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The male of *Tetanoptera leucodactyla* (Diptera: Sciomyzidae)

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Abstract. The male of *Tetanoptera leucodactyla* Verbèke, a genus and species of Sciomyzidae known until now only from one female specimen from the Congo, is described, and the genus is more fully characterized. The external morphology is illustrated and the male genitalia are described and figured for the first time. The relationships of *Tetanoptera* to genera of the *Sepedon* group and certain other genera of Tetanocerini are discussed. *Tetanoptera* appears to be related to *Verbekaria*, and intermediate in an evolutionary lineage between the relatively primitive *Tetanocera* and the advanced *Thecomyia*.

INTRODUCTION

The taxonomy of Sciomyzidae contributes to a phylogenetic classification that can serve as a framework for the study of the evolution of feeding behavior among mollusc-killing flies. Unfortunately, a few monotypic genera, as in most groups of insects, are known from only one or a few specimens, and from one sex. Of the 58 genera of Sciomyzidae, these mostly enigmatic genera are (distribution and known specimens in parentheses): *Ellipotaenia* Becker, 1908 (NE Tibet, 1♀); *Neodictya* Elberg, 1965 (Siberia, 1♂); *Oligolimnia* Mayer, 1953 (Morocco, 1♀); *Verbekaria* Knutson, 1968 (Tanzania, 2♀; 1♂ recently discovered but not described); and, until now *Tetanoptera* Verbèke, 1950 [Democratic Republic of Congo (formerly Zaire), 1♀]. A few other genera, e.g. *Trypetolimnia* Mayer, 1953 (Ukraine to Amur area) are represented by more material but are incompletely described and/or illustrated. Certain of these genera are especially important to include in phylogenetic and behavioral studies because of the nature of their characters, i.e., highly primitive or advanced, or because they show a peculiar mixture of characters. *Tetanoptera* is one such key genus.

In descriptions (without figures) of the genus *Tetanoptera* and species *T. leucodactyla*, Verbèke (1950: 4) commented: "Il est intéressant de retrouver au Congo Belge le genre *Tetanoptera* n. g., qui semble avoir certaines affinités avec le genre néotropical *Thecomyia* Perty", and p. 18 "Genre intermédiaire entre la sousfamille des Tetanocerinae, dont il présente l'aspect général, et la sousfamille des Sepedoninae, dont il possède la chétotaxie, et qui est particulier en outre par l'absence de bande médiane frontale et de soies postverticales [= postocellar]." "Nous estimons qu'il se rapproche davantage de la sousfamille des Tetanocerinae, mais le mâle étant inconnu, cela ne peut être établi definitivement; il devra probablement être placé dans une sousfamille ou une tribu séparée."

No additional specimens have been reported until now. Nothing is known about the biology of *Tetanoptera*. The senior author found a single male in the collection of the Institut National des Sciences Naturelles de Belgique (ISNB) during a visit in 1978. Herein we describe this unique male specimen, especially the complex characters of the genitalia, which provide a significantly more complete knowledge of the genus. With this new information and new, confirmed, or corrected information on external morphology, the genus is compared in a character matrix with other genera related to *Tetanoptera*, and we comment on its relationships.

When redescribing a genus previously known only from a single or a few specimens, we believe it is useful to follow the original description, if it is adequate, to maintain the concept of the genus and to aid the reader in comparing descriptions. Thus the genus is more completely redescribed below, following the format of Verbèke's description.

RESULTS

Genus *Tetanoptera* Verbèke, 1950

We examined the holotype female in the ISNB. Verbèke (1950: 18) stated that the "soies postverticales" (= postocellar bristles) are absent; this is an important character, showing relationships among the Sciomyzidae. These bristles are indeed absent in the female but there are inconspicuous, blackish swollen spots where these bristles normally arise. These are not sockets of bristles that have been broken off; the swollen spots in this specimen apparently represent undeveloped bristles, as the postocellar bristles *are* well developed in the male. The inner vertical bristles of the holotype female are broken off, but the sockets are clearly visible.

