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Seven new montane species of *Drosophila* in the Eastern Arc mountains and Mt Kilimanjaro in Tanzania attesting to past connections between eastern and western African mountains (Diptera: Drosophilidae)

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Key words. *Drosophila*, new species, new species complexes, biogeography, Eastern Arc mountains, Kilimanjaro, Tanzania, connections with Cameroon highlands.

Abstract. This report describes 7 new species of *Drosophila* found in the Eastern Arc mountains and on Mount Kilimanjaro in Tanzania: *D. baucipyga*, *D. gata*, *D. kilimanjarica*, *D. neogata*, *D. paragata*, *D. pilocornuta* and *D. usambarensis* spp.n. Two new species complexes, the *megapyga* species complex (*Sophophora* subgenus, *melanogaster* group, *montium* subgroup) and the *gata* species complex (*Drosophila* subgenus) are introduced. Only one species, *D. baucipyga* of the *montium* subgroup, has a geographical range matching the whole Eastern Arc, from the Usambara Mts. in the north-east of Tanzania to Mt. Uzungwa in the south-south west of the country. Five others, including one representative of the *dentissima* group of the *Sophophora* subgenus, *D. usambarensis*, and four representatives of the *Drosophila* subgenus, *D. gata*, *D. neogata*, *D. paragata* and *D. pilocornuta*, were found only in the Usambara Mts. Two of these five, *D. usambarensis* and *D. pilocornuta* were found only in West-Usambara, while two other related species, *D. gata* and *D. paragata*, were found only in East-Usambara. Only the distribution of *D. neogata* covers the whole of the Usambara mountains. Outside the Eastern Arc, another representative of the *dentissima* group, *D. kilimanjarica*, was found only on Mount Kilimanjaro. This new, highly specific, montane fauna of *Drosophila* further contributes to the unique biological diversity of the Eastern Arc Mts. The biogeographic affinities of the new taxa suggest past connections with the Virunga and Ruwenzori ranges and further west with the Cameroon Volcanic Line. It indicates, in particular, that the Eastern Arc forests have passed through a succession of coalescence and fragmentation events.

INTRODUCTION

The Eastern Arc mountain forests of Tanzania in East Africa is a range of fragmented residual submontane rainforests extending from the Indian Ocean coast at the north-easternmost border with Kenya to the northern shore of Lake Malawi. Miocene uplift of the central African plateau separated these coastal and montane forests from the main Guineo-Congolian forest of west and central Africa. Since then, the remarkable stability of the Indian Ocean currents that brought moisture to the tropical East African coast maintained, in the region, high rainfall throughout the Pleistocene droughts that caused the shrinkage of the African rainforest elsewhere on the continent. As a result, patches of the former Pan-African rainforest have survived on the east African mountains (Lovett, 1993a; Griffiths, 1993; Lovett & Wasser, 1993). Unlike the vast West and Central African forests, these highly fragmented forest relics are similar to intracontinental islands associated with localised areas of high rainfall, contrasting with the surrounding arid woodland. This NE-SW mainland "archipelago" includes ancient, Tertiary, crystalline mountains, most notably Mounts Usambara, Mt Guru, Mt Uluguru and Mt Uzungwa. Unlike the Eastern Arc mountains, Mount Kilimanjaro is a far more recent, Pleistocene, volcanic mountain, probably less than 1 My old (Wilkinson et al., 1986; Griffiths, 1993).

The antiquity, isolation and fragmented nature of the eastern African forests have resulted in remarkably high levels of endemism and diversity (Lovett & Wasser, 1993). Although great emphasis has been placed on the exceptional fauna and flora, including arthropods of the Eastern Arc and Mt Kilimanjaro (Kielland, 1990; De Jong & Congdon, 1993; Hoffman, 1993; Scharff, 1993), little attention has, as yet, been paid to the fauna of Drosophilidae. Since Lovett and Wasser's (1993) volume devoted to the biogeography and ecology of the rainforests of eastern Africa, one of us (D.L.) has made two *Drosophila* field surveys in Tanzania in 1995 and 1996. They revealed that the drosophilid fauna is as rich and unique as the other faunas and floras previously reported from the region, probably because of the fragmented nature of the rainforests and their varying antiquity. This paper describes seven new montane species of *Drosophila* from Tanzania, six from the Eastern Arc forests and one from the Mt Kilimanjaro forest. Their biogeographic affinities indicate past "montane" forest corridors linking the east African mountains with the western rift, Cameroon and Guinean highlands.

Collecting localities.

East Usambara mountains, Eastern Arc mountains, Tanga region, northeastern Tanzania, Amani Forest Reserve, 450–1050m a.s.l., 25-28 February-01 March 1995 (*D. Lachaise, M. Harry, C. Kerdelhué, J.Y. Rasplus*).

West Usambara mountains, Eastern Arc mountains, Lushoto region, northeastern Tanzania, Mazumbaï Forest Reserve, 1400m a.s.l., West Usambara mountains,

Lushoto region, 15–25 March 1996 (*D. Lachaise, M. Harry, J.Y. Rasplus*).

West-Usambara, Mt Magambo, Eastern Arc mountains, Gologolo, 1950 m a.s.l., 26 March 1996 (*D. Lachaise & M. Harry*).

Uzungwa mountains National Park, Eastern Arc mountains, eastern escarpment (Mwanihana scarp forest), south-central Tanzania (between Kidatu and Ifakara), Mang'ula (Mwanihana-Mang'ula scarp forest) 05–08 March 1995 (*D. Lachaise & M. Harry*).

Mount Kilimanjaro, Marangu, northern Tanzania, Forest Reserve, 1850 m a.s.l., 3 April 1996 (*D. Lachaise & M. Harry*).

We have used the spelling Uzungwa and Kilimanjaro instead of Udzungwa and Kilimandjaro throughout this paper.

Depositories. Holotypes and paratypes are deposited in the Museum National d'Histoire Naturelle, Paris (MNHN).

Drosophila, subg. *Sophophora* Sturtevant, 1939

melanogaster group, *montium* subgroup
megapyga species complex, n.

Definition. The new *Drosophila megapyga* species complex is characterized by the following traits: two long sexual combs, one on basal (20–34 teeth) and the other on second (14–20 teeth) fore tarsomeres; cercus bearing 4–5 huge strong teeth protruding from the male terminalia, about 1/20 the body size of the male; hypandrium with a long, marked medial extention sides of which are hirsute basally as well as the inner side of the lateral extensions of the novasternum; two paramedian short, strong bristles set apically on the medial extension; anterior parameres well differentiated and easily visible through the marked depressions between the medial and lateral extensions of the novasternum; posterior parameres almost as tall as the distiphallus. The complex includes three species: *D. baucipyga* Lachaise & Chassagnard, sp. n., this work; *D. eupyga* Tsacas, 1981; *D. megapyga* Tsacas, 1981.

Drosophila baucipyga sp.n.

(Figs 1–6)

Differential diagnosis. *Drosophila baucipyga* sp.n. differs

-from *D. megapyga* and *D. eupyga* by posterior parameres "bottine" (ankle-boot)-shaped,

-from *D. megapyga* by basitarsal comb comprising 17–26 teeth instead of 28–34,

-from *D. eupyga* by a long instead of truncated medial extension of the novasternum, and anterior parameres larger instead of smaller than the lateral expansions of the novasternum.

Description. Male.

Body length. *Holotype* = 2.29 mm, *paratypes* = 2.10–2.26 mm.

Head. Frons brownish-yellow, narrow yellow band ventrally; frons width and height subequal, fw/fh = 1.1–1.2; frons width/head width (fw/hw) = 0.43–0.45; orbital plate same colour as the frons but glossy; *or*1 slightly longer than *or*3, *or*2 ca. ½ length of *or*3 and arising closer to *or*1; proclinate orbital/posterior reclinate orbital (*or*1/*or*3) = 1–1.27, anterior reclinate orbital/posterior reclinate orbital (*or*2/*or*3) = 0.4–0.54; ocellar triangle reddish. Face: glossy greyish-white; facial carina narrow, ca. 2/3 length of face, with a white stripe on the edge; arista with 4–5 dorsal and 3 ventral rays plus terminal fork; 2nd peristomal bristle as long as the vibrissa; clypeus same colour as frons; palpus with one apical seta; gena narrow and yellow; genal width in line of greatest diameter of eye/greatest diameter of eye (g/e) = 0.04.

Thorax. Scutum brownish-yellow; anterior dorsocentral setae ca. ½ length of posterior; 8 rows of acrostichal setulae. Scutellum same colour as scutum, basal and subapical scutellar setae convergent and subequal (b/a = 0.84–0.9). Pleura same colour as scutum but slightly paler; anterior/posterior katepisternal setae (a/p) = 0.55–0.58, the mid-one setula-like. Legs uniformly light yellow; two long tarsal combs, the basitarsal very long and composed of ca. 24 teeth, the second tarsal comb consisting of ca. 19 shorter, uniform and more closely set-up teeth (Fig. 1). Wing: wing length = 2.16–2.31 mm; wing width/wing length (ww/wl) = 0.40–0.43; C = costal index a/b (i.e., length ratio of first to second costal section post-subcostal break) = 2.14–2.45; C3 fringe (percents) = 40.9–47.6.

Abdomen. Glossy; tergites 2 to 5 yellow with a narrow band posteriorly, brown for the first four tergites, black for the fifth, tergite 6 entirely black.

