Zootaxa 2638: 1–24 (2010)
www.mapress.com/zootaxa/
Copyright © 2010 · Magnolia Press

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

Coetzeemyia, a new subgenus of *Aedes*, and a redescription of the holotype female of *Aedes* (*Coetzeemyia*) *fryeri* (Theobald) (Diptera: Culicidae)

YIAU-MIN HUANG[1,5], WAYNE N. MATHIS[2] & RICHARD C. WILKERSON[3,4]

[1]*Department of Entomology, P.O. Box 37012, MSC C1109, MRC 534, Smithsonian Institution, Washington, D.C. 20013-7012, U.S.A. E-mail: huangy@si.edu*

[2]*Department of Entomology, P.O. Box 37012, MRC 169, Smithsonian Institution, Washington, D.C. 20013-7012, U.S.A. E-mail: mathisw@si.edu*

[3]*Walter Reed Biosystematics Unit (WRBU), MRC 534, Smithsonian Institution, Washington, D.C. 20013-7012, U.S.A. E-mail: wilkersonr@si.edu*

[4]*Division of Entomology, Walter Reed Army Institute of Research, Silver Spring, MD 20910 USA*

[5]*Corresponding author*

Abstract

Coetzeemyia, a **new subgenus** of *Aedes* Meigen (in the broad traditional sense, pre-Reinert 2000), is characterized and diagnosed. *Aedes fryeri* (Theobald) is removed from the subgenus *Levua* Stone and Bohart (genus *Levua* of Reinert *et al.* 2004) and placed in the new monotypic subgenus *Coetzeemyia* as its type species by present designation. Recognition of *Coetzeemyia* is based in part on a cladistic analysis of 16 species: seven outgroup species (four non-Aedini species and 3 aedine species) and nine within group species, including the three species that had been included in *Levua* and six other species belonging to three related subgenera in *Aedes (Geoskusea* Edwards, *Rhinoskusea* Edwards, and *Ochlerotatus* Lynch Arribalzaga). The type female and the male genitalia of *Ae. fryeri* are redescribed and illustrated. Its affinity to other subgenera of the genus *Aedes* is discussed. Information on the type data, distribution, bionomics, medical importance, and taxonomy of this species are presented. Some morphological characteristics of adults of the subgenera *Ochlerotatus* and *Levua* of *Aedes* are tabulated. Based on this cladistic analysis, it is evident that *Levua* is a monotypic lineage represented by a single known species, *Ae. geoskusea*. *Aedes dufouri* is transferred back to the subgenus *Ochlerotatus* and is distinguished from other congeners of this subgenus.

Key words: *Coetzeemyia*, new subgenus, *Aedes fryeri*, *Ae. dufouri*, *Ochlerotatus*, *Levua*, *Ae.* (*Levua*) *geoskusea* (= *suvae*), characteristics, systematics, Culicidae, Aldabra Island

Introduction

Several hypotheses regarding the classification of *Aedes* Meigen have recently been proposed (Reinert 2000; Reinert *et al.* 2004, 2006, 2008, 2009). Reinert (2000) divided *Aedes*, then with 43 subgenera, into two genera, *Aedes* and *Ochlerotatus*, and assigned 21 of the subgenera that had been included in *Aedes* to *Ochlerotatus*, keeping the remaining 22 subgenera in his redefined concept of *Aedes.* Reinert (2000) assigned the subgenus *Levua* to the genus *Ochlerotatus.* Thus, in Reinert's (2000) classification, *Aedes* (*Levua*) became *Ochlerotatus* (*Levua*).

Reinert *et al.* (2004: 289) subsequently wrote that "(ii) three small subgenera within the basal polytomy…are undoubtedly monophyletic, i.e. *Aedes* (*Huaedes*), *Ae.* (*Skusea*) and *Oc.* (*Levua*)…," and further (2004: 360) that "*Levua* Stone & Bohart, 1944, stat. nov., [be] raised to generic rank [comprising three species] *dufouri* (Hamon 1953), comb. nov., *fryeri* (Theobald 1912), comb. nov., [and] *geoskusea* (Amos 1944), comb. nov." Reinert *et al.* (2006: 93) continued to treat *Levua* as a genus but later (Reinert *et al.* 2008: 112) modified their classification to include *Levua* as a subgenus of *Ochlerotatus*. More recently, Reinert *et al.* (2009) proposed a more refined classification in which *Levua* was again accorded generic status.

Accepted by G. Courtney: 11 Sep. 2010; published: 6 Oct. 2010

The purpose of this paper is to re-examine the classification of species assigned to the subgenus *Levua* by responding to the following questions: (1) Are *Levua* and its included three species monophyletic? (2) What classification of these species is suggested by an analysis of the morphological evidence? (3) What is the morphological evidence?

As a summary of our results, we present herein a cladistic analysis of morphological evidence (132 characters), documenting that: (1) *Ae*. *fryeri* and *Ae*. *dufouri* should not be placed in *Levua* based on strikingly different morphological characters from those of *Ae.* (*Levua*) *geoskusea* (=*suvae*), and (2) that *Levua* now includes a single species, *Ae.* (*Levua*) *geoskusea*, that occurs in the Oceanian Region. In light of these results, we propose taxonomic changes that formally treat these modifications in the classification for *Ae*. *fryeri* (Theobald) with description herein of *Coetzeemyia*, a new monotypic subgenus that is morphologically distinct from other subgenera traditionally placed in the genus *Aedes* (sensu pre-Reinert 2000, the classification adopted herein). Included here are: (1) a discussion of the affinity of *Coetzeemyia* to other genus-group taxa in the genus *Aedes*, (2) a comparison of some morphological characteristics of the adults of the subgenera *Ochlerotatus* Lynch Arribalzaga and *Levua* Stone and Bohart, (3) a redescription and illustration of the holotype female and structures of the male genitalia of *Ae*. *fryeri*; (4) type data and information on distribution, bionomics, and medical importance, and a discussion on the taxonomy of this species. The suggested abbreviation for the subgenus *Coetzeemyia* is *Coe*.

The historical background for the species treated herein is reasonably straightforward and is as follows. Theobald (1912: 84, 86) described *Culicelsa fryeri* from females collected on Aldabra Island (Takamaka; J.C.F. Fryer collector) in 1908. Edwards (1932: 135–137) divided the subgenus *Ochlerotatus* Lynch Arribalzaga into eight groups with the letter designations of A–H, and *fryeri* was assigned to Group A (*taeniorhynchus* group: *Culicelsa*). Hamon (1953: 35) described *Ae. dufouri* from specimens collected on the island of Reunion (21°06’S, 55°36’E) and placed it in the subgenus *Ochlerotatus*. Danilov (1981: 86, 87), however, proposed that *Ae*. *fryeri* (Theobald) and *Ae*. *dufouri* Hamon should be transferred from the subgenus *Ochlerotatus* to *Levua* and that proposal has usually been followed to the present, most notably by Reinert (2000) and Reinert *et al*. (2004, 2006, 2008, 2009), even though they only included characters for *Ae*. *geoskusea* in their studies. Formerly, *Levua* was monotypic (*Ae*. *geoskusea* Amos = *suvae* Stone and Bohart) and was known to occur only on the Fiji Islands. After critical study of the type female and the topotypic (male and female) specimens of *Ae*. *fryeri*, it became apparent that *Ae*. *fryeri* should not be placed in *Levua* or in *Ochlerotatus*, but in the new subgenus, *Coetzeemyia*, that is described below.

Material and methods

This study is based primarily on specimens in the Department of Entomology, National Museum of Natural History, Smithsonian Institution [USNM]. Other specimens were borrowed from the individuals and institutions noted in the acknowledgments.

The terminology follows Harbach and Knight (1980, 1982) with the exception of “tarsal claws,” which is retained for “ungues.” The wing venation follows Belkin (1962). An asterisk (*) following the abbreviations M (= male), F (= female), P (= pupa), and L (= larva) indicates that all or some portion of that sex or stage is illustrated.

Sixteen species are included in this study. The ingroup consists of nine species of the genus *Aedes* Meigen (= nine species in the genus *Ochlerotatus* of Reinert 2000), representing four subgenera: (1) *Levua* Stone and Bohart, 3 species, [*geoskusea* (Amos), *fryeri* (Theobald), *dufouri* Hamon]; (2) *Geoskusea* Edwards, 2 species, [*baisasi* Knight and Hull, *longiforceps* Edwards]; (3) *Rhinoskusea* Edwards, 2 species, [*longirostris* (Leicester), *wardi* Reinert] and (4) *Ochlerotatus* Lynch Arribalzaga, 2 species, [*caballus* (Theobald), *vigilax* (Skuse)]. [Reinert (2000) assigned the subgenera *Levua*, *Geoskusea*, *Rhinoskusea* to the genus *Ochlerotatus*. Thus, in Reinert’s (2000) classification, *Aedes* (*Levua*), *Aedes* (*Geoskusea*), *Aedes* (*Rhinoskusea*) became *Ochlerotatus* (*Levua*), *Ochlerotatus* (*Geoskusea*), *Ochlerotatus* (*Rhinoskusea*); and the subgenera were afforded generic status in the studies that culminated in the classification of Reinert *et al*. (2009)].

TABLE 1. Selected morphological characters of *Aedes* (*Coetzeemyia*) *fryeri*, *Ae*. (*Ochlerotatus*) and *Ae*. (*Levua*) *geoskusea*.

Structure	Character	*fryeri*	*Ae.* (*Ochlerotatus*)	*geoskusea*
Adult Head	Maxillary palpus of male long, slightly shorter, as long as or longer than proboscis length	Yes	Yes	No
	Maxillary palpus of male short, about 1/5 length of proboscis	No	No	Yes
	Maxillary palpus of male long, 5-segmented, last two segments subequal in length and hairy	Yes	Yes	No
	Maxillary palpus of male short, 5-segmented, the last segment minute	No	No	Yes
	Proboscis speckled with pale scales	Yes	Yes/No	No
	Proboscis with all dark scales	No	Yes/No	Yes
Thorax	Lower prealar scale-patch present	Yes	Yes	No
	Paratergite with scales	Yes	Yes	No
	Subspiracular area with scales	No	Yes	No
	Postspiracular area with scales	Yes	Yes	No
	Lower mesepimeral setae absent	Yes	Yes/No	Yes
	Scutellum with narrow white scales on all lobes	Yes	Yes	No
Wing	Speckled with pale scales	Yes	Yes/No	No
	Scales all dark	No	Yes/No	Yes
Leg	Femora, tibiae, and tarsi all dark	No	No	Yes
	Femora and tibiae speckled with pale scales	Yes	Yes	No
Male genitalia	Gonostylus with pair of short, very stout, pointed gonostylar claws inserted under a hood (subapically)	No	No	Yes
	Gonostylus with pair of short, stout, pointed gonostylar claws inserted under a hood (apically)	Yes	No	No
	Gonostylus with long spine-like gonostylar claw inserted apically	No	Yes	No
	Gonocoxite with mesal membrane from base to apex	No	Yes	Yes
	Gonocoxite with mesal membrane from base not reaching apex	Yes	No	No
	Aedeagus large, broadened beyond base, rounded apically	No	No	Yes
	Aedeagus rather long, slightly broadened in middle	Yes	No	No
	Aedeagus smooth, scoop-shaped	No	Yes	No
	Claspette with slender, tapered spiniform setal appendage	No	No	Yes
	Claspette with short, stout setal appendage	Yes	No	No
	Claspette with flattened blade-like appendage	No	Yes	No
	Paraproct with long apical spine bifid for about half its length, strongly sclerotized and curved	No	No	Yes
	Paraproct with 2 or 3 blunt teeth at tip	Yes	No	No
	Paraproct with strongly sclerotized apical tooth	No	Yes	No
	Tergum IX with prominent lobes bearing strong setae distally	No	Yes	No

continued next page

TABLE 1. (continued.)