Head. General form and profile as *Tetanocera* Duméril, except the gena is narrower, gena to head ratio

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Fig. 1. Photo, *Tetanoptera leucodactyla*, male (scale bar = 1 mm).

1/3; frons entirely pruinose, without a median stripe extending from ocellar triangle, the latter weakly developed; lunule rather extensively exposed, equal in width to scape. A strong bristle at posteroventral corner of gena. No midfacial hairs. Antenna: shape of segments as in most *Tetanocera*; scape about same length as flagellum; arista white with short hairs, as in *Sepedon* Latreille.

Wing. Moderately broad, without maculation; dm-cu crossvein not curved.

Chaetotaxy reduced, similar to that of *Sepedon*.

Head. 1 pair of (posterior) orbital bristles; ocellar bristle microscopic, slightly longer than ocellar triangle; *postocellar bristle well developed*; inner and outer vertical bristles present, rather short.

Thorax. Prosternum with 2 pairs of bristles. Pleura essentially bare, a few prothoracic and katepisternal hairs; katatergite callus with 5 or 6 black hairs on lower part, about same size as hairs on ocellar triangle. No subalar (vallar) bristles. Two notopleural bristles, 1 supra-alar, 1 postalar, and 1 pair of strong prescutellar dorsocentral bristles. One (apical) pair of scutellar bristles. No proepisternal, postpronotal or presutural bristles; in the male, unlike the female, there are 4 small hairs on each postpronotal lobe. Mesoscutum not angulate anteriorly, mesoscutal suture incomplete. Scutellum triangular apically.

Legs. Coxae with 2 or 3 bristles on lower part, anteriorly and posteriorly; hind coxae with bristles on posterodorsal surface. Each tibia with weak dorsal preapical bristle, terminal spurs very short. Femora without ventral spinules, except on apical half of hind femur of male; no dorsal bristle on fore femur.

Abdomen. Without macrochaetae but with short, black hairs over most of surface, strongest near posterior margin. Male postabdomen at right angle to preceeding segments.

***Tetanoptera leucodactyla* Verbèke, 1950**

The species is redescribed below, following Verbèke's description, adding some characters, and indicating differences between the male and female.

Reddish-yellow species, body 7.0 mm long. Frons large, reddish-yellow pruinose, not rugose, moderately projecting, slightly enlarged anteriorly; anterior margin, including fronto-orbital spot and lateral borders, sparsely covered with black hairs. Fronto-orbital spot velvety black, large, more or less round in female, nearly square in male. Lunule exposed, shining yellow. Ocellar triangle reddish-brown in female, yellow in male. Orbital plate shining yellow, strongly tapered anteriorly and extending slightly beyond frontoorbital bristle. Occiput pruinose reddish-yellow like frons, covered with barely distinct whitish pruinosity which extends over cervix, shining yellow along margins, with very sparse black hairs or bristles over entire surface, bristles more numerous and larger posteriorly. Gena shining yellow, rather large, with stripe of silvery pruinosity along margin of eye, and extending slightly below eye. Face shining yellow, oblique below antennae, lower 1/5 perpendicular above mouth opening, with weak lateral carina along parafacial suture, and slightly pronounced median ridge in upper part. Eye round, slightly recurved along face below antenna; a few short, black hairs arising from whitish pruinosity in this area. Gena not quite as broad as 1/2 height of eye. Head subquadrangular in lateral view. Palp yellow, with row of about 7 short, strong bristles ventrally. Proboscis brownish, not unusually extended as in *Thecomyia*.

Antenna yellow, not as long as head; pedicel slightly enlarged from base toward apex, about as long as flagellum, with 8 or 9 moderately strong bristles along upper margin, apical bristle strongest; flagellum with upper margin very slightly concave, rounded apically. Arista yellow at base, rest whitish, with short, white hairs.

