

A NEW SPECIES OF *CRASPEDOXANTHA* AND A REVISED PHYLOGENY FOR THE GENUS (DIPTERA: TEPHRITIDAE)

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Abstract.—*Craspedoxantha bafut*, reared from *Vernonia calvoana* and *V. adoensis*, is newly described from specimens collected in Cameroon and Nigeria. A cladistic analysis of the 10 species of *Craspedoxantha* Bezzi with *Orellia punctata* (Schrank) as an outgroup was performed using Hennig86 (c). Using the “implicit enumeration” option of Hennig86, four trees of equal length (16 steps) were calculated from which a Nelson consensus tree was then generated. Using the successive weighting technique of Hennig86 further reduced the number of trees to two, which differed only in the sequence of Afrotropical species of the *manengubae* group. A Nelson consensus tree of these two trees is the same as the second tree. All trees that were calculated, including the Nelson trees, confirmed the validity of the two previously established species groups, *marginalis* and *manengubae*.

Key Words: *Craspedoxantha*, fruit flies, phylogeny, *Vernonia*

Freidberg (1985) recently revised *Craspedoxantha* Bezzi and included a discussion of its biology and phylogeny. His phylogeny divided the genus into two species groups: the *marginalis* group, with four Afrotropical species, and the *manengubae* group, with five species, of which three are Afrotropical and two are Oriental. The character data for the phylogeny were analyzed by hand, and the topology of the published tree was based in part on intuition.

During a recent field trip to Cameroon and Nigeria, a new species of *Craspedoxantha* was reared and collected from species of *Vernonia* (Asteraceae). Its discovery provides a good opportunity to test and refine the phylogeny of the genus with the addition of more characters and by using a computer program (Hennig86 (copyrighted), see Fitzhugh 1989 for description) for calculating and analyzing trees from the character data.

Craspedoxantha bafut Freidberg and Mathis, NEW SPECIES Figs. 1–4

Diagnosis.—This species is placed unambiguously in the *manengubae* group (Freidberg 1985: 189, 202) because of its similarity to the Afrotropical congeners, *manengubae* Speiser, *yaromi* Freidberg and *vernoniae* Freidberg, of that species group. In the key to species (loc. cit.), this species runs to couplet 8, which contains *vernoniae* and *manengubae*. It differs from *vernoniae* by the yellow marginal wing band, which does not widen opposite crossvein r-m. It differs from *manengubae* by the apical blackish spot on the wing, which does not broaden in cell r4+5 and is less than ¼ as wide as the length of the apical section of vein M. The terminalia, however, are more

similar to those of *C. yaromi*, especially the aculeus (Figs. 1–2), which is only slightly more rounded and wider at the tip, the spermatheca (Fig. 3), and the epandrium (Fig. 4), which is slightly different in lateral view but indistinguishable in ventral view. *C. bafut* can otherwise be distinguished from *C. yaromi* by its larger size (length of wing: 5.5–6.5 mm versus 4.5–5 mm in *C. yaromi*), by having predominantly dark, not pale, setulae on the scutellum, by the marginal wing band not widened opposite crossvein r-m, and by the lack of yellow pattern in and around the discal cell, although a microtrichial pattern, similar to the yellow pattern usually present on the wing of *C. yaromi*, is usually present in *C. bafut*.

Description.—Fitting the generic description (Freidberg 1985), with the following details.