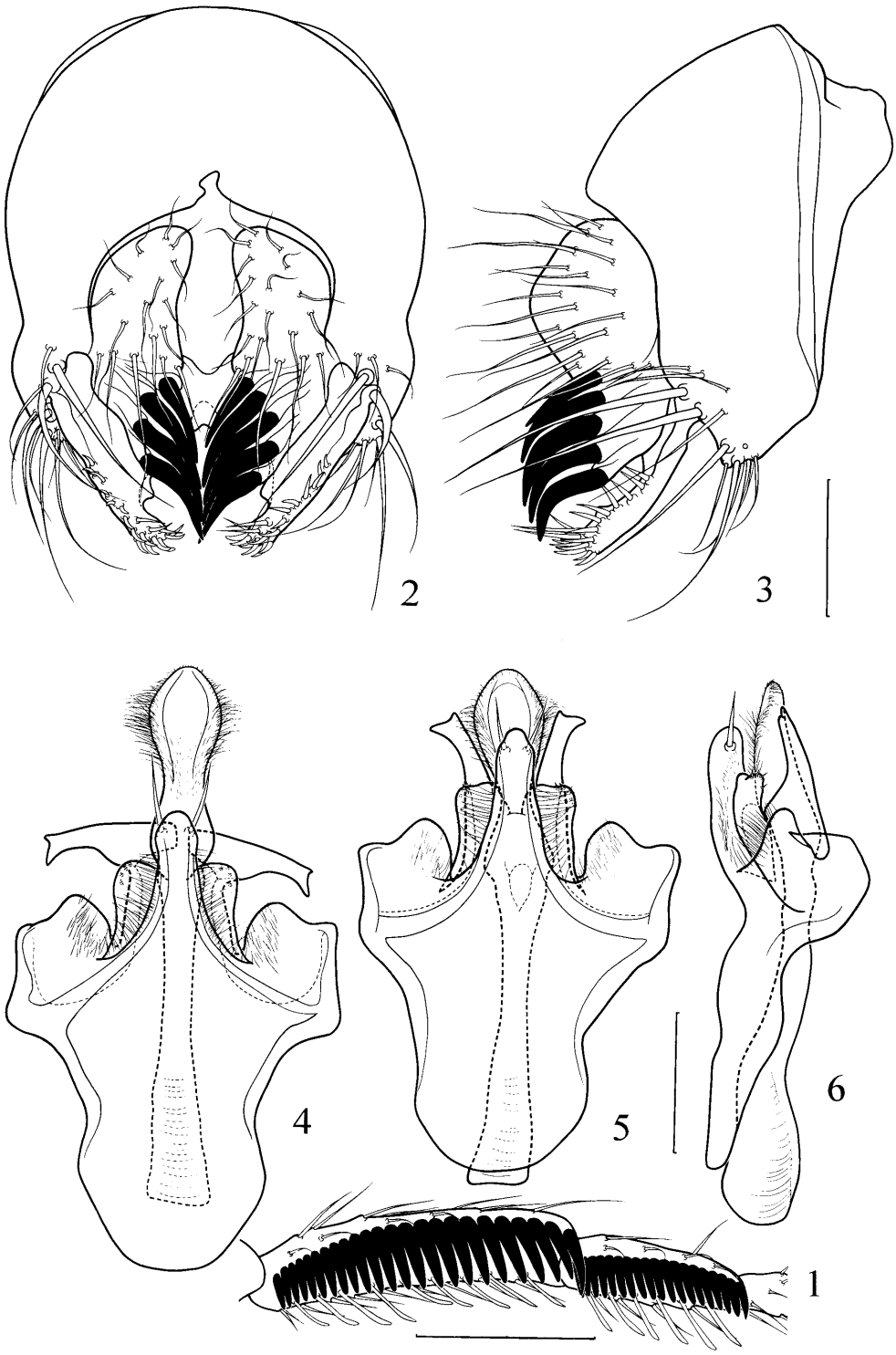
Male terminalia. Epandrium glossy black, large and bare; epandrial fragma narrow, long setae confined to the postero-ventral margin. Ventral part of cercus bearing 4–5 very large and strong teeth considerably protruding externally (ratio cercal teeth/body length: 1/20). Surstylus elongated, sharply narrowing ventrally, bearing a row of ca. 7 short setae and a cluster of ca. 10–11 short and long setae apically (Figs 2, 3). Hypandrium triangular, with a long medial extension of the novasternum, flanked by two short paramedian setae, and two hirsute lateral lobes; anterior parameres oblong and truncated, shortly spinulated postero-dorsally; posterior parameres "bottine" (ankle-boot)-shaped. Distiphallus hirsute, ca. ½ length of aedeagal apodeme (Figs 4–6).

Type material. Holotype, ♂ northeastern Tanzania: Mazumbaï, West-Usambara, on fruits of *Parinari excelsa*, 18–21.III.1996, D. Lachaise & M. Harry; Paratypes 4 ♂ *idem*; 15 ♂ northeastern Tanzania: Amani, East-Usambara, 25–28.II.1995; 1 ♂ *idem* but swept on *Ficus mucuso* figs, D. Lachaise & M. Harry; 7 ♂ Mazumbaï, West-Usambara, forest, 22.II.1995; 1 ♂ southern Tanzania: Mang'ula, Uzungwa Mountain National Park, Forest Reserve, traps by falls, 07.III.95 D. Lachaise & M. Harry (MNHN).

Other material. 22 ♂ northeastern Tanzania: Mazumbaï, West-Usambara, 18.III.1996; 118 ♂ *idem*, on fruits of *Parinari excelsa*, 19.III.1996, D. Lachaise & M. Harry; 2 ♂ northeastern Tanzania: Amani, East-Usambara, 8.III.1996, J.-Y. Rasplus & C. Kerdelhué (in absolute alcohol for DNA analysis, CNRS-Gif).

Etymology. From the Greek, βαυχις = bottine and πυγη = behind, allusion to the ankle-boot shaped posterior paramere.

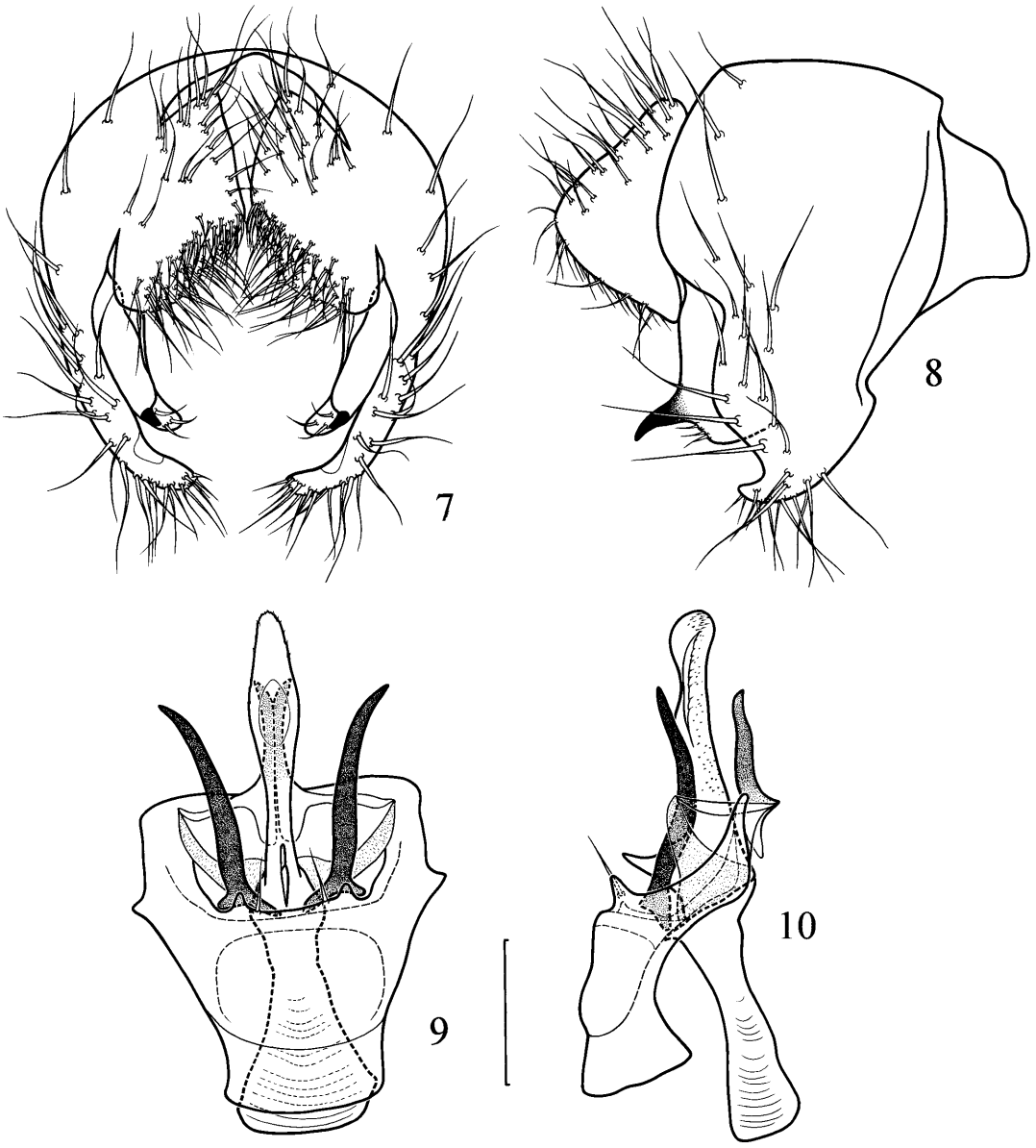
Distribution. Tanzania (Eastern Arc Mountains).



