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A REVISION AND PHYLOGENETIC STUDY OF *ACTOCETOR* BECKER (DIPTERA: EPHYDRIDAE)

Torsten Dikow and Wayne N. Mathis

(TD) Universität Rostock, Germany; National Museum of Natural History, Research Training Program, Smithsonian Institution, Washington, D.C. 20560-0169, USA (e-mail: torsten.dikow@stud.uni-rostock.de); (WNM) Department of Systematic Biology, Entomology Section, NHB 169, Smithsonian Institution, Washington, D.C. 20560-0169, USA (e-mail: mathis.wayne@nmnh.si.edu)

Abstract.—The genus *Actocetor* Becker is revised, including a phylogenetic analysis of the seven recognized species. Two new species, ***Actocetor afrus*** (Liberia and Senegal) and ***A. yaromi*** (Ethiopia), are described. *Actocetor hendeli* de Meijere, *A. margaritatus* (Wiedemann), and *A. panelii* Frey are **new junior synonyms** of *A. indicus* (Wiedemann), and *A. beckeri* de Meijere and *A. elegans* Hendel are **new junior synonyms** of *A. nigrifinis* (Walker). Lectotypes, all females, are designated for the following species: *Notiphila indica* Wiedemann, *Ephydra margaritata* Wiedemann, *Opomyza nigrifinis* Walker, and *Actocetor beckeri* de Meijere. The cladistic analysis is based on 29 morphological characters and resulted in 10 equally most parsimonious trees (length of 60 steps and consistency and retention indices of 0.83 and 0.83 respectively). Three trees then resulted from application of successive weighting, and from these a strict concensus tree was derived that is typologically identical to one of the original 10 trees. From the consensus cladogram, the following hypotheses can be made: (1) *Actocetor* is monophyletic and (2) the subgenera *Actocetor* Becker (4 species) and *Poecilostenia* Bezzi (3 species) are each monophyletic. Although we suggest an Afrotropical origin for *Actocetor*, the genus could have resulted from speciation events in the Oriental Region. Keys for the identification of all genera of Discomyzini and the species of *Actocetor* are provided. The distribution of all species of *Actocetor* and the biology of *A. indicus* from a coastal site in Israel are discussed.

Key Words: *Actocetor*, Discomyzini, Ephydridae, phylogeny

Shore flies are attractive to study because they are "... a family of flies in the full flower of its evolution" (Oldroyd 1964: 189). Although appealing for research, many nonspecialists consider the adults to be rather drab, being nondescript, usually dark colored, and tiny. There are a few large shore-fly species (>5 mm), and others are comparatively pale colored, but with few exceptions, the drab generalization holds. One notable exception is the genus *Actocetor* Becker, which comprises species with spotted wings and beautifully colored bodies. Like most shore-fly species, however, specimens of *Actocetor* are generally small, with body lengths of usually less than 3.5 mm. This paper is a revision of this distinctive genus.

Although specimens of *Actocetor* are easily recognized by their unique coloration and spotted wings, the species have never been treated comprehensively, and no key

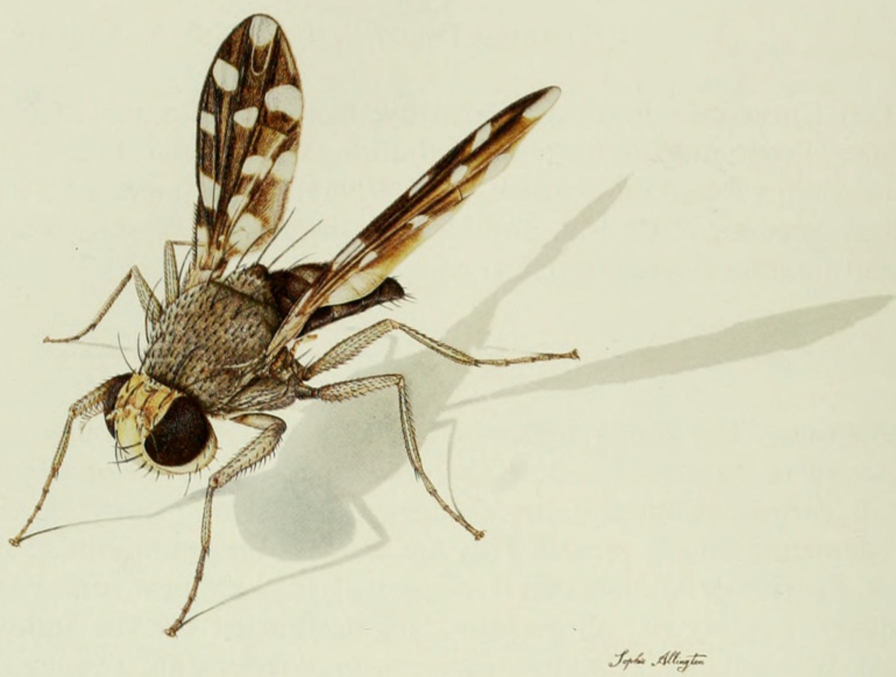


Fig. 1. Color habitus of *Actocetor indicus* (Wiedemann).

is available for all included species. Lacking adequate identification tools, some species were described more than once, sometimes from single females. The objectives of this revision are: (1) to clarify and redescribe all known species, (2) to investigate the phylogenetic relationships among them, (3) to summarize what we know about their biology, distribution, and biogeography, and finally (4) to present a key and illustrations for their identification. A key to the genera of the tribe Discomyzini Acloque is also presented.

Actocetor is known only from the Old World where the genus occurs primarily in the tropical zones of the Afrotropical and Oriental Regions. The most widely occurring species, *A. indicus* (Wiedemann; senior synonym of *A. margaritatus* (Wiedemann)), which is found in the Afrotropical, Oriental, and southern Palearctic Regions, is relatively well known because of its beautiful coloration and spotted wings. Not surprisingly, this species has been reported relatively often in the literature (see species' synonymy). The literature on the other species is meager at best, and virtually nothing about their natural history is recorded in the literature.

The nomenclatural history of *Actocetor* as a genus is mostly confined to the 20th Century when Becker (1903) first proposed the genus with *A. margaritatus* (= *A. indicus*) as its type species. The only generic synonym is *Poecilostenia* Bezzi (1908), which has been given generic or subgeneric status with the latter being more common in recent treatments and catalogs (Wirth 1955, Cogan 1980, Mathis and Zatwarnicki 1995).

The nomenclatural history at the species level, however, is more convoluted, with the type species being an example. Wiedemann (1830) named the type species in the genus *Notiphila,* apparently without realizing that six years earlier (1824) he had described the same species as *Ephydra indica.* This same species was described a third time (Hendel 1917) but using a preoccupied name, *A. beckeri.* De Meijere (1924) recognized the preoccupation and proposed *A. hendeli* as a replacement name. Frey (1958b) described this species yet again, but as a subspecies, *A. margaritatus panelii,* from specimens collected on the Cape Verde Islands. Two other species, *A. nigrifinis* (Walker) and *A. decemguttatus* (Bezzi), have similar histories, each having been described three times. Specimens of these three species are the most common in collections. The nomenclatural histories of the remaining four species of *Actocetor* are relatively uncommon, and correspondingly, not encumbered with synonyms.

Methods and Materials

The descriptive terminology, with the exceptions noted in Mathis (1986) and Mathis and Zatwarnicki (1990a), follows that published in the *Manual of Nearctic Diptera* (McAlpine 1981). Because specimens are small, usually less than 3.5 mm in length, study and illustration of the male terminalia required use of a compound microscope. We have followed the terminology for most structures of the male terminalia that other workers in Ephydridae have used (see references in Mathis 1986, and Mathis and Zatwarnicki 1990a, 1990b), such as surstylus, which in Dryxini is divided into a presurstylus (surstylus) and postsurstylus (clasper). Zatwarnicki (1996) has suggested that the pre- and postsurstylus correspond with the pre- and postgonostylus and that the subepandrial plate is the same as the medandrium. The terminology for structures of the male terminalia is provided directly on Figs. 30–32 and 37–38 and is not repeated for comparable illustrations of other species. Species' descriptions are composite and not based solely on the holotypes. One head and two venational ratios that are used in the descriptions are defined below (all ratios are based on three specimens: the largest, smallest, and one other. Gena-to-eye ratio is the genal height measured at the maximum eye height/eye height. Costal vein ratio is 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}. M vein ratio is the straight line distance along vein M between crossveins dm-cu and r-m/distance apicad of dm-cu.

The phylogenetic analysis was performed using Hennig86©, a computerized algorithm that produces cladograms by parsimony. Character data were polarized using outgroup procedures. Although autapomorphies were not included in the cladistic analysis (they were made inactive), which would skew the consistency and retention indices, we listed them on the cladogram and included them as part of generic treatments and phylogenetic considerations to document the monophyly of the lineages, particularly at the generic level.

Although most specimens are in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM), we also borrowed and studied numerous specimens from the following museums:

AMNH American Museum of Natural History, New York, USA.

BMNH The Natural History Museum (formerly the British Museum (Natural History)), London, England, United Kingdom.

CANZ Personal collection of Silvano Canzoneri, Venezia, Italy, now in Museo Regionale di Scienze Naturali (MRSN), Torino, Italy.

CNC Canadian National Collection, Ottawa, Canada.

MNHN Muséum National d'Histoire Naturelle, Paris, France.

MRAC Musée Royal de l'Afrique Centrale (Koninklijk Museum voor Midden Afrika), Tervuren, Belgium.

MRSN Museo Regionale di Scienze Naturali, Torino, Italy.
MZH Museum Zoological Helsinki, Helsinki, Finland.
NMSA Natal Museum, Pietermaritzburg, South Africa.
NMW Naturhistorisches Museum, Wien, Austria.
NMWL National Museum of Wales, Cardiff, Wales, United Kingdom.
SMN Staatliches Museum für Naturkunde, Stuttgart, Germany.
TAU Tel-Aviv University, Tel-Aviv, Israel.
UZMC Zoologisk Museum, Copenhagen, Denmark.
ZIL Zoological Institute, Lund University, Lund, Sweden.
ZMAN Instituut voor Taxonomische Zoologie, Zoölogisch Museum, Universiteit van Amsterdam, The Netherlands.
ZMHB Zoologisches Museum, Humboldt Universität, Berlin, Germany.

Systematics

Tribe Discomyzini

Discomyzini Acloque 1897: 486. Type genus: *Discomyza* Meigen 1830.

Key to Genera of Discomyzini

1. Vein R_{2+3} lacking a subapical stump vein . . 3
– Vein R_{2+3} bearing a subapical stump vein . . 2
2. Vein R_{4+5} basad of crossvein r-m bearing at most 1–2 tiny, black setulae; wing with irregular, transverse, wide white and brown bands; tibiae yellowish with brown rings; abdomen with maculate pattern of gray and brown microtomentum . . . . *Eremomusca* Mathis
– Vein R_{4+5} basad of crossvein r-m bearing 5–6 setae; wing generally dark with pattern of white spots; tibiae and femora unicolorous, lacking bands; abdomen mostly shiny, lacking maculate pattern . . . . . *Trypetomima* de Meijere
3. Wing hyaline or with anterior margin darkened but not spotted 5
– Wing generally dark with a pattern of white spots 4
4. Facial setae 3–5 but usually 4, all well developed; 1st flagellomere short, length subequal to height of pedicel; pseudopostocellar setae as well developed as large, proclinate, fronto-orbital seta; legs unicolorous . . . . *Actocetor* Becker
– Facial setae 2, only dorsal seta well developed; 1st flagellomere longer than height of pedicel; pseudopostocellar setulae distinctly smaller than large proclinate fronto-orbital seta; tibia or tarsus generally paler colored than femur . . . . *Guttipsilopa* Wirth, subgenus *Guttipsilopa*
5. Alula weakly developed, very narrow 9
– Alula well developed, earlike 6
6. Intrafrontal seta present; fronto-orbital setae 4 (anterior 2 setae proclinate, 3rd lateroclinate, 4th laterореclinate) . . . . . . *Paratissa* Coquillett
– Intrafrontal seta absent; fronto-orbital setae 2–3 7
7. Supra-alar seta well developed, length subequal to postalar seta . . . . *Rhysophora* Cresson
– Supra-alar seta moderately well developed, length about half postalar seta 8
8. Arista bearing 3–5 dorsal rays; facial setae 2, both inserted on ventral 3rd of face; vein R_{4+5} basad of crossvein r-m bearing 3–4 black setulae; legs unicolorous . . . . *Hostis* Cresson
– Arista bearing 7–9 dorsal rays; facial setae sometimes 2 but usually 4 (becoming larger dorsally; sometimes with larger gap between dorsalmost seta and those ventrad) in a vertical row that extends dorsad to midfacial height; vein R_{4+5} basad of crossvein r-m bare; legs dark with yellow tarsus, apical tarsomere dark . . . . *Guttipsilopa* Wirth, subgenus *Nesopsilopa* Mathis and Wirth
9. Prescutellar acrostichal seta absent; katepisternal seta 1; facial setae 3–5, all small and poorly developed; face conspicuously and deeply, transversely rugose; only the reclinate fronto-orbital seta well developed . . . . *Discomyza* Meigen
– Prescutellar acrostichal seta present; katepisternal setae 2, dorsal seta larger; facial setae 2, dorsal pair cruciate, ventral pair poorly developed; face at most with shallowly impressed, transverse striae; at least 1 proclinate fronto-orbital seta in addition to reclinate seta well developed 10
10. Pseudopostocellar setae well developed, length about ½ that of ocellar setae, divergent at usually less than 90° . . . . *Clasiopella* Hendel
– Pseudopostocellar setae weakly developed, length considerably less than ½ that of ocellar setae, orientation variable 11
11. Eye appearing bare; 1 well-developed proclinate fronto-orbital seta (2nd seta greatly reduced) inserted anterior of reclinate seta; presutural supra-alar seta weakly developed,

length less than anterior notopleural seta (except in *M. cressoni* Lizarralde de Grosso); vein R_{4+5} basad of crossvein r-m bearing 2 setulae; legs bicolored . . . *Mimapsilopa* Cresson

– Eye conspicuously setulose; 2 well-developed proclinate fronto-orbital setae, anterior proclinate seta at about same level as large, reclinate seta, posterior proclinate seta inserted posterior of reclinate seta; presutural supra-alar seta well developed, length greater than anterior notopleural seta; vein R_{4+5} basad of crossvein r-m lacking setulae; legs unicolorous, blackish brown . . . . . *Helaeomyia* Cresson

Genus *Actocetor* Becker

Actocetor Becker 1903: 169 [type species: *Ephydra margaritata* Wiedemann 1830 (= *Notiphila indica* Wiedemann 1824), by original designation]; 1926: 28–29 [review of Palearctic species].—Cresson 1929: 170–171 [discussion]; 1945: 66, 75 [distribution of species, key to genera]; 1946: 255–256 [review, Afrotropical fauna].—Wirth 1955: 51–53 [key to Afrotropical species].—Cogan 1980: 659 [Afrotropical catalog]; 1984: 139 [Palearctic catalog].—Mathis and Zatwarnicki 1995: 21–23 [world catalog].

Diagnosis.—Moderately small to medium-sized shore flies, body length 2.20–3.80 mm; head and thorax mostly yellowish with considerable whitish to cinereous microtomentum, abdomen reddish brown to black or dark blue (colors sometimes in combination), mostly bare, shiny.

Description.—*Head:* Insertion of antenna high on head, above dorsal ⅓ in lateral view; frons conspicuously wider than long; only reclinate fronto-orbital seta well developed; proclinate setae reduced, especially posterior seta, latter ½ of anterior seta; pseudopostocellar setae comparatively well developed, usually as large as larger proclinate fronto-orbital, mostly vertical, slightly to moderately divergent and reclinate; both inner and outer vertical setae present, well developed; vertex moderately creased; ocelli arranged in equilateral triangle, distance between posterior ocelli greater than between posterior ocellus and anterior ocellus; posterior ocelli situated immediately anterior to creased vertex. Antenna with 1st flagellomere short, length subequal to height of pedicel; scape not exerted; arista with 7–13 dorsal rays. Face densely invested with microtomentum, otherwise smooth, mostly flat, lacking pits or rugosity; usually 4 (sometimes 3 or 5) strong facial setae, inclinate, dorsalmost 1–2 setae large, cruciate. Eye appearing bare. Proboscis normally developed, not elongate.

Thorax: Generally yellow to pale brown or gray, with some cinereous microtomentum; supra-alar seta well developed, subequal or larger than postalar seta; acrostichal setae arranged in 6–8 irregular rows; prescutellar acrostichal setae present, well developed; postsutural supra-alar seta well developed; scutellum only slightly wider than long, disc densely setulose; basal scutellar seta over ½ length of apical seta; anepisternum with 1 large seta. Wing conspicuously maculate, guttate, generally dark with numerous white spots; subcostal break deeply incised; alula greatly reduced, a narrow band bearing setulae along posterior margin, or almost completely absent and lacking setulae; vein R_{2+3} extended normally to costal margin, lacking a subapical stump vein; vein R_{4+5} bearing 2–15 black setulae dorsally; halter whitish yellow to dark brown. Legs with forebasitarsus concolorous with remaining tarsomeres.

Abdomen: Generally bare of microtomentum, shiny, bronzish dark brown to black; 5th tergite bearing 4–8 well-developed, dorsally erect setae evenly spaced along posterior margin. Male terminalia (Figs. 31–38, 56–60): mostly symmetrical; epandrium generally thickly formed, U-shaped in posterior view, arms projected ventrad, well-developed erect setae along dorsum present or absent, numerous smaller setae present, lateral arms tapered gradually toward ventral apex; cercus in posterior view broadly oval, usually wider ventrally, dorsal apex more narrowly pointed; presurstylus (= surstylus) large, at ventral margin of epandrium, ventromedial surface with a small emargination; postsurstylus (= clasper) much longer than wide, bearing few to numerous setulae, especially apically, apex sometimes bilobed, bearing a postsurstylar process from basomedial surface, process medially and posteriorly directed, usually spatulate (often distinctly so); subepandrial plate broadly U-shaped, base longer than length of arms; aedeagus as a ring, sometimes angulate basally, and sometimes enlarged apically with phalanges that extend laterally or ventrally; aedeagal apodeme in lateral view more or less triangular, angle at attachment with hypandrium thicker; hypandrium bowl- or pouchlike, much narrower at articulation with aedeagal apodeme than with 5th sternite, becoming much wider toward anterior margin, concavity moderately deep.

Distribution.—Old World. Afrotropical (widespread), southern Palearctic (Canary Islands, Egypt, Israel, Oman, Spain, United Arab Emirates), and Oriental (widespread) regions.

Natural history.—The immature stages are unknown. Adults are often associated with sandy substrates, especially where there is highly organic matter, such as animal dung.

Variation.—A few species of *Actocetor* demonstrate variation in the degree and extent of microtomentum on abdominal tergites. The microtomentum usually forms transverse fascia toward the anterior and/or posterior margins and is usually more evident on the third and sometimes fourth tergites. Although most specimens have some microtomentum, there are occasional examples where none is evident or where the transverse fascia are very narrow and the microtomentum is sparse. Sometimes the overlap of the tergite immediately anterior partially obscures the fascia and artificially gives the impression of less or no microtomentum. The actual variation is expressed among conspecific specimens from the same locality and has led some workers to describe a species more than once.

As with microtomentum, the degree of coloration on the tergites can vary intraspecifically from yellow or more commonly yellowish red to metallic blackish blue. We suspect that the paler colored tergites correlate with more teneral specimens and that the dark, metallic color is characteristic of mature, fully sclerotized specimens.

We have used color of microtomentum on the scutellum and at the base of some thoracic setae as a character but caution against too much weight being given to these characters due to some variation. Although the extent of brown to blackish brown coloration is fairly dependable, this character varies and was not always entirely reliable.

Characters that were particularly reliable for diagnosing species were the pattern of wing spots and structures of the male terminalia, but even these demonstrated some variation. Variation in wing spots was mostly limited to size and shape rather than presence or absence. The shape of structures from the male terminalia varied far less. Of greater concern are slight changes in the aspect of a structure being observed and illustrated. These changes can easily give a false impression of variation and lead to misidentification.

Discussion.—*Actocetor* is one of the most easily recognized genera of shore flies, and we have discovered a number of synapomorphies that corroborate the monophyly of the genus. We have divided the corroborating characters into two groups: unambiguous synapomorphies and those with some homoplasy. The unambiguous characters are (parenthetic number as in discussion of characters and matrix): 1(1). 1st flagellomere short (length subequal to width of pedicel; an autapomorphy for *Actocetor*); 2(2). Position of antenna on head high, above dorsal ⅓ in lateral view (an autapomorphy for *Actocetor*); 3(7). Scutellum with apical ¼–¾ dark brown; 4(17). Vein R_{4+5} basad of crossvein r-m bearing 2 to several setulae. Characters showing some homoplasy are: 5(3). Pseudopostocellar setae well developed, as large as proclinate fronto-orbital seta (often or mostly slightly reclinate; a synapomorphy for *Actocetor, Eremomusca, Guttipsilopa,* and *Trypetomima*); 6(4). Face bearing 4 well-developed setae in a vertical row, dorsalmost 1–2 setae cruciate (a synapomorphy for *Actocetor* and *Guttipsilopa*); 7(9). Wing brown with white spots (a synapomorphy for *Actocetor, Guttipsilopa* (*Guttipsilopa*), and *Trypetomima*); 8(11). Alula reduced to a thin, bandlike lobe bearing numerous setulae (a synapomorphy for *Actocetor* (*Actocetor*) and genera *Eremomusca, Mimapsilopa,* and *Trypetomima*) or completely reduced and bearing no setulae (an autapomorphy for *Actocetor* (*Poecilostenia*); and 9(23). Setae on dorsum of epandrium well developed, dorsally erect (a synapomorphy for *Actocetor;* secondarily reduced in species of *Actocetor* (*Poecilostenia*).