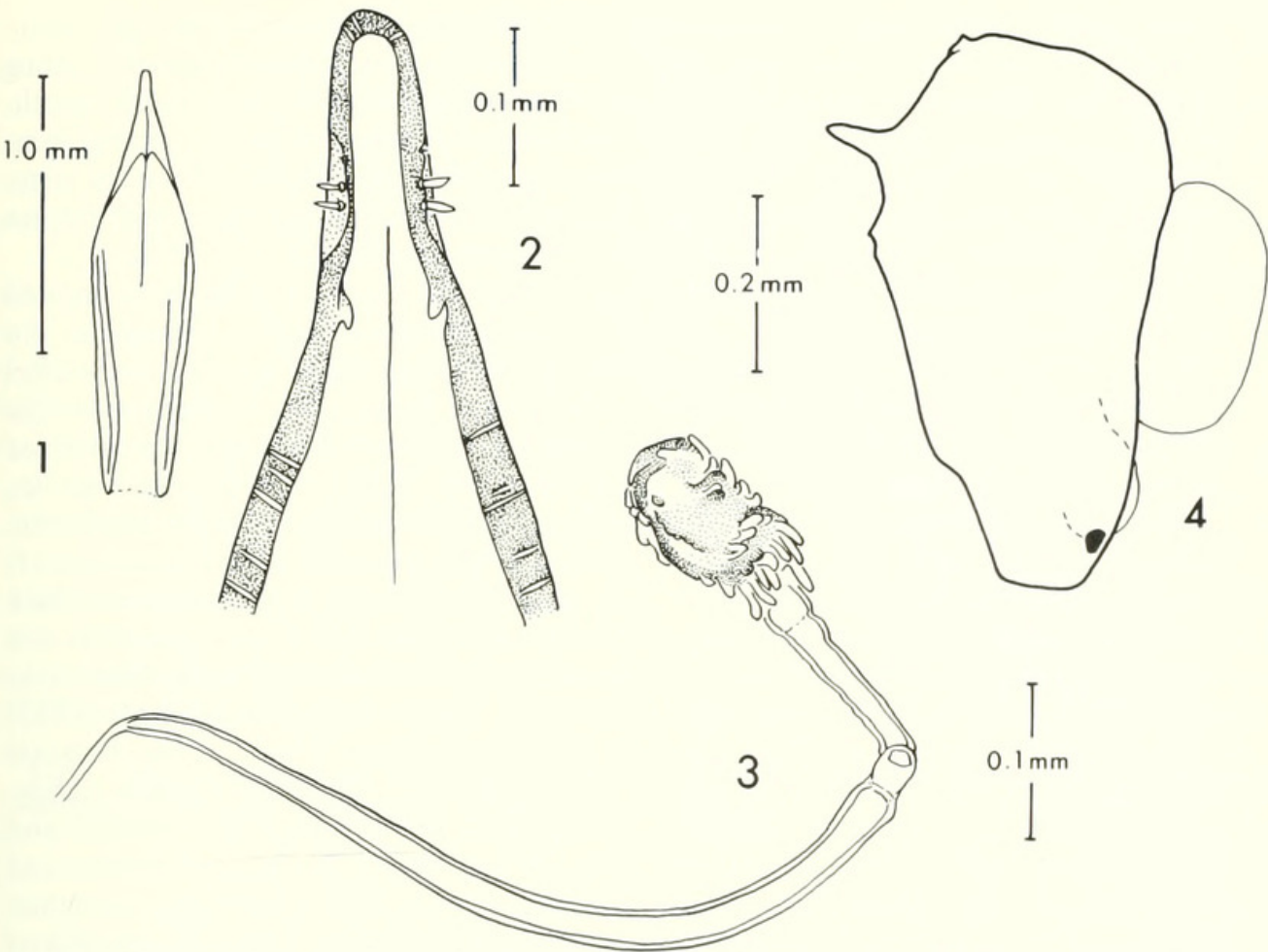
Head: Similar in shape to *C. marginalis* (Freidberg 1985, fig. 1), but with shorter 1st flagellomere, only 1.5–2 times as long as wide and 1.5 times as long as pedicel (in *C. marginalis* 2.5 times). Dull yellow, except face whitish and ventral facial margin shiny.