Structure	Character	*fryeri*	*Ae.* (*Ochlerotatus*)	*geoskusea*
	Tergum IX lobes prominent, strongly developed, rounded, with numerous setae on dorsal and ventral surfaces	No	No	Yes
	Tergum IX lobes prominent, strongly developed, with 8 or 9 slender setae on dorsal and ventral surfaces	Yes	No	No
Larva Abdomen	Comb in very large patch of numerous long scales	No	No	Yes
	Comb scales in 2 or 3 irregular rows	Yes	Yes	No

The outgroup includes seven species (as used by Reinert *et al.* 2008, 2009 [only four non-aedine outgroup taxa were used in the 2009 analysis]): (1) Non-aedine outgroup taxa, *Culiseta* (*Culiseta*) *inornata* (Williston), *Culex* (*Culex*) *quinquefasciatus* Say, *Mansonia* (*Mansonia*) *titillans* (Walker), *Orthopodomyia signifera* (Coquillett); and (2) aedine outgroup taxa, *Aedes* (*Abraedes*) *papago* Zavortink (=*Abraedes papago* as used in Reinert *et al*. 2008), *Aedes* (*Aedes*) *cinereus* Meigen, *Aedes* (*Aedes*) *esoensis* Yamada (=*Aedes cinereus*, *Aedes esoensis* as used in Reinert *et al*. 2008).

The phylogenetic analysis was performed with Hennig86© (Farris 1988), a computerized algorithm that produces cladograms by parsimony. Character data were polarized primarily using outgroup procedures.

We initially considered a subset of 196 adult characters from Reinert *et al.* (2009) in our analysis. Although Reinert *et al.* incorporated more characters, we did not include as many based on the following criteria. Characters of immature stages were not considered because these stages for the species included in our analysis are either not known or are inadequately documented (i.e., poorly illustrated or description too brief) for *Ae. fryeri* and *Ae. dufouri,* two of the species specifically being analyzed.

1. Eighteen characters (141, 149, 151, 163, 166, 169, 170, 171, 172, 184, 187, 207, 218, 220, 228, 229, 257 and 272 in Reinert *et al.* 2009) are all coded as state “1” for the species included in our study, i.e., these characters do not contribute information or signal to the analysis.
2. Twenty-seven characters (144, 150, 154, 174, 176, 177, 178, 190, 195, 196, 221, 222, 227, 230, 234, 236, 237, 238, 274, 299, 300, 301, 306, 308, 309, 311 and 335 in Reinert *et al.* 2009) are all coded as state “0” for the species included in our study, i.e., these characters do not contribute information or signal to the analysis.
3. Seventeen characters (153, 165, 185, 194, 199, 206, 225, 242, 243, 245, 250, 269, 296, 298, 319, 330 and 332 in Reinert *et al.* 2009) are autapomorphies for the species included in our study, i.e., like categories 1 and 2, these characters do not contribute information or signal to the analysis.
4. Three characters (307, 328, 331 in Reinert *et al.* 2009) have too many “??” and four characters (270, 314, 315 and 324 in Reinert *et al.* 2009) have no signal.

The 69 characters in categories 1–4 were omitted from our analysis. Thus we included in our analysis 127 of the morphological characters of adults (males and females) that were included in the study of Reinert et *al*. (2009). Of the 127 characters, 84 are binary and 43 multistate. Missing values, represented by question marks (?), were used for character states where assignments were not applicable, such as (?) = (-) as used by Reinert *et al.* (2009) in their analysis. We have largely adopted the character coding of these authors. However, where our observations are in conflict with their coding, we have modified the coding to reflect our observations, i.e, characters 145, 146, 168, 216, 217, 252, 258, 259, 302, 304 and 322 in Reinert *et al.* 2009. We have also modified 5 characters (152, 157, 217, 323, 326 in Reinert *et al.* 2009) and added 2 new characters (131, 132) for a total of 132 characters (89 binary, 43 multistate).

In the presentation on generic-level relationships that follows, the characters used in the analysis are listed 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 relationship based on cladistic analysis is presented and briefly discussed. The cladogram (Fig. 4) 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, a "0" indicates the state of the outgroup; and a "1" or "2" indicates the derived states. Multistate characters (2, 6, 9, 12, 13, 15, 16, 17, 20, 21, 26, 29, 35, 40, 42, 47, 56, 65, 66, 67, 68, 73, 75, 76, 81, 86, 87, 92, 95, 96, 102, 109, 112, 113, 116, 117, 118, 120, 122, 123, 125, 130, 131) were treated as nonadditive (-). The numbers used for characters in the presentation are the same as those on the cladogram, and the sequence is the same as noted in the character matrix (Table 2).

TABLE 2. Matrix of characters and taxa used in the cladistic analysis of some subgenera of Aedini (numbers for characters correspond with those used in the text).

Characters	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Cs.(*Cus.*) *inornata*	1	1	0	0	1	0	1	1	0	1	1	0	2	1	1
Cx.(*Cux.*) *quinquefasciatus*	1	1	0	0	1	0	1	1	0	1	1	0	1	1	1
Ma. (*Man.*) *titillans*	1	1	0	0	1	0	1	1	0	1	1	0	0	1	1
Or. signifera	1	1	0	0	1	0	1	1	0	1	1	0	0	1	0
Ae.(*Abr.*) *papago*	1	0	1	1	1	1	0	1	2	1	1	0	0	1	1
Ae. (*Aed.*) *cinereus*	1	2	0	1	1	0	1	1	0	1	0	2	?	0	?
Ae. (*Aed.*) *esoensis*	1	2	0	1	1	0	1	1	0	1	0	2	?	0	?
Ae. (*Lev.*) *geoskusea*	1	1	0	0	0	?	1	1	0	0	0	1	2	0	0
Ae. (*Lev.*) *dufouri*	1	1	0	1	1	0	1	1	0	1	1	0	0	1	1
Ae. (*Lev.*) *fryeri*	1	1	0	1	1	0	1	0	?	1	1	0	0	1	1
Ae. (*Geo.*) *baisasi*	1	0	1	0	0	?	1	1	0	0	0	1	2	1	0
Ae. (*Geo.*) *longiforceps*	1	0	1	0	0	?	1	1	0	0	0	1	2	0	0
Ae. (*Rhi.*) *longirostris*	0	0	1	0	0	?	1	1	0	0	0	1	2	0	?
Ae. (*Rhi.*) *wardi*	0	0	1	0	0	?	1	1	0	0	0	1	2	0	?
Ae. (*Och.*) *caballus*	1	1	0	1	1	0	1	1	1	1	1	0	0	1	1
Ae. (*Och.*) *vigilax*	1	1	0	1	1	0	1	1	0	1	1	0	0	1	1

continued.

Characters	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
Cs.(*Cus.*) *inornata*	2	0	1	1	2	0	1	0	1	0	2	0	1	1	1
Cx.(*Cux.*) *quinquefasciatus*	2	1	1	1	0	0	1	0	0	1	1	0	1	1	1
Ma. (*Man.*) *titillans*	2	1	1	1	0	0	1	0	0	0	2	0	1	1	1
Or. signifera	2	0	1	1	0	0	1	1	1	0	1	1	1	1	1
Ae.(*Abr.*) *papago*	2	0	1	1	1	2	1	1	1	1	2	0	1	1	1
Ae. (*Aed.*) *cinereus*	0	?	0	1	0	0	0	0	0	1	0	0	0	0	0
Ae. (*Aed.*) *esoensis*	0	?	0	1	0	0	1	0	0	1	0	0	1	0	1
Ae. (*Lev.*) *geoskusea*	0	0	0	0	?	0	0	0	0	1	0	0	0	0	0
Ae. (*Lev.*) *dufouri*	1	1	0	1	1	0	0	0	0	1	0	0	0	0	0
Ae. (*Lev.*) *fryeri*	2	1	1	1	0	0	1	0	0	1	3	0	1	2	1
Ae. (*Geo.*) *baisasi*	1	0	0	0	?	0	1	0	0	1	0	0	0	0	0
Ae. (*Geo.*) *longiforceps*	0	0	0	0	?	0	1	0	0	1	0	0	0	0	0
Ae. (*Rhi.*) *longirostris*	0	0	0	0	?	2	0	0	0	0	0	1	0	0	0
Ae. (*Rhi.*) *wardi*	0	0	0	0	?	2	0	0	0	0	0	1	0	0	0
Ae. (*Och.*) *caballus*	2	1	0	1	0	0	1	0	0	1	0	1	1	0	1
Ae. (*Och.*) *vigilax*	2	1	1	1	0	0	1	0	0	1	0	0	1	0	1

continued.

Characters	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45
Cs.(*Cus.*) *inornata*	0	0	1	1	2	0	1	0	1	1	1	0	1	1	1
Cx.(*Cux.*) *quinquefasciatus*	0	0	0	1	0	0	0	0	0	1	1	1	0	0	0
Ma. (*Man.*) *titillans*	0	0	0	1	0	1	0	0	0	2	1	1	0	0	0
Or. signifera	0	0	0	1	0	0	1	0	0	1	1	1	0	1	0
Ae.(*Abr.*) *papago*	1	1	1	1	1	1	0	1	1	1	1	2	0	1	1
Ae. (*Aed.*) *cinereus*	0	0	1	1	0	1	1	0	0	1	1	1	0	0	0
Ae. (*Aed.*) *esoensis*	0	0	1	1	0	1	1	0	0	1	1	1	0	0	0
Ae. (*Lev.*) *geoskusea*	0	0	0	1	2	1	0	0	0	1	0	1	0	0	0
Ae. (*Lev.*) *dufouri*	0	0	1	1	1	1	1	0	0	1	1	1	0	0	1
Ae. (*Lev.*) *fryeri*	0	0	1	1	2	1	1	0	0	1	1	1	0	0	1
Ae. (*Geo.*) *baisasi*	1	1	0	1	1	1	0	0	0	2	0	0	0	0	0
Ae. (*Geo.*) *longiforceps*	0	0	0	1	1	1	0	0	0	1	0	0	0	0	0
Ae. (*Rhi.*) *longirostris*	1	1	0	0	?	1	0	0	0	0	0	0	0	0	0
Ae. (*Rhi.*) *wardi*	1	1	0	0	?	1	0	0	0	0	0	0	0	0	0
Ae. (*Och.*) *caballus*	0	0	1	1	0	1	1	1	1	1	1	0	1	1	1
Ae. (*Och.*) *vigilax*	0	0	1	1	2	1	1	0	0	1	1	1	0	0	1

continued.

Characters	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60
Cs.(*Cus.*) *inornata*	1	0	1	0	1	0	1	1	1	0	3	1	1	0	0
Cx.(*Cux.*) *quinquefasciatus*	1	1	1	0	0	0	0	1	1	0	0	1	0	0	0
Ma. (*Man.*) *titillans*	1	0	1	0	0	0	0	1	0	?	3	1	0	1	0
Or. signifera	1	1	0	0	0	0	0	1	1	0	3	1	1	1	0
Ae.(*Abr.*) *papago*	1	1	0	0	0	0	0	1	0	?	1	1	0	0	1
Ae. (*Aed.*) *cinereus*	1	0	0	0	0	0	0	1	1	0	0	1	0	0	0
Ae. (*Aed.*) *esoensis*	1	0	0	0	0	0	0	1	1	0	1	1	0	0	0
Ae. (*Lev.*) *geoskusea*	0	?	0	0	0	0	0	1	1	0	0	1	1	0	0
Ae. (*Lev.*) *dufouri*	1	1	0	0	0	0	0	1	1	0	0	1	0	0	0
Ae. (*Lev.*) *fryeri*	1	1	0	0	0	0	0	1	1	0	3	1	0	0	0
Ae. (*Geo.*) *baisasi*	1	0	0	1	1	1	1	1	1	0	0	1	0	0	0
Ae. (*Geo.*) *longiforceps*	1	0	0	1	1	1	1	1	1	0	0	1	0	0	0
Ae. (*Rhi.*) *longirostris*	0	?	0	0	0	0	0	0	1	0	0	0	0	0	0
Ae. (*Rhi.*) *wardi*	0	?	0	0	0	0	0	0	1	0	0	0	0	0	0
Ae. (*Och.*) *caballus*	1	0	1	0	0	0	0	1	1	0	3	1	0	0	1
Ae. (*Och.*) *vigilax*	1	0	0	0	0	0	0	1	1	0	3	1	0	0	0

continued.