We suggest that the genus *Trypetomima* is close to or is the sister group of *Actocetor,* primarily based on its similar wing pattern. *Trypetomima* differs from *Actocetor* in having a shortened vein R_{2+3} that bears a subapical stump vein. *Actocetor* is distinguished from *Trypetomima* by the characters noted in the diagnosis and by most of the characters listed as synapomorphies for this genus. Although we have suggested that *Trypetomima* is the sister group, we also included three other genera (*Guttipsilopa* (*Guttipsilopa*), *Eremomusca,* and *Mimapsilopa*) as outgroups in the phylogenetic analysis.

Narrowing of the wing in *Actocetor* has occurred independently at least twice, in *A. afrus* of the subgenus *Actocetor* and in species of the subgenus *Poecilostenia.* The narrowing in species of *Poecilostenia* is more radical than in *A. afrus,* and the condition in the latter species is somewhat intermediate between *Poecilostenia* and other species of the subgenus *Actocetor* (details more specifically documented under *A. afrus* and *Poecilostenia*). We do not know the basis or any adaptive advantage for narrowing of the wing. Although flight is apparently still possible with the narrowed wing, that condition may affect its efficiency.

KEY TO SPECIES OF *ACTOCETOR*

1. Setulae on vein R_{4+5} basad and apicad of crossvein r-m; vein CuA_1 conspicuously sinuous along posterior margin of discal cell; discal cell with at most 1 white spot (subgenus *Poecilostenia*; Afrotropical) 5
– Setulae on vein R_{4+5} only basad of crossvein r-m; vein CuA_1 nearly straight along posterior margin of discal cell; discal cell with 2–3 white spots (subgenus *Actocetor*) 2
2. Cell r_1 with only 1 sub-basal white spot 4
– Cell r_1 with 2 white spots, 1 sub-basal spot and 1 subapical spot 3
3. Discal cell with 2 white spots (sub-basal spot broadly U-shaped; subapical spot often constricted medially, sometimes forming anterior and posterior spots); cell CuA_1 normally developed, broader than discal cell; basal half of cell CuA_1 white; base of 4th tergite generally with broad anterior band of gray microtomentum (sometimes thin lateral bands on 3rd and 5th tergites present or no microtomentum at all) (Afrotropical: widespread; Oriental: India, Malaysia, Sri Lanka; southern Palearctic: Canary Islands, Egypt, Israel, Oman, Spain, United Arab Emirates) . . . . *A. indicus* (Wiedemann)
– Discal cell with 3 white spots; cell CuA_1 narrower than discal cell, anal margin nearly straight; 1 white spot present in basal half of cell CuA_1; tergites 3–5 with broad bands of gray microtomentum basally (Afrotropical: Liberia, Senegal) . . . . *A. afrus,* new species
4. Cell r_{4+5} with 2 white spots; vein R_{4+5} bearing 2–4 setulae basad of crossvein r-m (Afrotropical: Madagascar) . . . . . *A. hovus* Giordani Soika
– Cell r_{4+5} with 3 white spots (sub-basal spot often small); vein R_{4+5} bearing 5–6 setulae basad of crossvein r-m (Oriental: widespread) . . . . *A. nigrifinis* (Walker)
5. Cell r_1 with 2 white spots, 1 sub-basal spot and 1 medial spot; discal cell without spots but with an apical, crescent-shaped, paler bulla; abdomen mostly microtomentose, tergites 3–7 entirely gray and brown microtomentose (Tanzania) . . . . *A. lindneri* Wirth
– Cell r_1 with only 1 medial, white spot; discal cell spots variable but without an apical bulla; abdomen mostly shiny, only tergites 3–4 with thin gray microtomentose, anterior bands . . . 6
6. Discal cell with 1 medial, white spot; scutellum with apical ½–¾ dark brown (widespread) . . . . *A. decemguttatus* (Bezzi)
– Discal cell without a white spot; scutellum entirely concolorous with yellowish to slightly brownish yellow scutum (Ethiopia) . . . . *A. yaromi,* new species

Subgenus *Actocetor* Becker

Actocetor Becker 1903: 169 [as a genus; type species: *Ephydra margaritata* Wiedemann 1830 (= *Notiphila indica* Wiedemann 1824), original designation].—Wirth 1955: 51 [key].

Diagnosis.—This subgenus is distinguished from the subgenus *Poecilostenia* by the following combination of characters:

Description.—*Thorax:* Mesonotum generally gray to brownish gray microtomentose. Wing alula greatly reduced, thin and bandlike, lobe bearing numerous short to long setulae along posterior margin; anal angle of wing moderately well developed, cell cua_1 much broader or narrower than discal cell; vein CuA_1 nearly straight along posterior margin of discal cell; dorsal surface of vein R_{4+5} bearing 2–6 setulae, only basad of crossvein r-m; discal cell with 2–3 white spots. Knob of halter variously shaped, white to brown.

Abdomen: 5th tergite of male bearing 6–8 well-developed setae along posterior margin; epandrium bearing 4–8 well-developed setae transversely along dorsum; aedeagus basally an angulate, well-sclerotized ring, apical ⅓–½ enlarged in some species as lateral or ventral phalanges; aedeagal apodeme simple, lacking a distinct keel; hypandrium simple, pouch like, narrowed at attachment with aedeagal apodeme, much wider at attachment with 5th sternite.

Discussion.—Specimens of this subgenus are relatively common in collections, and long series from a single locality were typically available, making assessment of variation more convenient and reliable. In addition to being relatively common, two species, *A. indicus* and *A. nigrifinis,* are widespread. The former occurs throughout the Oriental Region and the latter is found throughout Africa with extensions into the Indian Subcontinent and Malaysia as well as into the southern Palearctic Region (Spain, United Arab Emirates). The records from the Indian Subcontinent, the Seychelles, and Malaysia are occurrences in disjunct areas, and as such they may also represent introductions. Sampling error may also be a factor in the apparent disjunctions. A third species of this subgenus, *A. hovus,* is endemic to Madagascar and is the only species of *Actocetor* known from that island, and the fourth species, *A. afrus,* occurs in West Africa (Liberia and Senegal).

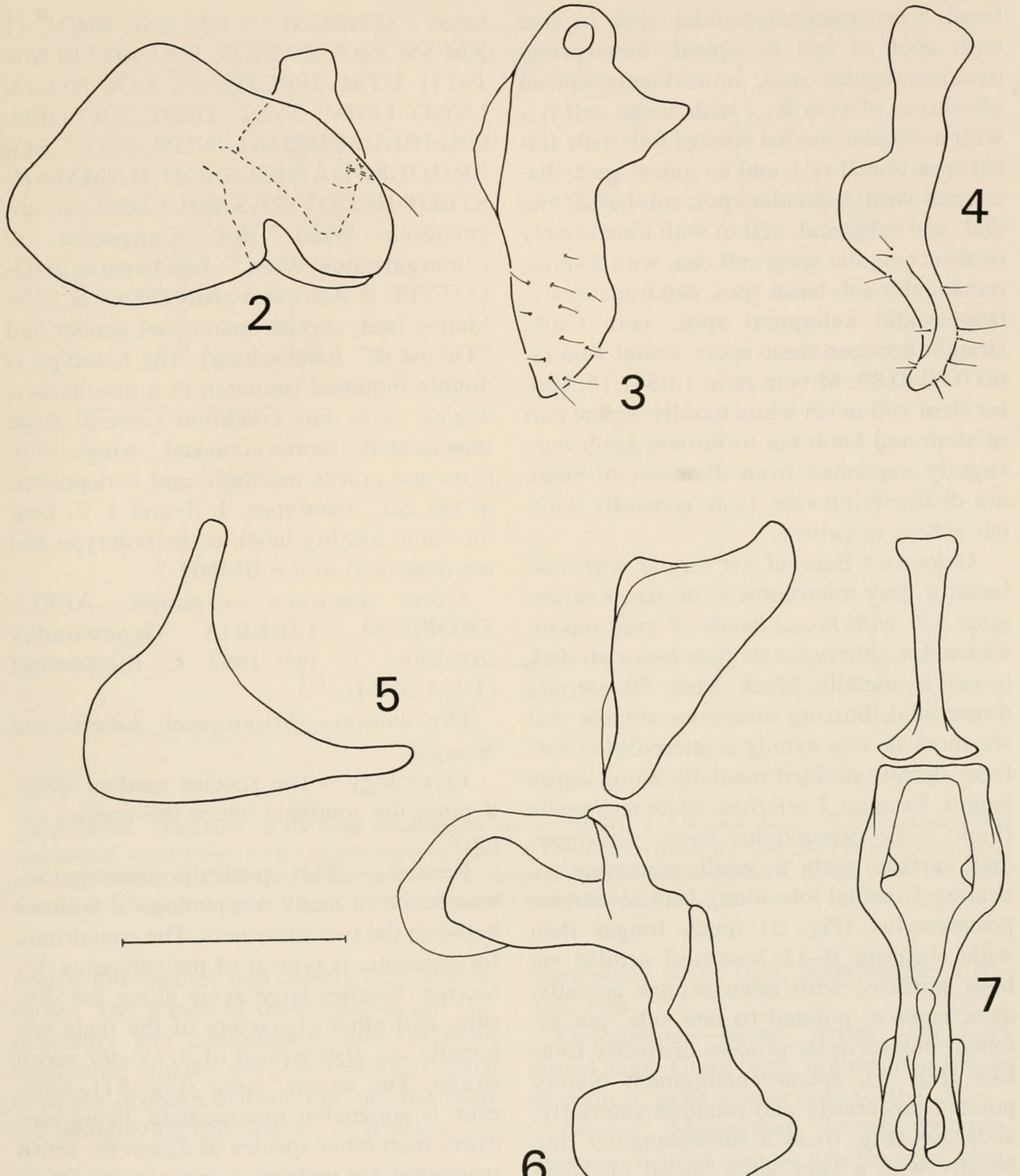
The subgenus *Actocetor* is monophyletic, as indicated on the cladogram (Fig. 65) and as substantiated by the following characters (characters marked with an * are unambiguous): 8*. Color surrounding base of prescutellar acrostichal, posterior dorsocentral, and basal scutellar setae distinctly dark brown; 15*. Discal cell with two white spots; 23*. Dorsum of epandrium bearing well-developed, dorsally erect setae; 25*. Male 5th sternite trapezoidal, divided medially into two sclerites; 26. Postsurstylar process present, expanded ventrally and projected to a point posteriorly (secondarily modified in *A. indicus* and *A. nigrifinis*); 28. Presurstylus bearing one round to oval lobe medially (secondarily modified in *A. indicus* and *A. hovus*).

Actocetor (*Actocetor*) *afrus* Dikow and Mathis, new species
(Figs. 2–7, 51)

Diagnosis.—This species is distinguished from congeners by the following combination of characters: moderately small to medium-sized shore flies, body length 2.10–3.10 mm.

Description.—*Head:* Arista with 9–12 dorsal rays. Gena-to-eye ratio 0.25–0.28.

Thorax: Mesonotum densely microtomentose, tannish gray to whitish gray, pleura whitish to silvery gray; 2 brown bars anteriorly, separated by width equal to that separating prescutellar acrostichal setae; rings at bases of larger setae (prescutellar acrostichal, posterior dorsocentral, basal scutellar setae) dark brown; scutellum with apical ⅓–¼ brown, basal portion concolorous with posterior portion of scutum. Wing (Fig. 51) very narrow, cell cua_1 narrower than discal cell, anal margin nearly straight;



Figs. 2–7. Structures of the male terminalia of *Actocetor afrus*. 2, Presurstylus, posterior view. 3, Postsurstylus, lateral view. 4, Same, posterior view. 5, Postsurstylar process, posterior view. 6, Aedeagus, aedeagal apodeme, dorsal view. 7, Same, lateral view. Scale bar equals 0.1 mm.

alula narrow, bandlike, bearing short setulae (length of setulae equal to height of alula) along posterior margin; vein R_{4+5} bearing 5 setulae basad of crossvein r-m; wing pattern as follows: cell c with basal half white; cell r_1 with transversely rectangular to trapezoidal, basal spot, and oval-rectangular subapical spot; cell r_{2+3} with 2 spots, basal rectangular/trapezoidal spot in line with spot in cell r_1, apical, transversely oval/rectangular spot, immediately apicad of merger of vein R_{2+3} with costa; cell r_{4+5} with a circular medial spot in line with apical spot in cell r_{2+3}, and an apical spot; discal cell with 3 circular spot, sub-basal, medial, and subapical; cell m with transversely oval/rectangular spot; cell cua_1 with 2 spots, rectangular sub-basal spot, and transversely trapezoidal subapical spot, vein CuA_1 straight between these spots; costal vein ratio 0.80–0.89; M vein ratio 1.05–1.15. Halter stem yellowish white basally, apical part of stem and knob tan to brown; knob only slightly expanded from diameter of stem, not distinctly clavate. Legs generally whitish yellow to yellow.

Abdomen: Base of 1st tergite with thin band of gray microtomentum; bases of tergites 3–5 with broad bands of gray microtomentum, otherwise tergites bronzish dark brown to metallic black. Male 5th sternite trapezoidal, bearing numerous setulae that are more or less evenly scattered over surface, sternite divided medially along entire length, forming 2 sclerites. Male terminalia (Figs. 2–7): presurstylus large, ventromedial surface with a small emargination, bearing 1 medial lobe along ventral margin; postsurstylus (Fig. 3) much longer than wide, bearing 9–11 scattered setulae on both surfaces, with more setulae apically, apex tapered, pointed to one side, not bilobed; postsurstylar process distinctly footlike (Fig. 5), apical enlargement bluntly pointed posteriorly and rounded anteriorly; aedeagus (Fig. 6) as a subrectangular ring basally with a very large lateral phalange that extends ventrally; aedeagal apodeme (Fig. 6) in lateral view subtriangular with angle at attachment with base of aedeagus extended and acutely formed; postgonite in ventral view as a sickle shaped process, broader toward attachment with aedeagal apodeme; pregonite short, simple, bearing 2 setulae apically; hypandrium broadly and deeply pouchlike.

Type Material.—The holotype ♂ is labeled "SENEGAL; 3 KM SSE BRIN, 11 KM SW ZIGUINCHOR. 9.XI.1977 [9 Nov 1977] UTM 28PCJ53-83. LOC.NO.22/ LUND UNIV. SYST. DEPT. SWEDEN-GAMBIA/SENEGAL NOV 1977-CEDERHOLM-DANIELSSON-HAMMARSTEDT-HEDQVIST-SAMUELSSON/margaritatus Wied. det. Canzoneri S. ["margaritatus Wied." handwritten]/HOLOTYPE ♂ Actocetor afrus Dikow & W.N. Mathis [red; species' name and gender and "Dikow &" handwritten]. The holotype is double mounted (minuten in a plastic rectangle), is in fair condition (several setae misoriented, thorax cracked, wings with tears and apices missing), and is deposited in the ZIL. Paratypes, 1 ♂ and 1 ♀, bear the same locality label as the holotype and are deposited in the BMNH.

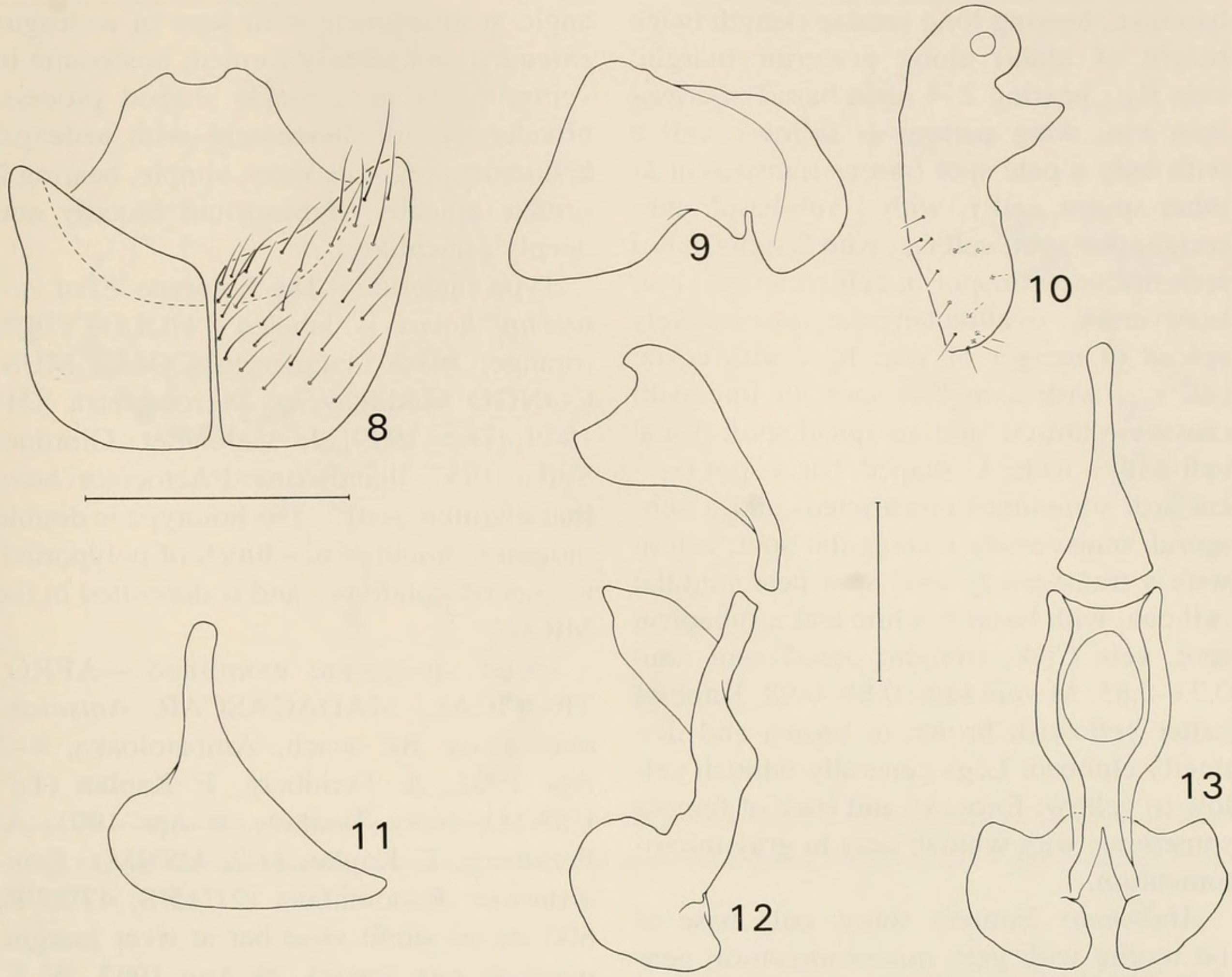
Other specimen examined.—AFROTROPICAL. LIBERIA. Genewonday (roadside), 17 Feb 1953, C. Blickenstaff (1♀; USNM).

Distribution.—Afrotropical: Liberia and Senegal.

Etymology.—The species epithet, *afrus,* denotes the continent where this species occurs.

Remarks.—This species is somewhat intermediate in many morphological features between the two subgenera. The epandrium, for example, is typical of the subgenus *Actocetor,* bearing large setae along the dorsum, and other characters of the male terminalia are also typical of *Actocetor* sensu stricto. The narrow wing (Fig. 51), however, is somewhat intermediate, being narrower than other species of *Actocetor* sensu stricto but not quite as narrow as species of *Poecilostenia.* The alula is narrow and bandlike, and bears some short setulae along the posterior margin, somewhat like *Actocetor* sensu stricto. The anal lobe, however, is narrower and straighter than *Actocetor* sensu stricto but not as narrow and straight as *Poecilostenia.*

The structures of the male terminalia are very similar to those of *A. hovus,* and based on these features alone, we would have sug-



Figs. 8–13. Structures of the male preabdomen and terminalia of *Actocetor hovus*. 8, Fifth sternite and hypandrium, ventral view (only left side showing setae). 9, Presurstylus, posterior view. 10, Postsurstylus, lateral view. 11, Postsurstylar process, posterior view. 12, Aedeagus and aedeagal apodeme, lateral view. 13, Same, dorsal view. Scale bar equals 0.3 mm for Fig. 8 and 0.1 mm for Figs. 9–13.

gested this species was closely related to *A. hovus*. The wings of these species are significantly and consistently different from each other, and the wing characters, coupled with the disjunct distribution, are the basis for recognizing this species as distinct.

Actocetor (*Actocetor*) *hovus* Giordani Soika
(Figs. 8–14, 48)

Actocetor hova Giordani Soika 1956a: 126.—Cogan, 1980: 659 [Afrotropical catalog].—Mathis and Zatwarnicki 1995: 22 [world catalog].

Diagnosis.—This species is distinguished from congeners by the following combination of characters: moderately small to medium-sized shore flies, body length 2.70–3.20 mm.

Description.—*Head:* Arista with 7–11 dorsal rays. Gena high, higher than height of pedicel, gena-to-eye ratio 0.29–0.31.

Thorax: Mesonotum densely microtomentose, tannish gray to whitish gray, pleura whitish to silvery gray; 2 short, dark brown bars anteriorly, separated by width equal to that separating prescutellar acrostichal setae; rings at bases of larger setae (prescutellar acrostichal, posterior dorsocentral, basal scutellar setae) dark brown; scutellum with apical ½–¾ dark brown, basal portion concolorous with posterior portion of scutum. Wing (Fig. 48) normally developed with wide anal angle; alula narrow, bandlike, bearing long setulae (length twice height of alula) along posterior margin; vein R_{4+5} bearing 2–4 setae basad of crossvein r-m; wing pattern as follows: cell c with only a pale spot (not as transparent as other spots); cell r_1 with 1 sub-basal, subrectangular spot; cell r_{2+3} with 2 spots, basal spot in line with spot in cell r_1, apical spot, transversely oval/rectangular, immediately apicad of merger of vein R_{2+3} with costa; cell r_{4+5} with a medial spot, in line with crossvein dm-cu, and an apical spot; discal cell with a wide, U-shaped, basal spot (apical arm sometimes constricted) and a subapical, transversely rectangular spot; cell m with a transversely oval spot near middle; cell cua_1 with basal ⅓ white and a subapical spot, vein CuA_1 straight; costal vein ratio 0.73–0.85; M vein ratio 0.89–0.98. Knob of halter yellowish brown to brown and distinctly clubbed. Legs generally whitish yellow to yellow; forecoxa and base of femora sometimes with whitish gray to gray microtomentum.