Thorax: Normal for genus; scutal length to width ratio = 1.1:1; dorsocentral setae aligned about midway between anterior supra-alar setae and suture; 1 anepisternal seta; dorsocentral and prescutellar black spots large; supra-alar spot and presutural spot slightly smaller than dorsocentral spot and often more elongate; scale-like setulae on scutum very dense, white or yellow, hardly extended beyond black, lyre-like pattern, which is discernable with difficulty. Scutellum unspotted, predominantly covered by blackish setulae, with yellowish setulae only near insertion of basal scutellar seta; pleura not striate; subscutellum and mediotergite brownish to blackish, densely covered by grayish-yellow microtomentum, except corners of subscutellum and ventral margin of mediotergite, which in posterior view appear less densely covered by microtomentum. Calypteres white to yellow, with or without brownish margins; halter yellow.

Legs: Yellow, elongate; femora without distinctly dense setulae ventrally. **Wing:** Length 5.5–6.5 mm; marginal band uniformly narrow, without a bump opposite crossvein r-m; apical blackish spot evenly narrow, as wide as $\frac{1}{6}$ – $\frac{1}{4}$ of terminal section of vein M; cell cup very lightly yellow; wing with microtrichial pattern in and around cell dm similar to the yellow pattern of *C. yaromi* (Freidberg 1985, fig. 13); microtrichia lacking from apical $\frac{1}{2}$ of cell br except near posterior part of crossvein r-m, from basal part of cell r4+5 except near posterior part of crossvein r-m, from cell bm and from base of cell dm; vein R4+5 with 2–8 setulae dorsally and ventrally at node.

Abdomen: Normal for genus; with predominantly yellow setulae, tergite 3 through last with 1 or few rows of brown setulae posteriorly; pattern of black spots reduced in ♂ to anterior band on tergite 5, which is microtomentose, matt, and a pair of small spots at posterior margin, and often entirely reduced in ♀, although in some ♀♀ a pair of small spots present at anterior margin of tergite 6 and at base of syntergosternite 7 (oviscape) and tip of syntergosternite 7 narrowly blackish; syntergosternite 7 about as long as combined length of posteriormost 4 tergites; ♂ terminalia as in Fig. 4; ♀ terminalia as in Figs. 1–3. The distiphallus is practically indistinguishable from that of *C. vernoniae* (Freidberg 1985, Fig. 29).

Type material.—*Holotype* ♀: “CAMEROON, Rt. N6 Bali-Batibo W. of Bamenda 20.XI.1987 A. FREIDBERG.” The allotype ♂, and four paratypes (2 ♂, 2 ♀) have the same label data as the holotype, except the collector of one ♂ is Fini Kaplan, and one ♀ is also labeled: ex. flowerhead of *Vernonia calvoana* 23 Nov 1987. Additional paratypes are as follows: CAMEROON. Northwest Province: Rt. P16 Mbengwi 25 Km W Bamenda, 23 Nov 1987, Fini Kaplan, 1 ♀; Rt. N11, Bafut 20 Km N. Bamenda, 17–24 Nov 1987, A. Freidberg, 1 ♀. NIGERIA. Plateau State: Kurra Falls, 60 Km SE Jos, 5–7 Dec 1987, A. Freidberg, 2



Figs. 1–4. *Craspedoxantha bafut*. 1, aculeus. 2, apex of aculeus. 3, spermatheca. 4, epandrium, lateral view.

♂ 2 ♀, of which 1 ♂ 2 ♀ are also labeled: ex. flowerhead of *Vernonia adoensis*, 10 Dec 1987; Keffi, Rt. 234, 4 Dec 1987, Fini Kaplan, 1 ♂. The holotype is in excellent condition, is pinned directly, and is deposited together with most paratypes in the Zoological Museum, Tel-Aviv University. Paratypes have also been deposited in the BMNH and USNM.

Biology and host plants.—All specimens were collected or reared from *Vernonia adoensis* Sch. Bip. ex Walp. or *V. calvoana* (Hook. f.) Hook. f. (Asteraceae). The specimens from Rt. N6, between Bali and Bati-bo, were collected together with numerous specimens of *C. manengubae*, a species that probably also breeds in *V. calvoana*, although this latter association has not been confirmed.

Etymology.—This species is named after Bafut, a picturesque village in the highlands of Cameroon, where this species was collected. The specific epithet is a noun in apposition.

