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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 consensus 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
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. nigri-finis* (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 *Actotector* 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 Ephyrididae have used (see references in Mathis 1986, and Mathis and Zatwarnicki 1990a, 1990b), such as surstylist, which in Dryxini is divided into a presur-stylist (surstylist) and poststurystylist (clasper). Zatwarnicki (1996) has suggested that the pre- and poststurystylus correspond with the pre- and postgonostylist and that the subependrial plate is the same as the mediantrum. 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. Genaal-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<sub>2</sub><sub>–5</sub> and R<sub>4</sub><sub>–5</sub>/distance between the apices of R<sub>1</sub> and R<sub>2</sub><sub>–3</sub>. M vein ratio is the straight line distance along vein M between crossoves 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.
- 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
\[ \ldots \quad 3 \]
- Vein R\(_{2,3}\) bearing a subapical stump vein \[ \ldots \quad 2 \]
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 micromomentum \[ \ldots \quad Eremomusca \quad Mathis \]
- Vein R\(_{4,5}\) basad of crossvein r-m bearing 5-6 setae; wing generally dark with pattern of white spots; tibiae and femoraunicolorous, lacking bands; abdomen mostly shiny, lacking maculate pattern \[ \ldots \quad Trypetomima \quad de \quad Meijere \]
3. Wing hyaline or with anterior margin darkened but not spotted \[ \ldots \quad 5 \]
- Wing generally dark with a pattern of white spots \[ \ldots \quad 4 \]
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, frono-orbital seta; legs unicolorous \[ \ldots \quad Actoceter \quad Becker \]
- Facial setae 2, only dorsal seta well developed; 1st flagellomere longer than height of pedicel; pseudopostocellar setulae distinctly smaller than large proclinate frono-orbital seta; tibia or tarsus generally paler colored than femur \[ \ldots \quad Gattipsilopa \quad Wirth, \quad subgenus \quad Gattipsilopa \]
5. Alula weakly developed, very narrow \[ \ldots \quad 9 \]
- Alula well developed, earlike \[ \ldots \quad 6 \]
6. Infradiscal seta present; frono-orbital setae 4 (anterior 2 setae proclinate, 3rd laterooclinate, 4th laterooclinate) \[ \ldots \quad Paratissa \quad Coquillett \]
- Infradiscal seta absent; frono-orbital setae 2\(-3\) \[ \ldots \quad 7 \]
7. Supra-alar seta well developed, length subequal to postalar seta \[ \ldots \quad Rhysophora \quad Cresson \]
- Supra-alar seta moderately well developed, length about half postalar seta \[ \ldots \quad 8 \]
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 \[ \ldots \quad Hostis \quad Cresson \]
- 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 dorsal to midfacial height; vein R\(_{4,5}\) basad of crossvein r-m bare; legs dark with yellow tarsus, apical tarsomere dark \[ \ldots \quad Gattipsilopa \quad Wirth, \quad subgenus \quad Nesopsilopa \quad Mathis \quad and \quad Wirth \]
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 frono-orbital seta well developed \[ \ldots \quad Discomyza \quad Meigen \]
- 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 frono-orbital seta in addition to reclinate seta well developed \[ \ldots \quad 10 \]
10. Pseudopostocellar setae well developed, length about ½ that of ocellar setae, divergent at usually less than 90° \[ \ldots \quad Clasioptella \quad Hendel \]
- Pseudopostocellar setae weakly developed, length considerably less than ½ that of ocellar setae, orientation variable \[ \ldots \quad 11 \]
11. Eye appearing bare; 1 well-developed proclinate frono-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 Lizzaralde de Grosso); vein R\textsubscript{2+3} basad of crossvein r-m bearing 2 setulae; legs bicolored ... Mimiplioopa 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 supraalar seta well developed, length greater than anterior notopleural seta; vein R\textsubscript{2+3} basad of crossvein r-m lacking setulae; legs unicolorous, blackish brown ....... Helaeomyia Cresson