Abdomen: Entirely shiny, only base of 1st tergite with gray microtomentum; generally metallic, dark blue, often totally dark blue but sometimes yellow to yellowish red at anterior and/or posterior margins. Male 5th sternite trapezoidal (Fig. 8), bearing numerous setulae that are more or less evenly scattered over surface, sternite divided medially along entire length, making 2 plates. Male terminalia (Figs. 9–13): presurstylus (Fig. 9) large, ventromedial surface with a small emargination, bearing 2 lobes along ventral margin, medial lobe much larger, 1 smaller, thumblike process between medial lobe and expanded base; postsurstylus (Fig. 10) much longer than wide, bearing 7–8 scattered setulae on both surfaces, with more setulae apically, apex bluntly formed and not bilobed; postsurstylar process (Fig. 11) distinctly footlike, apical enlargement pointed posteriorly and rounded anteriorly; aedeagus (Fig. 12) as a subrectangular ring basally with a very large lateral phalange that extends laterally; aedeagal apodeme (Fig. 12) in lateral view subtriangular with angle at attachment with base of aedeagus extended and acutely formed; postgonite in ventral view as a sickle shaped process, broader toward attachment with aedeagal apodeme; pregonite short, simple, bearing 2 setulae apically; hypandrium broadly and deeply pouchlike.

Type material.—The holotype ♂ of *Actocetor hovus* is labeled "HOLOTYPUS [orange; black submargin]/COLL. MUS. CONGO Madagascar: Maroansetra XII-1949 [Dec 1949] J. Vadon/det. Giordani Soika 1957 [handwritten]/Actocetor hova [handwritten; red]." The holotype is double mounted (minuten in a block of polyporus), is in good condition, and is deposited in the MRAC.

Other specimens examined.—AFROTROPICAL. MADAGASCAR. *Antseranana:* Nosy Bé beach, Ambatoloaka, 4–7 Apr 1991, A. Freidberg, F. Kaplan (1♂; USNM); Nosy Tanikely, 6 Apr 1991, A. Freidberg, F. Kaplan (1♀; USNM). *Fianarantsoa:* Ranomafana (21°15′S, 47°27′E; 600 m; on sunlit sand bar at river margin, montane rain forest), 29 Aug 1993, W. E. Steiner (2♀; USNM). *Toamasina:* Maroantsetra, Dec 1949, J. Vadon (1♂ holotype, MRAC; 1♀ paratype, USNM); Perinet, Dec 1955, B. Stuckenberg (1♂, 1♀; NMSA). *Toliara:* Fenerive (coastal forest), Dec 1955, B. Stuckenberg (1♂; NMSA); Ranohira (860 m), 26 Jan–4 Feb 1958, B. Stuckenberg (1♂; NMSA); Sud-Est Sainte Luce, Fort Dauphin (= Taolanaro; 10 m), 22–24 Feb 1953, B. Stuckenberg (1♀; NMSA).

Distribution (Fig. 14).—Afrotropical: Madagascar (Antseranana, Fianarantsoa, Toamasina, Toliara).

Remarks.—Variation is evident in the coloration of the abdomen and to a lesser degree in the size of the white spots in the wing. The abdomen is often entirely dark, metallic blue, but many specimens have some yellow to yellowish red color on the basal tergites, usually toward either the anterior or posterior margins.

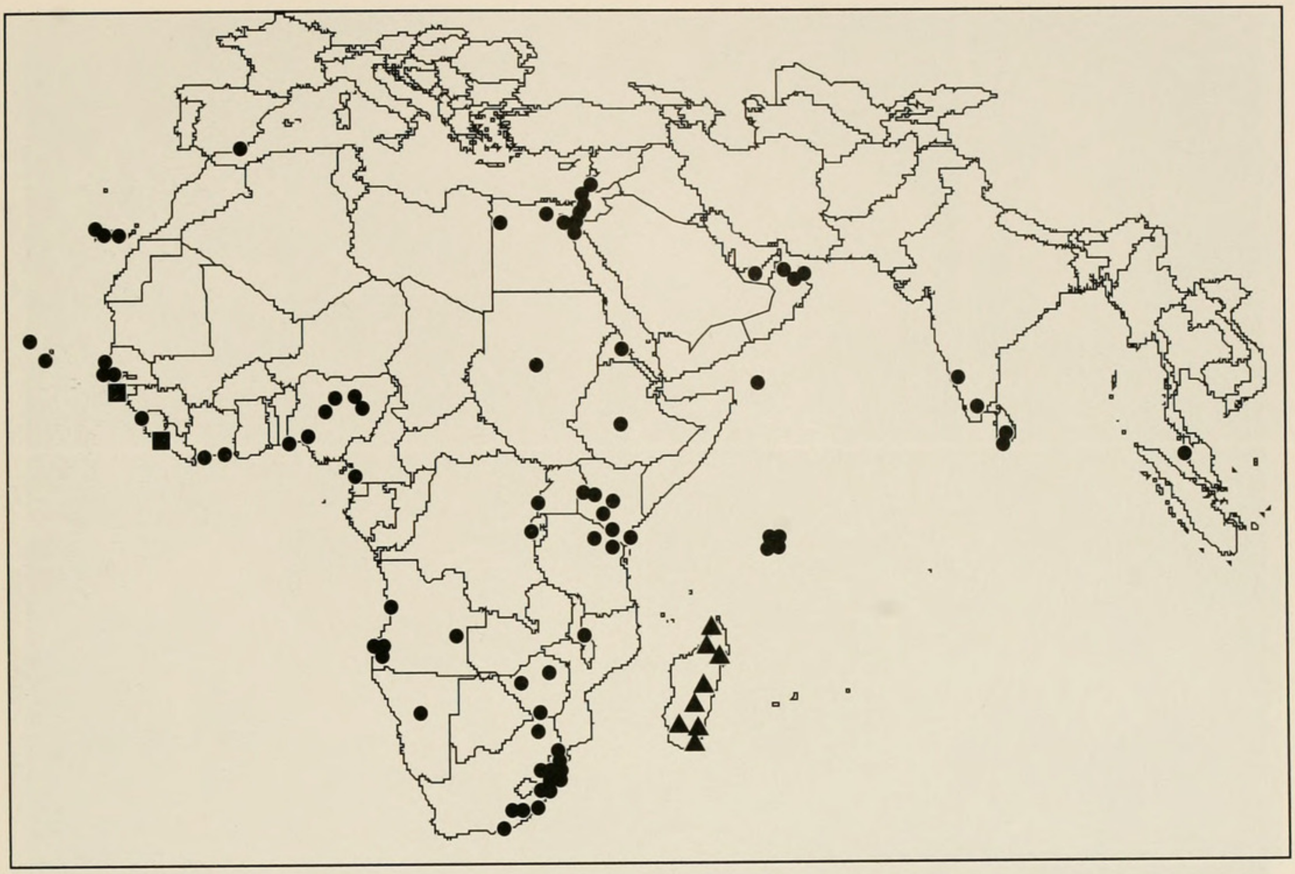


Fig. 14. Distribution map for *Actocetor afrus* (filled squares), *A. hovus* (filled triangles), and *A. indicus* (filled circles).

Actocetor (*Actocetor*) *indicus* (Wiedemann)
(Figs. 1, 14–38, 49)

Notiphila indica Wiedemann 1824: 58.

Actocetor indicus: Cogan and Wirth 1977: 328 [generic combination].—Mathis and Zatwarnicki 1995: 22 [world catalog].

Ephydra margaritata Wiedemann 1830: 594. **New synonym.**

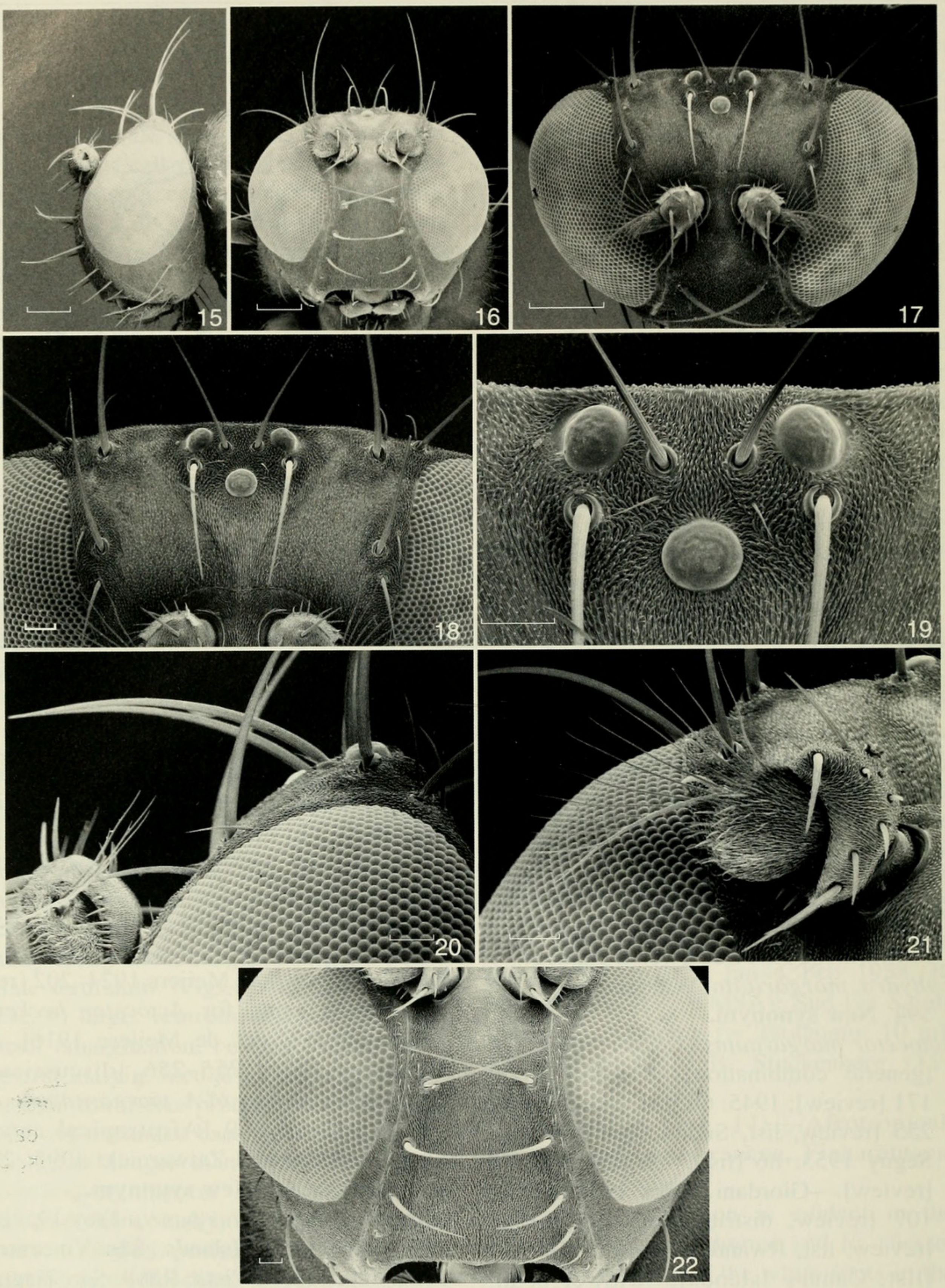
Actocetor margaritatus: Becker 1903: 170 [generic combination].—Cresson 1929: 171 [review]; 1945: 66 [list, India]; 1946: 255 [review, list, Sudan, Zimbabwe].—Séguy 1953: 86 [list].—Wirth 1955: 52 [review].—Giordani Soika 1956b: 106–107 [review, distribution]; 1956c: 503 [review, list, Rwanda].—Frey 1958a: 54 [list, Canary Islands].—Stower et al. 1958: 27 [scavenger in egg pods of desert locusts].—Greathead 1963: 452 [reared from damaged egg pods of desert locusts].—Cogan 1980: 659 [Afrotropical catalog].—Rossi 1988: 174–175 [parasite: *Stigmatomyces rampinii* Rossi (Laboulbeniaceae)].—Mathis and Zatwarnicki 1995: 22 [world catalog].—Canzoneri and Rampini 1996: 12 [list, Sierra Leone].

Actocetor beckeri Hendel 1917: 41 [preoccupied].—Cresson 1946: 255–256 [list].

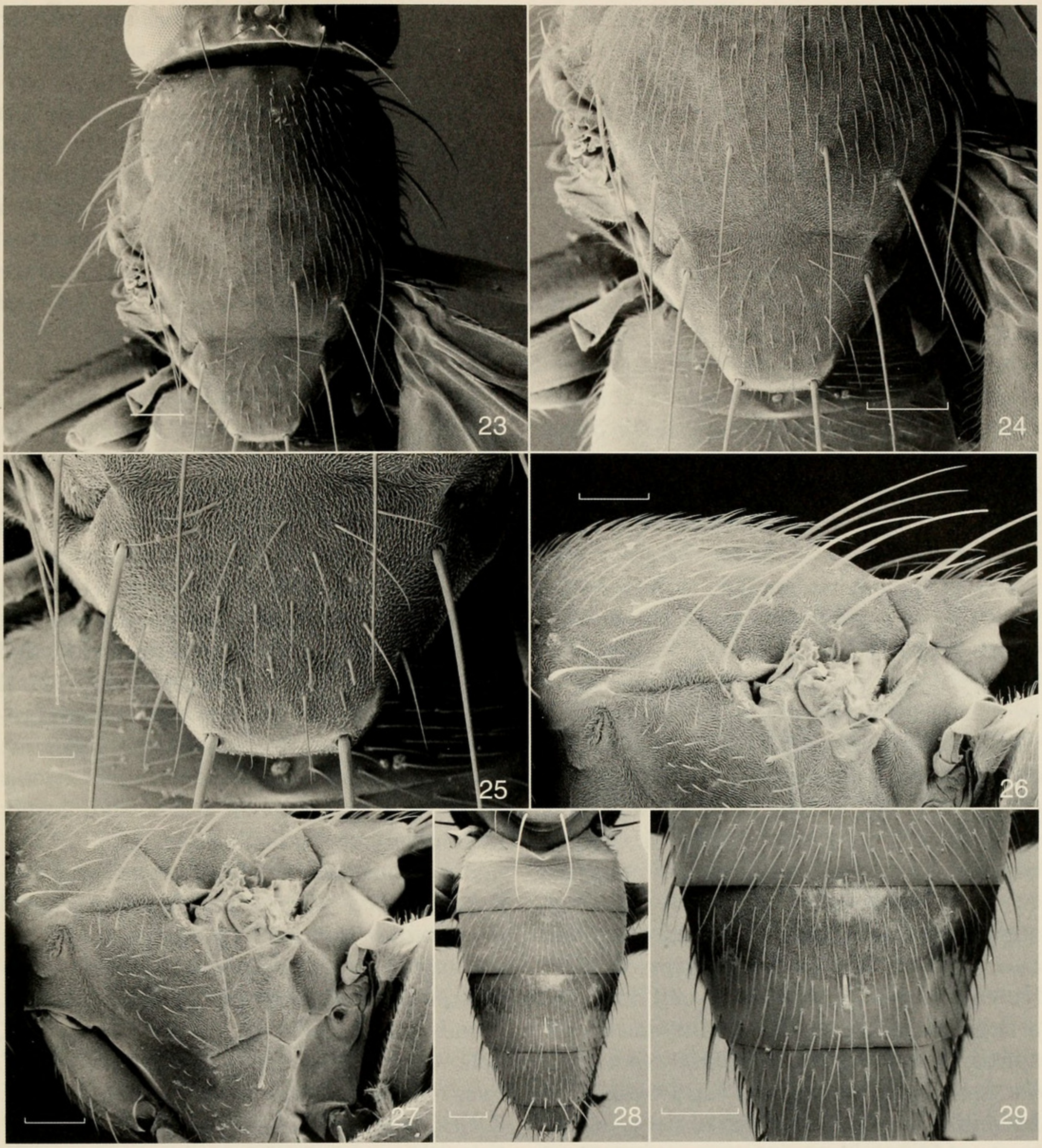
Actocetor hendeli de Meijere 1924: 202 [replacement name for *Actocetor beckeri* Hendel 1917, not de Meijere 1916].—Cresson 1946: 255–256 [discussion, probably a variety of *A. margaritatus*].—Cogan 1980: 659 [Afrotropical catalog].—Mathis and Zatwarnicki 1995: 22 [world catalog]. **New synonym.**

Actocetor margaritatus panelii Frey 1958b: 46 [Cape Verde Islands. São Vincente: Rib. Juliao. Boa Vista: Rabil. São Tiago: Rib. Charco; ST ♂♀, MZH].—Cogan, 1980: 659 [Afrotropical catalog]. **New synonym.**

Actocetor panelii: Mathis and Zatwarnicki 1995: 22 [revised status].



Figs. 15–22. Scanning electron micrographs of *Actocetor indicus.* 15, Head, lateral view (scale = 0.2 mm). 16, Same, anterior view (scale = 0.2 mm). 17, Same, anterodorsal view (scale = 0.2 mm). 18, Frons, anterodorsal view (scale = 50 μm). 19, Ocellar triangle, anterodorsal view (scale = 50 μm). 20, Dorsum of head, lateral view (scale = 50 μm). 21, Left antenna, anterolateral view (scale = 50 μm). 22, Face, anterior view (scale = 50 μm).



Figs. 23–29. Scanning electron micrographs of *Actocetor indicus*. 23, Mesonotum, dorsal view (scale = 0.2 mm). 24, Posterior portion of scutum and scutellum, dorsal view (scale = 0.2 mm). 25, Scutellum, dorsal view (scale = 50 μm). 26, Dorsum of mesonotum, lateral view (scale = 0.2 mm). 27, Pleura, lateral view (scale = 0.2 mm). 28, Abdomen, dorsal view (scale = 0.2 mm). 29, Abdominal tergites 3, 4, and 5, dorsal view (scale = 0.2 mm).

Diagnosis.—This species is distinguished from congeners by the following combination of characters: moderately small to medium-sized shore flies, body length 2.20–3.80 mm; habitus as in Fig. 1.

Description.—*Head* (Figs. 15–22): Arista with 9–12 dorsal rays. Gena high, higher than height of pedicel, gena-to-eye ratio 0.21–0.36.

Thorax (Figs. 23–27, 49): Mesonotum densely microtomentose, tannish gray to whitish gray, pleura whitish to silvery gray;

2 more or less short, dark brown bars may be present anteriorly, separated by gap equal to distance between prescutellar acrostichal setae (sometimes fused posteromedially, mesonotum in these specimens pale brown); rings at bases of larger setae (prescutellar acrostichal, posterior dorsocentral, and basal scutellar setae) usually not dark brown; scutellum with apical ¼–⅓ dark brown, basal portion concolorous with posterior portion of scutum. Wing (Fig. 49) normally developed with wide anal angle; alula narrow, bandlike, bearing long setulae (length twice height of alula) along posterior margin; vein R_{4+5} bearing 5–6 setae basad of crossvein r-m; wing pattern as follows: cell c with basal ½ white; cell r_1 with 2 spots, 1 sub-basal, subrectangular spot and 1 subapical rectangular to trapezoidal spot; cell r_{2+3} with 2 spots, basal spot in line with spot in cell r_1, apical spot, transversely oval/rectangular, immediately apicad of merger of vein R_{2+3} with costa; cell r_{4+5} with subcircular, medial spot, in line with crossvein dm-cu, and an apical spot (some specimens with a trace of a 3rd sub-basal spot); discal cell with a wide, U-shaped, basal spot (apical arm sometimes constricted) and a subapical, transversely oval-rectangular spot, sometimes divided into 2 circular spots; cell m with a transversely oval-rectangular spot near middle; cell cua_1 with a large, basal rectangular white and a subapical, transversely trapezoidal spot, vein CuA_1 straight; costal vein ratio 0.54–0.72; M vein ratio 0.84–1.0. Halter stem yellow; knob whitish yellow and distinctly clubbed. Legs generally whitish yellow to yellow; forecoxa and base of femora sometimes with whitish gray to gray microtomentum laterally.

Abdomen (Fig. 28–38): Mostly shiny, gray microtomentum almost always present and as follows: base of 1st tergite with thin band; 4th tergite with wide, anterior band; sometimes with thin, lateral bands on 3rd and 5th tergites or with medial spot on 3rd tergite; color generally metallic, dark blue to black, often with yellow to yellowish red at anterior and/or posterior margins or sometimes entirely yellowish red. 3rd and 4th sternites rectangular, broad, 1–2× longer than wide; 5th sternite of male (Fig. 30) trapezoidal with medial weakness or slight indentation on concave posterior margin. Male terminalia (Figs. 31–38): epandrium (Figs. 31–32) higher than wide; presurstylus (Fig. 33) large, ventromedial surface with a small emargination, bearing 2 round to oval lobes medially; postsurstylus (Fig. 34) much longer than wide, bearing 3–4, apical setulae, apex bilobed with a small, digitiform, medial, pointed process; postsurstylar process (Fig. 35) distinctly spatulate, rounded process, shaped like an halter; aedeagus (Fig. 37) as a subrectangular ring basally from which a lateral phalange extends apically; aedeagal apodeme (Fig. 38) in lateral view subtriangular with angle at attachment with base of aedeagus extended and acutely formed; postgonite in ventral view as a sickle shaped process, broader toward attachment with aedeagal apodeme; pregonite short, simple, bearing 2 setulae apically; hypandrium broadly and deeply pouchlike.