PHYLOGENY OF *CRASPEDOXANTHA*

Freidberg (1985) briefly discussed the phylogeny of *Craspedoxantha* and noted that the genus clearly formed a monophyletic group within the tribe Terelliini. The synapomorphies that establish the monophyly of the genus are those Freidberg used to distinguish it in his key to the genera of Terelliini. With one additional character, these synapomorphies are as follows:

- 1. Eye is 1.5–2 times higher than long.
- 2. Scutum with three pairs of black spots

that are uniquely arranged as follows: at the base or immediately behind the presutural supra-alar seta and at the base of the dorsocentral and prescutellar acrostichal setae.

3. Scutellar disc with at least some blackish setulae.
4. Wing with a complete, mostly yellow costal band. The apex of the band, from vein R2+3 to slightly beyond vein M, is mostly blackish, and there are usually three, seldom two, blackish, evenly spaced spots in cell r1.

Freidberg further noted that among terelliines the closest relative of *Craspedoxantha* was probably *Orellia* Robineau-Desvoidy, especially species in the *falcata* group, which includes *punctata* (Schrank) (the type species of *Orellia*), *falcata* (Scopoli), and *distans* (Loew.) Korneev (1985) removed from *Orellia* all species except those of Freidberg's *falcata* group, thus reducing the genus to a more firmly established monophyletic group.

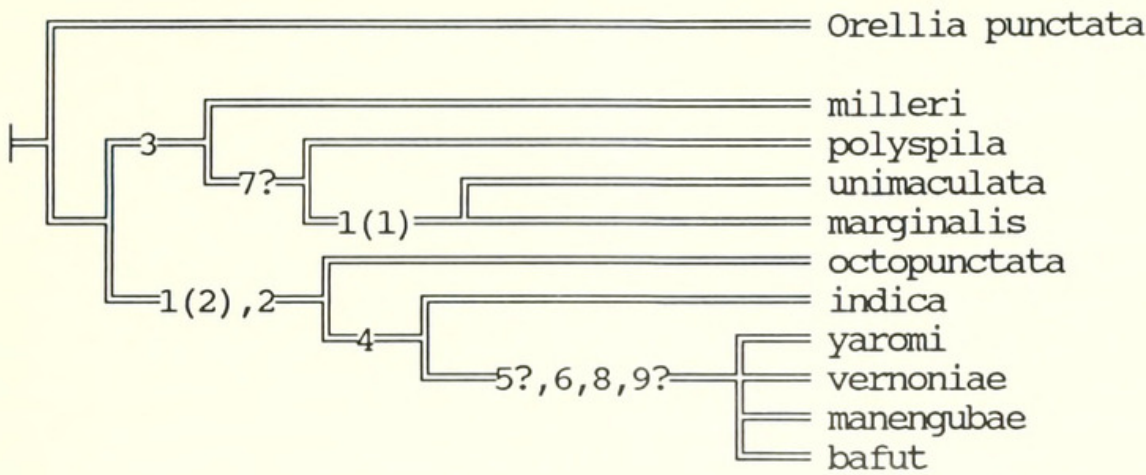
In the analysis to follow, *Orellia punctata*, the exemplar we chose to represent *Orellia*, was selected as the outgroup of *Craspedoxantha*. Although *O. punctata* appears to be a suitable candidate for this analysis, we are not completely satisfied with this selection. Our reservations derive from a lack of phylogenetic perspective on the tribe in general. Despite several recent publications on the taxonomy of the tribe (Freidberg 1985, Freidberg and Mathis 1986, Korneev 1982, 1985, 1987), very little has been reported on the phylogeny of the included taxa (e.g. Freidberg 1985). A better understanding of the phylogeny of the tribe and its six or seven currently recognized genera (seven in Freidberg (1985), six in Korneev (1987), who relegated *Cerajocera* Rondani to subgeneric status within the genus *Terellia* Robineau-Desvoidy) would have greatly facilitated the selection of an outgroup for *Craspedoxantha*. The main impediment to achieving a phylogeny for the tribe is our lack of knowl-

edge about the outgroup of the Terelliini. Terelliini is now generally thought to belong in the subfamily Tephritinae, and from other studies, we suggest that *Xyphosia* Robineau-Desvoidy could possibly be its sister group, although this and other possibilities await further study and resolution.