Characters	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75
Cs.(*Cus.*) *inornata*	1	1	1	0	0	3	4	0	0	1	0	0	0	0	2
Cx.(*Cux.*) *quinquefasciatus*	0	1	0	0	1	2	3	0	0	1	0	0	0	0	2
Ma. (*Man.*) *titillans*	1	1	1	1	0	1	2	0	0	0	1	1	1	1	0
Or. signifera	1	1	1	1	0	1	2	0	0	0	0	0	0	0	2
Ae.(*Abr.*) *papago*	1	1	0	1	0	0	1	0	1	0	0	0	?	0	0
Ae. (*Aed.*) *cinereus*	1	0	0	0	2	0	1	2	1	1	0	1	0	0	2
Ae. (*Aed.*) *esoensis*	1	0	0	0	2	0	1	2	1	1	0	1	0	0	2
Ae. (*Lev.*) *geoskusea*	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1
Ae. (*Lev.*) *dufouri*	0	0	1	1	2	3	3	1	1	1	0	1	0	1	1
Ae. (*Lev.*) *fryeri*	1	1	1	1	2	3	3	0	1	1	0	1	0	1	0
Ae. (*Geo.*) *baisasi*	0	0	0	0	0	3	3	0	0	0	0	0	0	1	1
Ae. (*Geo.*) *longiforceps*	0	0	0	0	0	3	3	0	0	0	0	0	0	1	1
Ae. (*Rhi.*) *longirostris*	0	0	0	0	0	0	1	0	1	0	0	0	0	1	1
Ae. (*Rhi.*) *wardi*	0	0	0	0	0	0	1	0	1	0	0	0	0	1	1
Ae. (*Och.*) *caballus*	1	1	1	1	2	3	4	2	1	1	1	1	0	1	2
Ae. (*Och.*) *vigilax*	0	1	1	1	2	2	3	0	1	1	0	1	0	1	1

continued.

Characters	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90
Cs.(*Cus.*) *inornata*	0	0	0	1	1	3	0	1	0	0	0	0	1	0	1
Cx.(*Cux.*) *quinquefasciatus*	0	0	0	1	1	3	0	1	0	0	0	0	1	1	1
Ma. (*Man.*) *titillans*	0	0	1	0	1	3	0	0	0	0	0	0	1	0	1
Or. signifera	0	0	0	1	1	0	0	1	0	0	2	0	1	0	1
Ae.(*Abr.*) *papago*	0	0	0	1	1	1	0	1	1	0	0	1	1	0	1
Ae. (*Aed.*) *cinereus*	0	0	1	1	1	4	0	1	1	0	2	1	1	0	0
Ae. (*Aed.*) *esoensis*	0	0	1	1	1	4	0	1	1	0	0	1	1	0	0
Ae. (*Lev.*) *geoskusea*	1	0	1	0	1	4	1	0	1	0	2	1	1	0	1
Ae. (*Lev.*) *dufouri*	2	1	1	0	0	0	0	0	1	1	2	2	1	1	1
Ae. (*Lev.*) *fryeri*	0	1	1	1	1	3	0	1	1	0	2	0	1	0	1
Ae. (*Geo.*) *baisasi*	1	1	1	0	1	0	1	0	1	0	2	1	1	0	1
Ae. (*Geo.*) *longiforceps*	1	1	1	0	1	0	1	0	1	0	2	1	1	0	1
Ae. (*Rhi.*) *longirostris*	0	0	1	0	1	3	0	0	1	0	2	0	0	0	1
Ae. (*Rhi.*) *wardi*	0	0	1	0	1	3	0	0	1	0	2	0	0	0	1
Ae. (*Och.*) *caballus*	1	1	1	0	0	0	0	0	1	0	2	1	0	0	1
Ae. (*Och.*) *vigilax*	1	1	1	0	0	0	0	0	1	0	2	0	0	0	1

continued.

Characters	91	92	93	94	95	96	97	98	99	100	101	102	103	104	105
Cs.(*Cus.*) *inornata*	1	1	0	0	1	0	1	0	1	1	1	1	1	0	0
Cx.(*Cux.*) *quinquefasciatus*	1	1	0	0	1	0	1	0	1	1	1	0	0	?	0
Ma. (*Man.*) *titillans*	1	0	1	0	2	0	1	0	1	1	0	?	0	?	0
Or. signifera	1	0	0	0	1	0	1	0	1	1	1	0	0	?	0
Ae.(*Abr.*) *papago*	1	0	0	1	0	0	1	0	0	0	1	0	1	0	0
Ae. (*Aed.*) *cinereus*	0	?	0	1	2	1	1	0	0	1	1	0	1	0	0
Ae. (*Aed.*) *esoensis*	0	?	0	1	2	1	1	0	0	1	1	0	1	0	0
Ae. (*Lev.*) *geoskusea*	1	0	1	0	2	2	1	0	1	1	1	0	1	0	0
Ae. (*Lev.*) *dufouri*	1	0	0	0	1	1	1	0	0	0	1	1	1	0	0
Ae. (*Lev.*) *fryeri*	1	0	1	1	0	1	1	0	0	0	1	1	1	0	0
Ae. (*Geo.*) *baisasi*	1	0	1	0	2	1	1	0	0	0	1	1	1	0	0
Ae. (*Geo.*) *longiforceps*	1	0	1	0	2	1	1	0	0	0	1	1	1	0	0
Ae. (*Rhi.*) *longirostris*	1	0	1	0	2	1	0	?	0	1	0	?	1	0	1
Ae. (*Rhi.*) *wardi*	1	0	1	0	2	1	0	?	0	1	0	?	1	0	1
Ae. (*Och.*) *caballus*	1	0	1	0	2	2	1	0	0	0	1	1	1	0	1
Ae. (*Och.*) *vigilax*	1	0	1	0	2	2	1	0	0	0	1	1	1	0	0

continued.

Characters	106	107	108	109	110	111	112	113	114	115	116	117	118
Cs.(*Cus.*) *inornata*	0	0	1	0	0	0	1	0	1	1	0	2	0
Cx.(*Cux.*) *quinquefasciatus*	0	0	1	0	0	0	1	0	1	1	0	3	1
Ma. (*Man.*) *titillans*	0	1	0	0	0	1	0	0	1	1	0	1	0
Or. signifera	0	1	1	0	0	0	1	0	1	1	0	3	1
Ae.(*Abr.*) *papago*	0	1	0	0	0	0	1	0	1	1	0	0	1
Ae. (*Aed.*) *cinereus*	1	1	0	0	1	1	0	0	0	0	?	?	?
Ae. (*Aed.*) *esoensis*	1	1	0	0	1	1	0	0	0	0	?	?	?
Ae. (*Lev.*) *geoskusea*	1	1	0	1	0	1	1	0	1	1	1	2	0
Ae. (*Lev.*) *dufouri*	1	1	0	0	0	1	1	0	1	1	1	2	0
Ae. (*Lev.*) *fryeri*	1	1	1	0	0	1	1	0	1	1	1	2	0
Ae. (*Geo.*) *baisasi*	0	1	0	?	0	0	1	0	1	1	0	0	1
Ae. (*Geo.*) *longiforceps*	0	1	0	0	0	0	1	0	1	1	0	0	1
Ae. (*Rhi.*) *longirostris*	1	1	1	0	0	0	2	2	1	1	0	3	1
Ae. (*Rhi.*) *wardi*	1	1	1	0	0	0	2	2	1	1	0	3	1
Ae. (*Och.*) *caballus*	1	1	0	0	0	0	1	0	1	1	0	0	1
Ae. (*Och.*) *vigilax*	1	1	0	0	0	0	1	0	1	1	0	0	1

continued.

Characters	119	120	121	122	123	124	125	126	127	128	129	130	131	132
Cs.(*Cus.*) *inornata*	0	0	?	?	0	1	2	0	1	1	1	0	?	0
Cx.(*Cux.*) *quinquefasciatus*	0	?	?	?	?	1	0	0	0	1	1	0	?	0
Ma. (*Man.*) *titillans*	0	1	0	1	2	0	1	0	0	1	0	0	?	0
Or. signifera	0	0	?	?	0	0	2	0	1	1	1	3	?	0
Ae.(*Abr.*) *papago*	0	1	0	0	2	0	0	0	0	1	0	3	?	1
Ae. (*Aed.*) *cinereus*	0	0	?	?	0	1	0	1	0	0	0	0	0	0
Ae. (*Aed.*) *esoensis*	0	0	?	?	0	1	0	1	0	0	0	0	0	0
Ae. (*Lev.*) *geoskusea*	0	1	0	0	1	0	1	0	0	1	0	4	0	0
Ae. (*Lev.*) *dufouri*	0	1	0	0	1	0	3	0	0	1	0	1	0	1
Ae. (*Lev.*) *fryeri*	0	1	0	0	2	0	1	0	0	1	0	1	1	0
Ae. (*Geo.*) *baisasi*	0	0	?	?	0	0	2	0	0	1	0	4	?	0
Ae. (*Geo.*) *longiforceps*	0	0	?	?	0	0	1	0	0	1	0	4	?	0
Ae. (*Rhi.*) *longirostris*	0	2	?	?	0	0	0	0	0	1	0	4	0	0
Ae. (*Rhi.*) *wardi*	1	2	?	?	0	0	0	0	0	1	0	4	0	0
Ae. (*Och.*) *caballus*	0	1	0	0	3	0	1	0	0	1	0	0	0	1
Ae. (*Och.*) *vigilax*	0	1	0	0	1	0	1	0	0	1	0	1	0	1

Characters used in the phylogenetic analysis (* = treated as nonadditive characters; # = only those character states of Reinert et *al*. (2009) found in the taxa analyzed herein are included). The character numbers of Reinert et *al*. (2009) are included in parentheses following our character numbers.

#1(142). Erect forked scales of head: (0) restricted to occiput; (1) on both occiput and vertex; (?) species without erect forked scales.

*2(143). Decumbent scales of vertex: (0) all broad; (1) all narrow; (2) both broad and narrow.

#3(145). Ocular scales: (0) all narrow; (1) all broad; (2) both narrow and broad.

#4(146). Eyes, immediately above antennal pedicels: (0) contiguous; (1) narrowly to moderately separated; (2) broadly to very broadly separated.

5(147). Interocular space, scales: (0) absent; (1) present.

*6(148). Interocular scales, shape: (0) all narrow; (1) all broad; (2) both narrow and broad; (?) species without interocular scales.

7(152, modified). Antennal pedicel, mesal surface, short, fine setae: (0) absent; (1) present.

8(152, modified). Antennal pedicel, mesal surface, scales: (0) absent; (1) present.

*9(152, modified). Antennal pedicel, mesal surface, characteristics of scales: (0) few small scales; (1) a patch of pale broad scales (not overlapping to only slightly overlapping) and mixed with few fine setae; (2) a patch of broad, entirely overlapping silvery scales; (?) species without scales.

#10(155). Antenna, flagellar whorls, development (males): (0) several moderately long to long setae, directed more or less dorsally and ventrally and several laterally; (1) numerous long setae, normally directed dorsally and ventrally.

11(156). Maxillary palpus, pale scales: (0) absent; (1) present.

*#12(157, modified). Maxillary palpomeres, development (males): (0) five, palpomeres 2 and 3 fused/ ankylosed; (1) four, palpomere 5 absent or minute; (2) three, palpomere 4 absent or vestigial; (3) two, palpomere 3 absent or vestigial.

*13(158). Maxillary palpomeres, position of palpomeres 4 and /or 5 relative to palpomere 3 (males): (0) down-turned; (1) up-turned; (2) nearly straight; (?) species without palpomeres 4 and /or 5.

14(159). Maxillary palpus, palpomere 3, ratio of length to length of proboscis (males): (0) < 0.14; (1) > 0.21.

*15(160). Maxillary palpus, palpomere 5, ratio of length to length of palpomere 4 (males): (0) < 0.58; (1) >0.66; (?) species without palpomeres 4 and/or 5.

*16(161). Maxillary palpus, ratio of length to length of proboscis (males): (0) < 0.27; (1) 0.48–0.80; (2) > 0.84.

*17(162). Maxillary palpus, setae on palpomeres 3 (distally) and 4 (males): (0) absent or few, short to moderately long; (1) moderate to numerous, long; (?) species without palpomere 4.

18(164). Proboscis, pale scales: (0) absent; (1) present.

19(167). Antepronotal scales: (0) absent; (1) present.

*20(168). Antepronotal scale shape: (0) all narrow; (1) all broad; (2) both narrow and broad; (?) species without scales on the antepronotum.

*21(173). Scutum, scale shape: (0) all narrow; (1) all broad; (2) both narrow and broad.

#22(175). Scutum, scale color: (0) all dark; (1) both pale and dark; (2) all pale.

23(179). Anterior dorsocentral area, pale-scaled stripe: (0) absent; (1) present.