Type material.—The lectotype ♀ of *Notiphila indica* Wiedemann, here designated to stabilize and make more universal the use of this name, is labeled "TYPE [red]/ Notiphila indica Wied. Ind[ia]. orient. [handwritten]/Notiphila indica Wied. Det. B.H. Cogan 1976. [species name and "76" handwritten]/Actocetor indicus (Wied.) Det. B.H. Cogan 1976. [species name and "76" handwritten]/LECTOTYPE ♀ Notiphila indica Wiedemann By Dikow & Mathis [all except "LECTOTYPE" and "By" handwritten; black submarginal border]." The lectotype is directly pinned, is in fair condition (the specimen is greasy and the pin bears some verdigris), and is deposited in the UZMC.

The lectotype ♀ of *Ephydra margaritata* Wiedemann, here designated to stabilize and make more universal the use of this name, is labeled "[a small pink square]/ Egypten [handwritten]/margaritata [handwritten] Coll. Winth. [black margin along longer sides of label]/Ephydra margaritata W Aegyptn. [handwritten]/Type [red]/LECTOTYPE ♀ Ephydra margaritata Wiedemann By Dikow & Mathis [all except "LECTOTYPE" and "By" handwritten; black submarginal border]." The lectotype is pinned directly, is in fair condition (several setae missing), and is deposited in the NMW. A ♂, presumably a syntype, is labeled "Egypten [handwritten]/margaritata [handwritten] Coll. Winth./margaritata W Egyptn [handwritten]." and is deposited in the NMW.

A ♂ paratype of *Actocetor margaritatus panelii* Frey from the type locality was examined, including structures of the dissected male terminalia.

The holotype ♂ of *Actocetor beckeri* Hendel (replaced with *A. hendeli* by de Meijere) is labeled "Algoa bay Capland 22 3 96 [22 Mar 1896; handwritten] Dr. Brauns./Actocetor Beckeri, n. sp. [2 black submarginal borders; handwritten]/violaceus nom. nov. det. Hendel [all except "det. Hendel" handwritten]/Coll. Hendel/HOLOTYPE ♂ Actocetor beckeri Hendel [red submarginal border; species name, author, and gender handwritten]". The holotype is double mounted (minuten in a cardboard card), is in poor condition (both wings are missing and several setae are broken), and is deposited in the NMW.

Other specimens examined.—AFROTROPICAL. ANGOLA. Bruco, 26 Feb–2 Mar 1972 (4♂, 4♀; BMNH); Cachoeiras (20 mi SW Gabela), 18–19 Mar 1972 (1♀; BMNH); Rio Curoca (7 mi N Rio Alexandre), 25–26 Feb 1972 (2♂, 2♀; BMNH); Rio Giraul (10 mi NE Mocamedes), 27–29 Feb 1972 (1♀; BMNH); Santa Clara, 19 Mar 1972 (1♀; BMNH); Tundavala (8 mi NW Sa da Bandeira), 27–29 Mar 1972 (1♀; BMNH).

BOTSWANA. River Semowane, 23–24 Apr 1972 (1♂, 1♀; BMNH).

CAMEROON. Kribi (Rt. N7; beach), 28–29 Nov 1987, A. Freidberg (2♀; USNM).

CAPE VERDE ISLANDS. São Vincente: Rib. Juliao, 26 Nov–2 Dec 1953, Lindberg (1♂; USNM). São Jorge dos Orgãos (alfalfa field), Jun 1986, A. van Harten (3♂, 1♀; NMWL).

DEMOCRATIC REPUBLIC OF CONGO. Rumonge (Urundi), 1932, A. Lestrade (1♀; MRAC).

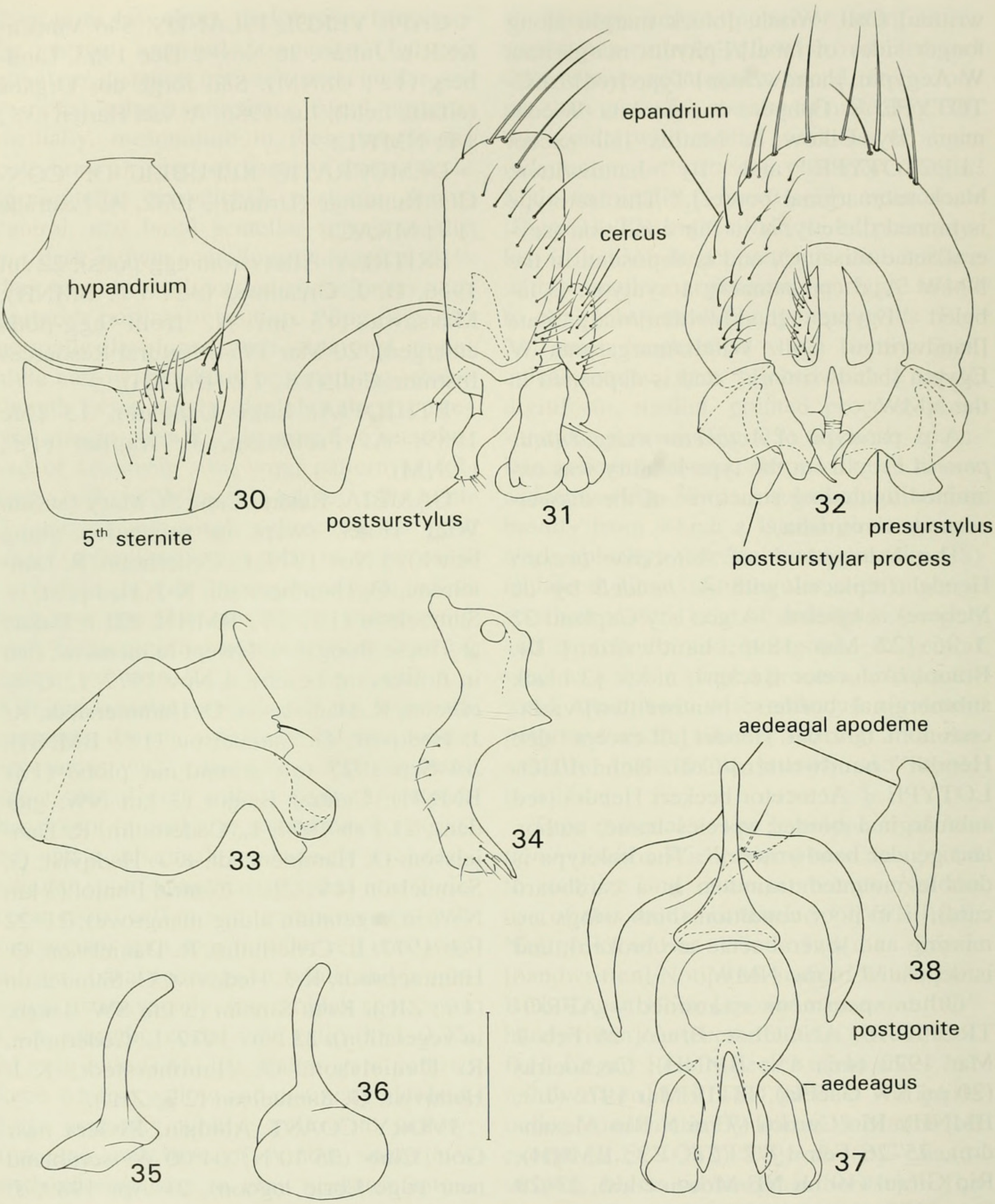
ERITREA. Ailet (from egg-pods), 22 Jul 1956, D. J. Greathead (3♂, 1♀; BMNH); Massawa (15 mi N, from egg-pods emerged), 20 Mar 1954, Natural Resources Institute Coll (1♂, 1♀; BMNH).

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

GAMBIA. Bakau, Cape St. Mary (at Sun Wing Hotel, swept in vegetation along beach), 5 Nov 1977, L. Cederholm, R. Danielsson, O. Hammerstedt, K-J. Hedqvist, G. Samuelson (1♂, 2♀; BMNH, ZIL); Bakau at Tropic Bungalow (swept in meadow, rich in flowers, at beach), 4 Nov 1977, L. Cederholm, R. Danielsson, O. Hammerstedt, K-J. Hedqvist, G. Samuelson (1♂; BMNH); Jul–Sep 1927 (on ground-nut plots) (1♂; BMNH). Central Banjol (3 km NW; garden), 21 Feb 1977, L. Cederholm, R. Danielsson, O. Hammerstedt, K-J. Hedqvist, G. Samuelson (1♀; ZIL). Central Banjol (3 km NW; in vegetation along mangrove), 21–22 Feb 1977, L. Cederholm, R. Danielsson, O. Hammerstedt, K-J. Hedqvist, G. Samuelson (1♀; ZIL). Kotu Stream (3 km SW Bakau; in vegetation), 23 Nov 1977, L. Cederholm, R. Danielsson, O. Hammerstedt, K-J. Hedqvist, G. Samuelson (2♀; ZIL).

IVORY COAST. Abidjan, Riviera near Golf Club (05°10'N, 04°00'W; scrubland near edge Ebrie lagoon), 21 Apr 1989, J. G. H. Londt (1♂, 4♀; NMSA). Banco National Park, N Abidjan (05°22'N, 04°03'W; edge of wide track in forest), 23–27 Apr 1989, J. G. H. Londt (1♂; NMSA). Fresco (15 km W; 05°06'N, 05°43'W; airfield/forest edge, near Palmindustrie), 24 Apr 1989, J. G. H. Londt (1♂; NMSA).

KENYA. Biretwo (40 km E Eldoret), 12 May 1991, A. Freidberg, F. Kaplan (1♀;



Figs. 30–38. Structures of the male preabdomen and terminalia of *Actocetor indicus*. 30, Fifth sternite and hypandrium, ventral view (only left side showing setae). 31, Epandrium, cerci, presurstylus, postsurstylus, gonite, and hypandrium, lateral view. 32, Same, posterior view. 33, Presurstylus, posterior view. 34, Postsurstylus, lateral view. 35, Postsurstylar process, posterior view. 36, Same, posteroventral view. 37, Aedeagus, aedeagal apodeme, dorsal view. 38, Aedeagal apodeme, lateral view. Scale bar equals 0.3 mm for Figs. 30–32 and 0.1 mm for Figs. 33–38.

USNM). Bungoma, 6–7 Nov 1983, A. Freidberg (1♀; USNM). Isolo (5 km S), 30 Nov 1986, A. Freidberg (1♀; TAU). Mombasa (beach) 5 Dec 1989, A. Freidberg, F. Kaplan (2♀; TAU, USNM). Mombasa (10 km N), 18 Aug 1996, A. Freidberg (1♂; USNM). Mombasa (20 mi S; Malaise trap), 23–25 Jan 1968, K. V. Krombein, P. J. Spangler (1♀; USNM). Nairobi (50 km SE; Rt. A109), 30 Apr 1991, A. Freidberg, F. Kaplan (1♀; TAU). Rift Valley, Ol Arabe Gorge, 11 Nov 1988, R. K. Butlin (1♂, 1♀; NMWL). Tsavo West, Ngulia Lodge, 16–17 Aug 1983, A. Freidberg (1♂, 3♀; USNM). Tseikuru, Jan 1957 (1♀; USNM). Mombasa, 9 Dec 1951, Deutche Ost Afrika Exp. (1♀; SMN).

MALAWI. Monkey Bay, Lake Malawi, 15 Aug 1943, R. C. Wood (1♀; BMNH).

NAMIBIA. Gross Barmen Resort (22°07′S, 16°42′E; roadside grass and dry river bed at camp), 29 Mar 1984, J. G. H. Londt, B. Stuckenberg (1♂; NMSA).

NIGERIA. Ile-Ife, 25 Apr 1969, J. T. Medler (1♀; USNM). Lagos (shore), 15 Dec 1987, A. Freidberg (2♂, 2♀; TAU). Lagos, Ikoyi, 14 Jan 1966, J. C. Deeming (1♀; CNC). Lagos, Victoria Island (shore), 15 Dec 1987, A. Freidberg (3♂, 1♀; TAU). Niger State, Mariga River (80 km W Mina), 11 Dec 1987, F. Kaplan (1♀; USNM). Yankori, 8–14 Nov 1987, P. Neuenschwander (1♀; TAU). Zaria, Samaru, May–Sep 1979, J. C. Demming (2♂, 4♀; NMWL).

SENEGAL. Dakar, 4–5 Oct 1978, J. Fortin, G. Hevel (1♂; USNM). Brin (3 km SSE), Iguinchor (11 km SW), 9 Nov 1977, L. Cederholm, R. Danielsson, O. Hammerstedt, K-J. Hedqvist, G. Samuelson (1♀; ZIL).

SEYCHELLES. *La Digue:* La Passe (4°20.8′S, 55°49.8′E), 14 May 1997, V. Hollmann (2♀; ZMHB); La Réunion (4°21.8′S, 55°49.6′E), 14 May 1997, V. Hollmann, W. N. Mathis (5♂, 10♀; USNM, ZMHB). *Mahé:* Airport, 7–8 Apr 1986, W. N. Mathis (2♂, 2♀; USNM); Anse aux Pins (4°41.4′S, 55°31.7′E), 2 Apr-3 May 1986, 1997, V. Hollmann, W. N. Mathis (1♂, 1♀; USNM, ZMHB); Anse Soleil (4°44.8′S, 55°27.9′E), 19 May 1997, W. N. Mathis (1♂, 1♀; USNM); Beau Vallon, 24 Mar 1965, W.T. Tams, I.B. Nye (1♂; BMNH); Police Bay (4°48.0′S, 55°31.3′E), 16 May 1997, V. Hollmann, W. N. Mathis (8♂, 5♀; USNM, ZMHB). *Praslin:* Anse Lazio (4°17.6′S, 55°42.1′E), 8–13 May 1997, W. N. Mathis (12♂, 6♀; USNM); Anse Kerlan (4°18.3′S, 55°41.1′E), 9 May 1997, W. N. Mathis (1♀; USNM); Anse Kerlan Farm (4°18.5′S, 55°41.2′E), 13 May 1997, V. Hollmann (1♀; ZMHB); Anse Lazio (4°17.6′S, 55°42.1′E), 8–13 May 1997, V. Hollmann, W. N. Mathis (20♂, 9♀; USNM); Baie Ste. Anne, Anse Takamaka (4°19.6′S, 55°46.3′E), 10–13 May 1997, V. Hollmann (2♂; ZMHB); Fond de L'Anse (4°20.1′S, 55°43.5′E), 11 May 1997, W. N. Mathis (1♂; USNM).

SIERRA LEONE. Freetown (6 km SW; 9°26′N, 13°16′W; in garden), 21 Nov 1993, L. Cederholm, R. Danielsson (1♂; ZIL).

SOKOTRA ISLAND. Hadibu Plains, 14 Dec 1898, W. R. O. Grant (1♂; BMNH).

SOUTH AFRICA. *Eastern Cape:* Algoa Bay, 22 Mar 1896, Brauns (1♂ holotype of *A. hendeli*; NMW); East London (3227Dd; 5 m; coastal dunes), 16 Mar 1972, M. E. and B. J. Irwin (1♀; NMSA); The Haven (3228Bb; coastal dunes), 24–28 Jun 1979, R. Miller, P. Stabbins (1♂; NMSA). *KwaZulu-Natal:* Dukuduku Forest (4 mi W St. Lucia; 2832Ad; 3 m), 26 Nov 1971, M. E. and B. J. Irwin (2♀; NMSA); Dukuduku Forest (E Mtubatuba; 2832Ad), 21 Jul 1973, M. E. Irwin (1♀; NMSA); Dukuduku (between St Lucia and Matubatuba), 7–8 Apr 1960, B. and P. Stuckenberg (2♀; NMSA, USNM); Durban, 27 Feb 1927, L. Bevis (1♀; BMNH); Gillitts (Pinetown District), 28 Dec 1961, B. and P. Stuckenberg (1♀; NMSA); Jamisons Drift (Tugela River), 12 Apr 1974, M. E. Irwin (1♂; NMSA); Kosi Bay Estuary (2632Dd; indigenous bush area), 16–19 Mar 1982, D. A. Barraclough (5♂, 1♀; NMSA); Lebombo Hills, H. A. Junod (1♂, 1♀, 1EX; BMNH); Mtubatuba, 24–25 Mar 1968, P. J. Spangler

(2♂, 1♀; USNM); Ndumu Reserve (Ingwavuma District), Tongaland, 1–10 Dec 1963, B. and P. Stuckenberg (1♀; NMSA); Near Lilani (Ahrens District), Apr 1962, B. and P. Stuckenberg (1♂; NMSA); Oribi Gorge Reserve, Umzinkulwana Valley, 21–28 Nov 1960, B. and P. Stuckenberg (1♂; USNM); Port St. Johns, 20–25 Nov 1961, B. and P. Stuckenberg (1♂; USNM); Salt Rock (28°29′S, 31°15′E; 10 m; caravan park), 5–12 Oct 1991, J. G. H. Londt (1ex; NMSA); Scottsburgh, 15 Nov 1963, B. and P. Stuckenberg (1♂, 3♀; NMSA); St. Lucia Park, 7–8 Oct 1983, A. Feidberg (1♀; USNM); Tugela Ferry (20 km W; 2830Ga; Malaise trap), 26–27 Feb 1977, R. Miller (1♀; NMSA); Umkomaas (NE; 3030Bb; along sand dunes), 21 Jun 1980, R. Miller, R. Stabbins (1♂; NMSA); Umkomaas, South Coast, 11 Oct 1983, A. Freidberg (4♂, 8♀; USNM); Umlalazi Nature Reserve (2831Dd, dune forest and edges), 2–10 Oct 1982, J. G. H. Londt (1♀; NMSA); Umlalazi Nature Reserve (28°57′S, 31°40′E; 20 m; dune forest), 28–29 Jan 1988, J. G. H. Londt (5♂, 7♀; NMSA); Umlalazi Nature Reserve (1.5 km E Mtunzini; 1831Dd; coastal dune vegetation), 30 Dec 1978, R. Miller (1♀; NMSA); Umlalazi Nature Reserve (1.5 km E Mtunzini; 1831Dd; coastal indigenous vegetation), 27 Jan 1979, R. Miller (1♂; NMSA); Umlalazi Nature Reserve (1.5 km E Mtunzini; 1831Dd; coastal indigenous vegetation), 24–25 Mar 1979, R. Miller (1♂; NMSA); Widenham Umbilo, 16 Dec 1914, L. Bevis (1♂, 1♀; BMNH). *Mpumalanga:* Ofcolaco, Selati River (2430Ab), 7–8 Dec 1976, R. Miller (1♀; NMSA). *Northern Province:* Entabeni For. Station, Zoutpansberg Range (2230Cc; grassland), Jan 1975, B. Stuckenberg (1♀; NMSA).

SUDAN. Um Baghot (among hantot ?), 22 Aug 1931, R. C. M. Darling (1♀; BMNH).

TANZANIA. Tarangire National Park (36°10′E, 03°50′S), Dec 1994, D. Grimaldi (1♂; AMNH).

UGANDA. Kilembe, Ruwenzori Range (4500 ft), Dec 1934–Jan 1935 (1ex; BMNH).

ZIMBABWE. Gwaai, 14 Oct 1926, R. H. R. Stevenson (1♀; NMSA). Harare, 9 Jun 1938, A. Cuthbertson (1♀; BMNH).

Country unknown. Torina (Deutsch Ost Afrika Expedition), 4–18 Mar 1952 (1♀; USNM).

ORIENTAL. INDIA. *Karnataka:* Mudigere, 6 Apr 1980, W. N. Mathis, A. Freidberg (1♀: USNM); *Tamil Nadu:* Palni Hills (Kodaikanal; 6500 ft), Mar–Apr 1953, P. S. Nathan (1♂; USNM).

MALAYSIA. Penang (at light trap), 16 Jul 1957, H. T. Pagden (1♀; BMNH).

SRI LANKA. *Central Province: Nuwara Eliya:* Horton Plains, 23 Apr 1980, W. N. Mathis, T. Wijeshine, L. Jayawickrema (2♀; USNM); *Southern Province: Hambantota:* Palatupana Tank, 6 Feb 1975, K. V. Krombein (1♀: USNM).

PALEARCTIC. UNITED ARAB EMIRATES. *Abu Dhabi:* Ruwais, 6 Nov 1985, M. J. Ebejer (1♀; NMWL).

CANARY ISLANDS. *Gran Canaria:* Las Plamas (on garden wall), 12 Nov 1927, Kisluik (3♂, 1♀; USNM); Las Palmas, R. Stora (1ex; BMNH); 1–15 May 1901 (1♂; ZMHB). *Tenerife:* Laguna (6–700 m), 8–30 Jun 1904 (1♀; ZMHB); Puerto de la Cruz (dry sand on shore), 21–26 Apr 1979, C. E. Dyte (2♂, 8♀; BMNH); Puerto Orotava (low herba and brass near beach), 20 Dec–2 Jan 1901 (6♂, 6♀; ZMHB); Jul 1907, Cabrera (1♀; ZMHB).

