomentose, gray; mesofrons, except for ocellar triangle, sparsely microtomentose, anterior portion mostly yellowish to reddish orange; 1 proclinate fronto-orbital seta inserted anterolaterad of reclinate seta. Antenna mostly yellowish

orange to orange; flagellomere 1 mostly yellow but with some brownish coloration toward base on dorsal surface, near insertion of arista; arista bearing 3 or 4 dorsal branches. Face densely microtomentose, whitish gray to silvery gray, bearing 3 lateral setae, each arising from subshiny, bare, shallow tubercle, sometimes with a smaller 4th seta ventrad to other setae; facial prominence bare at apex, bare area relatively small, usually less in diameter than width of pedicel. Gena high, eye-to-cheek ratio averaging 0.40; densely microtomentose, concolorous with face, bearing 1 larger and a few to several smaller black setae. Clypeus black with moderate to dense investment of gray microtomentum.

Thorax: Scutum and disc of scutellum mostly grayish tan with some faint golden luster; lateral margins of mesonotum slightly grayer, becoming progressively more so ventrad through notopleural area or farther onto the dorsum of the anepisternum; pleural sclerites gray and microtomentum with faint shiny luster; anepisternal setulae mostly on dorsal $\frac{1}{3}$, occupying an area that is more or less triangular, with a line of setulae to ventral portion of pleuron where several more setulae are inserted. Legs with coxae, trochanters, and femora mostly gray; fore femur lacking row of setae on anteroventral surface,



FIGURES 41, 42.—*Hecamede (Hecamede) socotra*: 41, male terminalia, lateral aspect; 42, internal structures of the male genitalia, lateral aspect. (Bar = 0.1 mm.)

mostly black on anterior surface, mostly gray posteriorly; middle and hind femora mostly gray anteriorly, posterior surface blackish; tibiae yellow with thin investment of whitish microtomentum; fore basitarsomere lacking black setae to base of posteroventral surface; tarsomeres mostly yellow except for apical 1–2, these dark brown. Wing with costal vein ratio averaging 0.35; M vein ratio averaging 0.50; last section of vein M shallowly sinuous.

Abdomen: Male terminalia (Figures 41, 42) as follows: 5th tergum with anterior $\frac{3}{4}$ to $\frac{7}{8}$ more lightly sclerotized and bearing numerous, evenly scattered cuticular microtrichia, from dorsal view with anterior and posterior margins broadly but shallowly emarginate, posterior $\frac{1}{4}$ to $\frac{1}{8}$ a sclerotized band bearing 8 to 11 setae along posterolateral margins; epandrium (Figure 41) a dorsal strap-like band, gradually but slightly enlarged posteriorly; surstylus (Figure 41) in lateral view very long and narrow, slightly along middle third, apex slightly enlarged and bearing about 12 stout setulae along anteroventral margin; cercus (Figure 41) long and narrow, length about twice that of epandrium, bearing a conspicuously longer seta (or setae) at posteroventral margin; gonite (Figure 42) roughly triangular in shape, with a narrow connection above aedeagus, ventral angle acutely pointed; aedeagal apodeme (Figure 42) roughly L-shaped, with arms curved, better developed toward angle; aedeagus (Figure 42) shaped like a pipe, long and narrow on apical $\frac{3}{4}$, tapered gradually to apex, basal $\frac{1}{4}$ bowl shaped, much broader, with right angle curve at basal $\frac{1}{4}$ to $\frac{1}{3}$; hypandrium slightly narrowly and deeply emarginate anteriorly, emargination U-shaped.

TYPE MATERIAL.—The holotype male is labeled "Ras Shoab, Sokotra [South Yemen], I[Jan]. [18]99. O. Simony/Hecam[ede]. albicans det. Becker [species name handwritten]/HOLOTYPE Hecamede socotra ♂ W.N.Mathis [species name and gender symbol handwritten, red]." Seven male paratypes, all bearing the same locality label as the holotype, are deposited in the ANSP (1), NMW (5), and USNM (1). The holotype is double mounted, is in good condition (the abdomen and hind legs have been removed and dissected; the parts are in an attached microvial), and is deposited in the NMW.

DISTRIBUTION (Figure 40).—Old World. Afrotropical. *South Yemen*. Socotra: Rás Shóab.

ETYMOLOGY.—The species epithet, *socotra*, is a noun in apposition and refers to the island where this species was collected.

DIAGNOSIS.—This species is very similar to *H. maritima*, and except for characters of the male terminalia, especially the shape of the gonite and surstylus (Figures 41, 42), I cannot distinguish between them.

The *planifrons* Group

SPECIES INCLUDED.—*Hecamede planifrons* (de Meijere).

DIAGNOSIS.—This species group is distinguished from other congeners of the subgenus *Hecamede* by the lack of intrafrontal

setae (not to be confused with the ocellar setae, which are inserted in front of the anterior ocellus); the mostly to entirely dark-colored flagellomere 1; the presence of an anteroventral and posteroventral row of stout setae on the fore femur; the lack of genal setae (pale setulae are present, however); and the genal height, which is nearly equal to the height of the eye.

DISTRIBUTION.—Australasian/Oceanian and Oriental Regions.

DISCUSSION.—The only species comprising this group is distinct from congeners (see diagnosis above) and is a monophyletic lineage that is characterized by several synapomorphies (see "Phylogenetic Considerations" on p. 39). Unfortunately virtually nothing is known about their natural history, and the immature stages are unknown.

Hecamede (Hecamede) planifrons (de Meijere)

FIGURES 43–47

Hemicyclops planifrons de Meijere, 1913:67.—Cresson, 1945:56 [notes].

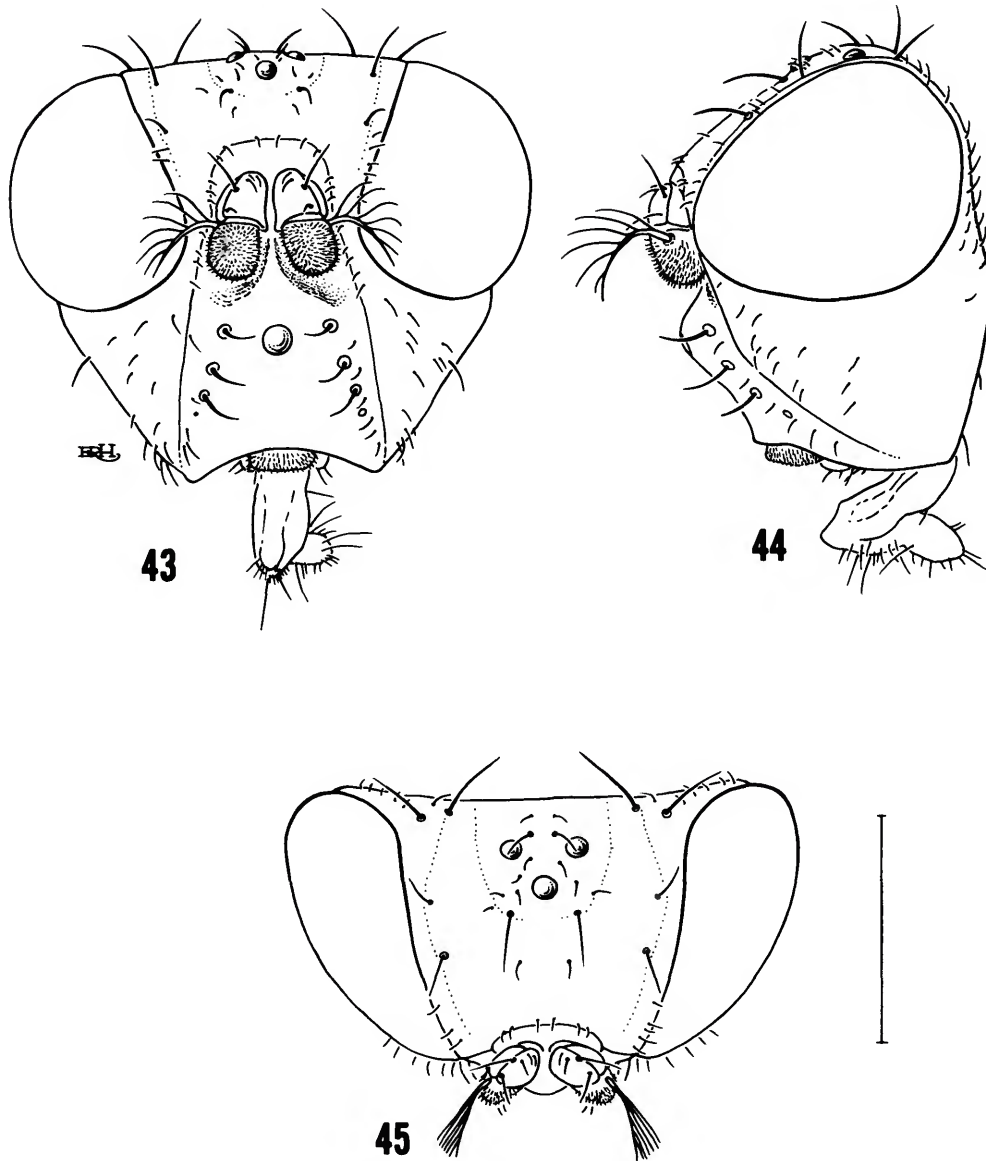
Hecamede planifrons.—Mathis, 1989a:641 [generic combination].

Hemicyclops maculipleuris de Meijere, 1914:248.—Cresson, 1945:56 [list].—Cogan and Wirth, 1977:325 [Oriental catalog]. [New synonymy.]

DESCRIPTION.—Moderately small to medium-sized shore flies, length 2.00 to 3.10 mm.