Genus Actocetero Becker


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 microtomum, 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 \( \frac{1}{2} \) in lateral view; frons conspicuously wider than long; only reclinate fronto-orbital seta well developed; proclinate setae reduced, especially posterior seta, latter \( \frac{1}{2} \) of anterior seta; pseudopostocular 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 microomentum, 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 microtomum; 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 \( \frac{1}{2} \) 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\textsubscript{2+3} extended normally to costal margin, lacking a subapical stump vein; vein R\textsubscript{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 microtomum, 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; poststurstylar (= clasper) much longer than wide, bearing few to numerous setulae, especially apically, apex sometimes bilobed, bearing a poststurysty lar process from basomedial surface, process medially and posteriorly directed, usually spatulate (often distinctly so); subependrial 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 tender 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 (parenthentic 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 ½ in lateral view (an autapomorphy for Actocetor); 3(7). Scutellum with apical ¾–¾ dark brown; 4(17). Vein R 2, 3 basad of cross-vein r-m bearing 2 to several setulae. Characters showing some homoplasy are: 5(3). Pseudostock celar setae well developed, as large as proclinate fronto-orbital seta (often
or mostly slightly reclinate; a synapomorphy for *Actocetor, Eremonusca, Guttipilopa, and Trypetomima*); 6(4). Face bearing 4 well-developed setae in a vertical row, dorsalmost 1–2 setae cruciate (a synapomorphy for *Actocetor and Guttipilopa*); 7(9). Wing brown with white spots (a synapomorphy for *Actocetor, Guttipilopa (Guttipilopa)*, and *Trypetomima*); 8(11). Alula reduced to a thin, bandlike lobe bearing numerous setulae (a synapomorphy for *Actocetor (Actocetor)* and genera *Eremonusca, 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 (*Guttipilopa (Guttipilopa), Eremonusca, 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 *ACTOCECTOR***

1. Setulae on vein $R_{1+3}$ basad and apicad of cross-vein r-m; vein $Cu_{1}$ conspicuously sinuous along posterior margin of discal cell; discal cell with at most 1 white spot (subgenus *Poecilostenia*; Afrotopical) ................................. 5

- Setulae on vein $R_{1+3}$ only basad of crossvein r-m; vein $Cu_{1}$ 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 $Cu_{1}$ normally developed, broader than discal cell; basal half of cell $Cu_{1}$ 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 Paleartic: Canary Islands, Egypt, Israel, Oman, Spain, United Arab Emirates) ........... A. indicus (Wiedemann)

- Discal cell with 3 white spots; cell $Cu_{1}$ narrower than discal cell, anal margin nearly straight; 1 white spot present in basal half of cell $Cu_{1}$; tergites 3–5 with broad bands of gray microtomentum basally (Afrotropical: Liberian, Senegal) ................. A. afrus, new species

4. Cell $r_{1+3}$ with 2 white spots; vein $R_{1+3}$ bearing 2–4 setulae basad of crossvein r-m (Afrotropical: Madagascar) .......... A. hoyus Giordani Soika

- Cell $r_{1+3}$ with 3 white spots (sub-basal spot often small); vein $R_{1+3}$ 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 microtomentum (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 microtomentum, anterior bands .... 6

6. Discal cell with 1 medial, white spot; scutellum with apical ½–¾ dark brown (widespread) ........ A. decemguttatus (Bazzi)