24(180). Posterior dorsocentral area, pale-scaled stripe: (0) absent; (1) present.

25(181). Scutal fossal scales: (0) sparse; (1) dense.

*26(182). Scutal fossa scales, color: (0) all dark; (1) contrasting pale scales in large patch; (2) contrasting lines or small patches of pale scales on lateral and/or mesal and/or posterior margins; (3) indefinite arrangement of pale and darker scales.

27(183). Prescutellar area, median and/or posterior parts, scales: (0) absent; (1) present.

28(186). Prescutellar area, pale scales on outer margin mesal to setae: (0) absent; (1) present.

*#29(188). Antealar area, scales on anterior part, color: (0) all dark; (1) all pale; (2) both dark and pale; (?) species without scales on the anterior part of the antealar area.

30(189). Supraalar area, pale scales: (0) absent; (1) present.

#31(191). Scutellum, scales on midlobe: (0) all narrow; (1) all broad; (2) both narrow and broad.

#32(192). Scutellum, scales on lateral lobes: (0) all narrow; (1) all broad; (2) both narrow and broad.

33(193). Paratergal scales: (0) absent; (1) present.

34(197). Postpronotal scales: (0) absent; (1) present.

*35(198). Postpronotal scales, shape: (0) all narrow; (1) all moderately broad to broad; (2) both narrow and moderately broad to broad; (?) species without scales on the postpronotum.

36(200). Postspiracular setae: (0) absent; (1) present.

37(201). Postspiracular scales: (0) absent; (1) present.

38(202). Hypostigmal scales: (0) absent; (1) present.

39(203). Subspiracular scales: (0) absent; (1) present.

*40(204). Upper proepisternal setae: (0) 1–4; (1) 5–19; (2) >20.

41(205). Upper proepisternal scales: (0) absent; (1) present.

*42(208). Mesokatepisternal scales: (0) in one large patch; (1) in two patches; (2) in three patches.

43(209). Upper prealar setae: (0) < 20; (1) > 21.

44(210). Upper prealar scales: (0) absent; (1) present.

45(211). Lower prealar scales: (0) absent; (1) present.

46(212). Mesepimeral scales: (0) absent; (1) present.

*47(213). Mesepimeral, scales: (0) in one patch; (1) in two patches; (2) in three patches; (?) species without scales on the mesepimeron.

48(214). Lower anterior mesepimeral setae: (0) absent; (1) present.

49(215). Mesepimeral fine setae: (0) absent; (1) present.

50(216). Metameron, vestiture: (0) absent; (1) present.

51(217, modified). Metameron, setae: (0) absent; (1) present.

52(217, modified). Metameron, scales: (0) absent; (1) present.

53(219). Upper calypter, setae or hair-like scales (males): (0) 0–3; (1) numerous, > 7.

54(223). Remigium, dorsal setae: (0) absent; (1) present.

#55(224). Remigium, insertion of dorsal setae: (0) distally; (1) proximally; (?) species without setae dorsally on the remigium.

*56(226). Costal scales: (0) all dark; (1) one pale-scaled patch at or near base; (2) > 3 pale-scaled patches; (3) pale and dark scales intermixed for all or most of length, not forming defined pattern.

57(231). Wing, dorsal tertiary fringe scales on proximal 0.50: (0) absent; (1) present.

58(232). Wing, dorsal tertiary fringe scales on proximal 0.50 (males): (0) absent; (1) present.

59(233). Wing, dorsal tertiary fringe scales, color: (0) uniform; (1) intermixed or patches of pale and dark.

60(235). Postprocoxal scales: (0) absent; (1) present.

61(239). Hindfemur, pale scales dorsally and/or anteriorly at apex: (0) absent; (1) present.

62(240). Hindtibia, scales, color: (0) dark only; (1) dark with pale-scaled areas.

63(241). Hindtarsomere 1, basal pale scales or band: (0) absent; (1) present.

64(244). Hindtarsomere 2, basal pale scales or band: (0) absent; (1) present.

*65(246). Foretarsal claws: (0) both simple; (1) one simple, one toothed; (2) both toothed.

*#66(247). Foretarsal claws (males): (0) larger one with one tooth, smaller one simple; (1) larger one with two teeth, smaller one simple; (2) both toothed, larger one with one tooth; (3) both toothed, larger one with two teeth.

*#67(248). Midtarsal claws (males): (0) larger one simple, smaller one toothed; (1) larger one with one tooth, smaller one simple; (2) larger one with two teeth, smaller one simple; (3) both toothed, larger one with one tooth; (4) both toothed, larger one with two teeth.

*68(249). Hindtarsal claws: (0) both simple; (1) one simple, one toothed; (2) both toothed.

69(251). Abdominal tergum I, laterotergite, scales: (0) absent; (1) present.

70(252). Abdominal tergum III, median dorsobasal pale-scaled area: (0) absent; (1) present.

71(253). Abdominal tergum III, median dorsoapical pale-scaled area: (0) absent; (1) present.

72(254). Abdominal terga, lateral setae (males): (0) relatively short to moderately long; (1) long.

*#73(255). Abdominal segment VII, cross-section shape: (0) dorsoventrally flattened; (1) cylindrical.

74(256). Intersegmental membrane between segments VII and VIII: (0) short to intermediate; (1) long to very long.

*75(258). Tergum VIII, posterior margin: (0) convex; (1) straight; (2) concave.

*76(259). Tergum VIII, length relative to width: (0) shorter; (1) longer; (2) equal.

77(260). Tergum VIII, one or more moderately long to long seta(e) on lateral margins of proximal 0.40: (0) absent; (1) present.

78(261). Tergum VIII, insertion of setae: (0) on distal 0.60 or less; (1) on distal 0.70 or more.

79(262). Tergum VIII, scales: (0) absent, occasionally with 1–3 adventitious scales; (1) present, > 14 scales.

#80(263). Sternum VIII, development: (0) mostly sclerotized, with a narrow, median, longitudinal, non-sclerotized area; (1) entirely sclerotized.

*81(264). Sternum VIII, posterior margin: (0) gently rounded; (1) more or less straight; (2) more or less uniformly sloping cephalad from apicolateral corners to midline; (3) median emargination separating broadly rounded lateral lobes; (4) median emargination separating sublateral lobes.

82(265). Sternum VIII, seta 2-S, insertion relative to seta 1-S: (0) noticeably posterior; (1) lateral at or near same level as seta 1-S.

83(266). Sternum VIII, scales: (0) absent, occasionally with 1–3 adventitious scales; (1) present, > 10 scales, often covering much of surface.

84(267). Tergum IX, width/length ratio: (0) > 2.0; (1) < 1.8.

85(268). Tergum IX, development: (0) single sclerite, usually with small to deep emargination on posterior margin; (1) two sclerites connected by membrane.

*86(271). Postgenital lobe, posterior margin: (0) rounded; (1) straight; (2) emarginate.

*87(273). Postgenital lobe, ventral index: (0) 0.47–1.64; (1) 1.65–2.81; (2) 2.90–4.32.

88(275). Upper vaginal sclerite: (0) absent; (1) present.

89(276). Lower vaginal sclerite: (0) absent; (1) present.

90(277). Insula, development: (0) tongue-like; (1) lip-like.

91(278). Insula setae: (0) absent; (1) present.

*92(279). Insula, insertion of setae: (0) in lateral patches; (1) in median patch; (?) species without setae on the insula.

#93(280). Cercus index: (0) < 2.88; (1) 2.94–4.06; (2) >4.21.

94(281). Cercal scales: (0) absent; (1) present.

*#95(282). Cercus, distal part: (0) gently oblique; (1) moderately to broadly rounded; (2) narrowly rounded; (3) truncate.

*96(283). Cercus/dorsal postgenital lobe index: (0) < 3.20; (1) 3.24–4.78; (2) > 4.90.

97(284). Accessory spermathecae: (0) absent; (1) present.

#98(285). Accessory spermathecae, development: (0) two large; (?) species without accessory spermathecae.

99(286). Tergum IX, posterior margin: (0) two small, relatively narrow lobes; (1) two moderately broad to broad lobes.

100(287). Tergum IX, position of lateral lobes on posterior margin: (0) close together; (1) widely separated.

101(288). Tergum IX, setae (males): (0) absent; (1) present.

*102(289). Tergum IX, setae (males): (0) all slender; (1) some or all stout; (?) species without setae on tergum IX.

103(290). Sternum IX, vestiture: (0) absent; (1) present.

104(291). Sternum IX, vestiture: (0) setae; (1) setae and scales; (?) species without vestiture on sternum IX.

105(292). Gonocoxite, dorsomesal apical lobe: (0) absent; (1) present.

106(293). Gonocoxite, dorsomesal basal lobe: (0) absent; (1) present.

107(294). Gonocoxite, scales: (0) absent; (1) present.

108(295). Gonocoxite, mesal surface: (0) entirely membranous; (1) partly or entirely sclerotized.

*109(297). Gonocoxite, setal development on basomesal area of dorsal surface: (0) all slender; (1) one or more stout or flattened; (?) species without setae on the basomesal area of the dorsal surface.

110(302). Gonostylus, attachment to gonocoxite: (0) apical; (1) subapical.

111(303). Gonostylus, proximal part: (0) narrow; (1) broad.

*112(304). Gonostylus, median part: (0) noticeably narrower than proximal part; (1) slightly narrower to slightly broader than proximal part; (2) noticeably broader than proximal part.

*113(305). Gonostylus, distal part: (0) narrower than proximal part; (1) slightly broader than proximal part; (2) much broader than proximal part.

114(310). Gonostylus, seta(e) on distal 0.33: (0) absent; (1) present.

115(312). Gonostylar claw(s): (0) absent; (1) present.

*116(313). Gonostylar claw(s), number: (0) one; (1) two; (2) three or more; (?) species without a gonostylar claw.

*117(316). Most proximal gonostylar claw, development: (0) relatively narrow spiniform; (1) moderately broad spiniform; (2) short, claw-like spiniform; (3) flattened, relatively broad, somewhat leaf-like structure; (?) species without a gonostylar claw.

*#118(317). Most proximal gonostylar claw, apex: (0) bluntly pointed; (1) truncate, rarely rounded but nearly truncate; (?) species without a gonostylar claw.

#119(318). Gonostylus / gonocoxite index: (0) 0.42–0.71; (1) >0.73.

*120(320). Claspette, development: (0) single basal setose plaque, columnar lobe absent; (1) single columnar lobe; (2) two basal lobes, columnar lobe absent; (3) two basal lobes, one columnar; (?) claspette is absent.

121(321). Claspette, subapical thumb-like projection on columnar stem: (0) absent; (1) present; (?) species without a columnar stem.

*122(322). Claspette, ratio of columnar stem length to length of aedeagus: (0) < 0.85; (1) > 0.90; (?) species without a columnar stem.

*123(323, modified). Claspette, vestiture: (0) two or more simple setae; (1) one slender, tapered spiniform setal appendage; (2) one stout spiniform appendage; (3) one flattened blade-like appendage; (?) claspette is absent.

124(325). Aedeagus, development: (0) single, tube-like, scoop-like or trough-like structure; (1) comprised of two lateral plates.

*125(326, modified). Aedeagus, width: (0) widest in distal 0.33; (1) widest in middle 0.33; (2) widest in proximal 0.33; (3) not widened, parallel-sided in basal 0.60.
126(327). Aedeagal teeth: (0) absent; (1) present.
127(329). Aedeagus, small distal spicules: (0) absent; (1) present.
128(333). Proctiger, cercal setae: (0) absent; (1) present.
129(334). Proctiger, apical teeth on paraproct: (0) absent; (1) present.
*130(336). Habitat of immature stages: (0) fresh-water ground pools; (1) brackish-water ground and rock pools; (2) fresh-water rock pools; (3) fresh-water containers (phytotelmata, small artificial containers, rock holes); (4) crab holes.
*131(new). Gonocoxite, basal dorsomesal lobe: (0) attached to basomesal area of dorsal surface (forming part of dorsal portion of gonocoxite); (1) attached basally to mesal surface (not forming part of dorsal portion of the gonocoxite); (?) species without dorsomesal basal lobe.
132(new). Paraproct, single, strongly sclerotized curved apical tooth: (0) absent; (1) present.