Figs 1–6. *Drosophila* (*S.*) *baucipyga* sp. n. 1– fore tarsi and sexual combs of basal and second tarsomeres; 2 – epandrium and associated structures, caudal view; 3 – *idem*, lateral view; 4 – hypandrium and associated structures, with posterior parameres down, ventral view; 5 – *idem*, posterior parameres up; 6 – *idem*, lateral view. Scale: 0.1 mm.

***dentissima* group (as revised by Tsacas, 1980)**
new species complex probable (not described here)
***Drosophila usambarensis* sp.n.**
(Figs 7–10, 12)

Differential diagnosis. *Drosophila usambarensis* sp.n. shows a new combination of traits (including: sexual comb on basal tarsomere long, sexual comb on second tarsomere slightly shorter; one long subapical oral seta, posterior parameres united but not fused, cercus fused to



Figs 7–10. *Drosophila* (*S.*) *usambarensis* sp. n. 7 – epandrium and associated structures, caudal view; 8 – *idem*, lateral view; 9 – hypandrium and associated structures, ventral view; 10 – *idem*, lateral view. Scale: 0.1 mm.

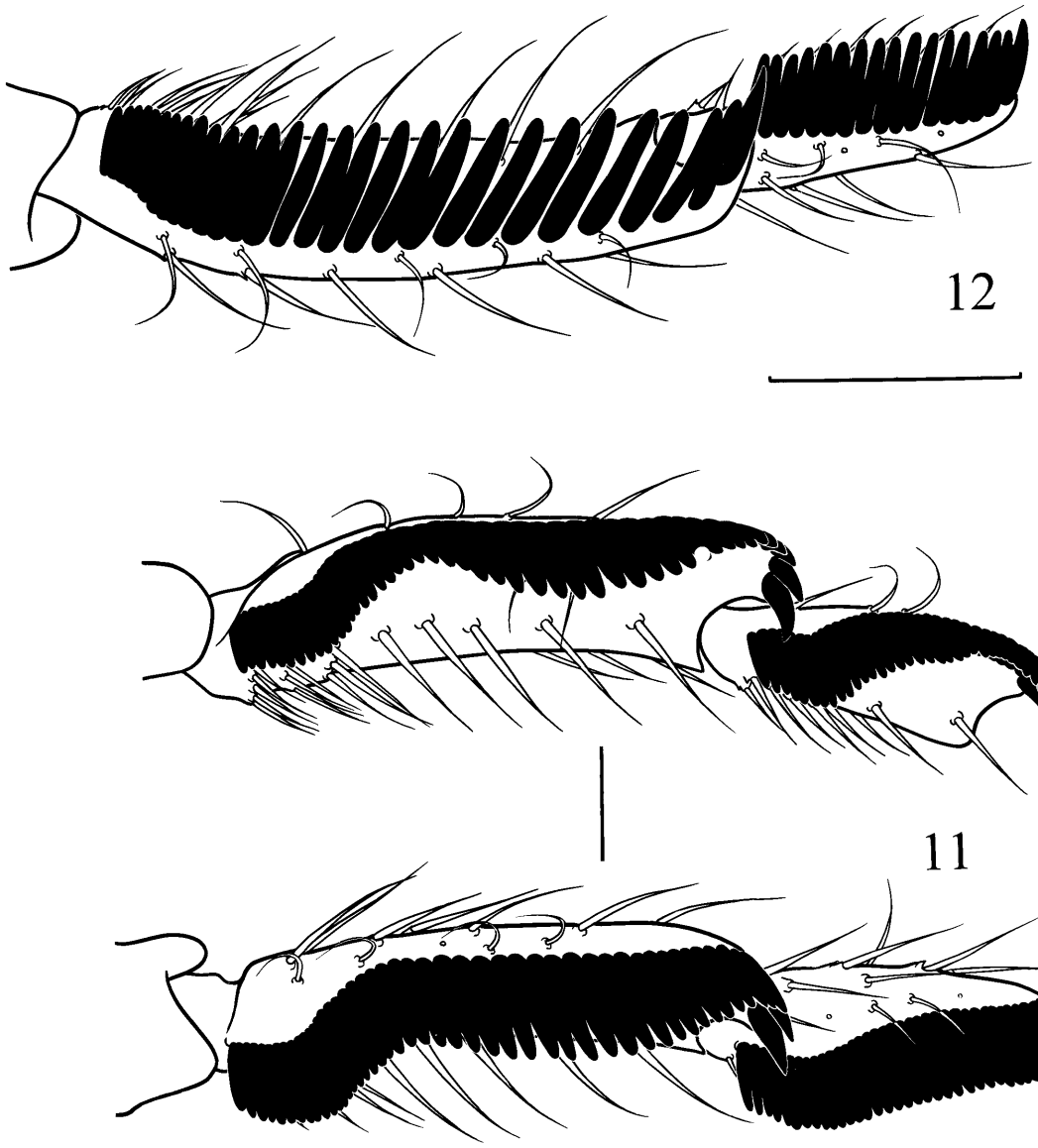
epandrium over nearly half its length), which does not fit any of the species complexes described by Tsacas (1980).

Description. Male.

Body length. 2.10–2.37 mm.

Head. Frons golden reddish; ocellar triangle and fronto-orbital plate almost same colour as anterior part of the frons, fw/fh = 1.28–1.43, fw/hw = 0.46–0.50; *or*1 and *or*3 nearly subequal, *or*1/*or*3 = 0.81–0.88, and *or*2 arising closer to *or*1, *or*2/*or*3 = 0.37–0.50, and placed as *or*3 in a markedly outer position. Face greyish white, paler than fronto-orbital plate, epistoma slightly browner than face and showing a upside down 'V'-like shape, facial carina remarkably hatchet-like, non-pedicellate above and not reaching epistoma. Antenna rusty-brown, arista with 3–4 dorsal and 2–3 ventral notably straight rays, subequal, plus terminal fork. Palpus yellowish, one long subapical oral seta; gena whitish and very narrow. Eye, g/e = 0.06–0.07.

Thorax. Scutum and scutellum same colour as frons; basal and apical scutellar setae subequal, b/a = 0.87–0.95, the former slightly convergent, the latter crossed; anterior dorsocentral setae markedly shorter than posterior ones; acrostichal setulae in about six rows. Pleura same colour as scutum but slightly paler, three major katepisternal setae, a/p = 0.55–0.60, the third (mid) one reduced to a setula. Legs same colour as pleura. Fore tarsomeres bearing two strong sexual combs, that on the basal tarsomere long, markedly incurvate, with ca. 29 teeth, the apical tarsomere with 17 teeth (Fig. 12). Wing length = 2.10–2.24 mm, ww/wl = 0.38–0.39; C = 2.3–2.5; C3 fringe = 40–45.



Figs 11–12. Fore tarsi and sexual combs of basal and second tarsomeres in two representatives of the *dentissima* species group: 11 – *Drosophila* (*S.*) *kilimanjarica* sp. n. (under two views) from Mt Kilimanjaro; 12 – *D.* (*S.*) *usambarensis* sp. n. from West-Usambara Mts. Scale: 0.1 mm.

Abdomen. T1-T4 rusty brown with a faint browner posterior fringe, T5-T6 black.