Head: Frons microtomentose, coloration subdued, grayish; ocellar triangle, area immediately adjacent to triangle, and fronto-orbits lightly tannish white to whitish gray, otherwise frons grayish tan to golden brown. Proclinate fronto-orbital setae 1, inserted anteriorly and slightly laterad of reclinate seta. Antenna with scape and pedicel and area immediately at base of flagellomere 1 yellowish orange, remainder of flagellomere 1 blackish; arista with 4 to 7 branching rays; face and gena lightly tannish to silvery white; facial setae 3 or 4; facial prominence bare, not much larger than shiny area at base of facial setae; eye horizontally obovate, more broadly rounded posteriorly than anteriorly; only the genal seta is evident although several pale setulae are present; gena high, subequal to eye height, eye-to-cheek ratio 0.75.

Thorax: Coloration of mesonotum and ventrally to dorsal $\frac{1}{4}$ of anepisternum lightly tannish gray, thereafter ventrally whitish to silvery gray; anterior half of katepisternum bare anteriorly, shiny, blackish brown. Prescutellar acrostichal and presutural setae variable, conspicuous to greatly reduced or absent; anepisternal setulae mostly on posterodorsal $\frac{1}{3}$, with a line of setulae to ventral portion of pleuron where a few additional setulae are inserted; posterior notopleural seta inserted distinctly above level of anterior seta. Costal vein ratio 0.35; M vein ratio 0.67; last section of vein M shallowly concave. Femora whitish gray; tibiae less densely microtomentose than femora, although invested with considerable whitish gray microtomentum but with yellowish orange microtomentum ventrally; tarsi mostly yellow, although apical tarsomere usually dark, brownish; fore femur bearing distinct row of setae along both anteroventral and posteroventral margins on apical



FIGURES 43-45.—*Hecamede (Hecamede) planifrons*: 43, head, anterior aspect; 44, head, lateral aspect; 45, head, dorsal aspect. (Bar = 0.5 mm.)

half of femur.

Abdomen: Microtomentum of terga finer and with slightly less luster than that of gena or femora, grayish white with pearly luster. Male terminalia (Figures 46) as follows: Epandrium in lateral view more or less rectangular, slightly wider at ventral margin; surstylus large and conspicuous, capitate, bearing large, stout setulae along broadly rounded apex; gonite lunate but with a medial, pointed prong with an

anteroventral orientation; aedeagus tapered toward apex, apex acutely pointed and with a small, membranous vesica preapically; aedeagal apodeme with a keel along outer margin, otherwise lunate.

TYPE MATERIAL.—The holotype female of *Hemicyclops planifrons* is labeled "Waigeo [Waigeo Island, Indonesia, NE Moluccas] 30.XII.09. [30 Dec 1909] AM./*Hemicyclops planifrons* det. de Meijere. Type [black submargin, species name and

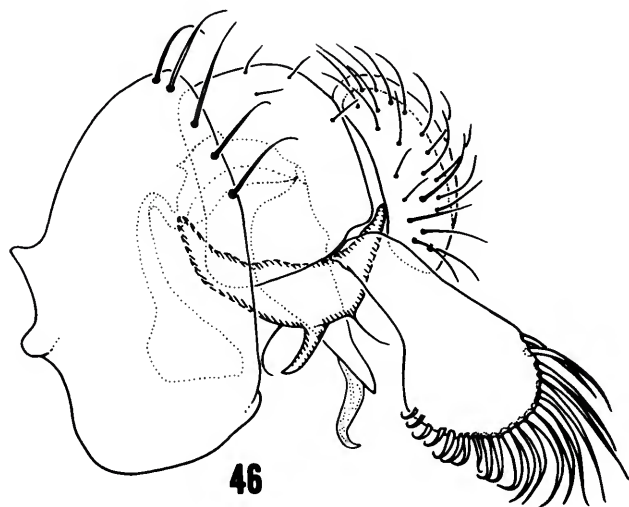


FIGURE 46.—*Hecamede (Hecamede) planifrons*: 46, male terminalia, lateral aspect. (Bar = 0.1 mm.)

“Type” handwritten]/HOLOTYPE [red with black border]/HOLOTYPE ♀ *Hemicyclops planifrons* Meij det. B.H. Cogan 1971. [handwritten except for “det B.H. Cogan 1971”].” The holotype is double mounted (minuten in a plastic foam rectangular block), is in poor condition (somewhat collapsed; the specimen appears to have been mounted when teneral), and is deposited in the ZMA.

The holotype male of *H. maculipleuris* is labeled “E.”

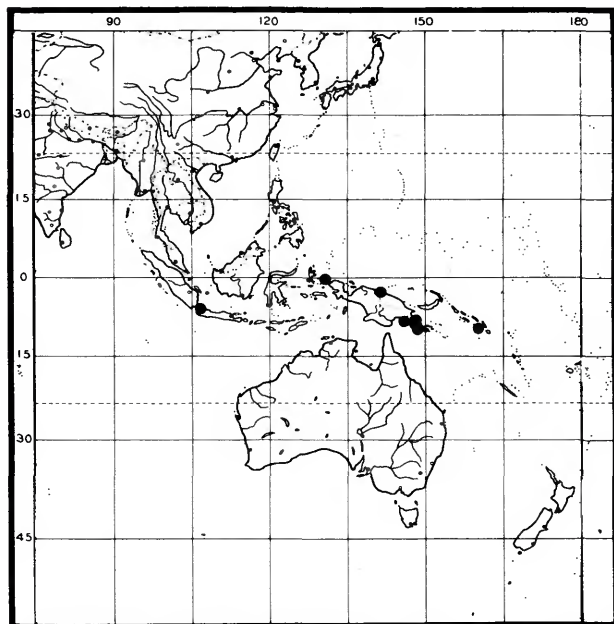


FIGURE 47.—Distribution map for *Hecamede (Hecamede) planifrons*.

Jacobson Moeara Antjol Batavia Nov 1908/*Hemicyclops maculipleuris* det. de Meijere. type [black submargin, species name and “type” handwritten]/HOLOTYPE [red with black border]/HOLOTYPE *Hemicyclops maculipleuris* deMe det. B.H. Cogan 1971. [handwritten except for “det. B.H. Cogan 1971”].” The holotype is double mounted (minuten in a plastic foam rectangular block), is in good condition (Most of the abdomen has been removed and dissected. The parts are in a microvial that is attached to the pin.), and is deposited in the ZMA.

OTHER SPECIMENS EXAMINED.—Australasian/Oceanian: PAPUA NEW GUINEA. Central Province: Cape Rodney (seashore), 24 Jul 1982, J.W. Ismay (1♂, 1♀; USNM); Gabagaba (beach), 2 Feb 1983, J.W. Ismay (1♂; USNM); Yule Island, 1 Jan 1983, J.W. Ismay (2♂, 10♀; USNM). North Province: Gira River near Popondetta (bank of river), 30 Jun 1982, J.W. Ismay (1♀; USNM). West Sepik Province: Wutung (seashore), 12 Nov 1985, J.W. Ismay (2♂; USNM).

SOLOMON ISLANDS. Guadalcanal: Malimbu Point, 12 Nov 1944, J. Laffoon (1♀; USNM).

DISTRIBUTION (Figure 47).—Old World. Australasian/Oceanian: Papua New Guinea and Solomon Islands. Oriental: Indonesia. (Djakarta, Java, Moluccas).

DIAGNOSIS.—As this species is the only known member of the *planifrons* group, the distinguishing characters noted in the “Diagnosis” section of the latter (p. 29) and in the key serve to distinguish this species.

NOTES ON VARIATION.—De Meijere (1914) noted the presence of four scutellar setae in the original description of this species, and the holotype specimen does have four setae on the left side of the scutellum. But only three setae occur on the right side of the scutellum, and the latter is the more typical number for species of *Hecamede*. I interpret the extra seta on the left side to be an aberration, similar to the extra (fourth) setal base on the left side of the face on the same specimen (on the right there are only three facial setae). Consequently I do not attribute much significance to the fourth scutellar seta on the left side. The males from Papua New Guinea has three facial and scutellar setae on each side.

There is also variation in the development of the prescutellar acrostichal setae and presutural seta, characters that had been used to distinguish between the the nominal species *maculipleuris* and *planifrons*. In the large and conspecific series from Papua New Guinea, including males and females, these setae varied from being well developed and conspicuous to either greatly reduced or absent. Thus these names undoubtedly represent a single species.

Subgenus *Soikia* Canzoneri and Meneghini

Soikia Canzoneri and Meneghini, 1969:1484 [type species: *Soikia argentata* Canzoneri and Meneghini, 1969 (= *Hecamede nuda* Wirth), by original designation].—Cogan, 1980:657 (Afrotropical catalog, as a synonym of *Hecamede*).

DESCRIPTION.—Small to medium-sized shore flies, length 1.65 to 3.50 mm; setae generally weak and sparse.

Head: Posterior portion of frons microtomentose and gray colored, (from anterior ocellus posteriad), anterior portion mostly yellow and at most thinly microtomentose; proclinate fronto-orbital seta weak, frequently lacking; intrafrontal setae lacking. Antenna entirely yellow. Conical facial prominence entirely microtomentose, similar to rest of face; clypeal vestiture variable.

Thorax: Mesonotum at most lightly tan, otherwise thorax gray except for tibiae and tarsi, lacking a pleural stripe; chaetotaxy generally weakly developed; acrostichal setae arranged in 3 to 4 more or less regular rows; prescutellar acrostichal setae, presutural seta, and katepisternal seta lacking; setulae on dorsal half of anepisternum reduced, pale colored, inconspicuous.