EGYPT. Heliopolis, 20–22 Oct 1964, E. Hargreaves (ex; BMNH). Egypten (1♀ holotype, 1♂; NMW). *Sinai:* Bir Zrir, 2 Sep 1970, J. Kugler (1♀; USNM); El-Arba'in (Sinai Mountains), 14 Jul 1974, F. Kaplan (1♀; USNM); Danav, 23 May 1981, W. N. Mathis (1♀; USNM); El 'Arīsh, 9 Jan 1917, E. E. Austen (1♀; BMNH); Ein Furtāga, 7 Jul 1969, Kugler (2♂, 3♀; USNM); Ein Hudra, 9 Jul 1969, A. Freidberg (2♀, 1ex; USNM); Et-Tūr, 25 Jun 1968 (4♂, 1♀; TAU); Feirān, 9 Apr 1973, D. Furth (1♂; TAU); Nuweibá, 14 May 1981, T. Furman (4♀, 5♂; USNM); Ofira (sewage), 21 May

1981, A. Freidberg, W. N. Mathis (11♂, 8♀, 1ex; TAU, USNM); Ofira, 22 Mar 1981, A. Freidberg (1♀; TAU); Ophira Airport, 22 Apr 1980, B. R. Pitkin (1♀; BMNH); Ras Mamlach, 11–15 Apr 1980, B. R. Pitkin (6♂, 4♀; BMNH); St. Katharina, 12 Jul 1969, J. Kugler (1♀; USNM); Taba (1 km S), 10 Apr 1980, B. R. Pitkin (1♀; BMNH); Wadi Feirān, 25 May 1971, A. Freidberg (2♂, 2♀; TAU, USNM); Wadi Hibrān, 11 May 1973, A. Freidberg, F. Kaplan (1♂, 1♀; TAU); Wadi Watīr, 5 Aug 1975, A. Freidberg (1♂; TAU).

ISRAEL. Arava Valley: Hazeva Field School (30°46.8′N, 35°14.6′E; 2 km N; Nahal Gidron; 110 m), 11 Mar–7 Jun 1995, M.E. Irwin (1♂, 14♀; TAU); Hazeva, Shezaf Nature Reserve (30°46′N, 35°15.4′E; north of water treatment plant, low sandy hummocks in small wadi; 80 m), 24 Mar–20 May 1995, M.E. Irwin (3♂, 4♀; TAU); Hazeva (30°46.3′N, 35°16.3′E; Hahal Shahaq, between agricultural fields; Malaise trap; 110 m), 15 Mar–16 Apr 1995, M.E. Irwin (10♂, 12♀; TAU); 'Iddan (30°48.9′N, 35°16.8′E; nahal running east of date palm orchard; 110 m; malaise trap), 13 Mar–5 Jun 1995, M.E. Irwin (21♂, 22♀; TAU); 'Iddan Springs (30°49′N, 35°17′E; in damp seep east of spring; 116 m), 13–17 Mar 1995, M.E. Irwin (3♀; TAU); 'Ir Ovot (30°56.8′N, 35°04.4′E; 3 km NW; water tank on hillside), 6 Apr 1995, M.E. Irwin (2♂, 1♀; TAU). Ashqelon, 5 Sep 1960, Fatal (2♂, 5♀; TAU, USNM). Biq'at Bet Zayda, 3 May–5 Aug 1973, 1986, A. Freidberg, I. Nussbaum (1♂, 1♀; TAU). 'En Yahav, 20 Sep 1995, A. Freidberg (10♂, 2♀; TAU, USNM). 'Enot Qane ['En Turaba], 30 Apr 1973, D. Furth (1ex; TAU). Herzliyya (beach; Malaise trap), 13 Jan–9 Nov 1975, 1981, 1982, 1994, A. Freidberg, F. Kaplan, D. Simon, I. Susman (31♂, 56♀; TAU, USNM). Mash'abbé Sade, 21 Aug 1986, A. Freidberg (1♂; TAU). Nahal Hatira, 19 Oct 1983, I. Nussbaum (1♀; TAU). Ne'ot ha-Kikkar, 20 May 1974, A. Freidberg (3♀, 1♂; TAU). Ne'ot Semadar, 21 Jun–29 Aug 1995, A. Freidberg (4♂, 4♀; TAU, USNM). Paran, 19 Sep 1977, A. Freidberg (2♂; TAU). Park HaYarden, 30 Sep 1982, F. Kaplan (1♂; TAU). Qalya, 20 Mar 1980, J. Kugler (1♀; TAU). Qezi'ot, 28 Aug 1986, I. Nussbaum (1♀, 1♂; TAU). Ramat-ha-Sharon, 18 Aug 1975, D. Simon (1♂; TAU). Rehovot, 30 Oct 1931, 1938, J. Aharoni (3♂; TAU, ZMHB). Tel Aviv, 22 Aug–27 Nov 1969, 1971, J. Kugler (13♀; TAU, USNM). Tel Aviv, Abu-Kabir, 13 Sep 1953, L. Fishelsohn (1♂; TAU). Upper Galilee, Park HaYarden, 5 Aug 1986, W. N. Mathis (2♂; USNM). Yotvata, 23 Sep 1962, J. Kugler (1♂, 4♀; TAU). Ze'elim, 6 Dec 1976, A. Freidberg (1♀; TAU). Zin Wilderness, Nahal Zin at 'En 'Aqrabbim (35°09′N, 39°E; cane-covered, sandy wadi; 61 m; Malaise trap), 27 Mar–15 May 1995, M.E. Irwin (2♂, 2♀; TAU).

OMAN. As-Seefa (coastal sand dunes), 4 Dec 1987, J. J. Ebejer (1♂, 1♀; NMWL). Ghuzayn (date culture), 10 Apr 1985, Paö (1♂; ZIL). Hazm (date palm grove beside Fort on maize, sorghum, and grasses), 19 Oct 1990, M. D. Gallaghler, J. C. Deeming (3♀; NMWL). Mazara (date cult), 6 Apr 1985, Paö (1♂, 5♀; ZIL). Muscat, 10 Apr 1985, P. Ardö (2♂, 2♀; ZIL). Qurm (hotel garden), 5 Apr 1985, Paö (1♂, 5♀; ZIL). Ruwi, Wattayeh, 1–7 Apr 1988, M. D. Gallagher (6♂, 6♀; NMWL). Viti Wadi, 7 Apr 1985, Paö (1♂, 1♀; ZIL). Wadi Bani Kharus (foothill of Jebel Akhdar Lilyah; 810 m; 23°11′N, 57°40′E), 18 Oct 1990, M. D. Gallaghar, J. C. Deeming (1♂; NMWL).

SPAIN. Almeria, Oct 1973, Boness (10♂, 6♀; BMNH).

Distribution (Fig. 14).—Afrotropical: Angola, Botswana, Cameroon, Cape Verde Islands (São Vincente), Democratic Republic of Congo, Eritrea, Ethiopia, Gambia, Ivory Coast, Kenya, Namibia, Nigeria, Rwanda (literature), Senegal, Seychelles (La Digue, Mahé, Praslin), Sierra Leone, Sokotra Island, South Africa (Eastern Cape, KwaZulu-Natal, Mpumalanga, Northern Province), Sudan, Tanzania, Uganda, Zimbabwe. Oriental: India (Karnataka, Tamil Nadu), Malaysia, Sri Lanka. Palearctic: Canary Islands (Gran Canaria, Tenerife), Egypt, Israel, Oman, Spain, United Arab Emirates (Abu Dhabi). This is the most widespread species of the genus, and its occurrence at some sites may represent introductions. We suspect this to be the case for the Seychelles and perhaps elsewhere, such as the Indian Subcontinent and Malaysia.

Natural history.—On islands of the Seychelles, the majority of specimens collected by Mathis were associated with sandy areas with sparse to no vegetation that were surrounded by or in close proximity to grass covered habitats. Occasionally this species was found associated with organic debris and other garbage that had accumulated at the high tide mark on sandy beaches.

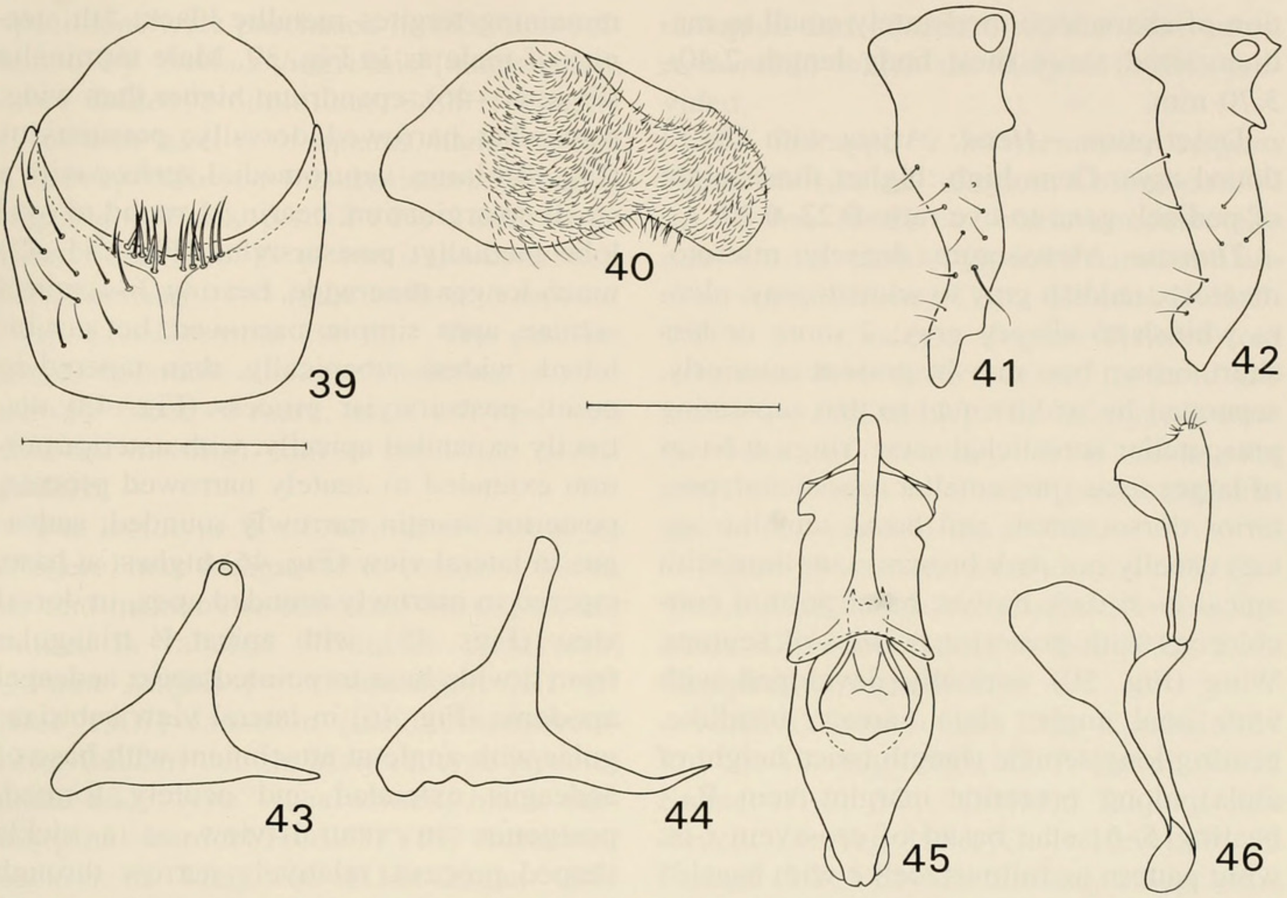
Larvae of this species apparently feed on varied sources of highly organic debris, probably as saprophages. Dr. Amnon Freidberg (personal communication) successfully reared this species on a medium of domestic cat dung in Israel, and Stower et al. (1958) and Greathead (1963) reared adults in Eritrea from damaged egg pods of desert locusts (*Schistocerca gregaria* Forskål).

Observations on mating behavior.—Date: 16 Aug 1986 (Saturday). Time: 10:30 am. Weather: Temperature about 30°C, very slightly breezy, sunny. Location: Beach at Herzliyya, Israel. Shaded area at base of hill, mostly a dune, immediately adjacent to beach (spray belt). Hill covered with *Oenothera* sp. (introduced; Onagraceae) and *Pancratium maritimum* L. (Amaryllidaceae). Observers: A. Freidberg and W. N. Mathis.

Several specimens were observed running over the sandy substrate, primarily in the shade. Their wings were parted at about 80° and occasionally the wings were quickly moved in a scissoring motion. A few females were observed to tap the substrate with their abdomens, perhaps searching for ovipositional sites. When a male came within 5–7 cm of a female, he would immediately pursue her and attempted to mount, apparently without any precopulatory behavior. Mounting was brief, usually 5 seconds or less (range 3–15 seconds based on 4 observations). For one pair we observed the tips of both abdomens touching but could not see if the genitalia of the male engaged those of the female (we assume that they did). After dismounting, the pair would face each other and touch their extended probosces intermittently for 10–20 seconds. While thus touching, the male and/or female would scissor its wings, the opposite sex would remain essentially stationary, with its wings parted at nearly 150°. We could not determine whether trophallaxis occurred with the touching of probosces. While touching probosces there was apparently some foreleg-to-head touching.

Remarks.—Wiedemann described this species twice and in two different genera. As species of *Actocetor* are striking and unlikely to be overlooked, we suspect that Wiedemann failed to examine specimens in his own collection (he may have returned some specimens and did not have ready access to them, did not consult his previously published description, or his memory faltered). Regardless, our study of Wiedemann's primary types clearly revealed that the syntypes of both names are conspecific, with *A. indicus* having priority as the senior synonym. In view of the widespread distribution of this species, particularly in the Afrotropical Region, it is unfortunate that the senior synonym, *A. indicus*, alludes to an area on the periphery of this species' distribution where it may represent an introduction.

The comparison of the male terminalia of the paratype of *A. margaritatus panelii* with those from India and Sri Lanka indicates that both are conspecific and thus the names are synonyms despite the lack of characteristic microtomentum on tergites 3–5. The microtomentum on the abdomen is also variable in other specimens, especially on the 4th tergite. This was particularly evident in specimens from a single site in Nigeria where a majority of the specimens have a wide band of microtomentum and a few,



Figs. 39–46. Structures of the male preabdomen and terminalia of *Actocetor nigrifinis*. 39, Fifth sternite and hypandrium, ventral view (only left side showing setae). 40, Presurstylus, posterior view. 41, Postsurstylus, lateral view (Sri Lanka. Padaviya). 42, Same (Malaysia. Sabah: Kota Kinabalu). 43, Postsurstylar process, posterior view (Sri Lanka. Padaviya). 44, Same (Malaysia. Sabah: Kota Kinabalu). 45, Aedeagus, aedeagal apodeme, dorsal view. 46, Same, lateral view. Scale bar equals 0.3 mm for Fig. 39 and 0.1 mm for Figs. 40–46.

including females, have sparse to no microtomentum. The structures of the male terminalia were compared directly in detail and are the same, and we are thus of the opinion that they are conspecific.

The holotype of *A. hendeli* de Meijere bears only a very narrow band of microtomentum on the 4th tergite and is otherwise metallic, bluish black. Although an entirely bluish black abdomen also occurs elsewhere, specimens often have some yellowish orange to red color on at least the basal 2–3 tergites. The structures of the male terminalia of the holotype are virtually identical to those of typical *A. indicus*, and we consider these specimens to be conspecific. Thus, *A. hendeli* is also a synonym of *A. indicus*.

Actocetor (*Actocetor*) *nigrifinis* (Walker)
(Figs. 39–47, 50)

Opomyza nigrifinis Walker 1860: 168.
Actocetor nigrifinis: Cogan and Wirth 1977: 328 [generic combination].
Actocetor beckeri de Meijere 1916: 264.—Cogan and Wirth 1977: 328 [Oriental catalog].—Mathis and Zatwarnicki 1995: 22 [world catalog].—de Jong 2000: 36 [status of syntypes]. **New synonym.**
Actocetor elegans Hendel 1917: 41.—Cresson 1929: 171 [comparison with *A. margaritatus*].—Cogan and Wirth 1977: 328 [synonymy with *A. beckeri*; Oriental catalog]. **New synonym.**

Diagnosis.—This species is distinguished from congeners by the following combination of characters: moderately small to medium-sized shore flies, body length 2.40–3.70 mm.

Description.—*Head:* Arista with 10–13 dorsal rays. Gena high, higher than height of pedicel, gena-to-eye ratio 0.22–0.30.

Thorax: Mesonotum densely microtomentose, reddish gray to whitish gray, pleura whitish to silvery gray; 2 more or less short, brown bars may be present anteriorly, separated by width equal to that separating prescutellar acrostichal setae; rings at bases of larger setae (prescutellar acrostichal, posterior dorsocentral, and basal scutellar setae) usually not dark brown; scutellum with apical ½–¾ dark brown, basal portion concolorous with posterior portion of scutum. Wing (Fig. 50) normally developed with wide anal angle; alula narrow, bandlike, bearing long setulae (length twice height of alula) along posterior margin; vein R_{4+5} bearing 5–6 setae basad of crossvein r-m; wing pattern as follows: cell c with basal ½ white; cell r_1 with 1 sub-basal rectangular spot; cell r_{2+3} with 2 spots, basal spot in line with spot in cell r_1, apical spot, transversely oval/rectangular, immediately apicad of merger of vein R_{2+3} with costa; cell r_{4+5} with sub-basal rectangular spot in line with anterior spot in cell r_1, a subcircular, medial spot, in line with crossvein dm-cu, and an apical spot; discal cell with a wide, U-shaped, basal spot (apical arm sometimes constricted or appears to be separated) and a subapical, transversely oval-rectangular spot; cell m with a transversely oval-rectangular spot near middle; cell cua_1 with a large, basal rectangular white and a subapical, transversely trapezoidal spot, vein CuA_1 straight; costal vein ratio 0.65–0.87; M vein ratio 0.94–1.17. Halter stem yellow; knob whitish yellow and distinctly clubbed. Legs generally whitish yellow to yellow; forecoxa and base of femora sometimes with whitish gray to gray microtomentum laterally.

Abdomen: Entirely shiny but with gray microtomentum on base of 1st tergite; color of tergites 1–3 more or less yellowish red, remaining tergites metallic black; 5th sternite of male as in Fig. 39. Male terminalia (Figs. 40–46): epandrium higher than wide, somewhat narrowed dorsally; presurstylus (Fig. 40) large, ventromedial surface with a small emargination, bearing 1 round to oval lobe medially; postsurstylus (Figs. 41–42) much longer than wide, bearing 3–4, apical setulae, apex simple, narrowed, but not bilobed, widest subapically, then tapered to point; postsurstylar process (Fig. 43) distinctly expanded apically, with anterior portion extended to acutely narrowed process, posterior margin narrowly rounded; aedeagus in lateral view (Fig. 46) highest at base, tapered to narrowly rounded apex, in dorsal view (Figs. 45), with apical ⅔ triangular from a wide base to pointed apex; aedeagal apodeme (Fig. 46) in lateral view subtriangular with angle at attachment with base of aedeagus extended and acutely formed; postgonite in ventral view as a sickle shaped process, relatively narrow through length; pregonite short, simple, bearing 2 setulae apically; hypandrium broadly and deeply pouchlike.

Type material.—The lectotype ♀ of *Opomyza nigrifinis* Walker, here designated to preserve stability and make more universal the use of this name, is labeled "SYN-Type [circular label, green submarginal border, SYN handwritten]/Mak [circular label, gray]/nigrifinis [handwritten]/684/Celebes: Makessar [handwritten]/Actocetor nigrifinis Walk. SYNTYPE 1860 Proc. Linn. Soc. Lond. IV p. 168 (Opomyza) det. J.C. Deeming 1964 [handwritten except for "det. J.C. Deeming 196'"]/LECTOTYPE ♀ Opomyza nigrifinis Walker By Dikow & Mathis [all except "LECTOTYPE" and "By" handwritten; black submarginal border]." The lectotype is double mounted (minuten in rectangular block of foam), is in good condition (left midleg and wing missing), and is deposited in the BMNH. A paralectotype ♀ is labeled "SYN-Type [circular label, green submarginal border, SYN handwritten]/Celebes [circular label, gray] 58 142 × [on underside of label, means that specimens were purchased in 1858 and collected by Wallace]/nigrifinis [handwritten, label folded]/Notiphilinae 3/8.01. Czerny [brownish label with squares, handwritten]/ Celebes: Makessar [handwritten]/Actocetor nigrifinis Walk. SYNTYPE 1860 Proc. Linn. Soc. Lond. IV p. 168 (Opomyza) det. J.C. Deeming 1964 [handwritten except for "det. J.C. Deeming 196′")." The paralectotype is double mounted (minuten in rectangular block of foam; head, left fore- and midlegs missing), and is deposited in the BMNH.

The lectotype ♀ of *Actocetor beckeri* de Meijere, here designated to preserve stability and make more universal the use of this name, is labeled "Batavia [Djakarta] (Moara Antjol) [= Moaraantjol] XII. 07 [Dec 1907] Jacobson [handwritten]/Actocetor Beckeri det. de Meijere. type [species name and "type" handwritten; black submarginal border]/HOLOTYPE Actocetor beckeri de Meij det. B.H. Cogan 1971 [handwritten except for "det. B.H. Cogan 197"]/Actocetor hendeli de Meij. Det. B.H. Cogan 1971. [handwritten except for "det. B.H. Cogan 197"]/Actocetor Beckeri de Meijere, 1916 ZMAN type DIPT.0437.1 [red]/LECTOTYPE ♀ Actocetor beckeri de Meijere By Dikow & Mathis [all except "LECTOTYPE" and "By" handwritten; black submarginal border]." The lectotype is double mounted (minuten in rectangular block of foam), is in good condition (minuten has verdigris on it), and is deposited in the ZMAN. In the original description, de Meijere mentioned "Sumpf" (swamp) as part of the type locality. There are also five ♀ paralectotypes that bear the same locality data as the lectotype with the addition of "by Bembex nest." Although Cogan wrote that this specimen is a holotype, de Meijere's original description noted "einige Exemplare" (some specimens) and thus a lectotype designation is needed. Cogan also attached a second label on which "Actocetor hendeli de Meij." was written. Cogan apparently confused the name of this species with *A. beckeri* Hendel, which is preoccupied and needed a replacement name, *A. hendeli,* which de Meijere (1924) provided.