- 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 *Poecilostenta* 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 cu, much broader or narrower than discal cell; vein CuA1 nearly straight along posterior margin of discal cell; dorsal surface of vein R4-5 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 ½–⅔ enlarged in some species as lateral or ventral phalanges; aedeagal apodeme simple, lacking a distinct keel; hypantrum 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. Postsurtystylar 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 ½–⅔ brown, basal portion concolorous with posterior portion of scutum. Wing (Fig. 51) very narrow, cell cu, 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 r₁, apical, transversely oval/rectangular spot, immediately apical of merger of vein R₂+₃ with costa; cell r₄+₅ with a circular medial spot in line with apical spot in cell r₂+₃, and an apical spot; discal cell with 3 circular spot, sub-basal, medial, and subapical; cell m with transversely oval/rectangular spot; cell cu₄ with 2 spots, rectangular sub-basal spot, and transversely trapezoidal subapical spot, vein Cu₄ 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, ventromedian 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 foot-like (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 la-
beled “SENEGAL: 3 KM SSE BRIN, 11 KM SW ZIGUINCHOR. 9.XI.1977 [9 Nov 1977] UTM 28PJC53-83. LOC.NO.22/ LUND UNIV. SYST. DEPT. SWEDEN-GAMBA/SENEGAL NOV 1977-CE- DERHOLM-DANIELSSON-HAMMAR- STEDT-HEDQVIST-SAMUELSSON/margaritatus Wied. det. Canzoneri S. [‘margaritatus Wied.’ handwritten] HO- LOTYPE ♂ Actoceter 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. Blickestaff (♀; 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 Actoceter, bearing large setae along the dorsal margin, and other characters of the male terminalia are also typical of Actoceter sensu stricto. The narrow wing (Fig. 51), however, is somewhat intermediate, being narrower than other species of Actoceter 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 Actoceter sensu stricto. The anal lobe, however, is narrower and straighter than Actoceter 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-
suggested 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)


Diagnosis.—This species is distinguished from congers 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 dorso-central, 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 R₄₋₅ 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 r₁ with 1 sub-basal, sub-rectangular spot; cell r₂₋₃ with 2 spots, basal spot in line with spot in cell r₁, apical spot, transversely oval/rectangular, immediately apical of merger of vein R₂₋₃ with costa; cell r₄₋₅ 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 sub-apical, transversely rectangular spot; cell m with a transversely oval spot near middle; cell cuₐ₁ with basal ½ white and a subapical spot, vein Cu₁ 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; posturstylus (Fig. 10) much longer than wide, bearing 7–8 scattered setulae on both surfaces, with more setulae apically, apex bluntly formed and not bilobed; posturstyal 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; postponite 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 poulchlike.

Type material.—The holotype δ of Ac-tocetor hovus is labeled “HOLOTYPEPUS [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 polypropus), is in good condition, and is deposited in the MRAC.

Other specimens examined.—AFRO-TROPICAL, MADAGASCAR. Antserana-ana: 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: Maroant-setra, 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 (Antseranaana, 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.
Actoceter (Actoceter) indicus (Wiedemann) (Figs. 1, 14–38, 49)


Actoceter panelii: Mathis and Zatwarnicki 1995: 22 [revised status].
Figs. 15–22. Scanning electron micrographs of *Actoceter 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).
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): Ares 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 postero-medially, mesonotum in these specimens pale brown); rings at bases of larger setae (prescutellar acrostichal, posterior dorso-central, and basal scutellar setae) usually not dark brown; scutellum with apical \( \frac{1}{3} - \frac{1}{2} \) 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 \( \frac{1}{2} \) 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 apical 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 \( cu_{1} \), 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 microomentum laterally.

**Abdomen** (Fig. 28–38): Mostly shiny, gray microomentum 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; presurstyly (Fig. 33) large, ventromedial surface with a small emargination, bearing 2 round to oval lobes medially; postsurstyly (Fig. 34) much longer than wide, bearing 3–4, apical setulae, apex bilobed with a small, digitiform, medial, pointed process; postsurstyly process (Fig. 35) distinctly spatulate, rounded process, shaped like an haler; 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. Dct. B.H. Cogan 1976. [species name and “76” handwritten]/Actocetor indicus (Wied.) dct. 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 [hand-

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

ERITREA. Ailet (from egg-pods), 22 Jul 1956, D. J. Greathed (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 ♀; NMWL).
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, posterovertral 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.

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. Londoit, B. Stuckenberg (1♂; NMSA).


SENEGAL. Dakar, 4–5 Oct 1978, J. Frottin, 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 Mtubatuba), 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♀; IEX; BMNH); Mtubatuba, 24–25 Mar 1968, P. J. Spangler
(2♂, 1♀; USNM); Ndumu Reserve (Ing-wavuma 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. Londo (1♂; NMSA); Scottburgh, 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; 28°30’Ga; Malaise trap), 26–27 Feb 1977, R. Miller (1♂; NMSA); Umkoamas (NE; 30°30’Bb; along sand dunes), 21 Jun 1980, R. Miller, R. Stabbins (1♀; NMSA); Umkoamas, South Coast, 11 Oct 1983, A. Feidberg (4♂, 8♀; USNM); Umlalazi Nature Reserve (28°31’Dd, dune forest and edges), 2–10 Oct 1982, J. G. H. Londo (1♀; NMSA); Umlalazi Nature Reserve (28°57’S, 31°40’E; 20 m; dune forest), 28–29 Jan 1988, J. G. H. Londo (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). Mpuamalanga: 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 hintamot?), 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 (1♂; BMNH).