Abdomen: Considerable diversity, see descriptions under the two included species.

DISTRIBUTION.—Maritime beaches in the Indian and western Pacific oceans. Afrotropical: Kenya, Madagascar, Mozambique, and South Africa. Australasian/Oceanian: Australia.

Palaearctic: Oman.

DISCUSSION.—The species of this subgenus demonstrate considerable variability in the number and coloration of setae, especially those on the head. Specimens of *N. bocki*, for example, sometimes have two fronto-orbital setae, but frequently there is only one seta, and occasionally three setae occur on each side. If there are two, it is not uncommon for one to be pale colored and the other black, the more typical condition. The same applies to the facial setae, the setulae of the antenna, the pedicel in particular, and to a lesser extent to the setae of the rest of the body. The variability is evident in long series (25+ specimens) from a single locality and collection date, and thus I am confident that the variation represents intraspecific differences.

In the key to species of this subgenus, I have recognized the population of *H. nuda* from Oman as distinct but conspecific with African populations. Systematists who accept and use the concept of subspecies would certainly apply it to the Omani population, which is distinct externally but has structures of the male terminalia that are virtually identical with the same structures in conspecific populations from subsaharan Africa.

Key to Species of the Subgenus *Soikia*

1. Facial setae 3 or 4; clypeus microtomentose, dull, grayish; fore femur lacking row of stout setae along posteroventral margin *H. bocki*, new species
Facial setae 2; clypeus bare, shiny black; fore femur with row of stout setae along posteroventral margin 2
2. Inner vertical seta lacking; facial setae pale, whitish; fore tibia entirely yellow, concolorous with mid and hind femora *H. tomentosa*, new species
Inner vertical seta present, although much smaller than outer seta; facial setae black; fore tibia with mid portion dark brown to black *H. nuda* Wirth

Hecamede (Soikia) nuda Wirth

FIGURES 1, 48–53

Hecamede nuda Wirth, 1956:379–380.—Cogan, 1980:657 [Afrotropical catalog].

Soikia argentata Canzoneri and Meneghini, 1969:1484.—Cogan, 1980:657 [synonymy with *H. nuda*].

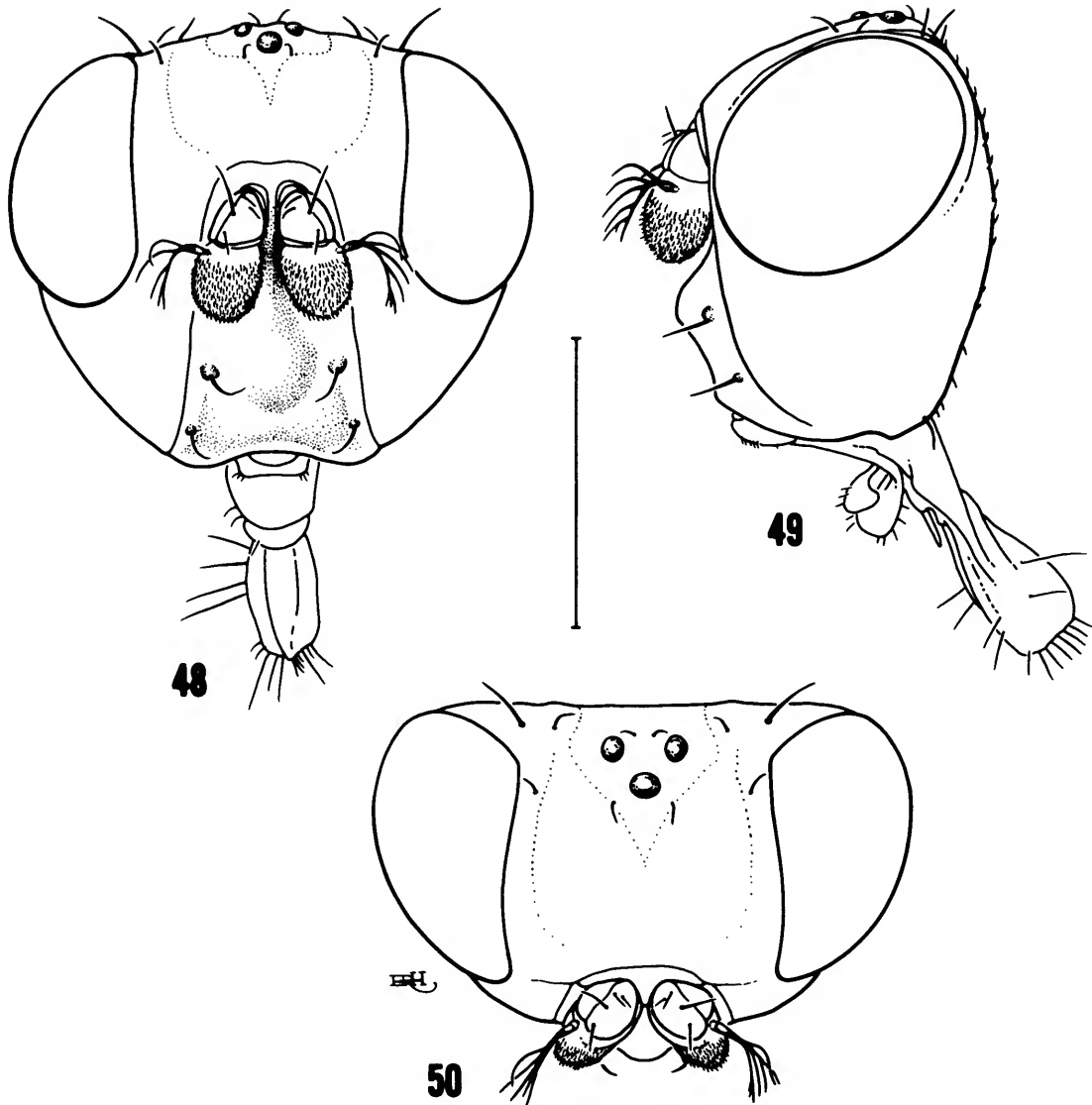
Soikia nuda.—Canzoneri, 1981:203–204 [generic combination, list, Senegal]; 1982:58 [list, Sierra Leone].

DESCRIPTION.—Small to medium-sized shore flies, length 1.90 to 3.5 mm.

Head (Figures 48–50): Fronto-orbits and ocellar triangle densely microtomentose, microtomentum white to whitish gray; mesofrons yellowish orange on anterior portion; setae of frons poorly developed, frequently only 1 fronto-orbital seta that is oriented posterolaterally, if a 2nd is present, proclinate and inserted anteriorly of reclinate seta; ocellar setae weakly developed, inserted slightly anteriorly of anterior ocellus; both inner and outer vertical setae present, although inner seta much

reduced, length about half that of outer seta. Antenna entirely pale, yellowish orange; arista mostly white to lightly mostly yellow, usually bearing 5 dorsal branches, occasionally with fewer. Face entirely microtomentose, microtomentum mostly white with pearly luster and some faint orangish coloration; conical facial prominence rounded in lateral view; facial setae 2, black, arising from bare, basal spots. Gena essentially concolorous with face, lacking black setae; gena high, eye-to-cheek ratio averaging 0.80. Clypeus bare, shiny black.

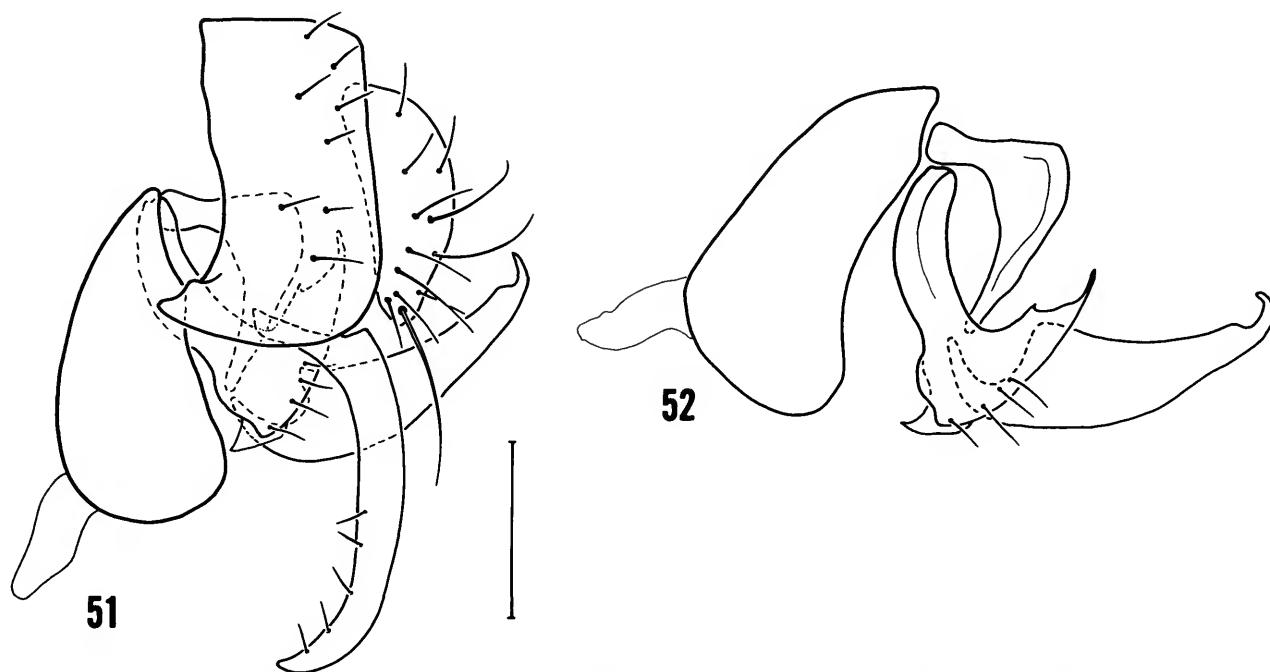
Thorax: Mesonotum densely microtomentose, gray to tan, except for portion immediately dorsad of cervix, which is shiny, black, dorsomedial margin as 2 short, extended areas; pleural areas gray to whitish gray; setae generally sparse and weakly developed, especially evident on disc of scutellum, with 20 or fewer setulae, and anepisternum, both of which have few setulae; acrostichal setulae in 3 or 4 regular rows; lacking a presutural, prescutellar acrostichal, or katepisternal seta and setae that are present frequently pale colored. Posterior surface of fore coxa and adjacent area of katepisternum black, shiny,