Analysis and results

Using the implicit enumeration (ie*) option of Hennig86, which is an exhaustive search, a single most parsimonious tree was generated from the analysis of the 132 characters. The cladogram has a length of 325 steps and consistency and retention indices of 0.50 and 0.62, respectively. 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 954 steps, and with stabilization, the consistency and retention indices increased to 0.70 and 0.79, respectively. The analysis of the characters for this cladogram is given in Table 3 and the weights of the various characters are given in Table 4. The placement and numbering of characters and character states on nodes of the cladogram are unambiguous.

In summary, and as indicated on the single cladogram (Fig. 4), the following results relating to the questions posed earlier are evident:

1. *Levua* is monotypic, including only *Ae*. *geoskusea*;
2. *Aedes geoskusea* is the sister of *Geoskusea* (2 species, *Ae*. *baisasi*, *Ae*. *longiforceps*) + *Rhinoskusea* (2 species, *Ae*. *longirostris*, *Ae*. *wardi*);
3. *Aedes dufouri* is basal to *Ae*. *geoskusea* and then *Geoskusea* (2 species, *Ae*. *baisasi*, *Ae*. *longiforceps*) + *Rhinoskusea* (2 species, *Ae*. *longirostris*, *Ae*. *wardi*);
4. *Aedes fryeri* is basal to *Ae*. *caballus*, *Ae*. *vigilax* + *Ae*. *dufouri* and secondly to *Ae*. *geoskusea* and finally to *Geoskusea* (2 species, *Ae*. *baisasi*, *Ae*. *longiforceps*) + *Rhinoskusea* (2 species, *Ae*. *longirostris*, *Ae*. *wardi*);
5. The species *Aedes cinereus* + *Ae*. *esoensis* together are the sister group of *Aedes fryeri* and secondly of *Ae*. *caballus*, *Ae*. *vigilax* + *Ae*. *dufouri* and thirdly of *Ae*. *geoskusea* and finally of *Geoskusea* (2 species) + *Rhinoskusea* (2 species).
6. Both *Ae*. *fryeri* and *Ae*. *dufouri* are basal to *Ae*. *geoskusea* and then to *Geoskusea* (2 species) + *Rhinoskusea* (2 species).

Based on this cladistic analysis, it is evident that *Levua* is a monotypic lineage represented by a single known species, *Ae. geoskusea.* Although two other species have been placed in *Levua*, *Ae. fryeri* and *Ae. dufouri*, their inclusion would result in an untenable, polyphyletic group. *Aedes dufouri* is here transferred back to the subgenus *Ochlerotatus* and is distinguished from other congeners of this subgenus by the pair of short, pointed gonostylar claws that are inserted under a hood. A more detailed, taxonomic discussion on *Ae*. *dufouri* will be treated in a separate paper. In this paper, we further consider only the taxonomy of *Ae. fryeri,* proposing a new subgenus for this species along with providing a re-evaluation and detailed description of this species.

Table 3. Analysis of characters (character number, steps, consistency index, retention index).

character/steps/ci/ri

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
1	3	2	2	1	1	1	1	2	1	2	2	3	3	2	4	3	3
100	66	50	50	100	100	100	100	100	100	50	100	66	33	50	50	33	33
100	80	75	83	100	100	100	100	100	100	83	100	80	60	66	66	60	66

19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37
1	3	2	3	2	2	3	4	3	2	2	2	3	3	3	1	6	1	3
100	66	50	33	50	50	33	75	33	50	100	50	33	33	33	100	33	100	33
100	0	50	50	0	50	50	66	33	83	100	83	33	33	71	100	33	100	71

38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56
2	3	3	1	4	2	3	4	2	5	3	1	2	1	2	1	2	0	5
50	33	66	100	50	50	33	25	50	20	33	100	50	100	50	100	50	100	40
0	0	50	100	60	0	33	40	50	0	33	100	50	100	50	100	0	100	50

57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75
1	2	2	2	3	2	4	4	3	7	7	3	2	4	2	3	1	2	4
100	50	50	50	33	50	25	25	66	42	57	66	50	25	50	33	100	50	50
100	50	0	0	71	85	50	50	80	42	50	50	80	57	0	66	100	80	71

76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94
3	3	2	2	2	6	2	2	1	1	3	5	2	2	1	1	2	3	2
66	33	50	50	50	50	50	50	100	100	33	40	50	50	100	100	50	33	50
75	60	66	83	50	57	50	83	100	100	50	50	66	0	100	100	0	66	66

95	96	97	98	99	100	101	102	103	104	105	106	107	108	109	110	111	112	113
4	3	1	0	2	4	2	3	2	0	2	2	2	3	1	1	4	3	1
50	66	100	100	50	25	50	33	50	100	50	50	50	33	100	100	25	66	100
50	83	100	100	75	50	50	60	50	100	50	83	0	60	100	100	40	66	100

114	115	116	117	118	119	120	121	122	123	124	125	126	127	128	129	130	131
1	1	3	7	5	1	4	0	1	5	3	6	1	1	1	1	5	1
100	100	33	42	20	100	50	100	100	60	33	50	100	100	100	100	60	100
100	100	0	33	0	100	66	100	100	50	33	57	100	100	100	100	71	100

132
3
33
33

Genus *Aedes* Meigen

Coetzeemyia Huang, Mathis & Wilkerson, new subgenus

Type species. *Culicelsa fryeri* Theobald. 1912, by present designation and monotypy.

Characteristics. The subgenus *Coetzeemyia* is characterized by the following combination of characters: *Adults* (both sexes): Vertex with erect forked scales numerous, not restricted to occiput; with decumbent scales largely narrow; maxillary palpus of male slightly shorter than proboscis, 5-segmented, dark; with white band at base of palpomeres 2–5, those on palpomeres 4,5 incomplete ventrally; palpomeres 2 and 3 ankylosed and long; palpomere 3 longest; apex of palpomere 3 somewhat swollen, slightly upturned; palpomeres 4 and 5 straight, slightly downturned; ventrolateral surface of apex of palpomere 3 and all of palpomere 4 with well-developed long setae; palpomere 4 slightly swollen; palpomeres 4 and 5 subequal in length and with setae (see Fig. 1A); maxillary palpus of female about 0.17 length of proboscis, with white scales at tip (Fig. 1B); proboscis speckled with pale scales; acrostichal setae present; paratergite with few broad white scales; postspiracular setae present; lower prealar scale patch present; subspiracular area without scales; postspiracular area with broad white scales; lower mesepimeral setae absent; scutellum with all narrow scales and with narrow white scales on all lobes; wing membrane not clouded on crossveins r-m and m-cu; wing speckled with pale scales; remigial setae present; femora, tibiae and tarsomere 1 speckled with pale scales; hindtarsomeres 1–5 with basal white bands. Male genitalia: Aedeagus simple, rather long, slightly broadened in middle; claspette present, stem slender with short, stout setal appendage; paraproct with 2 or 3 blunt teeth at tip; cercal setae present; gonostylus with pair of short, stout, pointed gonostylar claws inserted under a hood (apically); gonocoxite rather stout, with mesal membrane from base not reaching apex; basal dorsomesal lobe attached basally to mesal surface (not forming part of tergal part of gonocoxite as does the basal lobe in most *Ochlerotatus*); tergum IX lobes prominent, strongly developed, with 8 or 9 slender setae on dorsal and ventral surfaces; sternum IX with setae. The above combination of characters distinguishes *Coetzeemyia*, a polythetic generic-level taxon, from all other subgenera traditionally placed in the genus *Aedes*.

Table 4. Weights (varying between 1-10) and status (i.e., nonadditive = ?) of characters after successive weighing.

1	2	3	4	5	6	7	8	9	10	11	12	13	14	
10+[	5-[	3+[	4+[	10+[	10-[	10+[	10+[	10-[	10+[	4+[	10-[	5-[	2+[	
15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
3-[	3-[	2-[	2+[	10+[	0-[	2-[	1+[	0+[	2+[	1+[	5-[	1+[	4+[	10-[
30	31	32	33	34	35	36	37	38	39	40	41	42	43	44
4+[	1+[	1+[	2+[	10+[	1-[	10+[	2+[	0+[	0+[	3-[	10+[	3-[	0+[	1+[
45	46	47	48	49	50	51	52	53	54	55	56	57	58	59
1+[	2+[	0-[	1+[	10+[	2+[	10+[	2+[	10+[	0+[	10-[	2-[	10+[	2+[	0+[
60	61	62	63	64	65	66	67	68	69	70	71	72	73	74
0+[	2+[	4+[	1+[	1+[	5-[	1-[	2-[	3-[	4+[	1+[	0+[	2+[	10-[	4+[
75	76	77	78	79	80	81	82	83	84	85	86	87	88	89
3-[	5-[	2+[	3+[	4+[	2+[	2-[	2+[	4+[	10+[	10+[	1-[	2-[	3+[	0+[
90	91	92	93	94	95	96	97	98	99	100	101	102	103	104
10+[	10+[	0-[	2+[	3+[	2-[	5-[	10+[	10+[	3+[	1+[	2+[	2-[	2+[	10+[
105	106	107	108	109	110	111	112	113	114	115	116	117	118	119
2+[	4+[	0+[	2+[	10-[	10+[	1+[	4-[	10-[	10+[	10+[	0-[	1-[	0-[	10+[
120	121	122	123	124	125	126	127	128	129	130	131	132		
3-[	10+[	10-[	3-[	1+[	2-[	10+[	10+[	10+[	10+[	4-[	10-[	1+[		

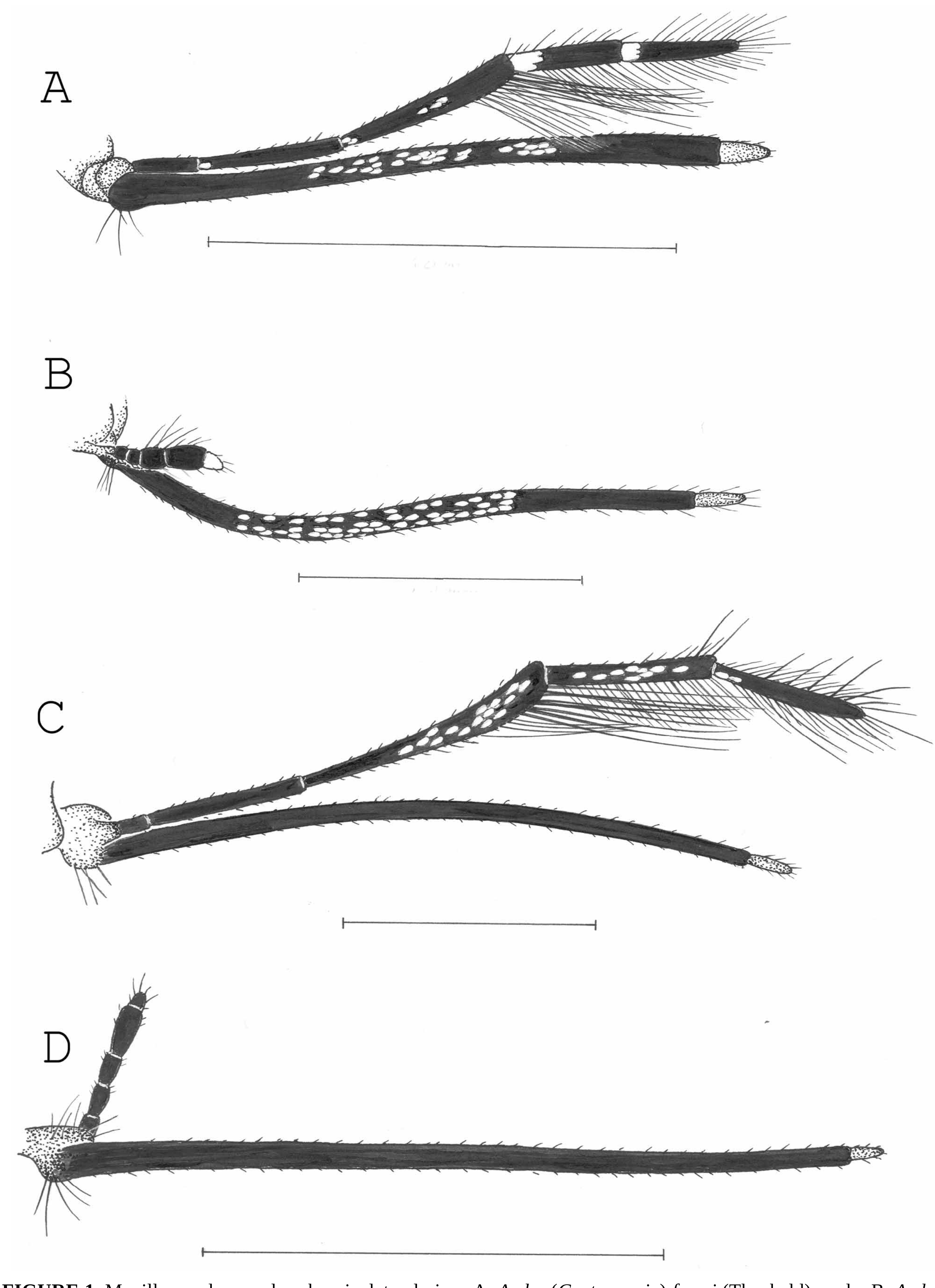

FIGURE 1. Maxillary palpus and proboscis, lateral view. A, *Aedes* (*Coetzeemyia*) *fryeri* (Theobald), male. B, *Aedes* (*Coetzeemyia*) *fryeri* (Theobald), female. C, *Aedes* (*Ochlerotatus*) *harrisoni* Muspratt, male. D, *Aedes* (*Levua*) *geoskusea* (Amos), male. Scales = 1.0 mm.