Despite not having a well-corroborated phylogeny from which an outgroup for *Craspedoxantha* could be selected, we feel that *Orellia* ought to be considered for the following reasons. *Orellia*, as characterized by Korneev (1985) and accepted by us, shares with *Craspedoxantha* three characters that are probably synapomorphies: (1) a generally similar arrangement of black mesonotal spots, (2) a relatively short and heavily sclerotized distiphallus that lacks elongate, distal tubes (Korneev's (1985) "paired sclerites of epiduct"—this character is also shared by *Chaetorellia* Hendel, *Chaetostomella* Hendel and some *Terellia*), and (3) the host plants of *Craspedoxantha* and *Orellia* tend to be in Asteraceae other than the tribe Cardueae, a character also shared by *Neaspilota* Osten Sacken.

Nine characters were used in the phylogenetic analysis, and most of these were illustrated previously (Freidberg 1985). In accordance with standard procedures for cladistic analysis, we ordered and polarized the characters. We then coded the characters, with the most plesiomorphic states, such as those of the outgroup, as 0, and the more apomorphic states as 1 and 2. The coding we assigned to character states is given in parentheses. For purposes of clarification, we have included, as needed, an explanation of the characters in the listing as follows:

1. Scutellum with 4 (0), 2 (1), or 0 (2) black spots.
2. Anepisternal setae numbering 2 (0), or 1 (1).
3. Femora slender and lacking dense investment of setulae (0), or swollen and densely setulose ventrally (1).



Tree length 17; Consistency Index 64; Retention Index 82

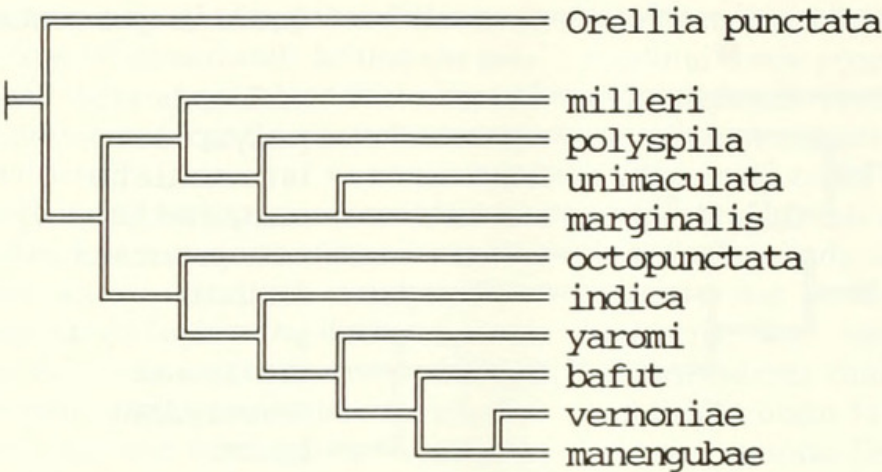
Character:	1	2	3	4	5	6	7	8	9
Steps:	3	1	1	1	2	1	3	3	2
Consistency Index:	66	100	100	100	50	100	33	66	50
Retention Index:	83	100	100	100	75	100	50	75	50

Fig. 5. Nelson consensus tree and its analysis for species of *Craspedoxantha* with *Orellia punctata* as the outgroup. A “?” denotes characters that are partially homoplasious.