FIGURES 48-50.—*Hecamede (Soikia) nuda*: 48, head, anterior aspect; 49, head, lateral aspect; 50, head, dorsal aspect. (Bar = 0.5 mm.)

bare, black area not extended dorsad above level of fore coxa. Legs with femora mostly gray, densely microtomentose; tibiae generally mostly yellow, but fore tibia usually with a ring of dark brown coloration, sometimes dark coloration more extensive; middle tibia with mostly white microtomentum on anterior surface; tarsi mostly yellow except for apical 1-2; fore femur with a conspicuous row of 10 to 12 stout setae along posteroventral margin; fore basitarsus with 2 or 3 black setae inserted toward base on posteroventral surface; hind basitarsus with 2 or 3 long, black setae inserted at base on anteroventral surface. Wing costal vein ratio averaging 0.40; M vein ratio averaging 0.60; last section of vein M straight.

Abdomen: Male terminalia (Figures 51, 52) as follows: 5th tergum more or less evenly sclerotized; epandrium (Figure 51) a more or less parallel-sided, dorsal band; surstylus (Figure 51) in lateral view long and narrow, curved anteriorly, tapered very gradually to acutely pointed apex, anterior margin with a few tiny setulae; cercus (Figure 51) moderately long and narrow, length less than height of epandrium in lateral view; gonite (Figure 52) irregularly and roughly triangular in shape in lateral view, with a narrow connection or gonial arch above aedeagus, lacking a larger, subapical seta; aedeagal apodeme (Figure 52) narrowly triangular in shape in lateral view; aedeagus (Figure 52) long and distinctly tapered toward apex; hypandrium



FIGURES 51, 52.—*Hecamede (Soikia) nuda*: 51, male terminalia, lateral aspect; 52, internal structures of the male genitalia, lateral aspect. (Bar = 0.1 mm.)

shallowly concave and with a median structure anterior, at juncture with sternum.

TYPE MATERIAL.—The holotype male of *Hecamede nuda* is labeled “beach at Umkomaas[,] Natal[,] S. Afr. 9 Dec. 1954[,] B. Stuckenberg/HOLOTYPUS ♂ *Hecamede nuda* ♂ W.W. Wirth [red, species name and gender handwritten]/*Hecamede nuda* Wirth det. W.W. Wirth [species name and author handwritten]/Type No 62814 USNM [red, number handwritten].” The holotype is double mounted (thin wire that is twisted around the main pin), is in excellent condition, and is deposited in the USNM (62814).

The holotype male of *Soikia argentata* is labeled “plage SOMONE SENEGAL 4. X. 1961 [handwritten]/dans detritus vegetaux [handwritten]/HOLOTYPUS ♀ *Soikia* gen. n. *argentata* sp. n. [red, handwritten except for “HOLOTYPUS”].” The holotype is double mounted (pin in a rectangular card), is in good condition (the abdomen has been removed and dissected, and the parts are in a microvial that is attached to the pin), and is deposited in the MNHN.

OTHER SPECIMENS EXAMINED.—Afrotropical: **KENYA**. Gazi (60 km S Mombasa, Rt. A14), 5 May 1991, A. Freidberg, F. Kaplan (2♀; USNM). Mombasa, 1–3 Jan 1971, A.E. Stubbs (5♂, 4♀; BMNH); Ngomeni (150 km N Mombasa), 4 Dec 1989, A. Freidberg, F. Kaplan (3♂, 2♀; TAU, USNM).

MADAGASCAR. Antseranana: Sambava (beach), 14 Apr 1991, A. Freidberg, F. Kaplan (2♂; USNM). Toamasina:

Fénérive (beach), Dec 1955, B. Stuckenberg (2♀; USNM). Toliara: Fort Dauphin (beach), 18 Apr 1991, A. Freidberg, F. Kaplan (27♂, 16♀; TAU, USNM); Morondava, 28–31 Mar 1990, W.E. Steiner, C. Kremen, V. Razafimahatratra (1♀; USNM).

MOZAMBIQUE. Lourenço Marques, 1 Jan 1956, B. Stuckenberg (1♂, 1♀; USNM).

OMAN. near Al Ashkara (21°64′N, 59°30′E, 5 m, coastal dunes, to light), 10 Oct 1990, M.D. Gallagher (1♂; NMWL); Dhofar, Mughsail beach (in burrow of turret-building crab, *Ocypode rotundata* Miers), 11 Oct 1990, M.J. Ebejer, J.C. Deeming (1♀; NMWL).

SOUTH AFRICA. Natal: Umkomaas, 11 Oct 1983, A. Freidberg (1♀; USNM); Umkomaas (beach), 9 Dec 1954, B. Stuckenberg (4♂, 1♀; ANSP, NMP, USNM).

DISTRIBUTION (Figure 53).—Old World. Afrotropical: Kenya, Madagascar, Mozambique, South Africa. Palearctic: Oman. Canzoneri (1981, 1982) reported this species from Senegal and Sierra Leone respectively, but I have not studied species from either country in West Africa.

NATURAL HISTORY.—Wirth (1956:380) reported that Stuckenberg, the collector of the type series, found adults of this species resting on the sides of crab burrows (crabs of the genus *Ocypode* Fabricius) within a few inches of the entrance. The burrows are very common in the intertidal zone on the beaches of Natal. The female from Oman was also collected from the

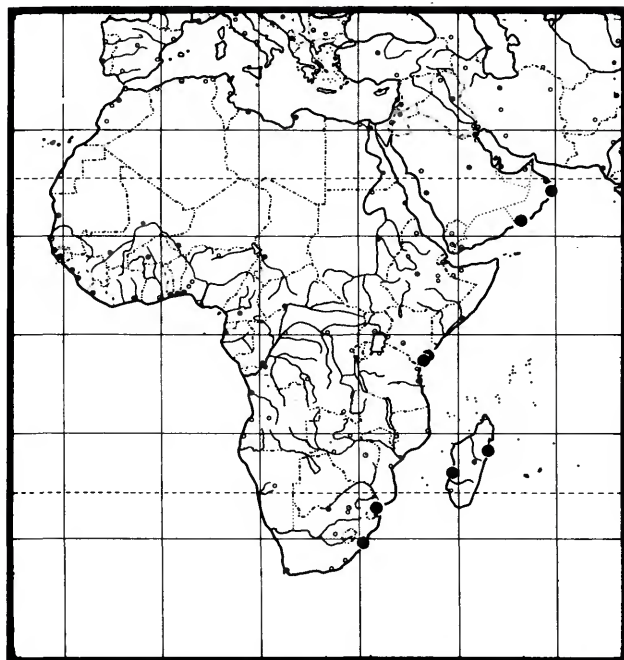


FIGURE 53.—Distribution map for *Hecamede (Soikia) nuda*.

burrow of a turret-building crab, specifically *Ocypode rotundata* Miers. This habitat is also where some Omani specimens of *H. maritima* (see p. 27) were collected and is not unique to this species or subgenus.

DIAGNOSIS.—This species and its sister species, *H. tomentosa*, are very distinctive and are not likely to be confused with any others. The two sister species, although similar, can be distinguished by the characters outlined in the key. In addition, the male terminalia of this species are diagnostic, especially the long, slender and curved surstylus, the gonite, which is pointed ventrally and lacks lobes, and the shorter and more robust aedeagus (Figures 51, 52).

NOTES ON VARIATION.—The population from Oman is quite distinct externally, and I have chosen to recognize its distinctiveness by describing here the external features that characterize it.

Head: Mesofrons yellowish orange on anterior portion; frons laterad and anterior of ocelli with 2 bare bands that extend anteriorly from ocelli; coloration immediately laterad and anterior of ocelli black; setae of frons poorly developed, frequently only 1 weak, fronto-orbital seta that is oriented posterolaterally, if a 2nd is present, proclinate and inserted anterior of reclinate seta; ocellar setae weakly developed, inserted slightly anterior of anterior ocellus. Gena high, eye-to-cheek ratio averaging 0.65.

Thorax: Mesonotum densely microtomentose, gray to tan, except for area immediately dorsad of cervix, which is shiny,

black, dorsomedial margin evenly rounded; pleural areas gray to whitish gray; setae generally sparse and weakly developed, especially evident on disc of scutellum, with 15 or fewer setulae, and anepisternum, both of which have few setulae. Area comprising lateral and posterior surfaces of fore coxa and adjacent area of katepisternum black, shiny, black area extended dorsad to include anterior spiracle. Legs with femora mostly gray, densely microtomentose; fore tibia mostly blackish, only apices mostly yellow; hind basitarsus with 2 to 4 black setae inserted near base on anteroventral surface. Wing costal vein ratio averaging 0.36; M vein ratio averaging 0.60; last section of vein M straight.

Abdomen: As in nominate description.