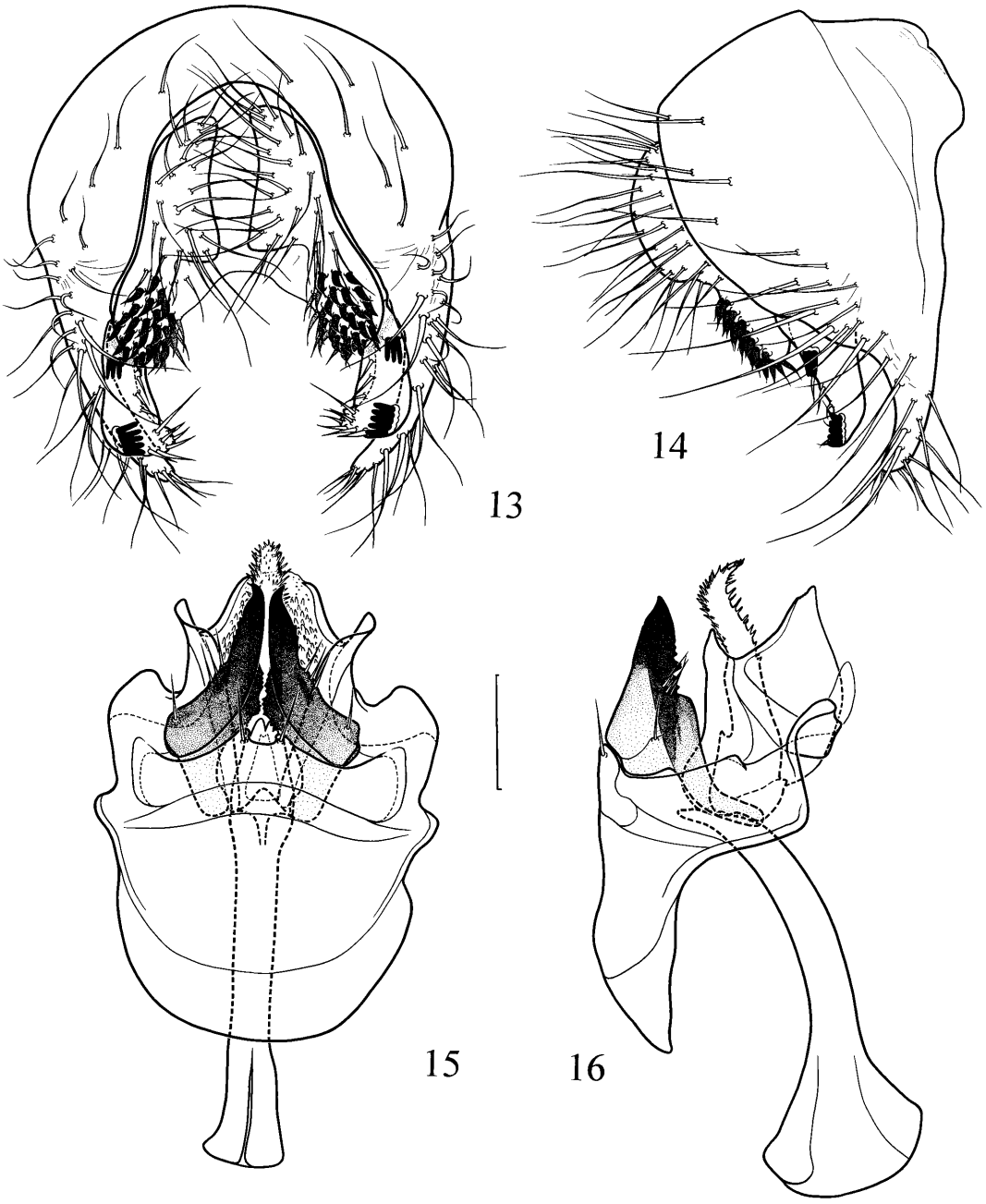
Male terminalia. Epandrium and cercus brownish black, glossy; lateral expansion of epandrium appearing narrow and finger-like in caudal view, wide dorsally and markedly narrowed in lateral view, a row of setae along the posterior edge of the epandrium; cercus short, triangular, markedly protruding posteriorly, and fused to epandrium in dorsal position, lower surface of cercus densely pilose; Surstylus finger-like in caudal view, rectangular in lateral view, bearing a strong black tooth subapically and three short apical setae (Figs 7, 8); Hypandrium with a short novasternum, considerably overtopped by distiphallus and anterior parameres, without medial indentation in between the paramedian setae; anterior parameres huge, sabre-like and dark; posterior parameres united but not fused, hidden behind aedeagus in ventral view, also sabre-like but half as long as the anterior ones; Aedeagus long, straight; slightly lozenge-shaped in ventral view, distiphallus swelling apically in lateral view; aedeagal apodeme short and wide (Figs 9, 10).

Type material. Holotype, ♂ northeastern Tanzania: West-Usambara, Mazumbaï, forest, on fruits of *Parinari excelsa*, 21.III.1996. Paratypes, 4 ♂ *idem* but on fruits of *Syzygium guineense*; West-Usambara, 16 ♂ Mt Magambo, Gologolo, 1950 m a.s.l., 26.III.1996, D. Lachaise & M. Harry (MNHN).

Other material. 34 ♂ northeastern Tanzania, West--Usambara, Mt Magambo, Gologolo, 1955m a.s.l., 25-26.III.1996, D. Lachaise & M. Harry (preserved in absolute alcohol for DNA analysis, CNRS-Gif).

Etymology. Allusion to the origin of the specimens from Mts Usambara.

Distribution. Tanzania (West Usambara in the north-east of the Eastern Arc Mountains).



Figs 13–16. *Drosophila* (*S.*) *kilimanjarica* sp. n. 13 – epandrium and associated structures, caudal view; 14 – *idem*, lateral view; 15 – hypandrium and associated structures, ventral view; 16 – *idem*, lateral view. Scale: 0.1 mm.

***altissima* complex**

***Drosophila kilimanjarica* sp.n.**

(Figs 11, 13-16)

Differential diagnosis. *Drosophila kilimanjarica* sp.n. has a combination of unique traits, including 1. sexual comb of basal tarsomere long (48 teeth); 2. two long subapical oral setae; 3. posterior parameres entirely fused; and 4. cercus not fused to epandrium. The new species can be ascribed to the *altissima* species complex, differing from other members by a more complete fusion of posterior parameres.

Description. Male.

Body length. 2.24–2.37 mm.

Head. Frons rusty yellow; ocellar triangle and fronto-orbital plate same colour as frons, fw/fh = 1.32–1.48, fw/hw = 0.46–0.49, a well marked paler band anteriorly, *or*1 hardly shorter than *or*3, *or*1/*or*3 = 0.77–0.94, and *or*2 arising closer to *or*1 and placed as *or*3 in a markedly outer position, *or*2/*or*3 = 0.32–0.42. Face darker brown than fronto-orbital plate, facial carina short, narrow, pedicellate above and not reaching epistoma. Antenna same colour as face, arista with four straight dorsal and three ventral rays, all of them subequal, except of terminal fork. Palpus paler and gena whiter than face, one long

subapical seta, gena narrowing anteriorly, two long subapical oral setae; g/e = 0.06–0.07.

Thorax. Scutum and scutellum yellowish-brown; anterior dorsocentral setae shorter than posterior ones, acrostichal setulae in about six rows; basal and apical scutellar setae subequal and convergent, b/a = 0.90–1.02. Pleura same colour as scutum; anepisternum and anepimeron brownish, katepisternum and meron yellow; two major katepisternal setae, the anterior about 2/3 the posterior seta, a/p = 0.50–0.62, the third mid one reduced to a setula. Legs same colour as katepisternum. Fore tarsomeres bearing two remarkably strong sexual combs, each of them being composed of exceptionally sinuous, inflected rows of teeth, the basal tarsomere with ca. 48 teeth, the apical tarsomere with 37 teeth, both ending in a stout tooth apically and hooking onto each other (Fig. 11). Wing length = 2.34–2.50 mm, ww/wl = 0.33–0.43, C = 2.89–3.15, C3 fringe = 35–42.

Abdomen. Predominantly dark; T6-T5 black; T4-T2 yellow with a large posterior brown band, T1 yellowish.

Male terminalia. Epandrium and cercus brownish black, glossy; cap-shaped in lateral view that is very large dorsally and tapering ventrally; a fringe of long setae along the posterior edge and the lateral expansion of the epandrium; cercus not fused to epandrium and most remarkable in being made up of two lobes separated by a deep medial indentation, the ventral lobe racket-like and bearing ca. 25 short strong teeth evenly distributed; surstylus elongated bearing a dorsal row of 3 prensisetae pointing downwards, a ventral row of 5 prensisetae pointing inwards, and a ventral inner lobe with 7 apical setae (Figs 13, 14). Hypandrium with a rectangular novasternum the height of which exceeds the width, with almost no medial indentation between the paramedian setae; anterior parameres exceptionally stout and dark, in ventral view suggesting the dorsal part of a crab claw with outer serration dorsally and inner serration medially; posterior paramere entirely fused into a high collar hirsute ventrally, very large in lateral view. Distiphallus prickly and hook-like in lateral view; aedeagal apodeme long, narrow and incurvated (Figs 15, 16).

Type material. Holotype, ♂ northern Tanzania: Mount Kilimanjaro, Marangu, Forest Reserve, 1850 m a.s.l., 3.iv.1996; Paratypes : 5 ♂ *idem*, D. Lachaise & M. Harry (MNHN).

Etymology. Allusion to the origin of the specimens from Mt Kilimanjaro.

Distribution. Tanzania (Mt Kilimanjaro).

subg. *Drosophila* Fallén, 1823

virilis section

***gata* complex, n.**

Definition. The *Drosophila gata* species complex belongs to *Drosophila* s. str. and can be arranged tentatively into the *virilis* section of the subgenus. Within the section, it shows general similarity with the Palaearctic *D. picta* Zetterstedt, 1847, as redescribed by Tsacas (1969), including more especially pleura yellowish with three brown stripes and symmetrical black spots on tergites. However, there is a more or less distinct medial line of abdominal spots in *D. picta*.

Epandrium elongated and hirsute; cercus hirsute and partially fused to epandrium at a mid dorso-ventral position of both cercus and epandrium; surstylus with 7-10 long and strong prensisetae; hypandrium short and rounded; distiphallus cornet-like evocative of a cat head in ventral view; novasternum hirsute posteriorly; with a marked paramedial indentation delineating two pairs of lobes, the inner one invaginated in the larger one and bearing one strong medial bristle; distiphallus large, with serrated "ears". Includes three species: *D.* (*D.*) *gata* Lachaise & Chassagnard, sp. n., *D.* (*D.*) *neogata* Lachaise & Chassagnard, sp. n; *D.* (*D.*) *paragata* Lachaise & Chassagnard, sp. n (this work).