The holotype ♀ of *Actocetor elegans* Hendel is labeled "Ceylon, Colombo./6/VI 02. [6 Jun 1902] Dr. Uzel./Actocetor elegans H. det. Hendel [species name and author handwritten]/Coll. Hendel/HOLOTYPE ♀ Actocetor elegans Hendel [red submarginal boarder; name, author, and gender handwritten]." The holotype is double mounted (minuten in a rectangular block of foam), is in very good condition, and is deposited in the NMW.

Other specimens examined.—ORIENTAL. AUSTRALIA. Cocos-Keeling Islands. Direction Island, 4 Jun 1952, T. G. Campbell (1♀; BMNH).

MALAYSIA: *Sabah:* Kota Kinabalu (17 km S), 19 Aug 1983, G. F. Hevel, W. E. Steiner (1♂, 5♀; USNM); Tanjung Aru Beach, 29 Aug 1983, G. F. Hevel, W. E. Steiner (1♀; USNM); Tomani, 1 Sep 1983, G. F. Hevel, W. E. Steiner (5♂; USNM).

PHILIPPINES. Palawan Brookes Point, Uring Uring, 25 Aug 1961, Noona Dan Expedition (1♀; UZMC). Batangas: Bo. Cale (14°07′N, 121°06′E; 7 km NW Tanauan; ex. *Zea mays* L.), 16 Jul 1977, A. T. Barrion (1♂; CNC).

SRI LANKA. *Central Province. Kandy:* Mahiyangana (51 mi NW; Malaise trap at Hasalaka Irrigation Bungalow), 30 Mar–9 Apr 1971, P. and P. Spangler (1♂; USNM); Peradeniya Botanical Gardens, 25 Jan 1977, W. N. Mathis, T. Wijesinhe, L. Jayawickrima (2♂, 8♀; USNM); Peradeniya (Malaise trap at Botanical Gardens), 26–28 Mar 1971, P. and P. Spangler (2♀; USNM). *Northern Province. Jaffna:* Klinochchi (80 ft), 25 Jan 1977, W. N. Mathis, T. Wijesinhe, L. Jayawickrima (1♀; USNM). *North Central Province. Anuradhapura:* Padaviya (180 ft), 2–8 Nov 1970, O. S. Flint, Jr. (1♀; USNM); Padaviya (180 ft; Irrigation Bungalow), 27 Feb–9 Mar 1970, D. R. Davis, W. Rowe (1♀; USNM). *Polonnaruwa:* Pimburettawa (13 mi S Mannampitiya; 1850 ft), 9–12 Oct 1970, O. S. Flint, Jr.

(3♂; USNM). *Province of Sabaragamuwa. Ratnapura:* Panamure (500 ft), 15–21 Oct 1970, O. S. Flint, Jr. (1♂, 1♀; USNM); Uggalkaltota (350 ft; Irrigation Bungalow), 31 Jan–8 Feb 1970, D. R. Davis, W. Rowe (2♀; USNM). *Southern Province. Galle:* Kanneliya, 27 Apr 1980, W. N. Mathis, T. Wijesinhe, L. Jayawickrima (2♂, 1♀; USNM). *Hambantota:* Kirinda, 25 Apr 1980, W. N. Mathis, T. Wijesinhe, L. Jayawickrima (1♂; USNM); Palatupana, 3–6 Feb 1975, K. V. Krombein, P. B. Karunaratne, P. Fernando, E. G. Dabrera (1♀; USNM); Palatupana Tank, 6 Feb 1975, K. V. Krombein (1♀; USNM). *Province of Uva. Badulla:* Digaluma Falls (1550 ft; black light), 17 Aug 1973, G. Ekis (1♂, 1♀; USNM); Girandurakotte Circ. Bungalow (10 mi NNE Mahiyangana; UV trap), 4–7 Sep 1980, K. V. Krombein, P. B. Karunaratne, T. Wijesinhe, L. Jayawickrema, V. Gunawardane (1♂, 2♀; USNM). *Monaragala:* Agunakolapelessa (on or in leaf litter), 8–9 Oct 1980, K. V. Krombein, P. B. Karunaratne, T. Wijesinhe, L. Jayawickrema, V. Gunawardane (1♂, 10♀; USNM); Agunakolapelessa (Malaise trap), 27–28 Mar 1981, K. V. Krombein, T. Wijesinhe, L. Weeratunge (2♂, 9♀; USNM). *North Province.* Kudattanai (6 mi SE Point Pedro), 13 Feb 1962, H. Andersson, P. Brink, L. Cederholm (1♀; ZIL). *Northwest Province.* Kadalmparu (15 mi N Negombo; at shore of lagoon), 31 Jan 1962, H. Andersson, P. Brink, L. Cederholm (1♂, 1♀; ZIL). *Western Province. Colombo:* Colombo, 18 Apr 1980, W. N. Mathis (8♀; USNM); Colombo, Museum Garden, 28–31 Jan 1975, 6 Jul 1976, K. V. Krombein, P. B. Karunaratne, P. Fernando (2♀; USNM); Colombo, 6 Jun 1902, Dr. Uzel (1♀; NMW); Colombo (swept waste ground), 17 Sep 1963 (1♀; BMNH); Katunayaka (near airport), 16 Jan 1977, K. V. Krombein (1♀; USNM); Ratmalana (9 mi S Colombo; dry grass on sandy beach), 7–13 Jan 1963, H. Andersson, P. Brink, L. Cederholm (2♂, 1♀; ZIL).

THAILAND. Chaing Mai, 5 Dec 1985, K. A. Spencer (1♀; NMWL). Hot (20 km W; 200 m), 17 Oct 1993, F. Kaplan, A. Freidberg (1♂; USNM); KhaoLak Beach (100 km N Phuket), 19 Oct 1993, F. Kaplan, A. Freidberg (1♂; USNM).

Distribution (Fig. 47).—Oriental: Cocos-Keeling Islands, Indonesia (Java, Sulawesi), Malaysia, Philippines, Sri Lanka, Thailand.

Natural history.—Like *A. indicus,* this species apparently also occurs around sandy habitats, at least in part. This suggestion is based on the observation that the paralectotypes of *A. beckeri* (see label data noted above) were collected by a nest of *Bembex,* a genus of solitary wasps known to construct nests in sand.

Remarks.—This is a widespread species in the Orient and is likely to occur in more countries than available locality records indicate. The lack of records from most of the countries of Southeast Asia is particularly noteworthy and probably reflects sampling error rather than the species' absence.

Cogan and Wirth (1977) determined previously that *A. elegans* was a junior synonym of *A. beckeri,* and here we have concluded that both names are junior synonyms of *A. nigrifinis,* a species name that was generally overlooked until Cogan and Wirth (1977) correctly assigned this species to *Actocetor* from *Opomyza* (family Opomyzidae).

Subgenus *Poecilostenia* Bezzi

Poecilostenia Bezzi 1908: 195 [as a genus; type species: *Poecilostenia decemguttata* Bezzi 1908, monotypy].—Wirth 1955: 51 [subgeneric status].

Diagnosis.—This subgenus is distinguished from *Actocetor* sensu stricto by the following combination of characters:

Description.—*Thorax:* Mesonotum generally yellow microtomentose. Wing alula completely reduced, bearing few or no setulae along posterior margin; anal angle straight, cell cua_1 narrower than discal cell; vein R_{4+5} bearing 5–6 setulae on dorsum, basad of crossvein r-m and 5–10 setulae apicad of crossvein r-m; vein CuA_1 conspic-

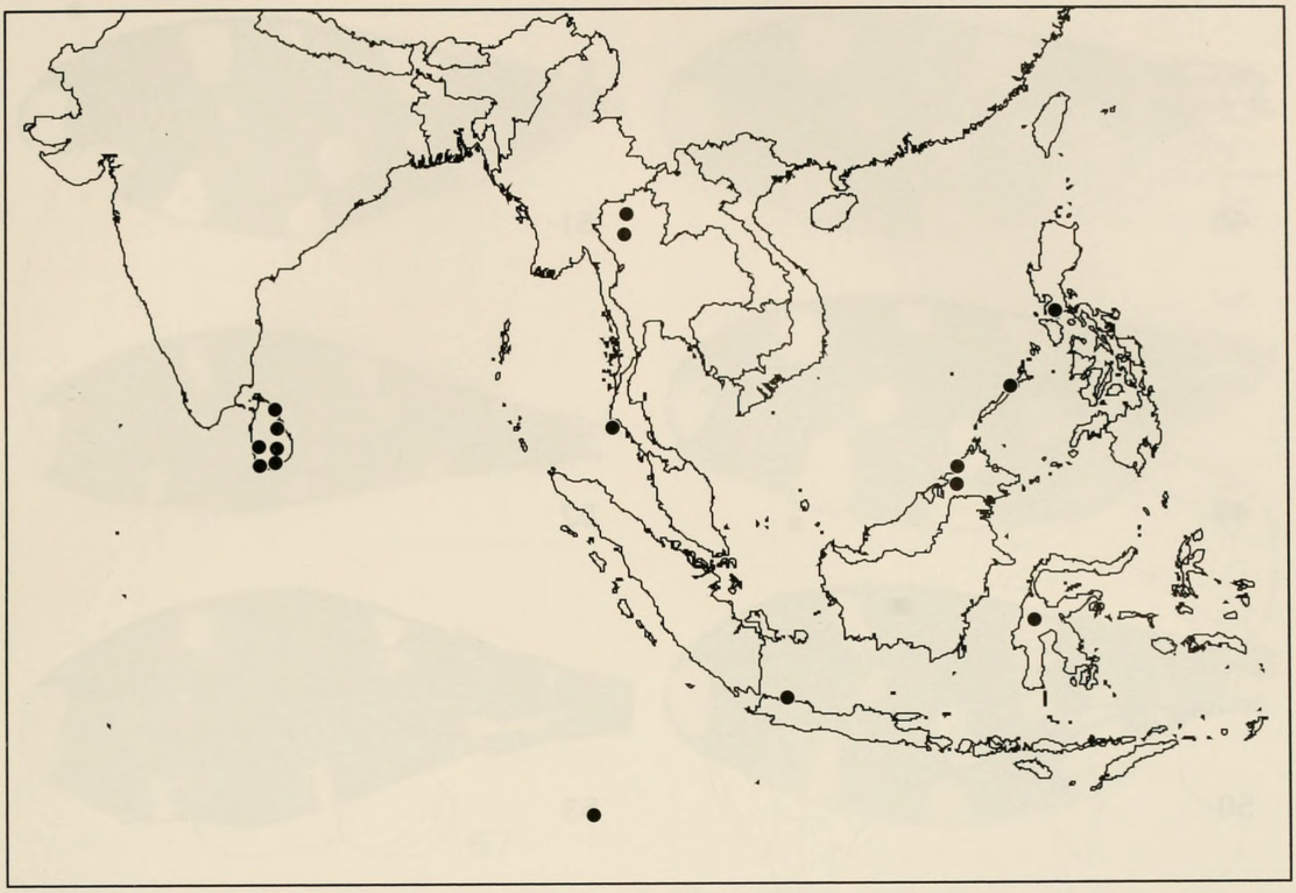


Fig. 47. Distribution map for *Actocetor nigrifinis*.

uously sinuous along posterior margin of discal cell; discal cell with at most 1 white spot. Knob of halter dark brown to black, not distinctly clubbed.

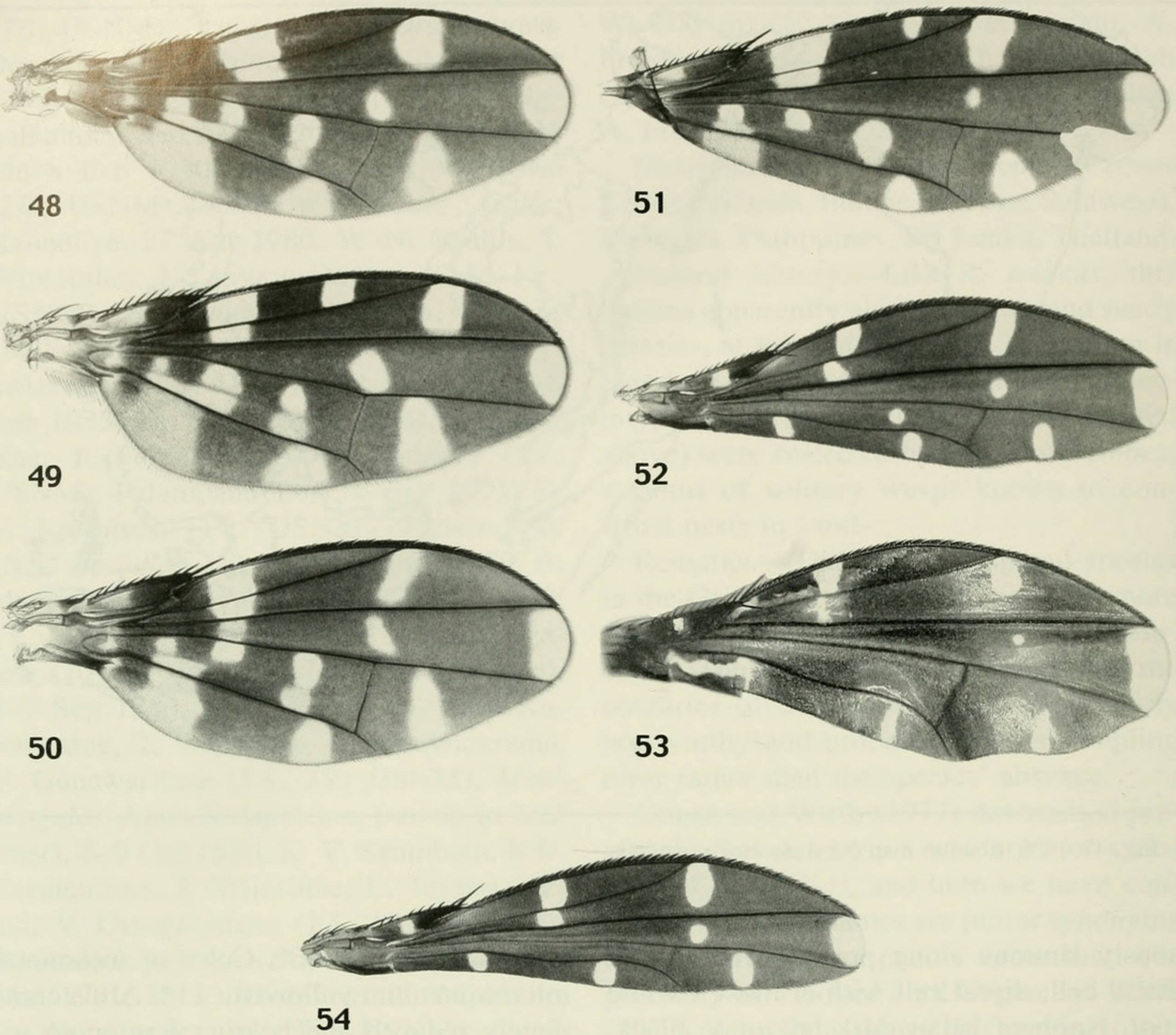
Abdomen: 5th tergite of male bearing 4 well-developed setae along posterior margin; epandrium lacking large setae along dorsum; other structures as in the species descriptions of *A. decemguttatus* and *A. lindneri*, the only species of *Poecilostenia* for which males are known.

Discussion.—Specimens of *Poecilostenia* are uncommon generally and more specifically when compared with *Actocetor* sensu stricto. Although the species can be determined fairly easily, some are represented by a single female. We suspect that additional species will be found in this subgenus as the Afrotropical Region is better sampled.

The subgenus *Poecilostenia* is monophyletic, as substantiated by the following synapomorphies (characters marked with an * are unambiguous): 6*. Color of mesonotal microtomentum yellowish; 11*. Alula completely reduced and bearing few or no setulae along posterior margin; 12*. Cell cua_1 generally narrower than discal cell, and anal margin nearly straight; 13*. Vein R_{4+5} bearing setulae basad and apicad of crossvein r-m; 14*. Anterior margin of vein CuA_1 basad of crossvein dm-cu slightly concave; 20*. Knob of halter dark brown to black; 21*. Knob of halter not distinctly clubbed (only slightly expanded from diameter of stem); 22. Microtomentum on anterior margins of 3rd and 4th tergites with narrow bands (secondarily modified in *A. lindneri*).

Actocetor (*Poecilostenia*) *decemguttatus* (Bezzi)
(Figs. 52, 55–59)

Poecilostenia decemguttata Bezzi 1908: 195 [Botswana. Kang-Khakhea, Kalahari; ST ♂♀, deposition unknown].—Cres-



Figs. 48–54. Wings. 48, *A. hovus*. 49, *A. indicus*. 50, *A. nigrifinis*. 51, *A. afrus*. 52, *A. decemguttatus*. 53, *A. lindneri*. 54, *A. yaromi*.

son 1946: 256 [review, list, South Africa].

Actocetor (*Poecilostenia*) *decemguttatus*: Wirth 1955: 51 [generic combination].—Cogan 1980: 659 [Afrotropical catalog].

Actocetor anormalipennis Séguy 1933: 40.—Cresson 1946: 256 [synonymy with *P. decemguttata* Bezzi].—Wirth 1955: 51 [key].—Canzoneri and Rampini 1995: 254 [list, Sierra Leone].—Mathis and Zatwarnicki 1995: 23 [world catalog]. **New synonym.**

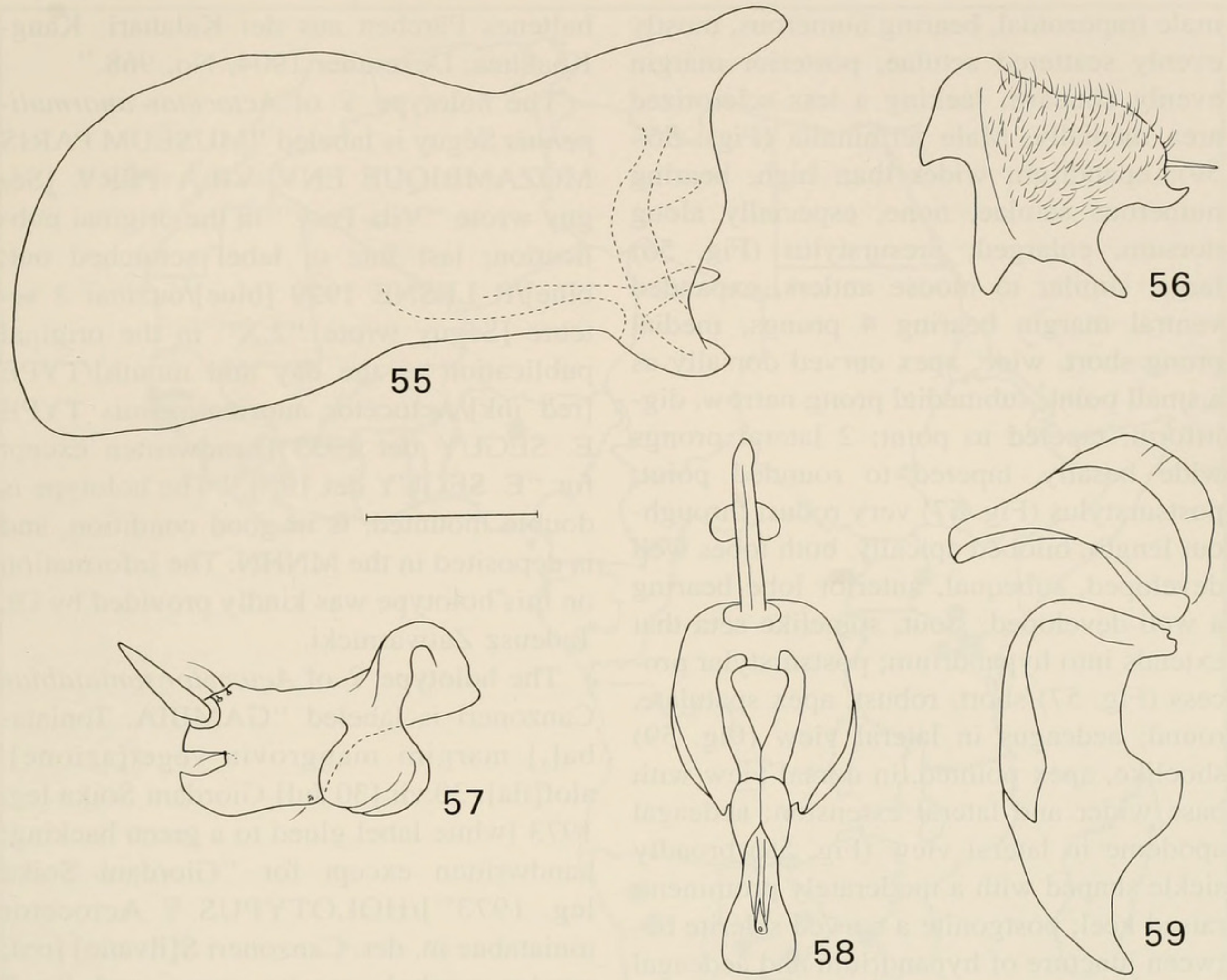
Actocetor abnormalipennis: Cresson 1946: 256 [lapsus, synonymy with *Poecilostenia decemguttata* Bezzi].—Cogan 1980: 659 [Afrotropical catalog].

Actocetor toniatabae Canzoneri 1981: 209 [habitus figure].—Mathis and Zatwarnicki 1995: 22 [world catalog]. **New synonym.**

Diagnosis.—This species is distinguished from congeners by the following combination of characters: moderately small shore flies, body length 2.30–2.90 mm.

Description.—*Head:* Arista with 8–9 dorsal rays. Gena-to-eye ratio 0.20–0.21.