4. Dorsocentral setae aligned with anterior supra-alar setae (0), or inserted more anteriorly (1).	7. Marginal band on the wing approaching (0) or not approaching (1) crossvein r-m. In some species of <i>Craspedoxantha</i> the marginal wing band is uniformly narrow and does not noticeably approach the junction of crossvein r-m and vein R4+5 (coded 1). In most other species the band has a small posterior bump that reaches or almost reaches this point. In <i>C. milleri</i> Freidberg and species of <i>Orellia</i> this bump is actually part of a transverse band. For all the latter taxa it was coded 0.
5. Cell cup distinctly (0), or indistinctly (1) yellow.	8. Posterior margin of the epandrium, the surface from which the cerci arise, in lateral view concave (0), straight (1) or convex (2).
6. Presutural black spots about as large as (0), or distinctly smaller than (1) dorsocentral spots.	9. Host plants: Host plant associations that are in part or exclusively with <i>Vernonia</i> (tribe Vernoniae) are hypothesized as the derived condition (1). We are unable to differentially treat other associations, whether they include plants of the tribe Cardueae (hosts of most Terelliini), Lac-

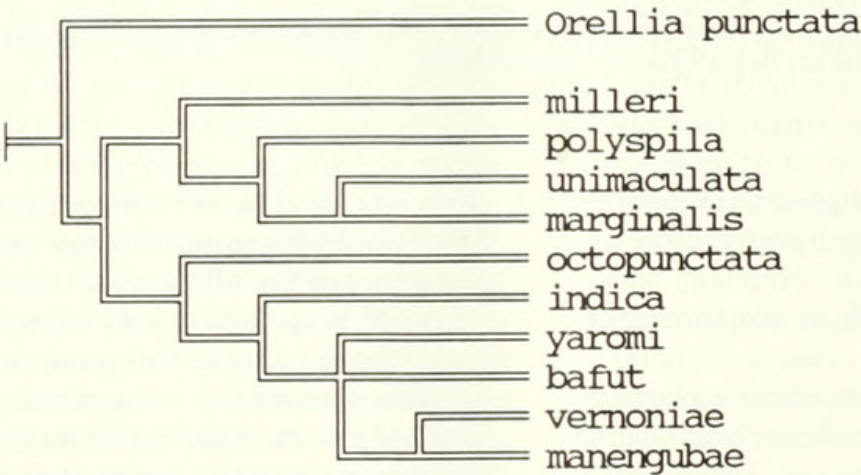
Table 1. Character matrix for *Orellia punctata* and species of *Craspedoxantha*. Missing or unavailable data are indicated by a ?.

Taxon	123456789 (Characters)
<i>Orellia punctata</i>	000000000
<i>C. unimaculata</i>	1010001??
<i>C. marginalis</i>	101000101
<i>C. milleri</i>	0010000??
<i>C. polyspila</i>	001010100
<i>C. octopunctata</i>	21000000?
<i>C. indica</i>	210100000
<i>C. yaromi</i>	210111011
<i>C. vernoniae</i>	210111021
<i>C. manengubae</i>	210111121
<i>C. bafut</i>	210111111



Tree length 88; Consistency Index 86; Retention Index 94

Character:	1	2	3	4	5	6	7	8	9
Steps:	3	1	1	1	2	1	3	2	2
Consistency Index:	66	100	100	100	50	100	33	100	50
Retention Index:	83	100	100	100	75	100	50	100	50



Tree length 88; Consistency Index 86; Retention Index 94

Character:	1	2	3	4	5	6	7	8	9
Steps:	3	1	1	1	2	1	3	2	2
Consistency Index:	66	100	100	100	50	100	33	100	50
Retention Index:	83	100	100	100	75	100	50	100	50

Figs. 6–7. Two trees calculated with the successive weighting technique and their analysis. The second Nelson consensus tree, which was calculated from these two trees, is identical with Fig. 7.

tuceae (hosts of *Orellia* species) or others and considered them all as primitive (0). Trees were calculated from the character data using the “implicit enumeration” option of Hennig86. This option generates the most parsimonious tree(s), i.e. the tree(s) of

minimal length or with fewest number of steps. Four trees of equal, minimal length (16 steps) were calculated, and a Nelson consensus tree (Fig. 5) was then generated from these four trees to demonstrate where branches and relationships are consistent (most of the lineages) or inconsistent (the