***Drosophila gata* sp.n.**

(Figs 17–20)

Differential diagnosis. Species with yellowish pleura crossed by three faint diffuse brown longitudinal stripes; abdominal tergites yellowish with a brown patterning gradually fragmenting antero-posteriorly; cercus partially fused to epandrium by a narrow lateral bridge at a mid dorso-ventral position of both cercus and epandrium; Male terminalia characterized by surstylus bearing a marginal row of 7–8 large, pointed prensisetae; aedeagus short and stocky; distiphallus cornet-like evocative of a cat head in ventral view, serrated for the most part.

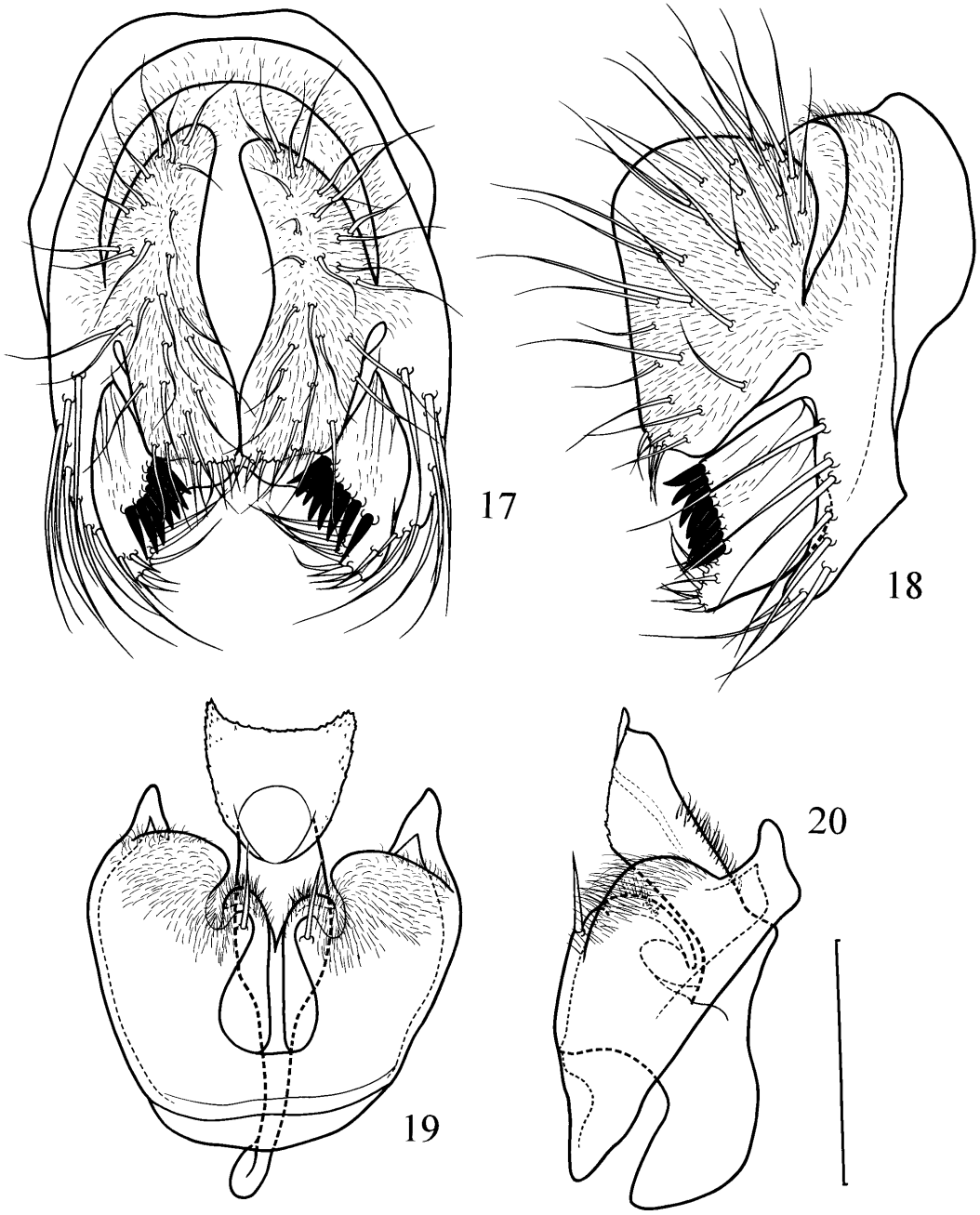
Description. Male.

Body length. 2.10 mm.

Head. Frons brownish-yellow, paler anteriorly; ocellar triangle dark, fronto-orbital plate same colour as anterior part of the frons, fw/hw = 0.45, *or*1 slightly shorter than *or*3, and *or*2 arising closer to *or*1 and placed in a markedly inner position, *or*1/*or*3 = 0.64, *or*2/*or*3 = 0.36. Face same colour as fronto-orbital plate, facial carina well-marked, flattened ventrally, pedicellate upside down but not reaching epistoma. Antenna yellowish-brown, arista with three straight dorsal and two ventral subequal rays plus terminal fork. Palpus and gena same colour as face, gena narrowing anteriorly. Eye light red, g/e = 0.13.

Thorax. Scutum and scutellum yellowish-brown, darker in between dorso-central setae and scutellar setae; basal and apical scutellar setae subequal, b/a = 0.91, the former convergent, the latter faintly convergent; anterior dorsocentral setae shorter than posterior ones; acrostichal setulae in about six rows. Pleura yellowish with three faint diffuse brown longitudinal stripes, the uppermost along the notopleural suture, the mid one across anepisternum and anepimeron, extending at the border between katatergite and anatergite and further on the base of the halter, and the lowermost stripe short, making an angle and fringing the upper katepisternum anteriorly; two major katepisternal setae, the anterior about 2/3 the posterior seta, a/p = 0.66, the third mid one reduced to a setula. Legs pale. Wing length = 2.05 mm; ww/wl = 0.4; C = 2.15; C3 fringe = 40.

Abdomen yellowish with symmetrical brown patterns separated by a yellow median band: T1 without pattern, T2 with crescent-shaped spots, T3-T5 with triangular patterns, T6 with a pair of spots, T3-T5 with additional



Figs 17–20. *Drosophila* (*D.*) *gata* sp. n. 17 – epandrium and associated structures, caudal view; 18 – *idem*, lateral view; 19 – hypandrium and associated structures, ventral view; 20 – *idem*, lateral view. Scale: 0.1 mm.

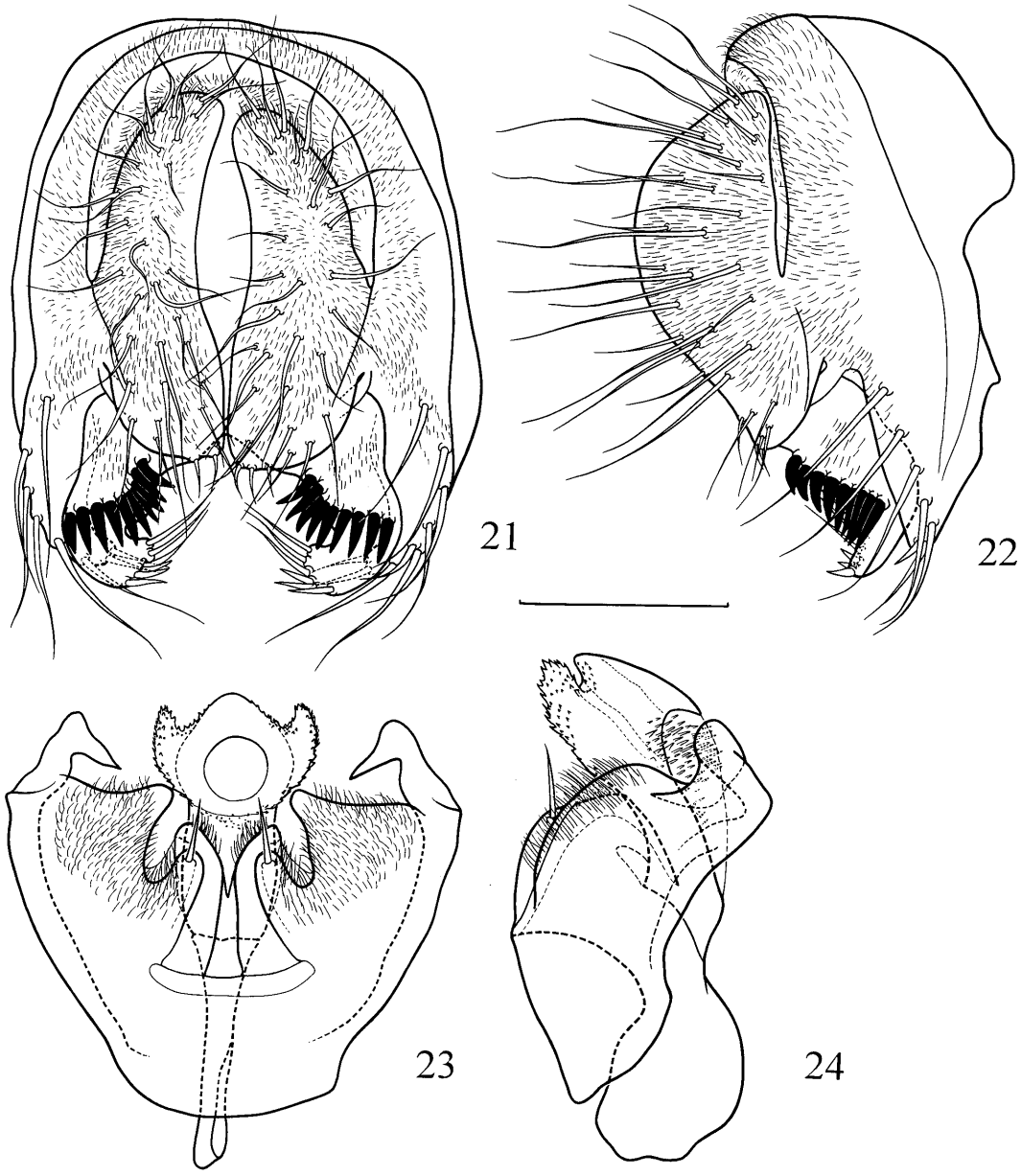
sublateral smaller spots, T2-T5 with a narrow marginal brown band fringing the lateral border of the tergites.