Available samples suggest that the Omani population is allopatric with those from the subsaharan Africa (Kenya to South Africa). I suspect, however, that additional collecting will reveal more or less continuous populations of this species along most if not all of the east coast of Africa and onto the Arabian peninsula. Moreover, I would be surprised not to find that the variation evident in the Omani population is clinal.

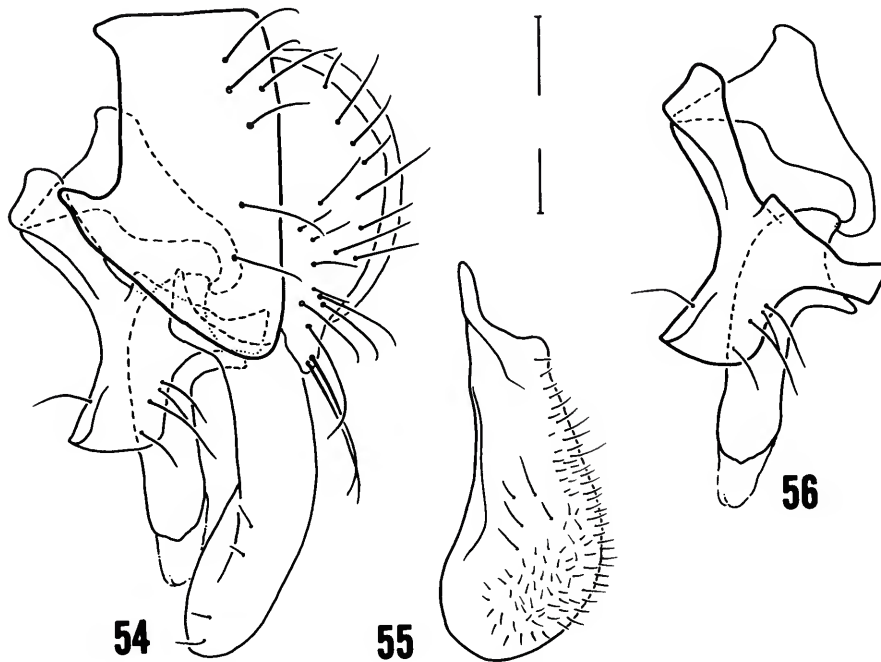
Hecamede (Soikia) tomentosa, new species

FIGURES 54–56

DESCRIPTION.—Moderately small shore flies, length 2.0 to 2.70 mm.

Head: Fronto-orbits and ocellar triangle densely microtomentose, microtomentum white to whitish gray; mesofrons yellowish orange on anterior portion; setae of frons poorly developed, usually no evident fronto-orbital setae; ocellar setae weakly developed, inserted very slightly anterior of anterior ocellus; inner vertical seta lacking, outer vertical seta well developed. Antenna entirely pale, yellowish orange; arista mostly white to lightly mostly yellow, usually bearing 5 dorsal branches, occasionally with fewer. Face entirely microtomentose, microtomentum mostly white with pearly luster and with some faint orangish coloration; conical facial prominence rounded in lateral view; facial setae 2, pale, whitish, arising from bare, basal spots. Gena essentially concolorous with face, lacking any black setae; gena high, eye-to-cheek ratio averaging 0.65. Clypeus mostly bare, shiny black.

Thorax: Mesonotum densely microtomentose, gray to tan, except for portion immediately dorsad of cervix, which is shiny, black, dorsomedial margin as 2 short, extended areas; pleural areas gray to whitish gray; setae generally sparse and weakly developed, especially evident on disc of scutellum with 20 or fewer setulae and anepisternum, both of which have few setulae; acrostichal setulae in 3 or 4 regular rows; lacking a presutural, prescutellar acrostichal, or katepisternal seta, any setae that are present frequently pale colored. Area comprising posterior surface of fore coxa, adjacent area of katepisternum black, subshiny to dull, microtomentose. Legs with femora



FIGURES 54–56.—*Hecamede (Soikia) tomentosa*: 54, male terminalia, lateral aspect; 55, surstylus, posterior aspect; 56, structures of the internal male genitalia, lateral aspect. (Bar = 0.1 mm.)

mostly gray, densely microtomentose; tibiae concolorous, generally mostly yellow; middle tibia with mostly white microtomentum on anterior surface; tarsi mostly yellow except for apical 1–2; fore femur with a conspicuous row of 10 to 12 stout setae along posteroventral margin; fore basitarsus with 2 or 3 black setae inserted toward base on posteroventral surface; hind basitarsus with 2 or 3 long, black setae inserted at base on anteroventral surface. Wing with costal vein ratio averaging 0.38; M vein ratio averaging 0.50; last section of vein M shallowly sinuous.

Abdomen: Male terminalia (Figures 54–56) as follows: 5th tergum more or less evenly sclerotized; epandrium (Figure 54) in lateral view with posterior margin straight, anterior margin with a median pointed process at attachment with internal structures, ventral margin broadly pointed; surstylus (Figures 54, 55) in lateral view 3–4 × longer than wide, slightly broader towards apex, in posterior view spatulate, very broadly rounded apically and microtrichiose along median and ventral surfaces; cercus (Figure 54) moderately long and narrow, length less than height of epandrium in lateral view; gonite (Figure 56) irregularly and roughly L-shaped in lateral view, arm laterad of aedeagus shorter, broader, and bearing a few setulae; aedeagal apodeme (Figure 56) narrowly and irregularly triangular in lateral view; aedeagus (Figure 56) 3–4 × as long as wide, base

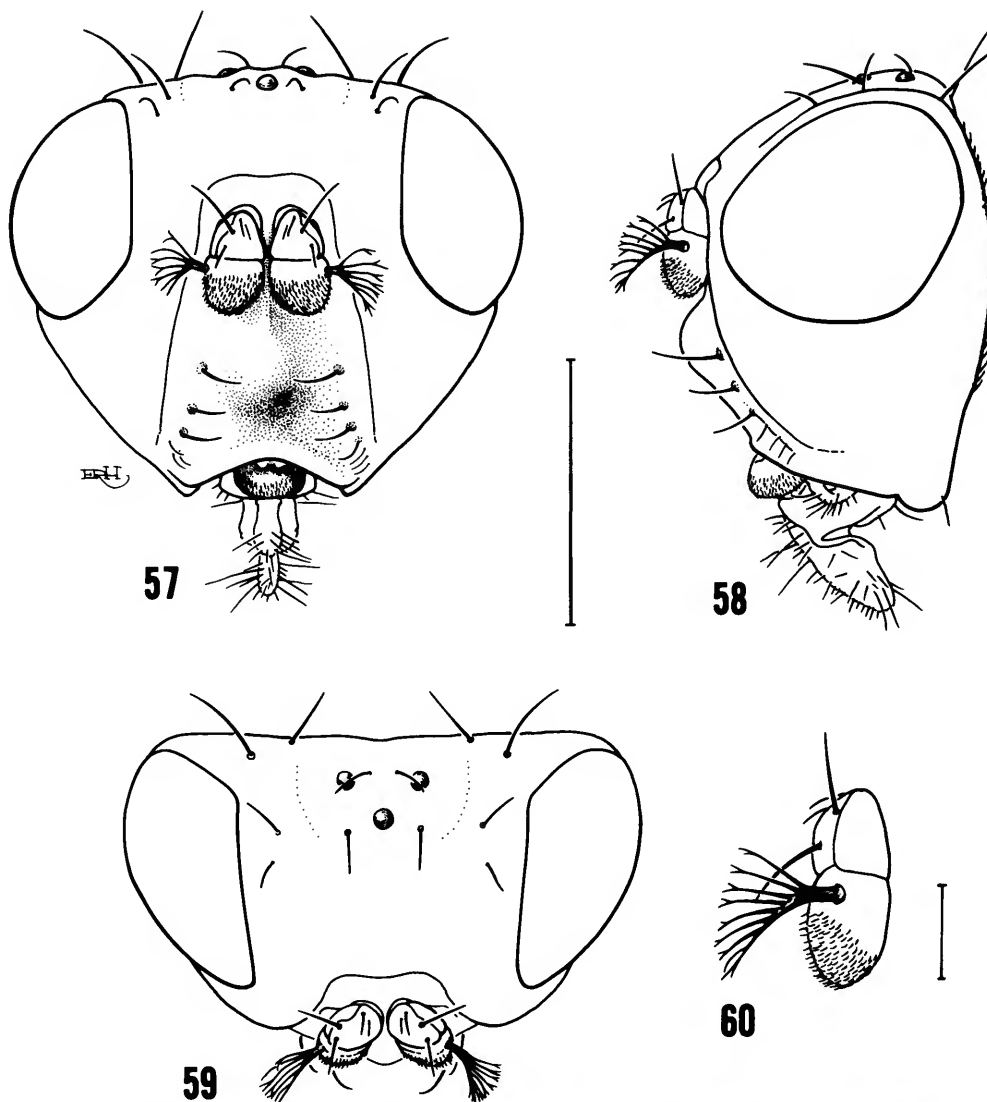
short and curved as right angle to main plain, slightly tapered towards apex; hypandrium shallowly concave, nearly flat, more or less trapezoidal, narrower end produced as 2 small projections that attach with remainder of terminalia.

TYPE MATERIAL.—The male holotype is labeled “NIGERIA Lagos (shore) 15.XII.1987 [15 Dec 1987] AMNON FREIDBERG.” The allotype female and three additional paratypes (3♀; USNM) are from Cameroon. Kribi (beach), 28–29 Nov 1987, A. Freidberg, F. Kaplan. The holotype is double mounted (minuten in a polyporus block), is in excellent condition (the abdomen has been removed, dissected, and the parts stored in an attached microvial), and is deposited in the USNM.