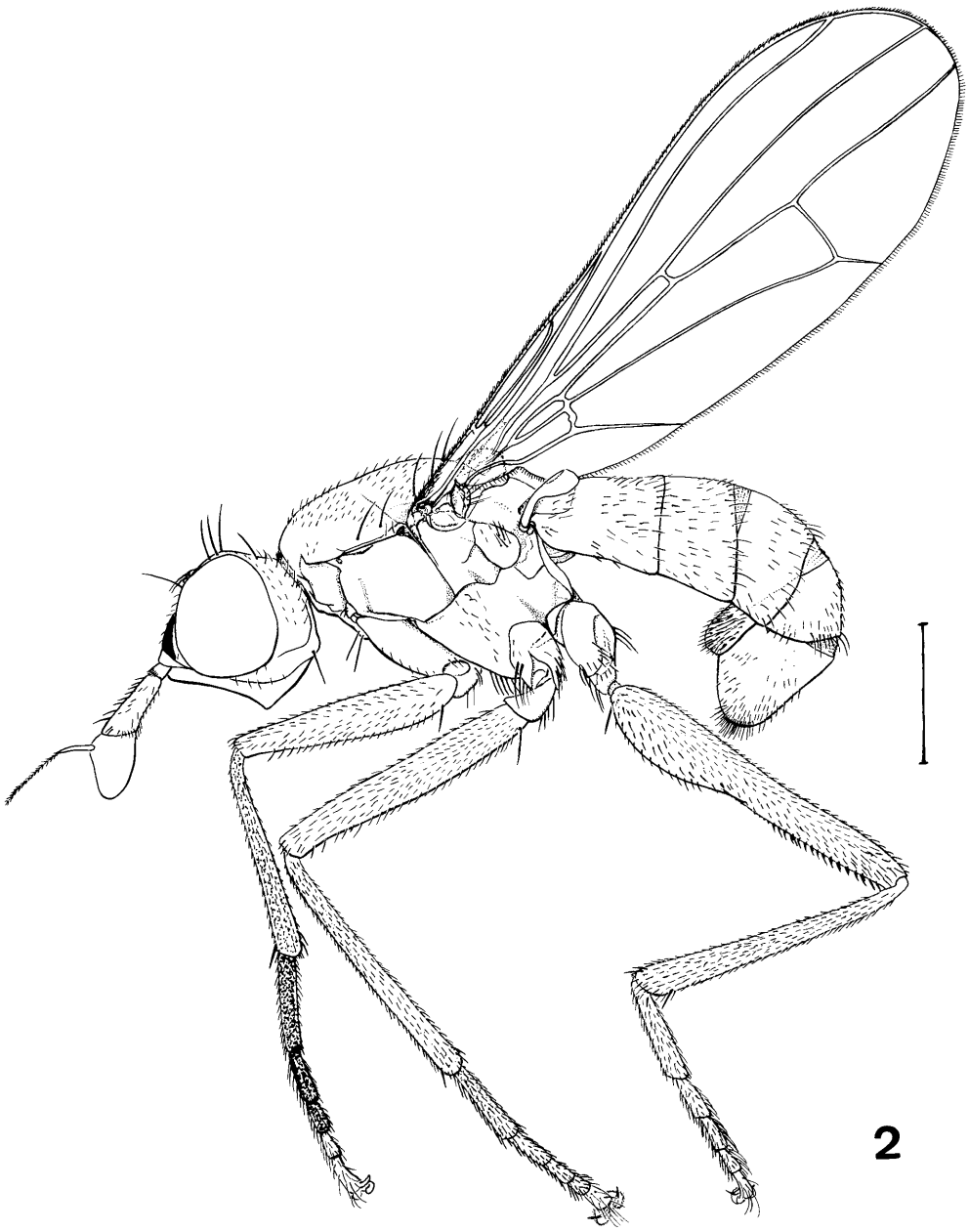