Thorax: Mesonotum densely microtomentose, yellowish brown, pleura concolorous; 2 pale brown bars anteriorly, separated by width equal to that separating prescutellar acrostichal setae; scutellum with



Figs. 55–59. Structures of the male preabdomen and terminalia of *Actocetor decemguttatus*. 55, Hypandrium, lateral view. 56, Presurstylus, posterior view. 57, Postsurstylus, lateral view. 58, Aedeagus, aedeagal apodeme, dorsal view. 59, Same, lateral view. Scale bar equals 0.1 mm.

apical ½ brown, basal portion concolorous with posterior portion of scutum. Wing (Fig. 52) very narrow, cell cua_1 narrower than discal cell, anal margin nearly straight; vein R_{4+5} bearing 5 setulae basad and 5 setulae apicad of crossvein r-m; wing pattern as follows: cell c with rectangular white spot basad of subcostal break; cell r_1 with rectangular, medial spot; cell r_{2+3} with 2 spots, basal rectangular/trapezoidal spot in line with spot in cell r_1, apical, transversely oval/rectangular spot, immediately apicad of merger of vein R_{2+3} with costa; cell r_{4+5} with a circular medial spot in line with apical spot in cell r_{2+3}, and an apical spot; discal cell with a circular, subapical spot; cell m with transversely oval-rectangular spot; cell cua_1 with 2 spots, rectangular sub-basal spot, and transversely trapezoidal spot in line with spot in discal cell, vein CuA_1 slightly concave between these spots; costal vein ratio 0.70–0.71; M vein ratio 1.17–1.18. Halter stem at base yellowish white, apical part of stem and knob dark brown to black; knob only slightly to moderately expanded from diameter of stem, not distinctly spatulate. Legs generally whitish yellow to yellow.

Abdomen: Mostly shiny, base of 1st tergite with gray microtomentum; base of 3rd and 4th tergites with tiny bands of gray microtomentum; generally metallic black but sometimes with reddish anterior and/or posterior margins of tergites; 3rd and 4th sternites of male rectangular, moderately narrow, 2–3× longer than wide; 5th sternite of male trapezoidal, bearing numerous, mostly evenly scattered setulae, posterior margin evenly concave, lacking a less sclerotized area medially. Male terminalia (Figs. 56–59): epandrium wider than high, bearing numerous setulae, none, especially along dorsum, enlarged; presurstylus (Fig. 56) large, similar to moose antlers, expanded ventral margin bearing 4 prongs, medial prong short, wide, apex curved dorsally as a small point; submedial prong narrow, digitiform, tapered to point; 2 lateral prongs wide basally, tapered to rounded point; postsurstylus (Fig. 57) very robust throughout length, bilobed apically, both lobes well developed, subequal, anterior lobe bearing a well-developed, stout, spinelike seta that extends into hypandrium; postsurstylar process (Fig. 57) short, robust, apex spatulate, round; aedeagus in lateral view (Fig. 59) shoelike, apex pointed, in dorsal view with base wider and lateral extension; aedeagal apodeme in lateral view (Fig. 59) broadly sickle shaped with a moderately prominent, raised keel; postgonite a curved sclerite between juncture of hypandrium and aedeagal apodeme and postsurstylus; postsurstylar process with short stalk, apex somewhat spatulate; pregonite not distinct, perhaps greatly reduced or fused indistinguishably with other structures; hypandrium (Fig. 55) greatly modified, narrow but extended anteriorly like a large, narrow, keel, pouch narrow but deep, bearing pronglike processes that are opposable to spinelike seta of postsurstylus.

Type material.—The syntypes, apparently 1 ♂ and 1 ♀, of *Poecilostenia decemguttata* Bezzi were not located despite searches in Italy (Museo Civico di Storia Naturale, Milano; Dr. Carlo Pesarini) and Germany (Zoologisches Museum, Humboldt Universität, Berlin; Dr. Hella Wendt), and our determination of this species is based on the original description, especially the illustration of the wing. Bezzi (1908) published the following locality data about the syntypes and type locality: "Ein gut erhaltenes Pärchen aus der Kalahari: Kang-Khakhea, Dezember 1904, No. 968."

The holotype ♀ of *Actocetor anormalipennis* Séguy is labeled "MUSÉUM PARIS MOZAMBIQUE ENV. VILA PERV. [Séguy wrote "Vila-Pery" in the original publication; last line of label scratched out; blue]/P. LESNE 1929 [blue]/ouzinai 2 setebre [Séguy wrote "2.X" in the original publication as the day and month]/TYPE [red ink]/Actocetor anormalipennis TYPE E. SÉGUY det 1933 [handwritten except for "E. SÉGUY det 19"]." The holotype is double mounted, is in good condition, and is deposited in the MNHN. The information on this holotype was kindly provided by Dr. Tadeusz Zatwarnicki.

The holotype ♀ of *Actocetor toniatabiae* Canzoneri is labeled "GAMBIA. Toniataba[,] margini mangrovia veget[azione]. alof[ila]. 30.vii [30 Jul] Giordani Soika leg. 1973 [white label glued to a green backing; handwritten except for "Giordani Soika leg. 1973"]/HOLOTYPUS ♀ Actocetor toniatabae m. det. Canzoneri S[ilvano] [red; gender symbol, species name, and "m." handwritten]/Actocetor decemguttatus (Bezzi) det. WNMathis 2000 [species name and year handwritten]." The holotype is double mounted (minuten in a rectangular card), is in excellent condition, and is deposited in the CANZ collection that is now in the MRSN.

Other specimens examined.—AFROTROPICAL. BOTSWANA. Kuke Pan, 21–30 Mar 1930, V.-L. Kal. Exp. (1 ♀; NMSA). Serowe (Malaise trap), 16–30 Apr 1985, P. Forchhammer (1 ♀; BMNH). Tlokweng, 15 Mar 1990, J. M. Mashonja, (6♂, 8♀; NMWL, USNM).

GAMBIA. *Western:* Bakau, 15 Nov 1993, J. C. Deeming (1 ♀; NMWL).

KENYA. Matembur (01°22′N, 35°02′E; 1550 m; Malaise trap), 26–27 May 1980, Lamoral (1 ♀; NMSA). Nairobi (50 km SE; Rt. A109), 30 Apr 1991, A. Freidberg, F. Kaplan (1 ♀; USNM). Rift Valley: Nguru-

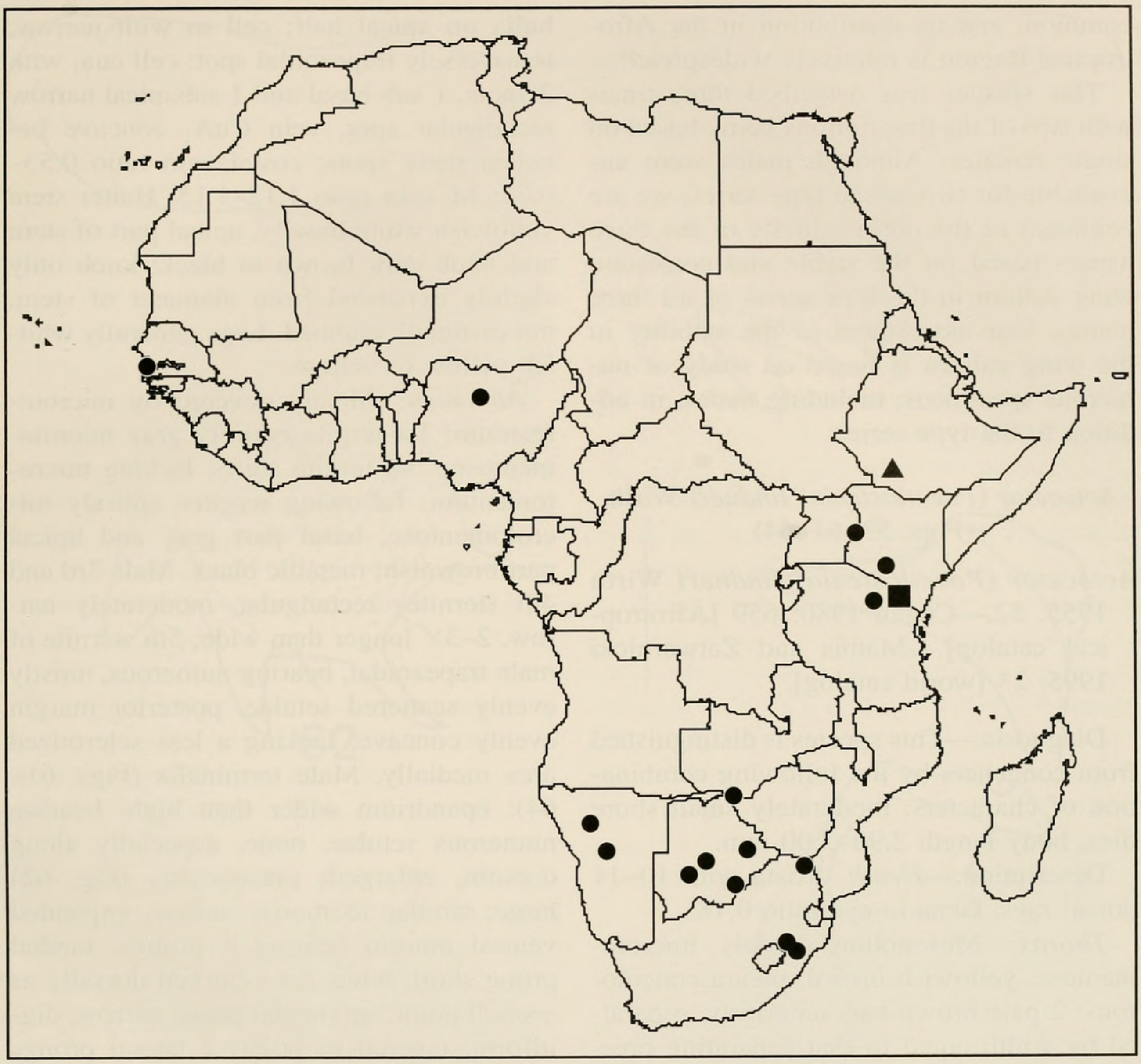


Fig. 60. Distribution map for *Actocetor decemguttatus* (filled circles), *A. lindneri* (filled square), and *A. yaromi* (filled triangle).

man, Oloibortoto River (1°48′S, 36°04′E; Malaise trap), 17–20 May 1999, R. Copeland (1♀; USNM).

NAMIBIA. Outjo (52 km W road 65; 20°14′S, 15°40′E; *Mopane* woodland on a rocky hillside), 24 Mar 1984, B. Stuckenberg, J. G. H. Londt (1♂; NMSA). Okahandja, 2–4 Feb 1972 (1♀; BMNH);

NIGERIA. Zaria, Samaru, Jun 1979, J. C. Demming (3♂, 6♀; NMWL, USNM).

SOUTH AFRICA. *KwaZulu-Natal:* Mhlopeni Nature Reserve (15 km S Muden; 2930Ab), 22 Dec 1983, J. G. H. Londt (1♀; NMSA). Weenen, Nov 1929, H. P. Thomasset (1♂, 1♀; BMNH, NMSA). *Mpumalanga:* Shingwedzi, 9 Feb 1988, D. Simon (2♀; USNM).

TANZANIA. Tarangire National Park (36°10′E, 03°50′S), Dec 1994, D. Grimaldi (2♂, 4♀; AMNH).

ZAMBIA. Livingstone, 16–20 Nov 1958, E. Lindner (1♀; SMN).

Distribution (Fig. 60).—*Afrotropical:* Botswana, Gambia, Kenya, Mozambique, Namibia, Nigeria, South Africa, Tanzania, and Zambia.

Remarks.—This is the only species of the subgenus *Poecilostenia* that is somewhat common, and its distribution in the Afrotropical Region is relatively widespread.

This species was described three times with two of the descriptions being based on single females. Although males were unavailable for two of the type series, we are confident of the conspecificity of the three names based on the stable and consistent wing pattern in the type series of all three names. Our assessment of the stability in the wing pattern is based on study of numerous specimens, including males, in addition to the type series.

Actocetor (*Poecilostenia*) *lindneri* Wirth
(Figs. 53, 61–64)

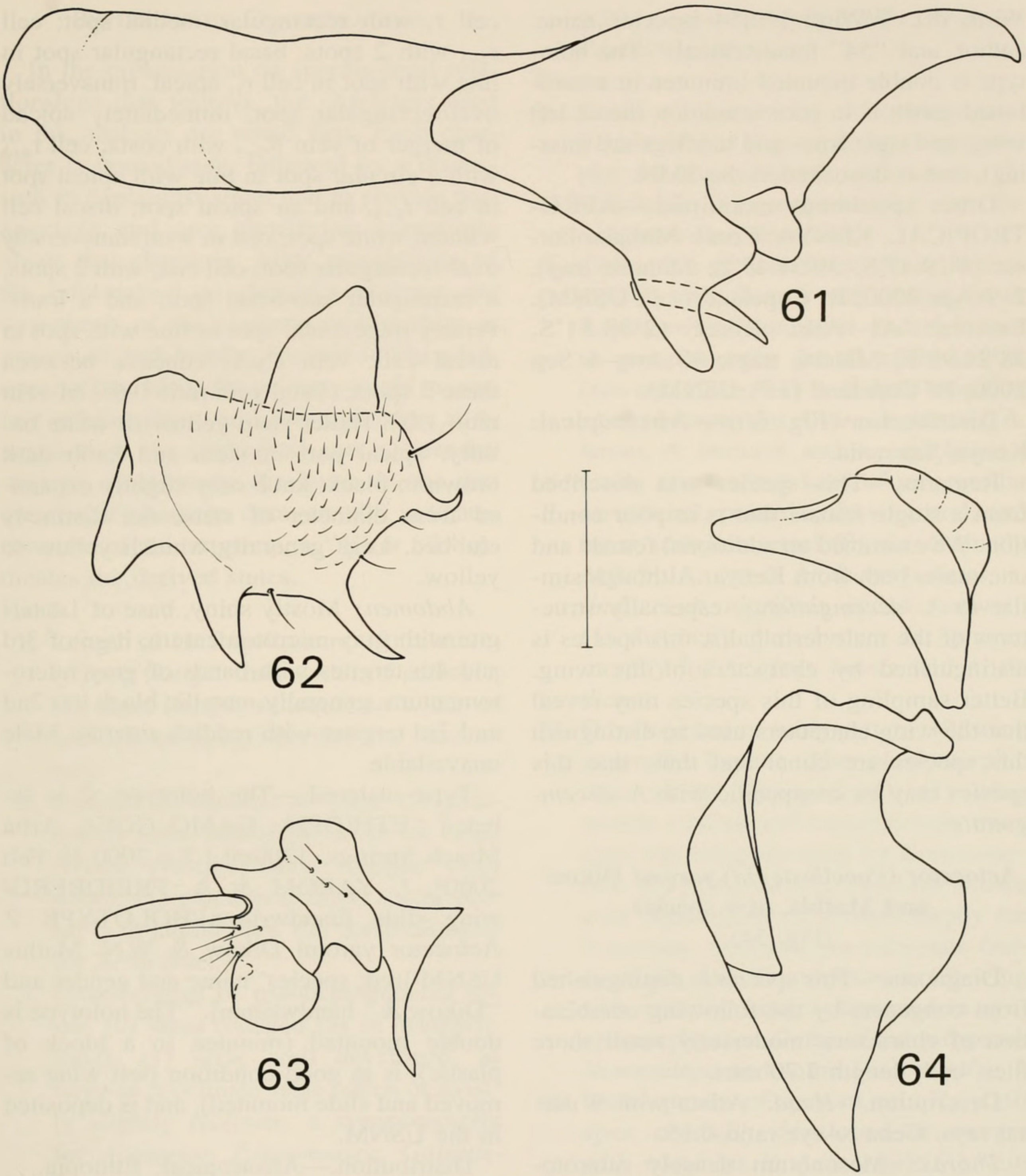
Actocetor (*Poecilostenia*) *lindneri* Wirth 1955: 52.—Cogan 1980: 659 [Afrotropical catalog].—Mathis and Zatwarnicki 1995: 23 [world catalog].

Diagnosis.—This species is distinguished from congeners by the following combination of characters: moderately small shore flies, body length 2.90–3.00 mm.

Description.—*Head:* Arista with 10–11 dorsal rays. Gena-to-eye ratio 0.18.

Thorax: Mesonotum densely microtomentose, yellowish brown, pleura concolorous; 2 pale brown bars anteriorly, separated by width equal to that separating prescutellar acrostichal setae; scutellum with apical ½ pale brown, basal portion concolorous with posterior portion of scutum. Wing (Fig. 53) very narrow, cell cua_1 narrower than discal cell, anal margin nearly straight; vein R_{4+5} bearing 7 setulae basad and 7 setulae apicad of crossvein r-m; wing pattern as follows: cell c with rectangular white spot basad of subcostal break; cell r_1 with a circular, sub-basal spot and a rectangular, medial spot; cell r_{2+3} with 2 spots, basal, transversely narrow, rectangular spot in line with spot in cell r_1, apical, transversely oval/rectangular spot, immediately apicad of merger of vein R_{2+3} with costa; cell r_{4+5} with a tiny circular, sub-apical spot, and an apical spot; discal cell without spots but with a paler-colored, crescent-shaped bulla on apical half; cell m with narrow, transversely trapezoidal spot; cell cua_1 with 2 spots, 1 sub-basal and 1 subapical narrow rectangular spot, vein CuA_1 concave between these spots; costal vein ratio 0.53–0.72; M vein ratio 1.12–1.15. Halter stem yellowish white basally, apical part of stem and knob dark brown to black; knob only slightly expanded from diameter of stem, not distinctly clubbed. Legs generally whitish yellow to yellow.

Abdomen: Mostly covered by microtomentum: 1st tergite entirely gray microtomentose; 2nd tergite shiny, lacking microtomentum, following tergites entirely microtomentose, basal part gray and apical part brownish; metallic black. Male 3rd and 4th sternites rectangular, moderately narrow, 2–3× longer than wide; 5th sternite of male trapezoidal, bearing numerous, mostly evenly scattered setulae, posterior margin evenly concave, lacking a less sclerotized area medially. Male terminalia (Figs. 61–64): epandrium wider than high, bearing numerous setulae, none, especially along dorsum, enlarged; presurstylus (Fig. 62) large, similar to moose antlers, expanded ventral margin bearing 4 prongs, medial prong short, wide, apex curved dorsally as a small point; submedial prong narrow, digitiform, tapered to point; 2 lateral prongs wide basally, tapered to rounded point; postsurstylus (Fig. 63) very robust throughout length, bilobed apically, both lobes well developed, subequal, anterior lobe bearing a well-developed, stout, spinelike seta that extends into hypandrium; postsurstylar process (Fig. 63) short, robust, apex spatulate, round; aedeagus in lateral view (Fig. 64) shoelike, apex pointed, in dorsal view with base wider and lateral extension; aedeagal apodeme in lateral view (Fig. 64) broadly sickle shaped with a moderately prominent, raised keel; postgonite a curved sclerite between juncture of hypandrium and aedeagal apodeme and postsurstylus; postsurstylar process with short stalk, apex somewhat spatulate; pregonite not distinct, perhaps greatly reduced or fused indistinguishably



Figs. 61–64. Structures of the male preabdomen and terminalia of *Actocetor lindneri*. 61, Hypandrium, lateral view. 62, Presurstylus, posterior view. 63, Postsurstylus, lateral view. 64, Aedeagus, aedeagal apodeme, lateral view. Scale bar equals 0.1 mm.

with other structures; hypandrium (Fig. 61) greatly modified, narrow but extended anteriorly like a large, narrow, keel, pouch narrow but deep, bearing pronglike processes that are opposable to spinelike seta of postsurstylus.

Type material.—The holotype ♀ is labeled "[Tanzania] Jipe-See 20.–23. V. 1952 D. O. Afrika Exp. [blue]/Jipe 21. V 52 [handwritten]/HOLOTYPE ♀ Actocetor linderni W. W. Wirth [red; species name handwritten]/Actocetor (Poecilostenia) lindneri

Wirth det. WWirth [19]54 [species name, author, and "54" handwritten]." The holotype is double mounted (minuten in a cardboard card), is in poor condition (head, left wing, and right fore- and hindlegs are missing), and is deposited in the SMN.

Other specimens examined.—AFROTROPICAL. KENYA. Coast: Muhaka Forest (4°19.47′S, 39°31.45′E; Malaise trap), 2–9 Apr 2000, R. Copeland (1♂; USNM). Eastern: At Athi River (2°38.51′S, 38°21.98′E; Malaise trap), 30 Aug–6 Sep 2000, R. Copeland (1♀; USNM).

Distribution (Fig. 60).—Afrotropical: Kenya, Tanzania.

Remarks.—This species was described from a single female that is in poor condition. We examined an additional female and one male, both from Kenya. Although similar to *A. decemguttatus*, especially structures of the male terminalia, this species is distinguished by characters of the wing. Better sampling of this species may reveal that the wing characters used to distinguish this species are clinal and thus, that this species may be conspecific with *A. decemguttatus*.

Actocetor (*Poecilostenia*) *yaromi* Dikow and Mathis, new species
(Fig. 54)

Diagnosis.—This species is distinguished from congeners by the following combination of characters: moderately small shore flies, body length 2.70 mm.

Description.—*Head:* Arista with 9 dorsal rays. Gena-to-eye ratio 0.15.

Thorax: Mesonotum densely microtomentose, yellowish brown, pleura concolorous; 2 pale brown bars anteriorly, separated by width equal to that separating prescutellar acrostichal setae; scutellum entirely concolorous with yellowish to slightly brownish yellow scutum. Wing (Fig. 54) very narrow, but cell cua_1 wider than discal cell, anal margin nearly straight; vein R_{4+5} bearing 6 setulae basad and 5 setulae apicad of crossvein r-m; wing pattern as follows: cell c with rectangular white spot medially; cell r_1 with rectangular, medial spot; cell r_{2+3} with 2 spots, basal rectangular spot in line with spot in cell r_1, apical, transversely oval/rectangular spot, immediately apicad of merger of vein R_{2+3} with costa; cell r_{4+5} with a circular spot in line with apical spot in cell r_{2+3}, and an apical spot; discal cell without white spot; cell m with transversely oval-rectangular spot; cell cua_1 with 2 spots, a rectangular sub-basal spot, and a transversely trapezoidal spot in line with spot in discal cell; vein CuA_1 concave between these 2 spots; costal vein ratio 0.66; M vein ratio 1.05. Halter stem yellowish white basally, apical part of stem and knob dark brown to black; knob only slightly expanded from diameter of stem, not distinctly clubbed. Legs generally whitish yellow to yellow.