Male terminalia. Epandrium narrow, bearing eight long setae along the posterior edge of the lateral expansion; cercus laterally fused to epandrium by a narrow bridge, with long cercal setae becoming shorter on the ventral truncated margin; cercus and dorsal half of epandrium densely pubescent. Surstylus bearing a marginal inner row of 7–8 large, pointed, closely set up prensisetae and a ventral lobe with 8–9 apical setae (Figs 17, 18). Hypandrium short and stocky with a deep medial indentation delineating two pairs of lobes, the more medial smaller and bearing one paramedian seta each; posterior part of hypandrium and anterior parameres densely pubescent. Aedeagus short and stocky; distiphallus cornet-like evocative of a cat head in ventral view, serrated all around and spinulated mediodorsally; aedeagal apodeme short and wide, laterally flattened (Figs 19, 20).

Type material. Holotype, ♂ northeastern Tanzania: Amani rainforest, Eastern Usambara, swept above fallen figs of *Ficus mucuso*, 25.II.1995, D. Lachaise & M. Harry (MNHN).

Etymology. From modern Greek γατα = cat, allusion to the cat-like shape of distiphallus in ventral view.

Distribution. Tanzania (East-Usambara).



Figs 21–24. *Drosophila* (*D.*) *neogata* sp. n. 21 – epandrium and associated structures, caudal view; 22 – *idem*, lateral view; 23 – hypandrium and associated structures, ventral view; 24 – *idem*, lateral view. Scale: 0.1 mm.

***Drosophila neogata* sp. n.**

(Figs 21–28)

Differential diagnosis. Differs from *D. gata* by

-the three brown pleural stripes darker and more marked;

-medial indentation of hypandrium more markedly widened anteriorly, and the two lobes less rounded;

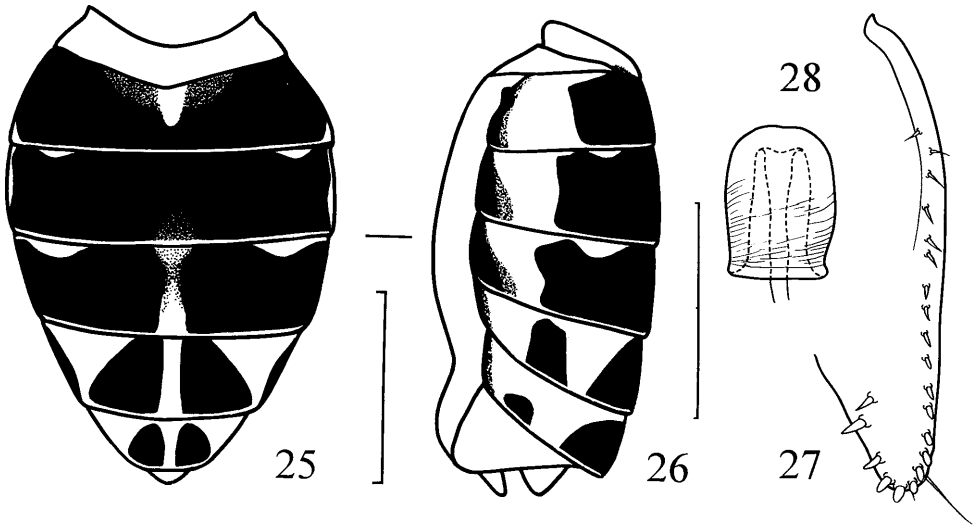
-distiphallus with two strongly serrated and denticulated dorsolateral expansions, showing in lateral view a small notch between the serrated and unserrated apical parts and with a patch of excrescences dorsally.

Description. Male.

Body length. 2.24–2.37 mm.

Head. Frons yellowish-brown, paler anteriorly, ocellar triangle dark, fronto-orbital plate greyish, fw/fh = 1.33 (♀), 1.37–1.43 (♂), fw/hw = 0.50–0.55; *or*1 slightly longer than 1/2 *or*3, *or*2 minute, arising very close to and more externally than *or*1, *or*1/*or*3 = 0.61–0.71, *or*2/*or*3 = 0.27-0.36. Face greyish yellow. Facial carina flattened, widening towards apex. Epistomal edge inflexed medially. Antenna same colour as frons but flagellomere (third antennal segment) darker, arista with three dorsal and two ventral subequal rays, plus terminal fork. Palpus with subapical seta followed by two more distal long setae; gena yellowish with straight ventral edge broadening posteriorly; eye dull red, e/g = 0.14–0.16.

Thorax. Scutum and scutellum with a variable yellowish brown colour; posterior dorsocentral setae almost twice as long as anterior ones; acrostichal setulae in about six rows, no prescutellar; scutellars damaged; pleura yellowish with three brown stripes as in *D. gata* but darker



Figs 25–28. *Drosophila* (*D.*) *neogata* sp. n. 25 – pigmentation pattern of female abdomen, dorsal view; 26 – *idem*, lateral view. Scale: 0.5 mm; 27 – ovipositor; 28 – spermatheca. Scale: 0.1 mm.

and more contrasting; two major katepisternal setae, a/p = 0.56–0.59, the third (mid) one reduced to a setula. Legs pale. Wing length = 2.24(♂)–2.42(♀), w/l = 0.40–0.42, C = 2.17–2.24, C3 fringe = 38.1–41.7.

Abdomen. Yellowish with a dark brown longitudinal dorsal band gradually breaking up along the antero-posterior axis into two spots on T4 and four spots on T5-6. T2 is also partially interrupted anteriorly; T2-6 with a dark-brown fringe laterally.

Male terminalia. Epandrium oblong, bearing 8–9 long setae along the posterior edge of the lateroventral expansion. Cercus fused to epandrium, with long cercal setae becoming shorter on the ventral edge; cercus and epandrium densely but unevenly pubescent. Surstylus bearing a characteristic wide array of 9–10 prensisetae and a strong protruding ventral lobe bearing 3 short and 3–5 longer setae apically (Figs 21, 22). Hypandrium short, with a medial indentation more markedly widened anteriorly than in *D. gata*, the two lobes less rounded than in *D. gata*. Anterior parameres pubescent, coupled to hypandrium inner edge of which is also pubescent. Aedeagus short; distiphallus with two strongly serrated and denticulated dorso-lateral expansions, showing in lateral view a small notch between the serrated and unserrated apical parts and with a patch of excrescences dorsally. Aedeagal apodeme swollen anteriorly in lateral view (Figs 23, 24).

Female.

Body length. 2.50 mm.

Thorax and abdomen. Pattern as in male (Figs 25, 26).

Ovipositor. Unspecialised, with a ventral row of short setulae turning to short blunt teeth apically and apico-dorsally (Fig. 27).

Spermatheca. Oblong, bell-shaped, with parallel sides (Fig. 28).

Type material. Holotype, ♂ northeastern Tanzania: Amani rainforest, Eastern Usambara, swept above fallen figs of *Ficus mucuso*, 25–27.II.1995, D. Lachaise & M. Harry; Paratypes : 1 ♂1 ♀ *idem*; 1 ♂ Mazumbaï, Western Usambara, swept above fallen figs of *Ficus sur*, 18–24.II. 1995, D. Lachaise & M. Harry (MNHN).

Etymology. From the modern Greek νεο = "novel", evoking the relatedness with *D. gata*.

Distribution. Tanzania (West and East-Usambara).

Drosophila paragata sp.n.