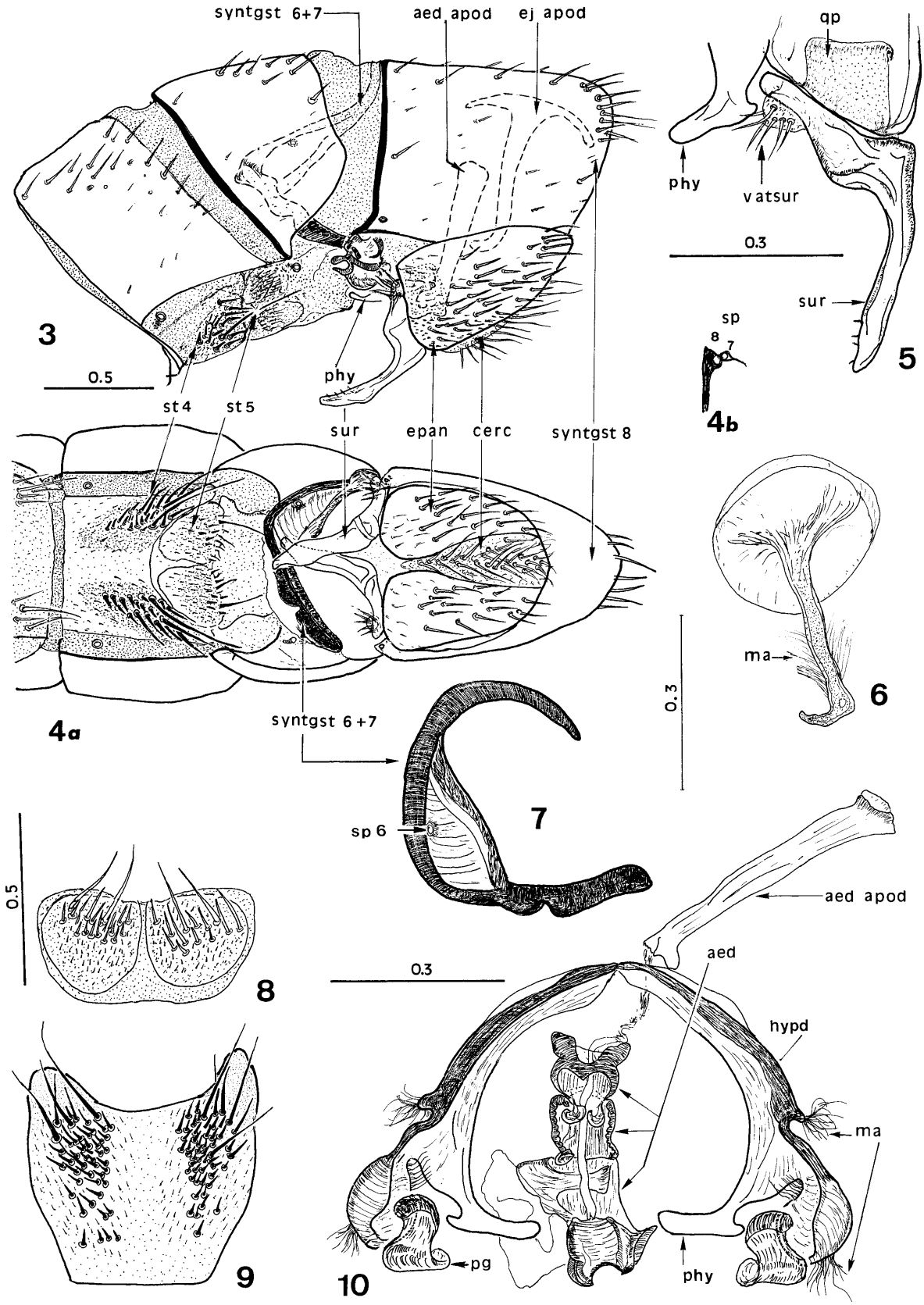