ZIMBABWE. Gwaii, 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).

INDIA. Karnataka: Mudigere, 6 Apr 1980, W. N. Mathis, A. Feidberg (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. Wijesshine, 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. Ebejeer (1♀; NMWL).

CANCARY ISLANDS. Gran Canaria: Las Plamas (on garden wall), 12 Nov 1927, Kisluik (3♂, 1♀; USNM); Las Palmas, R. Stora (1♂; 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’Arish, 9 Jan 1917, E. E. Austen (1♀; BMNH); Ein Furtaga, 7 Jul 1969, Kugler (2♂, 3♀; USNM); Ein Hudra, 9 Jul 1969, A. Feidberg (2♀, 1♂; USNM); Et-Tür, 25 Jun 1968 (4♂, 1♀; TAU); Feirän, 9 Apr 1973, D. Furth (1♂; TAU); Nuweibah, 14 May 1981, T. Furman (4♀, 5♂; USNM); Ofira (sewage), 21 May
1981, A. Freidberg, W. N. Mathis (110°, 80°, 1ex; TAU, USNM); Ofira, 22 Mar 1981, A. Freidberg (1♀; TAU); Ophirah 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 (19♂; BMNH); Wadi Feirán, 25 May 1971, A. Freidberg (2♂, 2♀; TAU, USNM); Wadi Hibrán, 11 May 1973, A. Freidberg, F. Kaplan (1♂, 1♀; TAU); Wadi Watür, 5 Aug 1975, A. Freidberg (1♂; TAU).


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


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 proboscies 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 proboscies. While touching proboscies 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 microomentum on tergites 3–5. The microomentum 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 microomentum and a few,
Actocetor (Actocetor) nigrifinis (Walker)  
(Figs. 39–47, 50)

Opomyza nigrifinis Walker 1860: 168.  
Actocetor nigrifinis: Cogan and Wirth 1977: 328 [generic combination].  
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 conegers by the following combina-
tion 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 \( \frac{1}{2}–\frac{3}{4} \) 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\(_{3+5}\) bearing 5–6 setae basad of crossvein r-m; wing pattern as follows: cell c with basal \( \frac{1}{2} \) 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 cu\(_A\) 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 \( \frac{1}{2} \) triangular from a wide base to pointed apex; aedeagal apodeme (Fig. 46) in lateral view subtringular 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 Oomyza nigrifinis Walker, here designated to preserve stability and make more universal the use of this name, is labeled “SYN-Type [circular label, gray, 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 (Oomyza) det. J.C. Deeming 1964 [handwritten except for “det. J.C. Deeming 196’”’]/LECTOTYPE ♀ Oomyza 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, gray, 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]/Actoceter 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 paralec- totypne is double mounted (minutes in rectangular block of foam; head, left fore- and midlegs missing), and is deposited in the BMNH.

The lectotype ♀ of Actoceter beckeri de Meijere, here designated to preserve stability and make more universal the use of this name, is labelled “Batavia [Djakarta] (Moara Antjol) [= Moaraantjol] XII. 07 [Dec 1907] Jacobson [handwritten]/Actoceter Beckeri det. de Meijere, type [species name and “type” handwritten; black submarginal border]/HOLOTYPE Actoceter beckeri de Meij det. B.H. Cogan 1971 [handwritten except for “det. B.H. Cogan 197’’]/Actoceter hendeli de Meij. Det. B.H. Cogan 1971. [handwritten except for “det. B.H. Cogan 197’’]/Actoceter Beckeri de Meijere, 1916 ZMAN type DIPT:0437.1 [red]/LECTOTYPE ♀ Actoceter beckeri de Meijere By dikow & Mathis [all except “LECTOTYPE” and “By” handwritten; black submarginal border].” The lectotype is double mounted (minutes in rectangular block of foam), is in good condition (minutes 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 ♀ paralecotypes that bear the same locality data as the lectotype with the addition of “by Bembex nest.” Although Cogan wrote that this species 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 “Actoceter hendeli de Meij.” was written. Cogan apparently confused the name of this species with A. beckeri Hendel, which is pre-occupied and needed a replacement name, A. hendeli, which de Meijere (1924) provided.