DISTRIBUTION.—Afrotropical: Cameroon and Nigeria.

ETYMOLOGY.—The species epithet, *tomentosa*, is of Latin derivation and refers to the completely microtomentose face of this species.

DIAGNOSIS.—This is the sister species of *H. nuda* and is distinguished from the latter by the lack of an inner vertical seta, the presence of pale colored facial setae, and the completely, mostly yellow fore tibia that is concolorous with the tibia of the mid and hindlegs. Characters of the male terminalia also distinguish this species, especially the surstylus (Figures 54, 55), which is broadly spatulate apically in posterior view, not thinly parallel sided as in *H. nuda*.



FIGURES 57-60.—*Hecamede (Soikia) bocki*: 57, head, anterior aspect; 58, head, lateral aspect; 59, head, dorsal aspect; 60, antenna, lateral aspect.

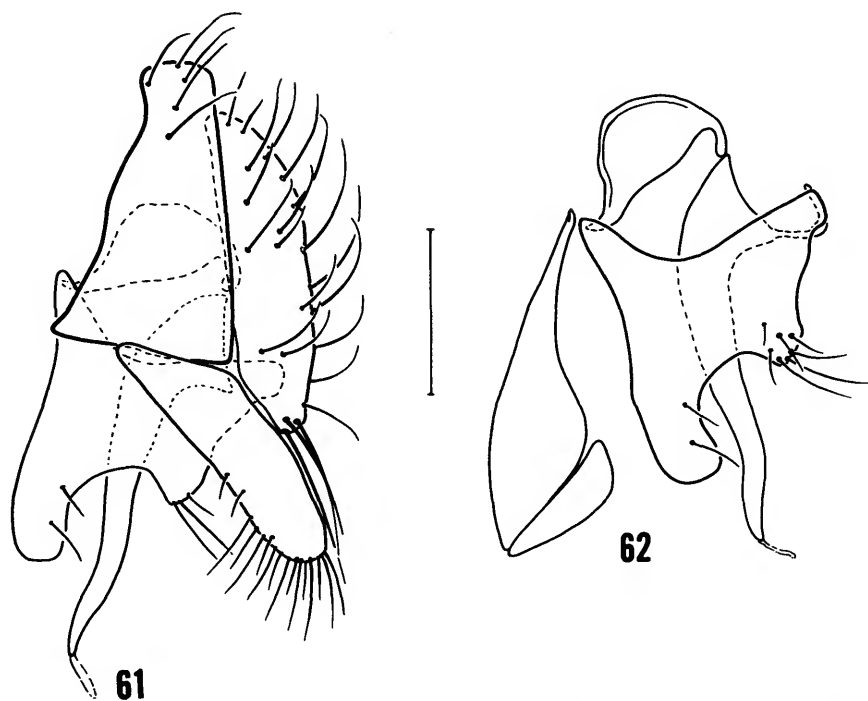
Hecamede (Soikia) bocki, new species

FIGURES 57-63

DESCRIPTION.—Small to medium-sized shore flies, length 1.65 to 3.00 mm.

Head (Figures 57-60): Fronto-orbits and ocellar triangle densely microtomentose, microtomentum white to whitish gray; mesofrons yellowish orange on anterior portion; setae of frons poorly developed, frequently only 1 fronto-orbital seta that is oriented posterolaterally, if a 2nd is present, proclinate and inserted anteriorly of reclinate seta; ocellar setae weakly

developed, inserted slightly anteriorly of anterior ocellus. Antenna entirely pale, yellowish orange; arista mostly white to lightly mostly yellow, usually bearing 5 dorsal branches, occasionally with fewer. Face entirely microtomentose, microtomentum mostly white with pearly luster and with some faint yellowish orange coloration; conical facial prominence rounded in lateral view; facial setae 3 or 4, arising from bare, basal spots. Gena essentially concolorous with face, lacking any black setae; gena high, eye-to-cheek ratio averaging 0.80. Clypeus black, but moderately invested with white microtomentum.



FIGURES 61, 62.—*Hecamede (Soikia) bocki*: 61, male terminalia, lateral aspect; 62, internal structures of the male genitalia, lateral aspect. (Bar = 0.1 mm.)

Thorax: Mesonotum densely microtomentose, gray to tan; pleural areas gray to whitish gray; setae generally sparse and weakly developed, especially evident on disc of scutellum and anepisternum, which lack large setulae; acrostichal setulae in 3 more or less regular rows; lacking a presutural, prescutellar acrostichal, or katepisternal seta, and any setae that are present frequently pale colored. Legs with femora mostly gray, densely microtomentose; tibiae, including fore tibia, generally yellow but with silvery white microtomentum; tarsi mostly yellow except for apical 1–2; fore femur unadorned; setae at base of hind basitarsus all yellowish orange. Wing costal vein ratio averaging 0.42; M vein ratio averaging 0.55; last section of vein M very shallowly curved posteriorly.

Abdomen: Male terminalia (Figures 61, 62) as follows: 5th tergum more or less evenly sclerotized; epandrium (Figure 61) a dorsal band that becomes wider ventrally; surstylus (Figure 61) in lateral view a broad, digitiform, parallel-sided process, straight, broadly rounded ventrally, ventral margin setulose; cercus (Figure 61) moderately long, length about equal to height of epandrium, and narrow; gonite (Figure 62) asymmetrically bilobed ventrally, anterior lobe larger, bluntly rounded ventrally, posterior lobe short, pointed ventrally, bearing several setae, connection or gonial arch above aedeagus, lacking a larger, subapical seta; aedeagal apodeme (Figure 62) semicircular in lateral view; aedeagus (Figure 62) long and narrow, tapered gradually to apex, shaped like a pipe, with nearly right angle curve at basal $\frac{1}{4}$ to $\frac{1}{3}$; hypandrium

becoming wider anteriorly, narrowly and shallowly emarginate along anterior margin.

TYPE MATERIAL.—The holotype male is labeled “[Australia] Deewhy, New South Wales 15, I.1957 [date handwritten]/ W W Wirth Collector/HOLOTYPE *Hecamede bocki* ♂ W.N. Mathis [species name and gender handwritten, red].” The allotype female and 49 paratypes (dates vary from Jan–Feb 1957; 17♂, 32♀; USNM) bear the same locality data as the holotype. The holotype is double mounted (minuten in a polyporus block), is in excellent condition, and is deposited in the ANIC. Other paratypes are as follows: **AUSTRALIA.** Australian Capital Territory. Cotter-M’bidgee R’s Junction, 29 Nov 1962, D.H. Colless (1♂, 1♀; ANIC). New South Wales. Como, Dec 1923, H. Petersen (1♀; USNM); Cronulla, 3 Feb–3 Apr, 1962, 1964, D.K. McAlpine (6♂, 7♀; AMS); Euston (9 mi E), Lake Benanee, 13 Jan 1964, Z. Liepa (2♂; ANIC); Toukley, 18 Jan 1963, Z. Liepa (1♂; ANIC).

DISTRIBUTION (Figure 63).—Australasian/Oceanian: Australia (ACT, NSW).

ETYMOLOGY.—It is a pleasure to name this species after Dr. Ian R. Bock, who has contributed much to our knowledge of Australian Ephydroidea, especially the family Drosophilidae but more recently on the Ephydriidae as well.

DIAGNOSIS.—This is the only species in the Australasian/Oceanian Region with a completely microtomentose face, including the apex of the conical, facial prominence. It is distinguished from *H. nuda* by the greater number of facial