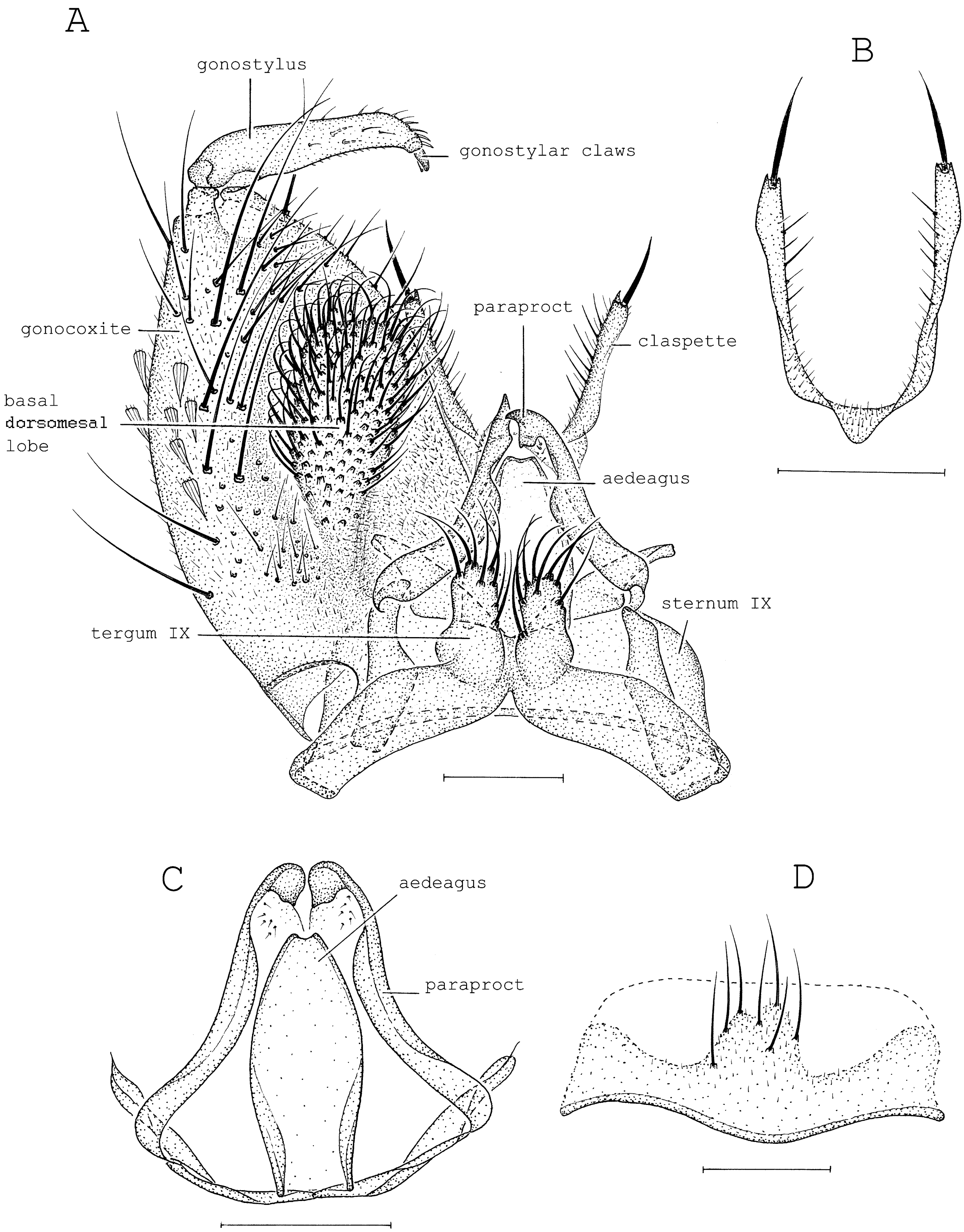

FIGURE 2. *Aedes* (*Coetzeemyia*) *fryeri* (Theobald). A, Tergal aspect of the male genitalia. B, Claspettes. C, Proctiger and aedeagus. D, Sternum IX. Scales = 0.1 mm.

Systematics. *Aedes fryeri* is very distinctive and has several unique features, as noted above, but it also shows some similarities with the subgenera *Ochlerotatus* and *Levua* (see Table 1). The male genitalia of *Ae. fryeri*, however, are strikingly different from all known species in these two subgenera, as well as from other subgenera of *Aedes*. Because of these differences, subgeneric status is accorded this species. The subgenus

Coetzeemyia possesses some basic characters in common with the subgenera *Ochlerotatus* and *Levua*, including: male maxillary palpus 5-segmented; aedeagus simple, without teeth; claspette present; proctiger with cercal setae; vertex with erect forked scales numerous, not restricted to occiput; with decumbent scales largely narrow; acrostichal setae present; scutellum with all narrow scales; wing membrane not clouded on crossveins r-m and m-cu and remigial setae present. These shared or common characters indicate an affinity of *Coetzeemyia* to these two subgenera.

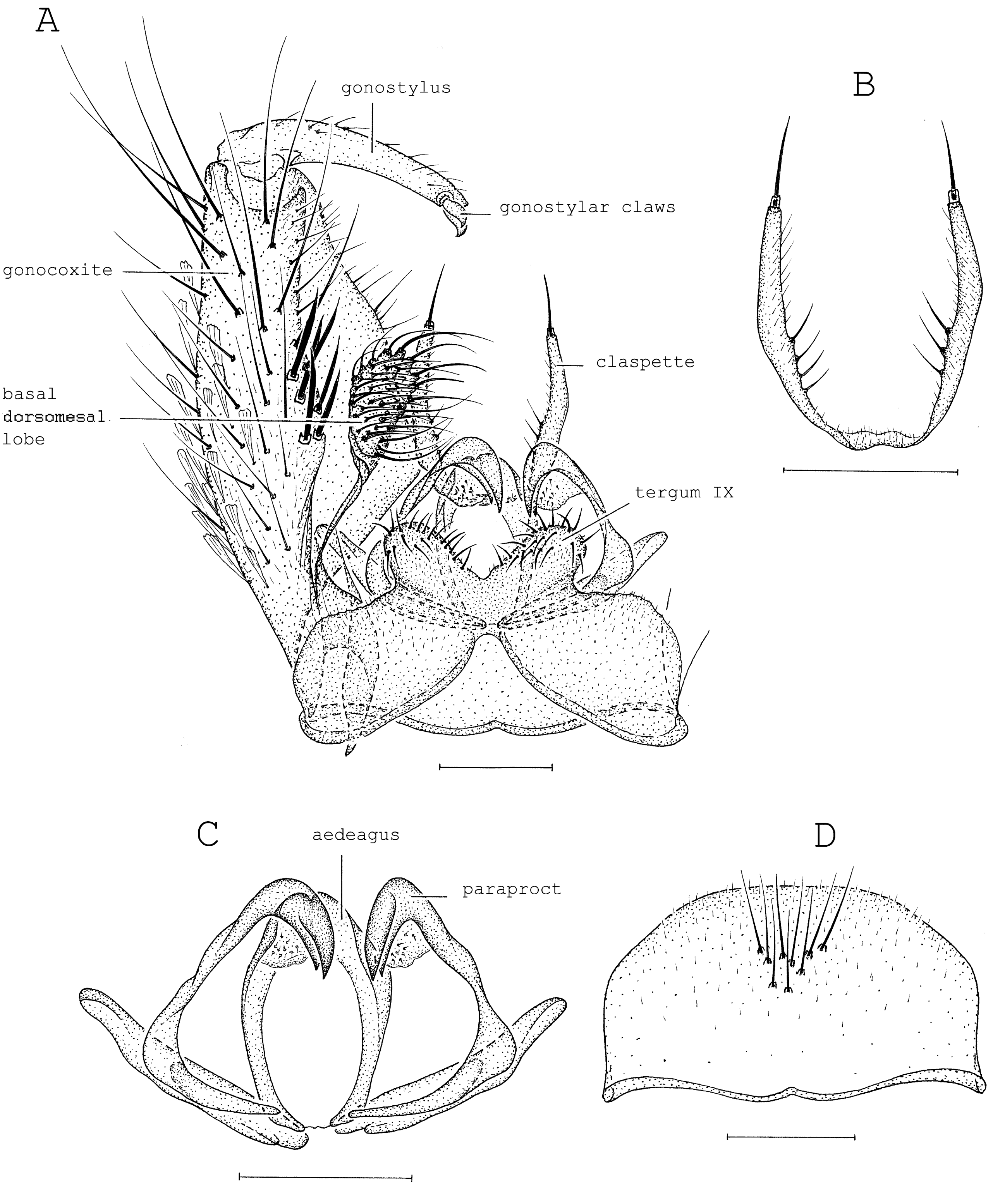

FIGURE 3. *Aedes* (*Levua*) *geoskusea* (Amos). A, Tergal aspect of the male genitalia. B, Claspettes. C, Proctiger and aedeagus. D, Sternum IX. Scales = 0.1 mm.

Adults of *Coetzeemyia* are very similar to those of *Levua* in having the vertex with decumbent scales largely narrow, with erect forked scales numerous, not restricted to occiput, and the subspiracular area without scales. However, this subgenus can easily be distinguished from *Levua* by the presence of a lower prealar scale-patch, the paratergite with a few broad white scales, the postspiracular area with broad white scales and the scutellum with narrow white scales on all lobes.

Males of *Coetzeemyia* are similar to those of *Levua* in having the maxillary palpus 5-segmented. They can be easily distinguished from *Levua* by the long maxillary palpus, a little shorter than the proboscis, with conspicuous, long setae, and the last two segments subequal in length and bearing setae (see Fig. 1A). In *Levua*, the maxillary palpus of the male is very short, at most 0.25 length of proboscis, without conspicuous long setae, and the last segment is minute (see Fig. 1D).

The male genitalia of *Coetzeemyia* (Fig. 2A) are very similar to those of *Levua* in having the aedeagus simple, without teeth, and the gonostylus with a pair of short, very stout, pointed gonostylar claws inserted under a hood. They can be distinguished from those of *Levua* in having the gonocoxite with the mesal membrane not reaching the apex; the claspette with a short, stout setal appendage (Fig. 2B); the paraproct with two or three blunt teeth at the tip; and the aedeagus rather long and slightly broadened in the middle (Fig. 2C).

In *Levua*, the male genitalia (Fig. 3A) have the gonocoxite with the mesal membrane reaching the apex; the claspette with a slender, tapered spiniform setal appendage (Fig. 3B); the paraproct with a long bifid apical spine about half its length, strongly sclerotized, and curved; and the aedeagus large, broadened beyond the base, and rounded apically (Fig. 3C). The maxillary palpus of *Coetzeemyia* males is very similar to that of species in subgenus *Ochlerotatus.* In *Ochlerotatus*, the maxillary palpus of males is slightly shorter, as long as or longer than the proboscis with conspicuous long setae on the distal half, and the last two segments subequal in length, downturned and without white bands at the base (see Fig. 1C).