Abdomen: Mostly shiny, base of 1st tergite with gray microtomentum; base of 3rd and 4th tergites with bands of gray microtomentum; generally metallic black but 2nd and 3rd tergites with reddish anterior. Male unavailable.

Type material.—The holotype ♀ is labeled "ETHIOPIA: GAMO GOFA, Arba Minch Springs, 1300m[,] 8.ii.2000 [8 Feb 2000], I. YAROM & A. FREIDBERG/ wing slide [handwritten]/HOLOTYPE ♀ Actocetor yaromi Dikow & W.N. Mathis USNM [red; species' name and gender and "Dikow &" handwritten]." The holotype is double mounted (minuten in a block of plastic), is in good condition (left wing removed and slide mounted), and is deposited in the USNM.

Distribution.—Afrotropical: Ethiopia.

Etymology.—The species epithet, *yaromi*, is a genitive patronym to honor and recognize the contributions of Dr. Ilan Yarom to the study of acalyptrate Diptera. Dr. Yarom collected the holotype.

Remarks.—We are describing this species now despite having only a single female specimen available to us. The species is distinctive, especially the characters of the wing, and confusion with congeners is unlikely.

Phylogenetic Considerations

In the presentation on species-level relationships that follows, the characters used in the analysis are noted first. Each character is immediately followed by a discussion to explain its states and to provide perspective and any qualifying comments about that character. After presentation of the information on character evidence, an hypothesis of the cladistic relationships is presented and briefly discussed. The cladogram (Fig. 65) is the primary mode to convey relationships, and the discussion is to supplement the cladogram and is intended only to complement the latter. In the discussion of character data, an "0" indicates the state of the outgroup; a "1" or "2" indicates the derived states.

Head:

1. Length of 1st flagellomere: (0) relatively long (longer than width of pedicel); (1) short (length subequal to width of pedicel; an autapomorphy for *Actocetor*).
2. Position of antenna on head: (0) positioned near midheight level of head (frons conspicuously longer than wide); (1) positioned high, above dorsal ⅓ in lateral view (an autapomorphy for *Actocetor*).
3. Development of pseudopostocellar setae: (0) setae reduced (as in *Mimapsilopa*); (1) setae well developed, as large as proclinate setae (often or mostly slightly reclinate; a synapomorphy for *Actocetor, Eremomusca, Guttipsilopa,* and *Trypetomima*).
4. Development of facial setae: (0) face bearing 2 well-developed setae; (1) face bearing 4 well-developed setae in a vertical row, dorsalmost 1–2 setae cruciate (a synapomorphy for *Actocetor* and *Guttipsilopa*).
5. Gena-to-eye ratio: (0) variable but gena generally short with ratios of 0.08–0.15; (1) 0.21–0.36 (a synapomorphy for the subgenus *Actocetor*); (2) 0.14–0.20 (a synapomorphy for the subgenus *Poecilostenia*).

Thorax:

6. Color of mesonotal microtomentum: (0) blackish; (1) grayish (a synapomorphy for the subgenus *Actocetor*); (2) yellowish (a synapomorphy for the subgenus *Poecilostenia*).
7. Coloration of scutellum: (0) scutellum entirely concolorous with scutum (as in *A. yaromi*); (1) apicad ¼–½ dark brown (a synapomorphy for *A. afrus* and *A. indicus*); (2) apicad ½–¾ dark brown (a synapomorphy for *A. decemguttatus, A. hovus, A. lindneri,* and *A. nigrifinis*).
8. Color surrounding base of prescutellar acrostichal, posterior dorsocentral, and basal scutellar setae: (0) not distinctly dark brown (as in *A. decemguttatus, A. lindneri, A. nigrifinis,* and *A. yaromi*); (1) distinctly dark brown (a synapomorphy for *A. afrus, hovus,* and *A. indicus*).
9. Development of wing pattern: (0) wing generally hyaline (the plesiomorphic state as in *Mimapsilopa*); (1) wing mostly whitish and conspicuously maculate (an autapomorphy for *Eremomusca*); (2) wing mostly blackish brown with white spots (a synapomorphy for *Actocetor, Guttipsilopa* subgenus *Guttipsilopa,* and *Trypetomima*); (3) wing with anterior margin darkened (a synapomorphy for *Guttipsilopa* subgenus *Nesopsilopa* and some *Discomyza*).
10. Development of apex of vein R_{2+3}: (0) apex normally developed at merger with costa (as in *Actocetor*); (1) vein R_{2+3} with a subapical stump vein (a synapomorphy for *Eremomusca* and *Trypetomima*).
11. Development of alula: (0) alula a well-developed lobe (as in *Guttipsilopa*); (1) reduced to a thin bandlike lobe bearing numerous short or long setulae along posterior margin (a synapomorphy for the subgenus *Actocetor* and the genera *Eremomusca, Mimapsilopa,* and *Trypetomima*); (2) completely reduced and

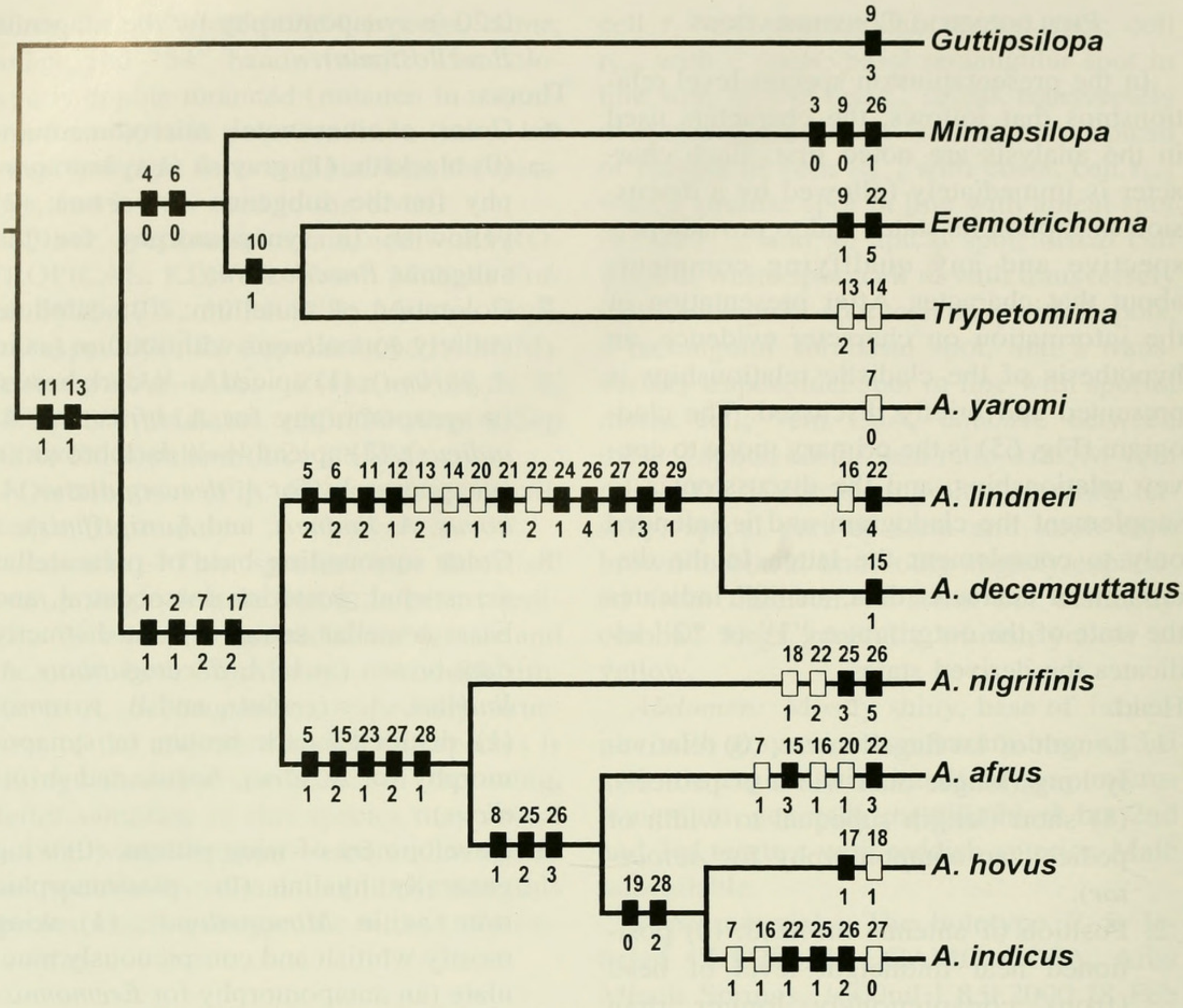


Fig. 65. Cladogram depicting hypothetical cladistic relationships among species of *Actocetor*.

bearing few or no setulae along posterior margin (an autapomorphy for the subgenus *Poecilostenia*).

12. Development of cell cua_1: (0) cell cua_1 broad, broader than discal cell, and anal angle moderately well developed (as in the subgenus *Actocetor*); (1) cell cua_1 generally narrower than discal cell, and anal margin nearly straight (an autapomorphy for the subgenus *Poecilostenia*).

13. Development of setulae on vein R_{4+5}: (0) no setulae present (as in *Guttipsilopa*); (1) setulae only basad of crossvein r-m (a synapomorphy for the subgenus *Actocetor* and the genera *Eremomusca* and *Mimapsilopa*); (2) setulae basad and apicad of crossvein r-m (a synapomorphy for the subgenus *Poecilostenia* and the genus *Trypetomima*).

14. Shape of anterior margin of vein CuA_1 basad of crossvein dm-cu: (0) straight (as in the subgenus *Actocetor*); (1) slightly concave (a synapomorphy for *A. decemguttatus, A. lindneri, A. yaromi,* and *Trypetomima*).

15. Number of white spots in discal cell: (0) no spot (as in *A. yaromi* and *A. lindneri*); (1) 1 spot (a synapomorphy for *A. decemguttatus* and *Trypetomima*); (2) 2 spots (a synapomorphy for *A. hovus, A. indicus,* and *A. nigrifinis*); (3) 3 spots (an autapomorphy for *A. afrus*).

16. Number of white spots in cell r_1: (0) 1 spot (as in *A. decemguttatus, A. hovus,*

A. nigrifinis, and *A. yaromi*); (1) 2 spots (a synapomorphy for *A. afrus, A. indicus,* and *A. lindneri*).

17. Number of setulae on vein R_{4+5} basad of crossvein r-m: (0) no setulae present (as in *Guttipsilopa*); (1) 2–3 setulae (an autapomorphy for *A. hovus*); (2) 4 or more setulae (a synapomorphy for *A. afrus, A. decemguttatus, A. indicus, A. lindneri, A. nigrifinis,* and *A. yaromi*).
18. Costal vein ratio: (0) 0.53–0.73 (as in *A. afrus, A. decemguttatus, A. indicus, A. lindneri,* and *A. yaromi*); (1) 0.73–0.87 (a synapomorphy for *A. hovus* and *A. nigrifinis*).
19. M vein ratio: (0) 0.84–1.00 (as in *A. hovus* and *A. indicus*); (1) 1.01–1.21 (a synapomorphy for *A. afrus, A. decemguttatus, A. lindneri, A. nigrifinis,* and *A. yaromi*).
20. Color of knob of halter: (0) white to yellow (as in the subgenus *Actocetor*); (1) dark brown to black (a synapomorphy for *A. afrus, A. decemguttatus, A. lindneri,* and *A. yaromi*).
21. Shape of knob of halter: (0) distinctly clubbed (as in the subgenus *Actocetor*); (1) knob of halter not distinctly clubbed (only slightly expanded from diameter of stem; an autapomorphy for the subgenus *Poecilostenia*).

Abdomen:

22. Development of microtomentum on abdomen (in addition to microtomentose anterior margin of 1st tergite): (0) entirely bare (as in *A. hovus* and *A. nigrifinis*); (1) anterior margin of 4th tergite with distinct band (an autapomorphy for *A. indicus*); (2) anterior margins of 3rd and 4th tergites with narrow bands (a synapomorphy for *A. decemguttatus* and *A. yaromi*); (3) anterior margins of 3rd, 4th, and 5th tergites with distinct bands (a synapomorphy for *A. afrus*); (4) tergites 3–7 entirely gray and brown microtomentose (an autapomorphy for *A. lindneri*); (5) entirely microtomentose (genus *Eremomusca*).
23. Development of setae on dorsum of epandrium: (0) bearing small setae only (as in *A. decemguttatus* and *A. lindneri*); (1) bearing well-developed, dorsally erect setae (a synapomorphy for *A. afrus, A. hovus, A. indicus,* and *A. nigrifinis;* no male available for *A. yaromi*).
24. Shape of male 3rd and 4th sternites: (0) rectangular, broad, 1–2× longer than wide (as in *A. afrus, A. hovus, A. indicus,* and *A. nigrifinis*); (1) rectangular, moderately narrow, 2–3× longer than wide (a synapomorphy for *A. decemguttatus* and *A. lindneri*; no male available for *A. yaromi*).
25. Shape of male 5th sternite: (0) trapezoidal with slightly concave posterior margin (as in *A. decemguttatus* and *A. lindneri*); (1) trapezoidal with medial weakness or slight indentation on concave posterior margin (an autapomorphy for *A. indicus*); (2) trapezoidal, divided medially into two sclerites (a synapomorphy for *A. afrus* and *A. hovus*); (3) trapezoidal with concave posterior margin with medial weakness and 4–5 setulae on either side of weakness (a synapomorphy for *A. nigrifinis*; no male available for *A. yaromi*).
26. Postsurstylar process: (0) absent; (1) present, cylindrical (an autapomorphy for *Mimapsilopa*); (2) present, clubbed with rounded knob (an autapomorphy for *A. indicus*); (3) present, expanded ventrally and projected to a point posteriorly (a synapomorphy for *A. afrus* and *A. hovus*); (4) present, clubbed but not stalked (a synapomorphy for *A. decemguttatus* and *A. lindneri*); (5) present, distinctly expanded apically, with anterior portion extended to narrow process, posterior margin narrowly rounded (an autapomorphy for *A. nigrifinis*; no male available *A. yaromi*).
27. Postsurstylus: (0) bilobed subapically with a small, digitiform, medial, pointed process (as in *A. indicus*); (1) bilobed apically, both lobes well devel-

Table 1. Matrix of characters and taxa used in the cladistic analysis of *Actocetor* (numbers for characters correspond with those used in the text).

	Characters
	00000 0000111111111122 22222222
	12345 6789012345678901 23456789
Taxa	
Guttipsilopa (Nesopsilopa)	00110 1003000000?0??00 00000000
Mimapsilopa	00000 0000010100?0??00 00001000
Eremomusca	00100 0001110100?0??00 50000000
Trypetomima	00100 000211021000??00 00000000
Actocetor (A.) hovus	11111 1212010102011000 01023220
Actocetor (A.) indicus	11111 1112010102120000 11012020
Actocetor (A.) nigrifinis	11111 1202010102021100 21035210
Actocetor (A.) afrus	11111 1112010103120110 31023210
Actocetor (P.) yaromi	11112 2002021210020111 2???????
Actocetor (P.) lindneri	11112 2202021210120111 40104131
Actocetor (P.) decemguttatus	11112 2202021211020111 20104131

oped, subequal (a synapomorphy for *A. decemguttatus* and *A. lindneri*); (2) apex not bilobed, bluntly formed or angulate, tapered to a point toward one side (a synapomorphy for *A. afrus, A. hovus,* and *A. nigrifinis*; no male available for *A. yaromi*).

28. Presurstylus: (0) variable in form, but usually rather simple structures, longer than wide; (1) bearing 1 round to oval lobe medially (a synapomorphy for *A. afrus* and *A. nigrifinis*); (2) bearing 2 lobes along ventral margin, medial lobe much larger, 1 smaller, thumblike process between medial lobe and expanded base (a synapomorphy for *A. hovus* and *A. indicus*); (3) bearing 4 lobes (a synapomorphy for *A. decemguttatus* and *A. lindneri*; no male available for *A. yaromi*).
29. Shape of hypandrium: (0) pouchlike, often moderately deep (as in the subgenus *Actocetor*); (1) very deeply formed, with an extended keel-like process that extends into the abdomen (a synapomorphy for *A. decemguttatus* and *A. lindneri*; no male available for *A. yaromi*).

Analysis, Results, and Conclusions

Multistate characters 5, 6, 7, 9, 13, 15, 17, 22, 25, 26, 27, and 28 were treated as nonadditive (−); character 11 is a multistate character that was intuitively kept additive; characters 24 and 29 are autapomorphies that were made inactive (]) for the analysis so that they did not contribute to the calculations of the consistency and retention indices. The autapomorphies were kept in the matrix (Table 1) so that they would appear on the cladogram as evidence corroborating the monophyly of the lineages they support.

Using an exhaustive search, the implicit enumeration (ie*) option of Hennig86, 10 most parsimonious tree (Fig. 65) were generated from the analysis of the 29 characters. These cladograms have a length of 60 steps and consistency and retention indices of 0.83 and 0.83 respectively. The basal nodes in each of the 10 cladograms are identical with variation only in the more derived species within the two subgenera of *Actocetor*.

The matrix was then subjected iteratively to successive weighing (xs w, ie*, cc) to determine a character's contribution or weight (Carpenter 1988, Dietrich and McKamey 1995). The successive weighing stabilized at 418 steps and produced three cladograms that are identical to three of the first 10. A consensus of these three trees resulted in a tree that is identical to one of

Table 2. Analysis of characters based on the cladogram (Fig. 61).

Characters	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Steps	1	1	1	1	2	2	4	1	3	1	2	1	3	2	3
Con. Index	100	100	100	100	100	100	50	100	100	100	100	100	66	50	100
Ret. Index	100	100	100	100	100	100	50	100	100	100	100	100	66	66	100
Characters	16	17	18	19	20	21	22	23	24	25	26	27	28	29	
Steps	3	2	2	1	2	1	6	1	1	3	5	3	3	1	
Con. Index	33	100	100	100	50	100	83	100	100	100	100	66	100	100	
Ret. Index	0	100	100	100	66	100	50	100	100	100	100	66	100	100	

the three weighed trees and to one of the original 10 trees. The consensus tree, although with one unresolved lineage (a tritomy), is our cladogram of choice (Fig. 65). The analysis of the characters for the cladogram is given in Table 2 and the weights of the various characters are given in Table 3. Given these character weights, the analysis of the cladogram resulted in revised consistency and retention indices of 0.94 and 0.95 respectively.

Two basal, monophyletic clades are immediately evident within *Actocetor,* and as genus-group names are available for these clades, we are recognizing them as subgenera, *Actocetor* and *Poecilostenia* (otherwise, recognition of these clades as species-groups would have been adequate).

Poecilostenia comprises three species that occur exclusively in the Afrotropics and form an unresolved tritomy. One of these species, *A. yaromi,* is represented by a single female, and as we noted previously, we suspect that additional Afrotropical species will yet be discovered in this subgenus. The most widespread of these three species is *A. decemguttatus.* We predict that the character states found in *A. decemguttatus* and *A. lindneri,* such as the lack of well-developed setae on the dorsum of the epandrium, will also apply to *A. yaromi.*

The subgenus *Actocetor* includes four species, and most of these have widespread distributions. An exception is *A. afrus,* which is thus far only in Senegal and Liberia and which has a partially attenuate wing. The placement of *A. afrus* within *Actocetor* sensu stricto and as the sister species of the lineage giving rise to *A. indicus* and *A. hovus* indicates that an attenuate wing, as found in *A. afrus* and conspicuously so in species of *Poecilostenia,* arose twice. As there are specific and evident differences in the narrowing (see descriptions), we suggest that its independent occurrence in two separate lineages is quite plausible.

A concluding discussion point concerns the geographic origins of *Actocetor.* With *Poecilostenia* being exclusively Afrotropical in distribution, and with most species of the subgenus *Actocetor* also occurring primarily in the Afrotropical Region, we suggest that the genus arose there. We would advocate this more strongly if we had con-

Table 3. Weights (varying between 1–10) and status (additive = +, nonadditive = −, active = [, inactive =]) of characters after successive weighing.

Characters	1	2	3	4	5	6	7	8	9	10
Weight, status	10+[	10+[	10+[	10+[	10−[	10−[	2−[	10+[	10−[	10+[
Characters	11	12	13	14	15	16	17	18	19	20
Weight, status	10+[	10+[	4−[	3+[	10−[	0+[	10−[	0+[	10+[	3+[
Characters	21	22	23	24	25	26	27	28	29	
Weight, status	10+[	4−[	10+[	10+[	10−[	10−[	4−[	10+[	10+[	

clusive evidence on the sister group of *Actocetor.* We suggest that the occurrence of *A. indicus* in the southern Palearctic Region and perhaps in the Oriental Region may represent subsequent dispersion of this species from its Afrotropical origins. An alternative hypothesis is suggested by the cladogram. If *Trypetomima,* which is Oriental and Oceanian in distribution, is the sister group to *Actocetor* and if *A. nigrifinis,* which also occurs in the Orient, is the basalmost species, then the genus could have originated from speciation events in the Orient/Oceanian area with subsequent dispersion to the Afrotropics. It is evident that numerous speciation events occurred in the Afrotropical Region, resulting in the present Afrotropical fauna being comparatively rich.

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