Fig. 2. Habitus, *Tetanoptera leucodactyla*, male (scale bar = 1 mm).

Dorsal surface of thorax including scutellum red-wellow, slightly shining, flattened posteriorly, with almost even distribution of short, black hairs except on narrowly bare lateral areas from behind head to supra-alar bristles; postpronotal lobe with 4 minute hairs in male, bare in female; prothorax above front coxa with a few minute hairs. Presutural part of scutum slightly shorter than postsutural part. Prosternum with pair of bristles mid laterally on each side. Pleura red-yellow, shining; lower margin of prothorax, katepisternum, and meron covered with weak silvery pruinosity. Abdomen uniformly yellow, without dark median stripe.

Coxa I yellow, II and III slightly reddish, with silvery pruinosity; femora I, II, and III yellow, with weak bristles over surface and 1 long, fine bristle ventrally at base; femur III of male slightly swollen ventrally on basal 1/3, swollen portion densely clothed with fine black hairs, with double row of stronger bristles ventrally on apical half; tibia I brown-yellow, slightly darker than tibiae II and III; tarsus I of male and female with first 3 segments black, third segment covered with silvery pruinosity, fourth and fifth pure white satin in color; segments yellow on tarsi II and III.

Wings 6.5 mm long, broad with membrane slightly but uniformly yellow and veins uniformly yellow; crossvein r-m small, situated slightly beyond middle of discal cell; crossvein dm-cu straight; cross veins not shaded. Vein R1 short of level of crossvein r-m by length of the crossvein; veins R4+5 and M parallel at apex; apical section of vein M1+2 distinctly longer than section between cross veins. Anal vein distinctly reaching margin, weaker on apical half. Alula with pale marginal hairs. Knob of haltere pale brown.



Figs 3–10. Abdomen, *Tetanoptera leucodactyla*, male. 3 – abdomen, lateral view (syntergosternum 8 shifted dorsally); 4a – abdomen, ventral view; 4b – spiracles 7 and 8, right side; 5 – surstylus, lateral view; 6 – ejaculatory apodeme; 7 – syntergosternum 6 + 7; 8 – sternum 5; 9 – sternum 4; 10 – hypandrium and aedeagus. aed – aedeagus; aed apod – aedeagal apodeme; cerc – cerci; ej apod – ejaculatory apodeme; epan – epandrium; phy – posterior process of hypandrium; hypd – hypandrium; pg – posterior gonapophysis; ma – muscle attachments; qp – quadrate plate; sp 6, 7, 8 – spiracles 6, 7, 8; st 4, st 5 – sternum 4, sternum 5; sur – surstylus (= gonostylus); syntgst 6+7 – syntergosternum 6+7; syntst 8 – syntergosternum 8; tg 5 – tergum 5; v atsur – vestige of anterior surstylus. Scales in mm; 7, 8, 9 at the same scale.

TABLE 1. Character matrix of some genera of Tetanocerini presumed to be related to *Tetanoptera*. Abbreviations: 1) Characters: ab f2 – anterior bristle on mid femur; l – long; m – moderate; 0 – none; pd br cx3 – posterodorsal bristles on hind coxae; ps dc – prescutellar dorsocentral bristles; s – short; sl – slight; st – strong; tb – thoracic bridge between hind coxae; w – white; wk – weak; ? – unknown. 2) Character states: + present; – absent. 3) Distribution: A – Australian-Oceanian; AF – Afrotropical; H – Holarctic; N – Nearctic; O – Oriental; P – Palaearctic.