(Figs 29–32)

Differential diagnosis. Differs from *D. gata* and *D. neogata* by

-facial carina more bulbous; and

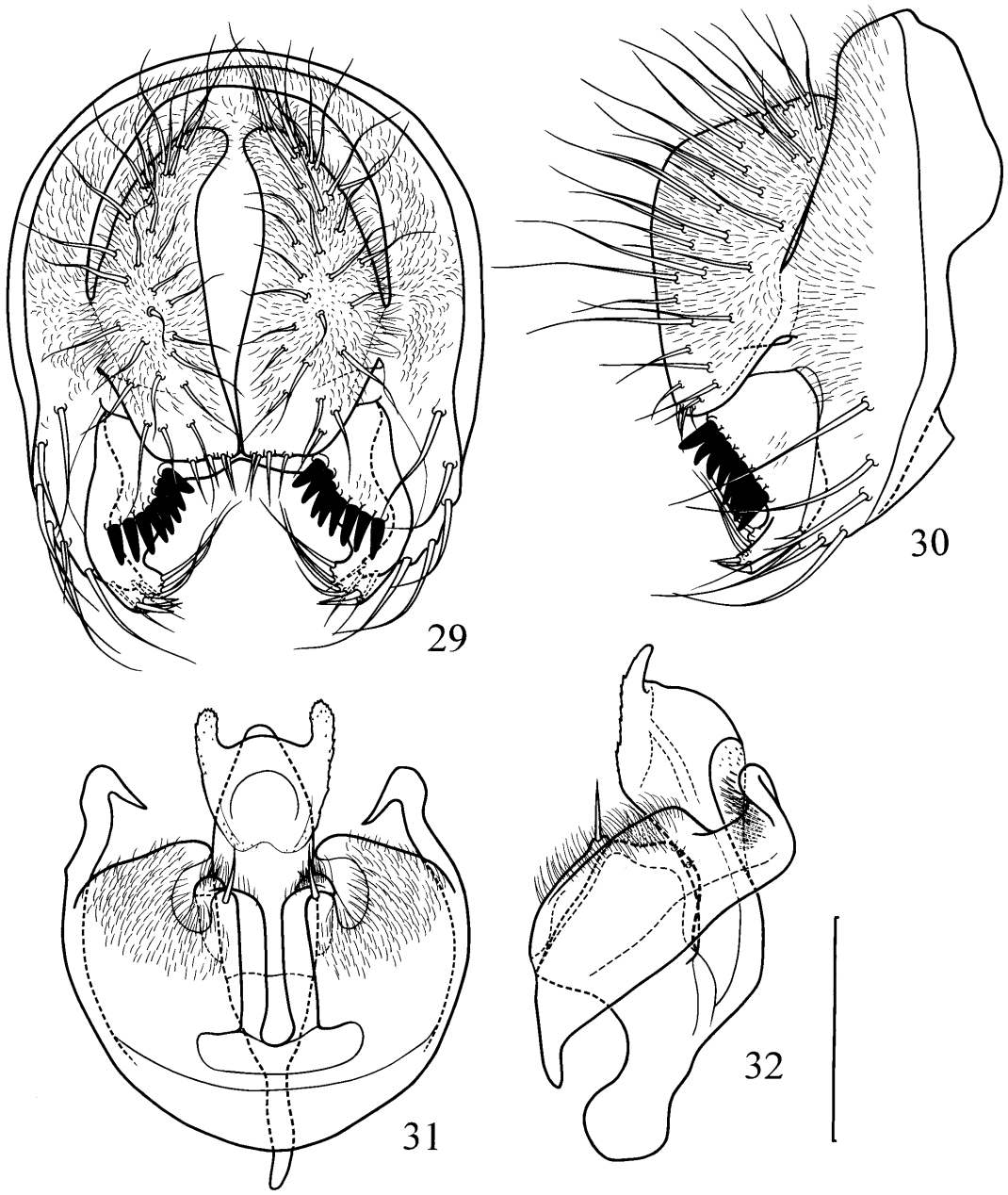
-distiphallus with two long apical expansions faintly serrated and separated from one another by a bare gently undulating border.

Description. Male.

Body length. 2.05 mm.

Head. Frons yellowish-brown, slightly paler anteriorly; ocellar triangle brownish; fronto-orbital plate not contrasting with frons, fw/fh = 1.42, fw/hw = 0.51; *or*1 significantly shorter than *or*3, *or*2 minute, close to and placed externally to *or*3, *or*1/*or*3 = 0.76, *or*2/*or*3 = 0.33. Face yellow, facial carina more bulbous than in *D. gata*, not reaching epistoma, the edge of which is inflexed medially. Antenna yellowish, left arista with 3 dorsal and 2 ventral, short and subequal straight rays plus terminal fork (right arista damaged). Palpus with one apical and one more basal setae both of medium size; gena yellow narrowing anteriorly. Eye light red, g/e = 0.03.

Thorax. Scutum and scutellum yellowish-brown with diffuse darker pattern; Anterior dorsocentral setae shorter than posterior ones; six rows of acrostichal setae; basal and apical scutellar setae convergent. Pleura yellowish, with three brown stripes very similar as in *D. gata*; two major katepisternal setae, the posterior stronger than the anterior one, a/p = 0.52, and one additional minute setula in mid position. Legs pale. Wings greyish and iridescent, wing length = 1.97, ww/wl = 0.40; C = 2.10; C3 = 36.8.



Figs 29–32. *Drosophila* (*D.*) *paragata* sp. n. 29 – epandrium and associated structures, caudal view; 30 – *idem*, lateral view; 31 – hypandrium and associated structures, ventral view; 32 – *idem*, lateral view. Scale: 0.1 mm.

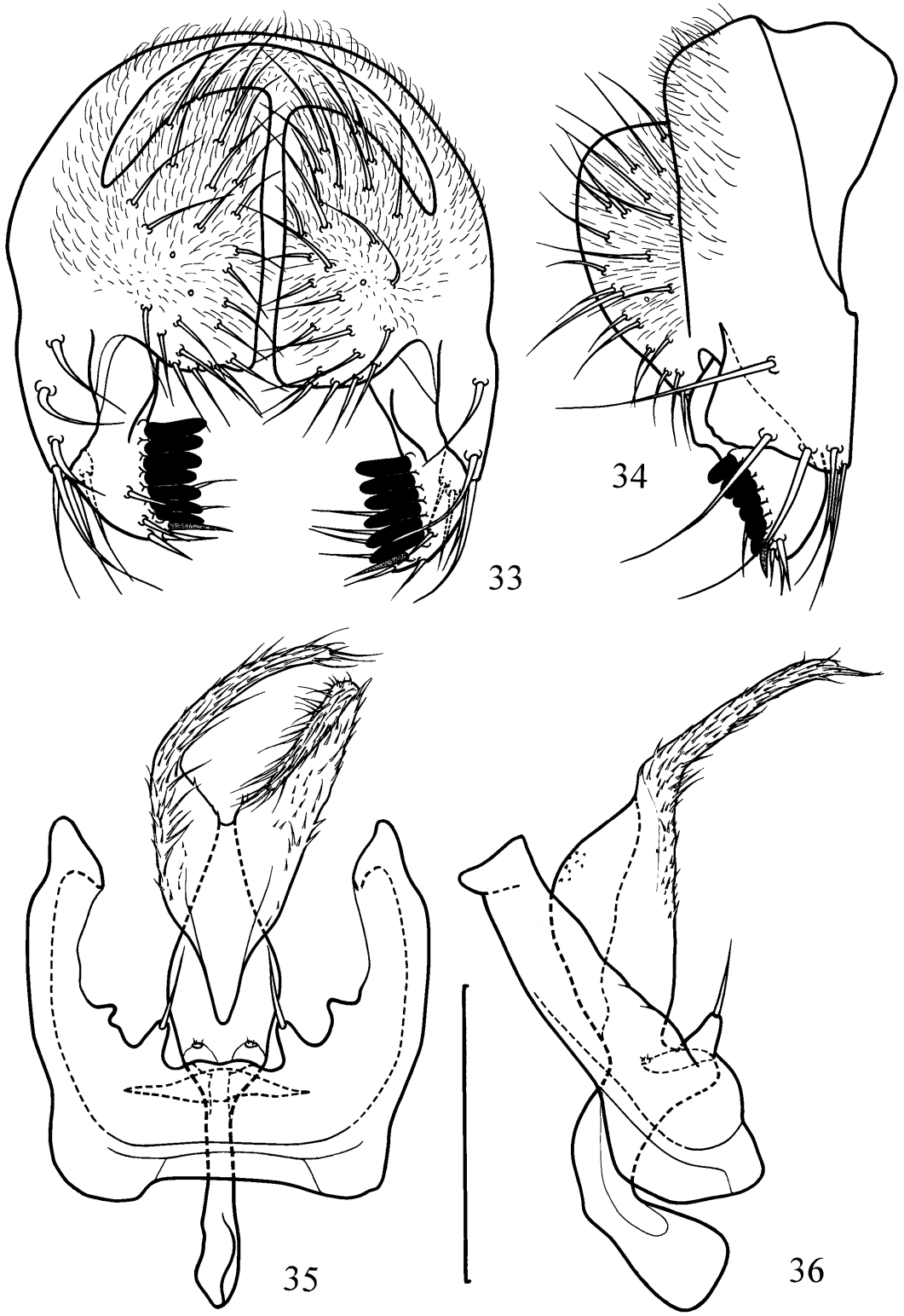
Abdomen. Yellowish with a dark brown longitudinal dorsal band interrupted in mid-dorsal line resulting in two symmetrical brownish patterns very similar to *D. gata* but paler.

Male terminalia. Epandrium oblong bearing 6 long setae along the posterior edge of the lateroventral expansion and a few shorter setae apically on this expansion. Cercus fused to epandrium, with long cercal setae becoming shorter on the ventral truncated edge. Cercus and upper part of epandrium densely pubescent. Surstylus bearing a slightly convex row of six prensisetae and a strong protruding lobe bearing 2–3 short and 3–4 longer setae apically (Figs 29, 30). Hypandrium rounded, with a notch-shaped medial indentation; the posterior margin of hypandrium protruding into two more medial lobes, pubescent, bearing one paramedian seta. Aedeagus short; distiphallus with two long apical expansions faintly serrated and separated from one another by a bare gently undulating border, a patch of excrescences can be seen dorsally in lateral view (Figs 31, 32).