African members of the *manengubae* group). The overall consistency index for this Nelson tree is 0.64, with a "retention index" of 0.83 (formula for the "retention index" is in Fitzhugh 1989). An analysis of this tree indicates that about half of the characters (2, 3, 4 and 6) have a perfect consistency index and that the characters that are most homoplasious (as judged by the indices) are characters 5, 7 and 9. Characters 5 and 7 deal with wing pattern, a feature that is often subject to homoplasy in Tephritidae. Character 9 involves host-plant data and in addition to having some apparent homoplasy, also suffers from a lack of information for three of the species.

As more than one tree resulted from the "implicit enumeration" option, we then used the successive weighting technique (Farris 1969, Carpenter 1988) to further resolve and assist in the selection of a tree. Two trees resulted from this procedure (Figs. 6–7) and were summarized in the form of a second Nelson consensus tree (Fig. 7). The two trees differ only in the African part of the *manengubae* group, which is the clade containing *bafut*, *manengubae*, *vernoniae* and *yaromi*. Both of these trees place *manengubae* and *vernoniae* as a monophyletic group (sister species), and the other two species either form an unresolved trichotomy with this monophyletic group (Fig. 6), or have *bafut* as the sister group to *manengubae* + *vernoniae*, and *yaromi* as a sister group to the other three species (Fig. 7). The second Nelson tree was identical with the second successive weighting tree (Fig. 7). At the moment we prefer the unresolved possibility of the first Nelson consensus tree (Fig. 5) over the other trees, because we feel that the relationships between these four species are as yet unresolved.

Two characters that have not been used in the cladistic analysis, should be mentioned. The first is the superficial similarity between the wing pattern of *yaromi* and the microtrichial pattern of *bafut*, which, together with the great similarity in the ter-

minalia of both species, may indicate sister-group relationships between these species. The second is the zoogeographical pattern of the four species, with *vernoniae* and *yaromi* apparently restricted to East Africa, and *bafut* and *manengubae* apparently restricted to West Africa. This zoogeographical pattern may indicate the actual sister-group relationships between these four species, which differs from that suggested by the previous character. Although these species are very closely related and similar, at least in the adult stage, it is possible that studies of immature stages will resolve this quadrichotomy.

It is interesting to compare the Nelson trees (Figs. 5, 7) of this study (which includes *bafut* n. sp.) with Freidberg's (1985) intuitive tree. The similarity is rather striking. The two previously established species groups (*marginalis* and *manengubae*) are as clear in all trees that were calculated using Hennig86 and the composition of the groups is the same. There are, however, two discrepancies. In the *marginalis* group, *milleri* is placed by Hennig86 as a sister species to the other species of this group; whereas in the intuitive tree it is the sister species to *polyspila* Bezzi only. In the *manengubae* group, *octopunctata* is placed as a sister species to the other species of this group; whereas in the intuitive tree it is the sister species to *indica* Zaka-ur-Rab only. These discrepancies are mainly the result of previously underestimating single characters, such as the wing pattern of *milleri*, which differs markedly from other patterns of its species group, and using zoogeographical considerations that were not used in the present analysis. *C. indica* and *octopunctata* were considered sister species in the intuitive tree because, in addition to overall morphological resemblance, they are the only Oriental congeners, a fact that was given more weight than some morphological evidence.

In summary, the use of Hennig86 or similar computerized algorithms is strongly rec-

ommended mainly because of their objectivity and their ability to analyze large numbers of taxa and characters quickly. In addition, a prerequisite to using Hennig86 is the preparation of a well-documented character matrix, which undoubtedly improves the thoroughness of revisionary work.

ACKNOWLEDGMENTS

We wish to thank Fini Kaplan and Y. Zvik for collecting flies for this study, Allen L. Norrbom and Jon K. Gelhaus for critically reviewing this paper and Elaine R. S. Hodges for inking the illustrations.

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