The holotype ♀ of Actoceter elegans Hendel is labeled “Ceylon. Colombo./6/VI 02. [6 Jun 1902] Dr. Uzel./Actoceter elegans H. det. Hendel [species name and author handwritten]/Coll. Hendel/HOLO- TYPE ♀ Actoceter elegans Hendel [red submarginal boarder; name, author, and gender handwritten].” The holotype is double mounted (minutes 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).


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. Jayawickrama (2♂, 8♀; USNM); Peradeniya (Malaise trap at Botanical Gardens), 26–28 Mar 1971, P. and P. Spangler (2♀; 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 paralecotypes 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 Oomyzidae).

**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 distinguishable from *Actocetor* sensu stritctro 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 narrower than discal cell; vein R₄,₅ bearing 5–6 setulae on dorsum, basal of crossvein r-m and 5–10 setulae apical of crossvein r-m; vein CuA₁, conspicuous...
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 microomentum yellowish; 11*. Alula completely reduced and bearing few or no setulæ along posterior margin; 12*. Cell cuₐ generally narrower than discal cell, and anal margin nearly straight; 13*. Vein R₄₅ bearing setulæ basad and apicad of crossvein r₅m; 14*. Anterior margin of vein Cuₐ 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. Microomentum 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-Khakhe, Kalahari; ST ♂ ♀, deposition unknown].—Cres-
Actocetor (Poecilostenia) decemguttatus: Cogin 1946: 256 [review, list, South Africa].


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. Genal-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
apical \( \frac{1}{2} \) 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 microomentum; base of 3rd and 4th tergites with tiny bands of gray microomentum; 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 even 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; submedian prong narrow, digitiform, tapered to point; 2 lateral prongs wide basally, tapered to rounded points; postsurstylus (Fig. 57) very robust throughout, bilobed apically, both lobes well developed, subequal, anterior lobe bearing a well-developed, stout, spinedlike 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 bronglike processes that are opposable to spinedlike seta of postsurstylus.

Type material.—The syntypes, apparently 1 ♂ and 1 ♀, of Poecilostentia decempunctata 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 er-

haltenes Pärchen aus der Kalahari: Kang-Khakheia, Dezember 1904, No. 968.”

The holotype ♀ of Actoceter anormalipennis Séguy is labeled “MUSEUM 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]/Actoceter 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 Actoceter toniatabiae Canzoneri is labeled “GAMBIA. Toniataba[,] margini mangrovia veget[azione]. alo[]la[] 30.vii [30 Jul] Giordani Soika leg. 1973 [white label glued to a green backing; handwritten except for “Giordani Soika leg. 1973”]/HOLOTYPUS ♀ Actoceter toniatabae m. det. Canzoneri S[ilvano] [red; gender symbol, species name, and “m.” handwritten]/Actoceter decempunctatus (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.


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-
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. Stucken-berg, 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).


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 Afro-tropical 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)


**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 cu₁ narrower than discal cell, anal margin nearly straight; vein R₁-₅ 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 r₁ with a circular, sub-basal spot and a rectangular, medial spot; cell r₂-₃ with 2 spots, basal, transversely narrow, rectangular spot in line with spot in cell r₁, apical, transversely oval/rectangular spot, immediately apicad of merger of vein R₂-₃ with costa; cell r₁-₅ 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 cu₄ with 2 spots, 1 sub-basal and 1 subapical narrow rectangular spot, vein CuA₁ 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, 2.3–3 × 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, spine-like 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
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 poststyrstylus.