The male genitalia of *Coetzeemyia* are strikingly different from all known species in these two subgenera, as well as from other traditionally recognized subgenera of *Aedes*. These differences include: gonocoxite rather stout, with mesal membrane not reaching the apex; basal dorsomesal lobe attached basally to the mesal surface (not forming part of the tergal part of the gonocoxite as does the basal lobe in most *Ochlerotatus*); claspette with a short, stout setal appendage; gonostylus with a pair of short, stout, pointed gonostylar claws inserted under a hood (apically); paraproct with two or three blunt teeth at the tip; aedeagus simple, without teeth, rather long, slightly broadened in the middle; and tergum IX lobes prominent, strongly developed, with 8 or 9 slender setae on the dorsal and ventral surfaces. In *Ochlerotatus*, the male genitalia have the gonocoxite with mesal membrane from base to apex (Edwards 1941: 115, Fig. 35, b); the claspette with a flattened, blade-like appendage (Edwards 1941: 115, Fig. 35, c); the gonostylus with a long spine-like gonostylar claw inserted apically; the paraproct with a strongly sclerotized apical tooth; the aedeagus simple, smooth, scoop-shaped; and tergum IX with prominent lobes bearing strong setae distally (Edwards 1941: 115, Fig. 35, a).

Etymology. The subgeneric name, *Coetzeemyia*, honors Prof. (Dr.) Maureen Coetzee (feminine, formed from her surname and *myia*, the Greek noun for fly) of the Vector Control Reference Unit, National Institute for Communicable Diseases (NICD), Johannesburg, South Africa. We are grateful for her kindness in collecting egg batches from individual females of several species of *Stegomyia* while Yiau-Min Huang was studying African *Stegomyia* at the Department of Medical Entomology, South African Institute for Medical Research (SAIMR), Johannesburg, South Africa. The subgeneric name also recognizes her many contributions to our knowledge of the mosquito fauna of Africa.

Distribution. *Aedes fryeri* is presently known from the Seychelles (Aldabra Island, Takamaka), and Kenya (Mombasa, Magogongi swamp, near Witu). Edwards (1941: 117) recorded *Ae*. *fryeri* from the Seychelles (Cosmoledo Is.), and Madagascar (Majunga). Smith and Corbet (1975: 285) recorded it from Tanzania. Knight and Stone (1977: 132) included records from Eritrea and Mozambique. White (1980: 130) recorded it from South Africa.

Based on the previous collection records, *Ae*. *fryeri* occurs along maritime coasts in eastern Africa and islands in the Indian Ocean.

Bionomics. *Aedes fryeri* was collected from Aldabra Island and from the coast of Kenya, where it probably breeds in brackish water. No individual rearings have been done. Hopkins (1952: 123) incorrectly described the larva of *Ae. (Aedimorphus)* species as *Ae. fryeri* from two unassociated whole larvae, deposited in the BMNH.

In Tanzania, Smith and Corbet (1975: 285, 286) reported finding *Ae*. (*Och*.) *fryeri* in saline pools on the coastal margins of coral islands near Dar es Salaam. The coral rock pools were shallow (10–30 cm) and contained water to a depth of a few centimeters, lying over a coral bottom. The pools were as saline as samples of sea water taken at the surface of the ocean near the island. *Aedes fryeri* was the only mosquito species found in the pools. The pools in coral rock probably constitute an important larval habitat for this species. Females are autogenous in the first ovarian cycle and anautogenous in the second ovarian cycle. During the dry season, in Kenya, Van Someren and Furlong (1964: 115) reported *Ae*. *fryeri* larvae in tidal marshes at the heads of mangrove creeks.

Van Someren *et al.* (1958: 657) reported that females of *Ae*. *fryeri* were mainly nocturnal, although biting also occurred throughout the day. The biting cycle had two clear peaks, at sunset and dawn. The evening peak occurred between 1800 and 1900 hr and was higher than the morning peak, which was slightly longer in duration, between 0500 to 0700 hr.

Medical importance. McIntosh *et al.* (1962: 686) reported that Spondweni virus was isolated from a pool of 42 female mosquitoes identified as *Ae.* (*Ochlerotatus*) *fryeri* or *Ae.* (*Aedimorphus*) *fowleri* collected at Lumbo, Mozambique.

Aedes (*Coetzeemyia*) *fryeri* (Theobald)

(Figs. 1A, 1B, 2A, 2B, 2C, 2D)

Culicelsa fryeri Theobald, 1912: 84 [F*].
Ochlerotatus fryeri.─Edwards 1917: 218, 220 [M*, F; generic combination].
Aedes (*Ochlerotatus*) *fryeri*.─Edwards 1932: 137 [generic combination]; 1941: 116 [M*, F].
Aedes (*Ochlerotatus*) *mombasaensis* Mattingly, 1963: 165 [M, F, L*].─Van Someren 1972: 90 [synonymy].
Aedes (*Levua*) *fryeri*.─Danilov 1981: 87 [subgeneric combination].
Levua fryeri.─Reinert *et al.* 2004: 360 [*Levua* Stone and Bohart, 1944, stat. nov., raised to generic rank]; 2006: 93; 2009: in Appendix 2 [same as Reinert *et al.* 2004].
Ochlerotatus (*Levua*) *fryeri*.─Reinert *et al.* 2008: 112 [subgenus *Levua* Stone and Bohart, 1944, stat. rev.].

Redescription of the type female of *Aedes fryeri* (Theobald, 1912). The description below is based on the type female of Theobald from Aldabra Island in the BMNH. The type female has four labels: (1) *Culicelsa fryeri* Type female Theo (handwritten), (2) Aldabra. Takamaka. J.C.F. Fryer (handwritten), (3) Seychelles Expd. Pres. by Committee of the Percy Sladen Trust Fund. 1911–99 (printed), and (4) SYN-TYPE (green circular paper, printed).

Female. *Head*: Proboscis dark-scaled, speckled with pale scales on basal 0.66, with apical 0.33 all dark, about as long as forefemur; maxillary palpus (Fig. 1B) about 0.17 length of proboscis, dark, with white scales at tip; antennal pedicel with short, fine setae on mesal surface; flagellomere 1 with few small dark scales on mesal surface; clypeus bare; erect forked scales numerous, not restricted to occiput; vertex largely with white narrow curved scales on middle area, with broad white and dark scales on lateral areas. *Thorax*: Scutum mottled with light and dark brown, narrow scales; acrostichal setae present; dorsocentral setae present and well developed; scutellum with narrow white scales on all lobes; antepronotum with narrow white curved scales; postpronotum with broad flat dark scales and some narrow curved scales dorsally; paratergite with 2 broad white scales; prespiracular setae absent; postspiracular setae present; postspiracular area with broad white scales; hypostigmal area without scales; subspiracular area without scales; lower prealar scale-patch present; patches of broad white scales on propleuron, upper and lower areas of mesokatepisternum, and mesepimeron; lower mesepimeron without setae; metameron and mesopostnotum bare. *Wing*: With dark scales, speckled with pale scales; wing membrane not clouded on crossveins r-m and m-cu; remigial setae present; upper calypter fringed with many hair-like setae; alula with a row of fringe scales; vein 1A ending well beyond base of fork of vein Cu; vein R_{2+3} shorter than R_2. *Halter*: With white scales. *Legs*: Coxae with patches of white scales; white knee-spot present on all femora; femora, tibiae and tarsomere 1 speckled with pale scales; foreleg (right side) with basal white bands on tarsomeres 1–3 (tarsomeres 4 and 5 missing); (left side) with basal white band on tarsomere 1 (tarsomeres 2–5 are missing); midleg (right side) missing. (left side) with basal white bands on tarsomeres 1–4; hindtarsus with basal white band on tarsomeres 1–5, ratio of length of white band on dorsal surface to total length of tarsomere 0.12–0.13, 0.25, 0.25, 0.33 and 0.50, respectively; midleg with tarsal claws equal, both toothed; hindleg with tarsal claws equal, both simple. *Abdomen*: Tergum I with large median patch of white scales, and white scales on laterotergite; terga II–VI each with basal white band and sub-basolateral white spots which do not connect with basal white band; terga VI–VII each with row of small white scales along posterior border; tergum VII with basal median patch of white scales; segment VIII completely retracted; cerci long.

The description below is based on a topotypical specimen from Aldabra, Takamaka, in the BMNH: male, with three printed data labels: (1) "At light", (2) "ALDABRA: South Island, Takamaka Pool, 1–17.ii. 1968, B. Cogan & A. Hutson", (3) "Aldabra Atoll, Royal Society Expedition, 1967-68. B.M. 1968-333.", with associated genitalia on microscope slide (2009/1).

Male. *Genitalia* (Fig. 2): Gonocoxite rather stout, with large, distinct basal dorsomesal lobe but no apical dorsomesal lobe; basal dorsomesal lobe attached basally to mesal surface (not forming part of the tergal part of the gonocoxite as does the basal lobe in most *Ochlerotatus*), expanded portion with numerous setae; mesal membrane not reaching the apex. Claspette present, stem slender, with short, stout seta at its tip. Gonostylus short and stout, gradually narrowed to apex, with several setae on dorsal and ventral surfaces, with pair of short, stout, pointed gonostylar claws inserted under a hood (apically). Aedeagus simple, rather long, slightly broadened in middle. Paraproct with 2 or 3 blunt teeth at tip, with 6 cercal setae on each side. Tergum IX lobes prominent, strongly developed, with 8 or 9 slender setae on dorsal and ventral surfaces; sternum IX short, with 7 setae.

Type data. *Culicelsa fryeri* Theobald, syntype female (*Culicelsa fryeri* type female of Theobald (handwritten)/Aldabra Takamaka J.C.F. Fryer (handwritten)/ Seychelles Expd. Pres. by Committee of the Percy Sladen Trust Fund. 1911–99.), in BMNH; type locality: Aldabra Island, Takamaka, SEYCHELLES. *Aedes* (*Ochlerotatus*) *mombasaensis* Mattingly, holotype male, Kenya, Mombasa, 3.V.1916 (J.O. Shircore), in BMNH; type locality: Mombasa, KENYA. Four paratypes (2 males and 2 females): paratype male (Brit. E. Africa, Mombasa, 3.V.1916, Dr. J.O. Shircore (handwritten)/ Pres. by Imp. Bur. Ent. 1919. 140/ with genitalia on a plastic plate); paratype female (Brit. E. Africa, Mombasa, In house, 24.IV.1916, Dr. J.O. Shircore (handwritten)/ Pres. by Imp. Bur. Ent. 1919. 140)/ *Ae*. (*Ochl*) m*ombasaensis* Mattingly (handwritten)); paratype male (Gede, Kenya, March 1954, J.O. Harper/ Salt water pools, Batch 1. T. no. 4 (handwritten)/ *Ae*. (*Ochl*) *mombasaensis* Mattingly (handwritten)); paratype female (Brit. E. Africa, Magogongi Swamp, near Witu. 29 Feb. 1912, S.A. Neave/ Pres. by Ent. Res. Committee, 1912. 396/ *Ae*. (*Ochl*) *mombasaensis* Mattingly (handwritten)), all in BMNH.

Other material examined. ALDABRA: 1 male and 1 female (at light/ Aldabra: South Island, Takamaka Pool, 1–17. ii. 1968, B. Cogan & A. Hutson/ Aldabra Atoll, Royal Society Expedition, 1967–68. B.M. 1968–333)/ with associated male genitalia on slide (2009/1) and female genitalia on slide (2009/2)); 1 male and 1 female (at light/ Aldabra: South Island, Cinq Cases, 23–29. i. 1968, B. Cogan & A. Hutson/ Aldabra Atoll, Royal Society Expedition, 1967–68. B.M. 1968-333); 1 pinned male (Aldabra, S. Island, Takamaka, well, 3: X: 1966, C.A. Wright (handwritten)/ terminalia on slide (handwritten)); 1 male genitalia slide (Aldabra, South Island, Takamaka , 1–17. ii. 1968, B. Cogan & A. Hutson, B.M. 1968-333); all in BMNH.

Distribution. We examined specimens from the Seychelles (Aldabra: Takamaka, Cinq Cases) and Kenya (Mombasa, Gede, Magogongi Swamp, near Witu).

Taxonomic discussion. The adult male and female of *Ae*. *fryeri* are very similar to that of *Ae*. (*Och*.) *breedensis* Muspratt (= '*Ochlerotatus*' *breedensis* of Reinert *et al*. 2008), in having the proboscis, wing, femora, and tibiae speckled with pale scales. Males and females of *Ae*. *fryeri* can easily be distinguished from *Ae*. (*Och*.) *breedensis* and all other African *Ochlerotatus* species by the absence of subspiracular scales, and a basal white band on hindtarsomeres 1–5. The female of *Ae*. *fryeri* can be distinguished from females of *Ochlerotatus* species by having few short, fine setae on the mesal surface of the antennal pedicel.