	Elgiva	*Hedria*	*Oligolimnia*	*Verbekaria*	*Tetanoptera*	*Dichetophora*	*Neosepedon**	*Sepedon*	*Sepedonea*	*Sepedoninus*	*Sepedomerus*	*Sepedonella*	*Thecomyia*
midfrontal stripe	+	+	+	–	–	+	+	–	–	–	–	–	–
lunule exposed	+	+	+	+	+	+	+	+	+	+	+	+	+
palpi	+	+	+	+	+	+	+	+	+	+	+	+	–
gena/head ratio	1/2	1/2	?	1/4	1/3	1/3	1/2–1/3	1/1	1/1.5	1/4	1/1.5	1/2	1/2
pedicel/flagellum ratio	1/1	1/1	1/1	1/1	1/1	1/1	1/1.5	1/1–2/1	1/1	2/1	1.5/1	1.5/1	4/5
aristal plumosity	w-s	w-s	w-s	w-s	w-s	w-s	w-s	w-s	w-s	w-s	w-s	w-s	w-l
fronto-orbital bristles	2	2	2	1	1	1–2	0–1	0–1	1–2	0–2	1	1	0–1
ocellar bristles	st	–	+	st	wk	st	0–wk	0–wk	–	–	–	–	–
postocellar bristles	+	+	+	+	+	+	+	+	+	+	–	–	–
pd br cx3	+	–	–	+	+	wk	0–wk	–	+	wk	+	wk	–
tb cx3	–	–	?	–	–	–	–	–	–	–	–	–	+
ab f2	+	+	–	–	–	+	+	+	+	–	–	–	+/–
wing spots	wk	wk	+	+	–	+	+	–	–	–	–	–	–
dm-cu crossvein curved	+	+	–	–	–	–	sl	–	–	–	–	–	–
postpronotal bristle	+	+	+	–	–	+	+	–	–	–	–	–	–
notopleural bristles	2	2	2	2	2	2	2	1–2	2	1	2	1	1
postalar bristles	2	2	2	1	1	1–2	1–2	1	1	1	0–1wk	1	1
subalar bristles	–	+	–	–	–	+	+	+	+	+	+	+	+
supra-alar bristles	+	0–wk	1	1	1	–	–	–	+	–	–	–	–
katatergite callus setae	–	–	?	+	+	–	–	+/–	–	–	+	–	–
no. ps dc bristles	1	1–2	1	1	1	1–2	1	0–1	1	1	1	1	1
prosternum setose	+/–	–	–	–	+	–	+/–	+/–	+	–	+	–	–
cochleate vesicle	–	–	?	–	–	–	–	+/–	–	–	–	–	–
posterior surstyli fused	–	–	?	–	–	–	–	–	+	–	–	–	–
distribution	H	N	P	AF	AF	P,O,A	A	H,AF, A,O,N	N	AF	N	AF	N

* Subgenus of *Dichetophora*.

Male abdomen (Figs 3–10). Segment 1 short, fused with 2. Segments 3, 4, and 5 normal, membranes between them broad. Spiracles 4 and 5 in membrane. Sterna (st) 3, 4, and 5 weakly sclerotized along midline, lateral portions heavily setose, sterna 4 and 5 appearing as a pair of plates. Syntergosternum 6+7 (syntgst 6+7) highly modified, strongly asymmetrical, almost a complete ring, ventral end heavily sclerotized, sinistral portion somewhat sickle-shaped with pair of subequal, anterior protuberances, spiracle 6 (sp 6) at border of pigmented portion (Fig. 7). Syntergosternum 8 (syntst 8) at right angle to preceding segments, conical posteriorly, apex with many long, hairlike bristles; only 1 spiracle seen in lower left corner (Fig. 4a), 2 in lower right corner (Fig. 4b). Ventral sclerite absent. Epandrium (epan, Figs 3, 4a, 5) well developed, setose, not closed below cerci, pair of quadrate plates (= medandrium; Zatwarnicki, 1996) (qp, Fig. 5) on inner surface, attached to ventral margin. L-shaped posterior surstyli (Figs 3, 4, 5, sur) not fused; articulated with ventral margin of epandrium; small, bristled lobe at proximal end of surstylus may be a vestige of the anterior surstylus (v atsur). Cerci (cerc) not fused, bristled (Figs 3, 4a). Hypandrium (hypd) well developed, strongly sclerotized, collar-like, long posterior process (phy); muscle attachements (ma) shown in Fig. 10. A pair of massive posterior gonapophyses (pg). Aedeagal complex (aed) well developed, aedeagal filaments absent. Aedeagal apodeme (Fig. 10, aed apod) a large, straight rod. Ejaculatory apodeme (ej apod) about same length as aedeagal apodeme, dorsal end expanded, spherical, umbrella-like (Fig. 6).