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

Figs. 61–64. Structures of the male preabdomen and terminalia of Actocetor lindneri. 61, Hypandrium, lateral view. 62, Presurusstylus, posterior view. 63, Postsurstylus, lateral view. 64, Aedeagus, aedeagal apodeme, lateral view. Scale bar equals 0.1 mm.
Wirth det. W.Wirth [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 micromentose, 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 cu₂ with wider than discal cell, anal margin nearly straight; vein R₄₅ bearing 6 setulae basad and 5 setulae apicad of crossvein r-m; wing pattern as follows: cell r₁ with rectangular, medial spot; cell r₂₃ with 2 spots, basal rectangular spot in line with spot in cell r₁, apical, transversely oval/rectangular spot, immediately apicad of merger of vein R₂₃ with costa; cell r₄₅ with a circular spot in line with apical spot in cell r₂₃, and an apical spot; discal cell without white spot; cell m with transversely oval-rectangular spot; cell cu₃ with 2 spots, a rectangular sub-basal spot, and a transversely trapezoidal spot in line with spot in discal cell; vein Cu₁ concave between these 2 spots; costal vein ratio 0.66; M vein ratio 1.05. Halter stem yellowish white based, 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 microomentum; base of 3rd and 4th tergites with bands of gray microomentum; 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.i.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 Actoceter).

2. Position of antenna on head: (0) positioned near midheight level of head (frons conspicuously longer than wide); (1) positioned high, above dorsal ½ in lateral view (an autapomorphy for Actoceter).

3. Development of pseudopostocular setae: (0) setae reduced (as in Mimapsilopa); (1) setae well developed, as large as procinete setae (often or mostly slightly reclinate; a synapomorphy for Actoceter, Eremomusca, Guttipisilopa, and Tryptomima).

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 Actoceter and Guttipisilopa).

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 Actoceter); (2) 0.14–0.20 (a synapomorphy for the subgenus Poecilostenia).

Thorax:

6. Color of mesonotal microomentum: (0) blackish; (1) grayish (a synapomorphy for the subgenus Actoceter); (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 Actoceter, Guttipisilopa subgenus Guttipisilopa, and Tryptomima); (3) wing with anterior margin darkened (a synapomorphy for Guttipisilopa subgenus Nesopsilopa and some Discomyzida).

10. Development of apex of vein R2+3: (0) apex normally developed at merger with costa (as in Actoceter); (1) vein R2+3 with a subapical stump vein (a synapomorphy for Eremomusca and Tryptomima).

11. Development of alula: (0) alula a well-developed lobe (as in Guttipisilopa); (1) reduced to a thin bandlike lobe bearing numerous short or long setulae along posterior margin (a synapomorphy for the subgenus Actoceter and the genera Eremomusca, Mimapsilopa, and Tryptomima); (2) completely reduced and
bearing few or no setulae along posterior margin (an autapomorphy for the subgenus Poecilostenia).

12. Development of cell cuₐ: (0) cell cu₁ broad, broader than discal cell, and anal angle moderately well developed (as in the subgenus Actocetor); (1) cell cu₁ generally narrower than discal cell, and anal margin nearly straight (an autapomorphy for the subgenus Poecilostenia).

13. Development of setulae on vein R₄₊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 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 r₁: (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 R4,5 basad of cross vein 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 microomentum on abdomen (in addition to microomentumose 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 microomentumose (an autapomorphy for A. lindneri); (5) entirely microomentumose (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 times longer than wide (as in A. afrus, A. hovus, A. indicus, and A. nigrifinis); (1) rectangular, moderately narrow, 2–3 times 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. Posturstylar 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. Posturstylus: (0) bilobed subapically with a small, digitiform, medial, point ed process (as in A. indicus); (1) bilobed apically, both lobes well devel-
opposed, subequal (a synapomorphy for A. decemguttatus and A. lindneri); (2) apex not bilobed, bluntly formed or angular, tapered to a point toward one side (a synapomorphy for A. afrus, A. hovus, and A. nigrinis; 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. nigrinis); (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 Actuceror); (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 (I) 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 Actuceror.

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
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 epi-drium, 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 Senegalese 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-

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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. nigirifinis, which also occurs in the Orient, is the basal-most 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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