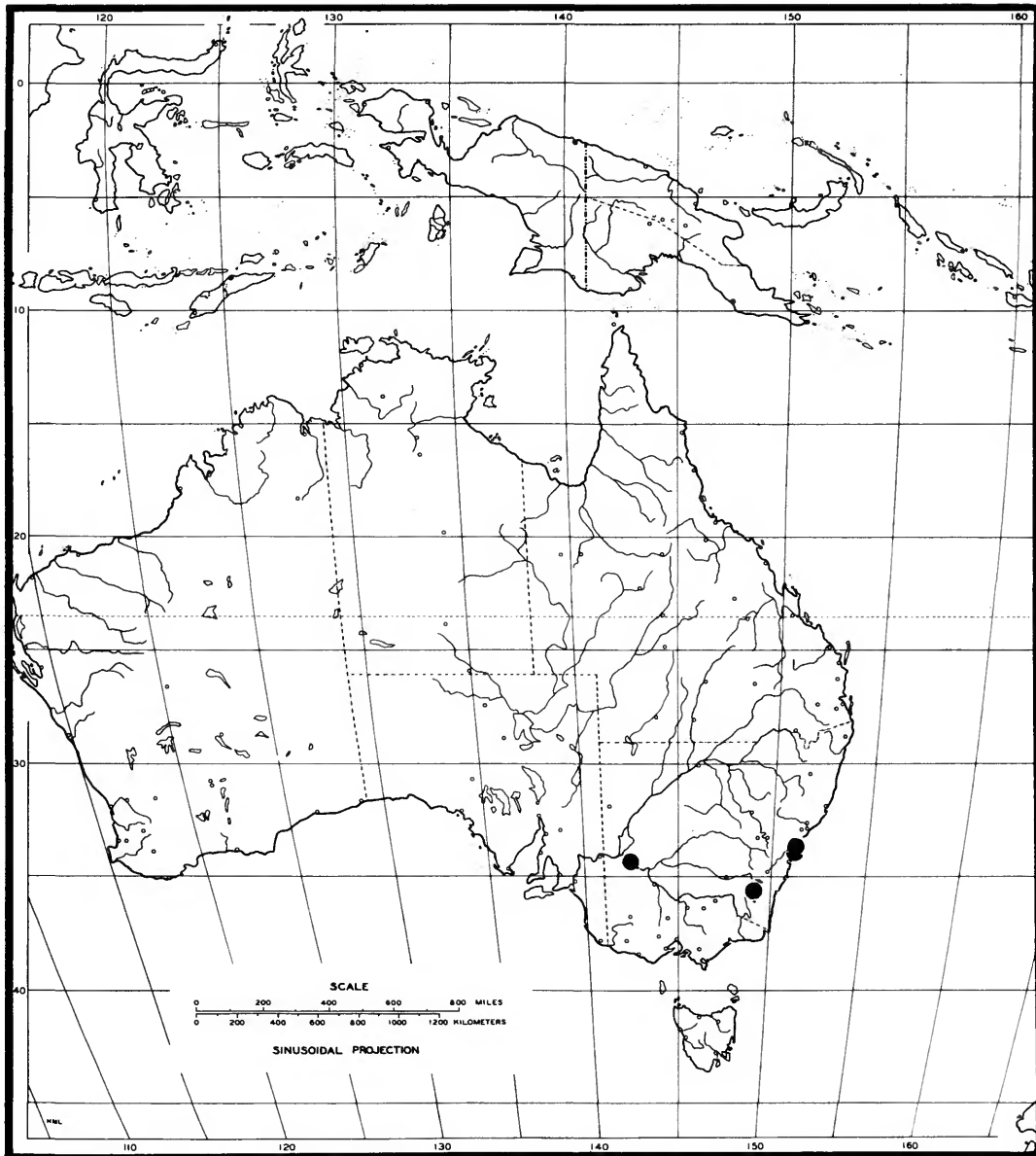


FIGURE 63.—Distribution map for *Hecamede (Soikia) bocki*.

setae, 3 or 4 all pale, by the microtomentose clypeus, and by the lack of a row of setae along the posteroventral margin of the fore femur. The structures of the male terminalia differ significantly from those of *H. nuda*, especially the bilobed gonite, finger-like and straight surstylus, and more slender aedeagus (Figures 61, 62).

Phylogenetic and Biogeographical Considerations

Hecamede is the nominate genus of the tribe Hecamedini

(Mathis, 1991), and within this tribe, it is most closely related to *Allotrichoma* Becker (sensu lato, including *Pseudohecamede* Hendl as a subgenus) and *Eremotrichoma* Giordani Soika. These three genera form a clade that is distinguished from related taxa by the following synapomorphies that also establish its monophyly: 4th segment of male abdomen elongate, 5th segment usually not visible, at least dorsally, retracted within 4th; oral margin narrow; clypeus narrow; ventral margin of face concave; middle of face with slight to pronounced conical or carinate prominence (the degree of facial prominence is quite variable). Of the two other genera

that comprise this group, *Hecamede* appears to be more closely related to *Eremotrichoma*, with confirming synapomorphies as follows: palpus pale and tibiae generally pale colored, usually yellow to yellowish orange but often with some to considerable investment of microtomentum that is white to gray. This sister-group relationship (*Hecamede* + *Eremotrichoma*), however, is based on characters of color, and the status of these characters as synapomorphies must be considered provisional as elsewhere in the Ephydriidae this kind of character is known to vary. Because I am not wholly convinced of the sister-group relationship between *Hecamede* and *Eremotrichoma*, given the lack of more and better collaborative evidence (congruence with other characters), I have considered *Allotrichoma* plus *Eremotrichoma* as the outgroup of *Hecamede* and as the basis by which the character states are polarized. This approach is somewhat between the strict use of an outgroup, a specific taxon such as the type species of *Eremotrichoma*, and Hennig's system of a "groundplan," which uses an hypothetical taxon.

Before proceeding with the analysis of species relationships within *Hecamede*, it is important to establish the monophyly of the genus. Unlike the putative sister-group relationships, the monophyly of *Hecamede* is rather compelling and is established by several synapomorphies as follows: fore femur swollen, especially when compared with femora of the middle and hind legs; postgenal margin sharp (this character has apparently developed independently in other lineages such as the tribe Gymnomyzini); gena high, over $\frac{1}{2}$ height of eye; katapisternum with one large seta and numerous smaller setae anteriorly of larger seta; scutellar disc with numerous, scattered setae; scutellum bearing three large pairs of setae along lateral margin (first noted by Dahl, 1959); wing membrane lacteous (this character also occurs in some Gymnomyzini); and acrostichal setulae in 3 or more rows. With the integrity of *Hecamede* as a monophyletic lineage intact, the next step in the phylogenetic analysis is to focus on the relationships among the included species.

In the presentation on species relationships that follows, the characters used in the analysis are noted first. Each character is immediately followed with a discussion to explain its states and to provide perspective and any qualifying comments on that character. After presentation of the information on a character, an hypothesis of the cladistic relationships is presented and discussed. The cladogram (Figure 64) is the primary mode to convey these relationships; the discussion is a supplement to the cladogram and is intended only to complement the latter. In the discussion of character data, a "0" indicates the state of the outgroup, "1" and "2" indicate respectively more derived states except for specific characters that are nonadditive. The coding for nonadditive characters is reviewed on a character by character basis as indicated in the text. The numbers used in the presentation are the same as those on the cladogram (Figure 64), and the sequence is the same as noted in the character matrix (Table 1).

CHARACTERS USED IN THE PHYLOGENETIC ANALYSIS

HEAD

1. Number of proclinate fronto-orbital seta. 0 = 1; 1 = 2; 2 = weakly developed or lacking. In most shore flies there is but one proclinate fronto-orbital seta. The presence of two such setae is a synapomorphy. This character is coded to reflect a transformation series for which both derived states arose independently from the ancestral state (nonadditive); thus for purposes of coding state "1" is ancestral, and "0" and "2" are the two independent, derived states, each one step from the ancestral state. The computer interprets this coding as the two desired states, each one step away from the ancestral or plesiomorphic state.
2. Insertion of posterior proclinate fronto-orbital seta. 0 = inserted distinctly anteriorly of reclinate seta; 1 = inserted slightly anteriorly of reclinate seta (distance between subequal to width of median ocellus); 2 = essentially aligned with reclinate seta. This character is coded to reflect the increasing posterior insertion of this seta.
3. Intrafrontal seta. 0 = lacking or greatly reduced; 1 = present, inserted in front of anterior ocellus.
4. Coloration of antenna. 0 = mostly to entirely dark colored; 1 = mostly to entirely yellow to yellowish orange, at most flagellomere 1 very faintly black dorsally, pedicel mostly yellowish orange, sometimes mostly black dorsally; 2 = flagellomere 1 mostly to entirely blackish orange laterally, more orange medially, pedicel with dorsal surface blackish, otherwise reddish orange.
5. Number of arisal branches. 0 = 5; 1 = 3 or 4.
6. Conical facial prominence. 0 = microtomentose; 1 = bare and shiny.
7. Shape of apex of conical facial prominence (in profile). 0 = rounded; 1 = flat.
8. Genal setae. 0 = a few or several black setae, more or less evenly scattered; 1 = 1 black seta near middle; 2 = bare of setae. This character is coded to reflect a transformation series where both derived states arose independently from the ancestral state; thus the coding for this character is the same that was done for character 1.
9. Height of gena. 0 = conspicuously shorter than eye height; 1 = almost as high as eye height.
10. Clypeal vestiture. 0 = bare; 1 = microtomentose; 2 = bare secondarily.

THORAX

11. Acrostichal setae. 0 = in 4 more or less regular rows; 1 = in about 6 irregular rows.
12. Prescutellar acrostichal setae. 0 = distinctly larger than surrounding setulae; 1 = much reduced, only slightly larger than surrounding setulae.
13. Presutural setae. 0 = well developed; 1 = either greatly reduced or absent.
14. Number of setulae on scutellar disc. 0 = sparse (less than 15); 1 = numerous (more than 20).