The ejaculatory apodeme (Fig. 6) is highly unusual and may represent a stage in the development of the unique cochleate vesicle of Afrotropical and Oriental species of

Sepedon (*Parasepedon*) and the Afrotropical *Sepedon curvisetus* Verbèke (rudimentary stage). The proximal part (end attached to sperm duct) is rod-like, with a mass of surrounding muscles (ma) and the apex foot-shaped, the distal (free) part is broadly expanded into an umbrella-like structure. Stages leading to the development of a cochleate vesicle perhaps involved further expansion of the umbrella-like structure into a globe covering the stem, this stem eventually becoming the minute vestige of the ejaculatory apodeme seen attached to the inner surface of the closed end of the cochleate vesicle (Steyskal & Knutson, 1975, Figs 3, 5a). This apodeme varies greatly in size and shape in the Sciomyzidae, the proximal and/or distal ends may be variously enlarged, but none has the distal end greatly enlarged in the shape of an umbrella.

The female is labeled "vers Rweru (volc. Mikeno), 2,400 m, 12.VII.1934". The volcano Mikeno is south of Rutshuru, Democratic Republic of Congo. Rutshuru is situated at 1°10′ S and 29°26′ E, about halfway between Lake Edward and Lake Kivu, just east of the Rutshuru River and Kivu Park in the Democratic Republic of Congo, near the Rwanda border. The male is labeled, "Congobelge, Rutshuru, V, 1937, J. Ghesquiere, R. Mus. Hist. Nat. Belg. I. G. 10.482." "L. Knutson det. 1978 *Tetanoptera leucodactyla* Verbèke, compared with type".

DISCUSSION

All authors have placed *Sepedon* and related genera in the Tetanocerini or equivalent Tetanocerinae except Acloque (1897) in his Sepedonini; Cresson (1920) in his Sepedontini of his subfamily Euthycerinae (= modern Tetanocerini) (including *Sepedon*, *Thecomyia* and *Dichetophora*); Malloch (1928) in Sepedonini (including the same 3 genera); and Verbèke (1950 and subsequently) in his Sepedoninae (including *Sepedon*, his new genera *Sepedoninus*, *Sepedomyia*, and *Sepedonella*, but not *Dichetophora* and *Thecomyia*). Also Hennig (1965), in describing the fossil *Sepedonites baltica*, analysed the subfamily and tribe classifications of Steyskal (1965) and Verbèke (1950) in detail and recognized Sepedoninae Verbèke as a subfamily and monophyletic group.

A cladistic analysis of 50 of the 58 genera of Sciomyzidae has recently been prepared by Marinoni and Mathis (Marinoni, 1996; Marinoni & Mathis, in prep.), but *Tetanoptera* was not included. They confirmed the monophyly of the family Sciomyzidae and two subfamilies, Salticellinae and Sciomyzinae, the latter with 2 monophyletic tribes, Sciomyzini and Tetanocerini. They confirmed the monophyly of Steyskal's (1973) *Sepedon* group (*Thecomyia*, *Sepedon*, *Sepedonella*, *Sepedoninus*, *Sepedomerus* and *Sepedonea*) but with the addition of the genera *Ethiolimnia* and *Teutonomyia*, placed it in the Tetanocerini, and noted it "is the most corroborated lineage within this analysis". In defining the *Sepedon* group, Steyskal (1973) stated: "The African genus *Tetanoptera* Verbèke (1950: 18) was placed by its author in the Tetanocerinae rather than in the Sepedoninae, but with the statement that it is intermediate between these two groups. The genus is based on a single female specimen. When a male is available, I believe the genus will be found synonymous with *Sepedon*." Miller (1995, p. 198) agreed, noting "...it is most likely that when a male becomes available by association or further collecting, the genus will be found to be synonymous with *Sepedon*, particularly since *S. testacea* Loew has two notopleural bristles likewise. The absence of postocellars in the type must be checked very closely".

As noted above, the postocellar bristles are well developed in the male of *T. leucodactyla*. We do not place critical, generic-level importance on the presence of two notopleural bristles. Although Verbèke (1950) stated that *Tetanoptera* appears to have certain affinities with *Thecomyia* the genera are abundantly distinct. In many characters, *Tetanoptera* is most similar to *Verbekaria* as shown in Table 1. Primarily on the basis of characters of the male postabdomen, we believe that *Tetanoptera* should be maintained as a distinct genus.