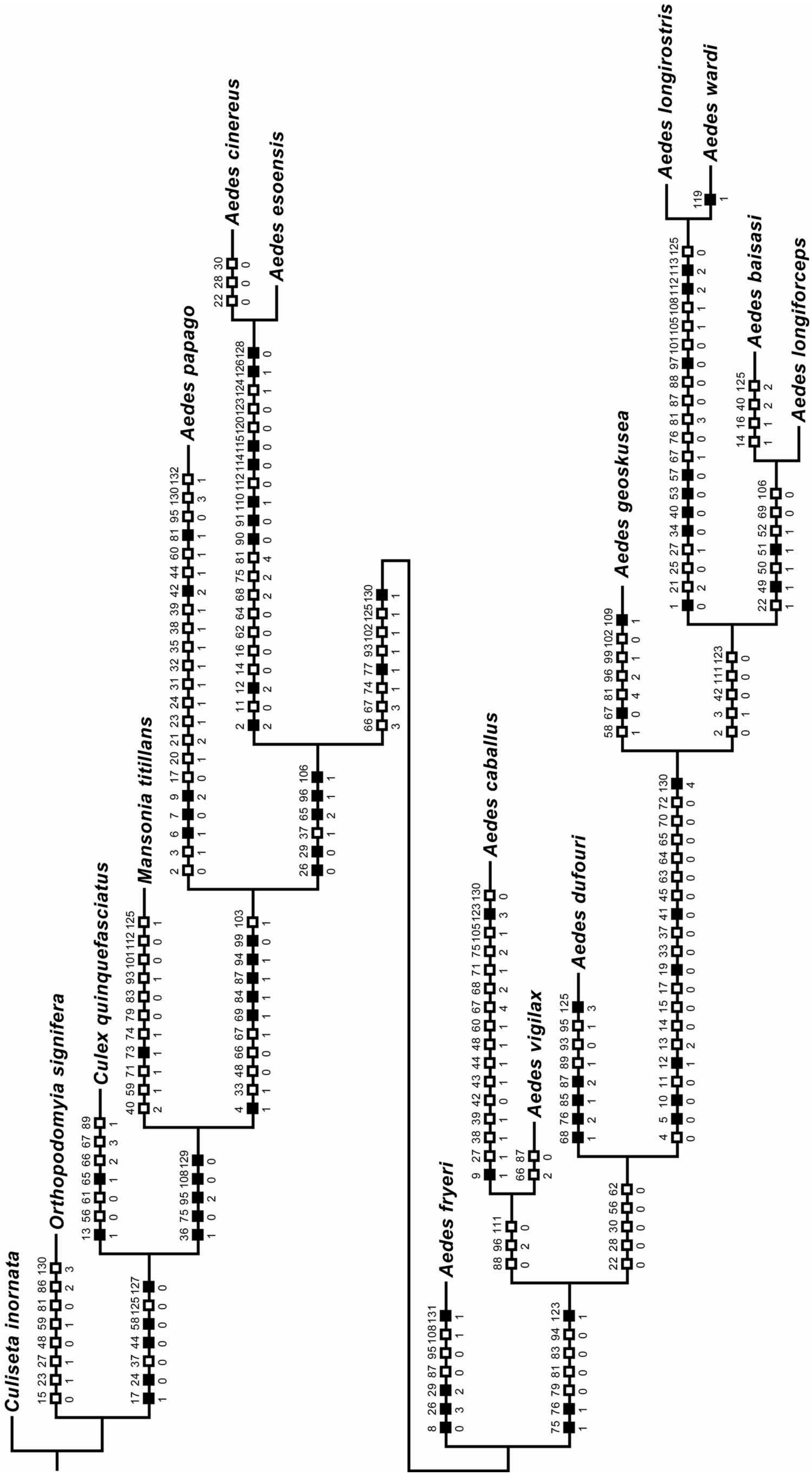

FIGURE 4. Cladogram depicting reconstructed relationships of some generic-level taxa of Aedini (954 steps, consistency index 0.70, retention index 0.79).

The maxillary palpus of *Ae*. *fryeri* male (see Fig. 1A) is slightly shorter than the proboscis, with conspicuous long setae on about the distal half, and the last two palpomeres subequal in length and with white bands at base. This condition differs from all the known species in these two subgenera, as well as from other subgenera of *Aedes*.

The male genitalia of *Ae*. *fryeri* (see Fig. 2) are strikingly different from all the known species in these two subgenera, as well as from other subgenera of *Aedes* (see the description of the male genitalia of *Ae*. *fryeri*).

Acknowledgments

We express our sincere appreciation and gratitude to the Department of Entomology, Smithsonian Institution for providing funding for the publication; to Drs. Leopoldo M. Rueda and Desmond Foley, Walter Reed Biosystematics Unit (WRBU), for critically reviewing this manuscript, and for their valuable comments. We also thank Ms. Karolyn Darrow, Scientific Illustrator, Department of Entomology, Smithsonian Institution, who helped produce the cladogram (Fig. 4).

We are most grateful to Miss Theresa M. Howard, Collection Manager, Department of Entomology, The Natural History Museum, London, England, for the loan of several types and other specimens. We also acknowledge with sincere appreciation the following: Dr. E. De Coninck and Mr. Stephane Hanot, Entomologie Section, Musee Royal d'Afrique Centrale (MRAC), Tervuren, Belgium, for the loan of *Aedes dufouri* specimens in the [MRAC/ (CMT)]; Prof. Maureen Coetzee, Vector Control Reference Unit, National Institute for Communicable Diseases (NICD), Johannesburg, South Africa, for the loan of several types and other specimens in the [NICD/ (SAIMR)]; and Dr. Leopoldo M. Rueda, (WRBU), for his kindness in bringing for us the loan specimens from Johannesburg, South Africa.

This research was performed under a Memorandum of Understanding between the Walter Reed Army Institute of Research and the Smithsonian Institution, with institutional support provided by both organizations. The material to be published reflects the views of the authors and should not be construed to represent those of the Department of the Army or the Department of Defense.

References

Amos, D.W. (1944) *Mosquito Control Training Manual*. Suva, Fiji. Times & Herald. 43 pp.

Belkin, J.N. (1962) *The mosquitoes of the South Pacific (Diptera, Culicidae)*. University California Press, Berkeley and Los Angeles. 2 vols., 608 and 412 pp.

Carpenter, J.M. (1988) Choosing among multiple equally parsimonious cladograms. *Cladistics*, 4, 291–296.

Danilov, V.N. (1981) On the mosquito fauna (Diptera: Culicidae) of the Ethiopian Zoogeographical region. I. A subgenus of the genus *Aedes* new for the region. (In Russian). *Meditsinskaya Parazitologiyai Parazitarnye Bolezni*, 50, 86–87.

Dietrich, C.H. & McKamey, S.H. (1995) Two new Neotropical treehopper genera and investigation of the phylogeny of the subfamily Membracinae (Homoptera: Membracidae). *Proceedings of the Entomological Society of Washington*, 97, 1–16.

Edwards, F.W. (1917) Notes on Culicidae, with descriptions of new species. *Bulletin of Entomological Research*, 7, 201–229.

Edwards, F.W. (1932) Diptera. Family Culicidae. *In*: Wytsman, P. (Ed.), *Genera Insectorum*. Desmet-Verteneuil, Brussels. Fascicle, 194, 258 pp., 5 pl.

Edwards, F.W. (1941) *Mosquitoes of the Ethiopian region. III. Culicine adults and pupae.* British Museum (Natural History), London. 499 pp.

Farris, J.S. (1988) Hennig86 version 1.5. Copyright J. S. Farris.

Hamon, J. (1953) Une nouvelle especie d' *Aedes* de l' Ile de la Reunion (Diptere: Culicidae). *Naturaliste Malgache* 5, 35–41.

Harbach, R.E. & Knight, K.L. (1980) *Taxonomists' glossary of mosquito anatomy.* Plexus Publishing, Inc., Marlton, New Jersey. 415 pp.

Harbach, R.E. & Knight, K.L. (1982) Corrections and additions to *taxonomists' glossary of mosquito anatomy. Mosquito Systematics* (1981), 13, 201–217.

Hopkins, G.H.E. (1952) *Mosquitoes of the Ethiopian region. I. –Larval bionomics of mosquitoes and taxonomy of culicine larvae.* 2nd Ed. with notes and addenda by P.F. Mattingly. British Museum (Natural History), London. 355 pp.

Knight, K.L. & Stone, A. (1977) *A catalog of the mosquitoes of the world (Diptera: Culicidae)*, Second edition. *Thomas Say Foundation*, *Entomological Society of America*, 6, 611 pp.

Mattingly, P.F. (1963) New and remarkable *Aedes* (Diptera: Culicidae) from Africa. *Proceedings of the Royal Entomological Society of London* (B), 32, 165–170.

McIntosh, B.M., Weinbren, M.P., Worth, C.B. & Kokernot, R.H. (1962) Isolation of viruses from mosquitoes collected at Lumbo, Mozambique. III. Isolation of Spondweni virus from *Aedes* (*Ochlerotatus*) *fryeri* (Theobald) and / or *Aedes* (*Aedimorphus*) *fowleri* (D'Emmerez de Charmoy). *American Journal of Tropical Medicine and Hygiene*, 11, 685–686.

Reinert, J.F. (2000) New classification for the composite genus *Aedes* (Diptera: Culicidae: Aedini), elevation of subgenus *Ochlerotatus* to generic rank, reclassification of the other subgenera, and notes on certain subgenera and species. *Journal of the American Mosquito Control Association*, 16, 175–188.

Reinert, J.F., Harbach, R.E. & Kitching, I.J. (2004) Phylogeny and classification of Aedini (Diptera: Culicidae) based on morphological characters of all life stages. *Zoological Journal of the Linnean Society*, 142, 289–368.

Reinert, J.F., Harbach, R.E. & Kitching, I.J. (2006) Phylogeny and classification of *Finlaya* and allied taxa (Diptera: Culicidae: Aedini) base on morphological data from all life stages. *Zoological Journal of the Linnean Society*, 148, 1–101.

Reinert, J.F., Harbach, R.E. & Kitching, I.J. (2008) Phylogeny and classification of *Ochlerotatus* and allied taxa (Diptera: Culicidae: Aedini) base on morphological data from all life stages. *Zoological Journal of the Linnean Society*, 153, 29–114.

Reinert, J.F., Harbach, R.E. & Kitching, I.J. (2009) Phylogeny and classification of tribe Aedini (Diptera: Culicidae). *Zoological Journal of the Linnean Society*, 157, 700–794.

Smith, S.M. & Corbet, P.S. (1975) Observation on the reproductive biology of *Aedes* (*Ochlerotatus*) *fryeri* (Theo.) (Diptera, Culicidae). *Bulletin of Entomological Research*, 65, 285–293.

Stone, A. & Bohart, R.M. (1944) Studies on mosquitoes from the Philippine Islands and Australasia (Diptera: Culicidae). *Proceedings of the Entomological Society of Washington*, 46, 205–225.

Theobald, F.V. (1912) No. V.– Diptera, Culicidae. *Transactions Linnean Society of London* (2), 15, 81–94.

Van Someren, E.C.C. (1972) On the status of *Aedes* (*Ochlerotatus*) *fryeri* (Theobald) and *Aedes* (*Ochlerotatus*) *mombasaensis* Mattingly. *Mosquito Systematics*, 4, 90.

Van Someren, E.C.C., Heisch, R.B. & Furlong, M. (1958) Observation on the behaviour of some mosquitoes of the Kenya coast. *Bulletin of Entomological Research*, 49, 643–660.

Van Someren, E.C.C. & Furlong, M. (1964) The biting habits of *Aedes* (*Skusea*) *pembaensis* Theo. and some other mosquitoes of Faza, Pate Island, East Africa. *Bulletin of Entomological Research*, 55, 97–124.

White, G.B. (1980) Family Culicidae, p. 114–148. *In*: Crosskey, R.W. (Ed.), *Catalogue of the Diptera of the Afrotropical Region.* British Museum (Natural History), London. 35 pp.