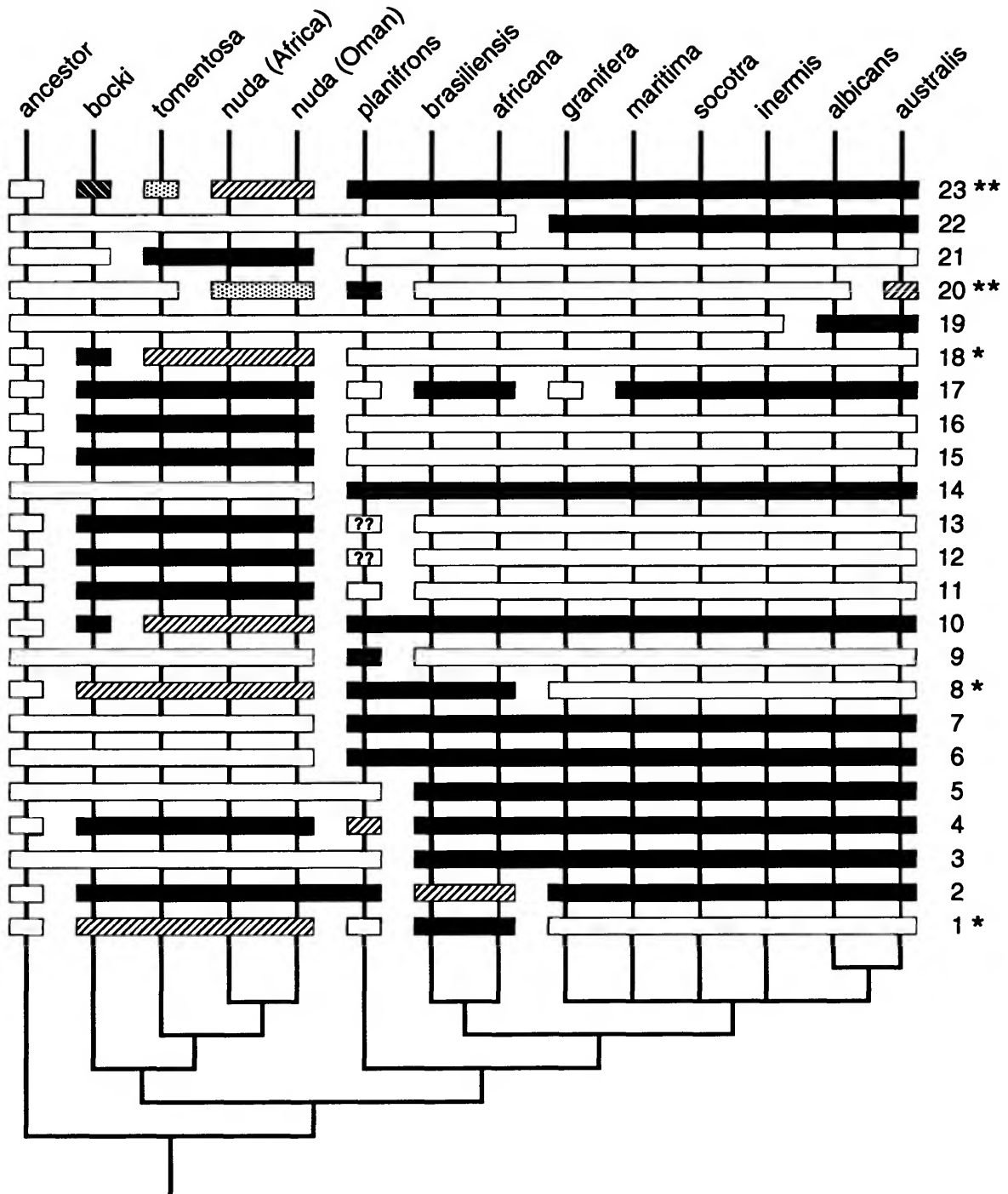


FIGURE 64.—Hypothetical phylogeny for species of *Hecamede*. Numbers correspond with those used in the text.

- 15. Anepisternal setulae. 0 = present, especially on dorsal $\frac{1}{3}$; 1 = reduced and/or lacking.
- 16. Katepisternal seta. 0 = well developed; 1 = absent.
- 17. Adornment of anteroventral surface of fore femur. 0 =

- unadorned, lacking a distinct row of setae along anteroventral margin; 1 = bearing a distinct row of short, slightly stout setae along anteroventral margin.
- 18. Adornment of posteroventral surface of fore femur. 0 =

TABLE 1.—Matrix of Character Data.

| Species | Head (1-10) | Thorax (11-21) | Abdomen (22-23) |
|----------------------|-------------|----------------|-----------------|
| <i>ancestor</i> | 100000100 | 0000011000 | 00 |
| <i>nuda</i> (Africa) | 2101000202 | 01101112031 | 02 |
| <i>nuda</i> (Oman) | 2101000202 | 01101112031 | 02 |
| <i>tomentosa</i> | 2201000202 | 01101112001 | 03 |
| <i>bocki</i> | 2101000201 | 01101110000 | 05 |
| <i>planifrons</i> | 1102011011 | 1??10001010 | 04 |
| <i>africana</i> | 0211111001 | 10010011000 | 01 |
| <i>brasiliensis</i> | 0211111001 | 10010011000 | 01 |
| <i>granifera</i> | 1111111101 | 10010001000 | 11 |
| <i>maritima</i> | 1111111101 | 10010011000 | 11 |
| <i>socotra</i> | 1111111101 | 10010011000 | 11 |
| <i>inermis</i> | 1111111101 | 10010011000 | 11 |
| <i>albicans</i> | 1111111101 | 10010011100 | 11 |
| <i>australis</i> | 1111111101 | 10010010120 | 11 |

bearing 5 to 7 setae on apical $1/2-2/3$; 1 = lacking setae along this surface; 2 = setae along this surface greatly enlarged. This character is coded to reflect a transformation series where both derived states arose independently from the ancestral state; thus the coding for this character is the same that was done for character 1.

19. Fore basitarsus. 0 = lacking black setae at base of posteroventral surface; 1 = bearing 2 or 3 black setae inserted toward base of posteroventral surface.
20. Tibial coloration. 0 = mostly yellow, similar to basal tarsomeres, at most with thin investment of mostly white microtomentum; 1 = fore tibia reddish orange, usually invested with gray to dark gray microtomentum; 2 = especially the fore tibia, mostly grayish, only apices of fore tibia mostly yellow; 3 = fore tibia dark brown medially, mostly yellow at apices. This character was made nonadditive, as polarization beyond that indicated by the outgroup could not be determined.
21. Setae at base of hind basitarsus. 0 = mostly yellow; 1 = 2 to 4 black setae inserted near base on anteroventral surface.

ABDOMEN

22. Length of cerci. 0 = subequal to height of epandrium; 1 = much longer than epandrium.
23. Shape of surstylus in lateral view. 0 = only slightly longer than wide; 1 = long and moderately narrow, posterior margin straight, anterior margin sinuous, narrow at middle, then slightly to moderately enlarged apically, length as long as epandrial height in lateral view; 2 = long and very narrow, curved anteriorly, pointed apically; 3 = long and narrow, curved anteriorly, rounded apically; 4 = broadly expanded and rounded apically; 5 = long, moderately wide, parallel-sided. This character was made nonadditive, as polarization beyond that indicated by the outgroup could not be determined.

The matrix resulting from these data is shown above.

From this matrix, using the implicit enumeration procedure of Hennig86, a single, most parsimonious tree resulted (Figure 64) that has a length of 36 steps, an overall consistency index of 0.94, and a retention index of 0.96. The analysis of each character is given in Table 2.

The two basal lineages or sister groups, which are here recognized as subgenera, are the first division of the cladogram within the genus *Hecamede*. One lineage of this sister-group relationship, the subgenus *Soikia*, comprises but three species; the other, the subgenus *Hecamede*, includes the remaining species of the genus. The latter assemblage, *Hecamede* sensu stricto, is further divided into the two clades that are denoted here as the *planifrons* and *albicans* species groups. The *planifrons* group has only two species, both from the Oceanian Region, and the *albicans* group has eight species that occur throughout much of the Old World and along portions of the eastern coast of the New World.

With the exception of the *albicans* species group, the cladogram is well resolved, and corroboration of the basal relationships is substantiated by numerous synapomorphies. The degree of resolution and abundance of evidence gives one confidence that the relationships at this level on the cladogram are reasonably accurate. Certainly the evidential requirements for the lineages giving rise to the two basal divisions are well met, as are those for the basal lineages of the two species groups within *Hecamede*, sensu stricto. The largely unresolved condition among species in the *albicans* group is problematic, however. Indeed, the species comprising this group are very similar externally, and except for *H. africana* and *H. brasiliensis*, which comprise a monophyletic lineage that is the sister group to the remainder of the *albicans* species group, no additional synapomorphies were discovered that would further resolve the relationships among these species. Although two species, *H. albicans* and *H. australis*, are linked as sister

species in the analysis and cladogram, the evidence for this relationship is weak (the occurrence of the black seta on the ventral surface of the hind basitarsus is apparently quite variable), indicating a questionable sister-group relationship.

The Old World (including Oceania), with 12 species, has a comparatively diverse fauna of *Hecamede* than does the New World, which has but two species. Moreover, the latter two species, *H. albicans* and *H. brasiliensis*, also occur on the Old World. The distributions of these two species and the sister-group relationship between *H. brasiliensis* and the East African endemic *H. africana*, lead one to suspect that both species are adventive to the New World. If this is the case, it would make the name of *H. brasiliensis* somewhat of an anomaly. Although occurring in Brazil, this species may have dispersed there from Africa, where it occurs along with its sister species, *H. africana*.

Recent evidence suggests that *H. brasiliensis* may be susceptible to being transported and introduced, probably passively, as was noted previously in the "Natural History" section under that species (p. 11). It is not surprising, therefore, that it now ranges from the west coast of Africa to the tropical coasts of the Atlantic seaboard of the New World (Brazil to Belize) and finally to the islands of the Galápagos Archipelago.

As both *Eremotrichoma*, the putative sister group of *Hecamede*, and all of the known species of *Hecamede* occur in the Old World, it is likely that the lineage that gave rise to these

taxa originated there. Based on the present-day distributions of the included species, especially those that arose from basal lineages, a reasonable case could be advanced for an origin of the genus (at least its basal most lineage) to have occurred along the maritime coasts somewhere within the basin of the Indian Ocean. Thereafter, through a succession of speciation events associated with range expansion (dispersal), division (vicariance), and isolation, that lineage became subdivided into at least the 12 species that now comprise the genus. The two species that now occur in the New World, probably dispersed there from Old World origins through subsequent range expansion or introductions.

In summary, the genus *Hecamede* is a monophyletic assemblage of 12 known species within the tribe Hecamedini. The included species are arrayed, according to the proposed phylogeny, into a classification of two subgenera, *Soikia* (three species) and *Hecamede* (nine species). In the latter subgenus there are two species groups, the *planifrons* group, with one species, and the *albicans* group, with eight species. The relationships between species of the *albicans* group are at present largely unresolved. The sublineages of the genus just elaborated are also monophyletic. The genus probably had its origin in the Old World, perhaps within the basin of the Indian Ocean where there is greatest species diversity and where taxa from all major lineages within the genus and the outgroup are represented.

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