The genera included in Table 1 are those placed in the *Sepedon* group by Steyskal (1973) and other genera considered by various authors as related to the *Sepedon* group. The characters in Table 1 are those traditionally found important in defining genera of Tetanocerini. For the genus *Oligolimnia*, we used characters mentioned by Mayer in his original description of the unique female specimen (still the only specimen known) and by Rozkošný (1987) who examined this specimen. For the genus and species *Verbekaria punctipennis* Knutson, 1968, described from two females, Table 1 includes information on the undescribed male recently found in the Museum of Zoology, University of Bergen, Norway, by L. Greve.

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REFERENCES

ACLOQUE A. 1897: *Faune de France, contenant la description des espèces indigènes disposées en tableau analytique et illustrée de figures représentant les type caracteristique des genres. Vol. 2. Orthoptères, etc.* J.-B. Baillière, Paris, 516 pp., 1235 figs.

CRESSON E.T. JR. 1920: A revision of the nearctic Sciomyzidae (Diptera, Acalyptratae). *Trans. Am. Entomol. Soc.* **46**: 27–89.

ELBERG K.J. 1965: New palaearctic genera and species of flies of the family Sciomyzidae (Diptera, Acalyptrarta). *Entomol. Obozr.* **44**: 189–196. (English transl. In *Entomol. Rev.* **44**: 104–109.

HENNIG W. 1965: Die Acalyptratae des baltischen Bernsteins. *Stuttg. Beitr. Naturkd.* No. 145, 212 pp.

KNUTSON L.V. 1968: A new genus and species of Sciomyzidae from Tanzania, with a key to the genera of the Ethiopian region and distributional notes (Diptera: Acalyptratae). *J. Entomol. Soc. Sth. Afr.* **31**: 175–180.

MALLOCH J.R. 1928: Notes on Australian Diptera, No. XV. *Proc. Linn. Soc. N. S. W.* **53**: 319–335.

MARINONI L. 1996: Cladistic analysis of Sciomyzidae Fallén 1820 (Diptera). *Proc. XXth Int. Congr. Entomol., Firenze, Italy. August 25–31, 1996,* p. 64 (abstract).

MARINONI L. & MATHIS W.N. (in press): A cladistic analysis of Sciomyzidae Fallén (Diptera). *Proc. Biol. Soc. Wash.*

MAYER H. 1953: Beiträge zur Kenntnis der Sciomyzidae (Diptera Musc. acalyptr.). *Ann. Nat. Mus. Wien* **59**: 202–219.

MILLER R.M. 1995: Key to genera of Afrotropical Sciomyzidae (Diptera: Acalyptratae) with new records, synonymies and biological notes. *Ann. Natal Mus.* **36**: 189–201.

ROZKOŠNÝ R. 1987: A review of the Palaearctic Sciomyzidae (Diptera). *Folia Fac. Sci. Nat. Univ. Purk. Brun. (Biology) (Brno)* **86**: 1–101.

STEYSKAL G.C. 1965: The subfamilies of Sciomyzidae of the world (Diptera: Acalyptratae). *Ann. Entomol. Soc. Am.* **58**: 593–594.

STEYSKAL G.C. 1973: A new classification of the Sepedon group of the family Sciomyzidae (Diptera) with two new genera. *Entom. News* **84**: 143–146.

STEYSKAL G.C. & KNUTSON L.V. 1975: The cochleate, a highly specialized device for sperm transfer in male sciomyzid flies. *Ann. Entomol. Soc. Am.* **68**: 367–370.

VERBÈKE J. 1950: Sciomyzidae (Diptera Cyclorrhapha). *Exploration du Parc National Albert, Mission G.F. de. Witte, (1933–1935). Fascicule 66.* M. Hayez, Bruxelles, 97 pp.

ZATWARNICKI T. 1996: A new reconstruction of origin of eremoneuran hypopygium and its implications for classification (Insecta: Diptera). *Genus* **7**: 103–175.

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