Type material. Holotype, ♂ northeastern Tanzania: Amani rainforest, Eastern Usambara, 8.III.1996, J.Y. Rasplus & C. Kerdelhué (MNHN).

Etymology. From the modern Greek παρα = "close to", evoking the relatedness with *D. gata*.

Distribution. Tanzania (East-Usambara).



Figs 33–36. *Drosophila* (*D.*) *pilocornuta* sp. n. 33 – epandrium and associated structures, caudal view; 34 – *idem*, lateral view; 35 – hypandrium and associated structures, ventral view; 36 – *idem*, lateral view. Scale: 0.1 mm.

Unclassified in a species complex.
***Drosophila pilocornuta* sp.n.**
(Figs 33–36)

Differential diagnosis. Although more or less distantly related to species of the *gata* species complex, it differs by its ringed femora and the lampbrush-like projections of the distiphallus.

Description. Male.

Body length. 1.84 mm.

Head. In a poor state. Frons golden yellow; ocellar triangle brownish; fronto-orbital plate not contrasting with frons, fw/fh = 1.36, fw/hw = 0.55; *or*1 lacking, *or*3 of normal length, *or*2 lacking, close to and externally positioned relatively to *or*1. Face yellow, facial carina slightly bulbous, not reaching epistoma, the edge of which is inflexed medially. Antenna yellowish. Palpus with one large apical, one medial and one basal medium-sized seta each; gena yellow; g/e = 0.12.

Thorax. Scutum and scutellum yellowish-brown, three faint, diffuse darker longitudinal bands visible under some views: two lateral bands ending at the level of anterior dorsocentral setae, and one medial band reaching the scutellum where it divides into two larger bands. Anterior dorsocentral setae shorter than posterior ones; acrostichal setulae in six rows; basal scutellar setae almost parallel, apical ones stronger and convergent, b/a = 0.87. Pleura yellow with two faint longitudinal brownish stripes: the uppermost running step-like across upper third of anepisternum, and then across mid anepimeron, lower third of katatergite + anatergite and upper border of katepisternum; two major katepisternal setae, the anterior shorter than the posterior one (a/p = 0.52), plus a minute setula in a medial position. Legs pale yellow, mid femora with a faint apical brownish ring, hind femora with two (subbasal and subapical) brownish rings, hind tibia with a small basal brownish ring. Wings greyish and iridescent, wing length = 1.58 mm, ww/wl = 0.43; C = 2.5; C3 = 35.7.

Abdomen. Yellow with a dark brown longitudinal dorsal band interrupted in mid-dorsal line resulting in two transverse extensive spots on T2, four large triangular spots on T3, two large saddle-shaped marks on T4, and two smaller spots on T5 and T6; T1 to T4 with two small marginal brownish spots.

Male terminalia. Epandrium as wide as high with a lateral expansion square in lateral aspect bearing 5–6 long setae on the ventral edge and 1–2 others more dorsally. Cercus widely fused to epandrium, densely pubescent as well as epandrium dorsally, and uniformely covered with setae of moderate size. Surstylus bearing a row of 6–7 strong blunt prensisetae accompanied by 4–5 apical and 2–4 inner setae (Figs 33, 34). Hypandrium bare showing a typical " U "-shaped ventral pattern, very narrow anteriorly with a posterior edge markedly denticulate, the most prominent denticles bearing a long paramedian setae; anterior parameres cryptic, rounded in ventral view and elongate in lateral view, with 2-3 sensillae. Aedeagus long; medially swollen; distiphallus hairy suggesting a double flexible lampbrush; aedeagal apodeme narrow and bent (Figs 35, 36).

Type material. Holotype, 1 ♂ northeastern Tanzania: Mazumbaï, West-Usambara, on *Ficus chirindensis* fallen figs, 16.III.1996, J.Y. Rasplus (MNHN).

Etymology. From Latin, evoking the lampbrush of the distiphallus.

Distribution. Tanzania (West-Usambara).

DISCUSSION

The Eastern Arc forests harbour a range of endemics in different forest types and of different affinities and therefore it is thought that the Eastern Arc cannot have suffered a major loss of forest or a sustantial lowering in the altitude of forest types, at least in the last 30 000 years (Lovett, 1993b). The centres of endemism probably resulted from the persistence of moist forests during the Pleistocene droughts. In particular, the Usambara mountains contain the highest known diversity and endemism of plant and animal species in East Africa (Newmark, 1991). The seven remarkable new species of *Drosophila* found in the Eastern Arc mountains and on Mount Kilimanjaro and described in the present work provide futher evidence that the highly fragmented montane forests of Tanzania have long been centres of speciation.

The new species, *D. baucipyga*, is undoubtedly among the most spectacular representatives in the Afrotropical region of the basically Oriental *montium* species subgroup. It is also most interesting for its biogeography. The geographical range of *D. baucipyga* is at once localized and widespread, matching the range of the supposedly old forests (in a geological sense) of the overall Eastern Arc, from Mount Usambara to the north-east of Tanzania to Mount Uzungwa to the south-south west of the country. Otherwise, the species is seemingly absent from the much younger forests of Mt Kilimanjaro and Mt Meru (D.L. unpublished). Should this distribution be confirmed, it probably means that the species has little propensity to migrate and the subdivided extant populations result from the fragmentation of the species home range. If this is so, *D. baucipyga* would be a palaeoendemic, a relic of the formerly continuous submontane Eastern Arc forests. This would support further the view that these ancient crystalline mountain forests have been interconnected, and isolated from distant forest blocks for a relatively long period of evolutionary time (Lovett & Wasser, 1993). Worth noting in this respect is the striking similarity of *D. baucipyga* to the species pair *D. megapyga* from Ruwenzori and the Cameroon Volcanic Line, and *D. eupyga* from the Cameroon highlands and Gabon (Tsacas, 1981). The three species, *D. baucipyga, D. megapyga* and *D. eupyga* of the *montium* species subgroup all have very similar overall phenotypes, sexual combs on the basal and second fore tarsomeres, and similar – albeit distinct - epandrium and hypandrium. Noticeably, all three species have a row of 4–5 huge cercal teeth protruding from the male abdomen, making them very easy to identify. They are undoubtedly closely related and we propose to place them all in a new species complex, the *megapyga* species complex. The finding of *D. baucipyga* in the Eastern Arc forests is of great interest for understanding biogeographical patterns throughout tropical African mountains, since it clearly indicates an old connection between Usambara, Ruwenzori and the Cameroon highlands. The presence of *D. eupyga* at lower elevations in northeastern Gabon (500 m a.s.l. at Makokou), and at mid (800 m a.s.l. at N'Kolbisson by Yaoundé) and higher elevations (2000 m at Bafut N'Guemba on Mt Lefo) in Cameroon indicates

that these basically montane species could migrate between forest blocks.

Two of the new *Drosophila* species described here belong to the *dentissima* species group, as revised by Tsacas (1980). This group of strictly tropical African species is basically comprised of "montane" species, whose range lies mostly between 1400 and 2750 m (a.s.l.). Although the core distribution is throughout the East African mountains (Virunga, Ruwenzori ranges, and Kenyan highlands), there are notable radiations in the Cameroon Volcanic Line and a few outlying species can be found still further west on the remote Mt Nimba in Guinea. To the south, species of the *dentissima* group have been recorded on the Nyika and Viphya plateaux in northern Malawi and further south in the eastern escarpment of Zimbabwe and those of the Drakensberg in South Africa (Chassagnard et al., 1997). A few rare species extend to lower elevations up to the Cape peninsula in South Africa.

The *Drosophila dentissima* group is probably one of the major groups of invertebrates shedding light on the palaeogeography of the East African highlands and their connections with the Cameroon highlands. Apart from a few rare outlying species, the core distribution of the *dentissima* species group matches what has long been called the "Victorian areotype" (Sharpe, 1893) (by reference to Victoria city by Mt Cameroon, Lake Victoria in Kenya/Tanzania, and Victoria Falls in Zimbabwe). The two new species described here are the first records of *dentissima* relatives reported from the Eastern Arc mountains and from Mt Kilimanjaro, and more generally from Tanzania.

Drosophila usambarensis, found in two locations of West-Usambara (Mazumbaï and Mt Magambo), contributes to the uniqueness of Mt Usambara. The species cannot be ascribed to any known species complexes of the *dentissima* group recognized by Tsacas (1980). It exhibits a combination of traits so far unknown and particularly extraordinary, including a long sexual comb of basal tarsomere; one long subapical oral seta; united but not fused posterior parameres; and the cercus fused to the epandrium over nearly half its length. This last major character has not been seen in the *dentissima* group. It is probably the first representative of a new species complex. However, we will delay the description of this latter until related taxa are found.

Outside the Eastern Arc, another representative of the *dentissima* group, *D. kilimanjarica*, is only reported from the relatively recent forests of Mount Kilimanjaro. The species has a combination of quite original traits, including a long sexual comb of basal tarsomere; two long subapical oral setae; posterior parameres entirely fused; and a cercus not fused to the epandrium. The new species could be tentatively assigned to the *altissima* species complex, differing by a more complete fusion of posterior parameres from *D. kilimanjarica.* The *altissima* species complex is represented by *D. altissima* Tsacas, 1980 from the Aberdare range in Kenya and the Virunga range in Zaïre, and *D. oreia* Tsacas 1980 from the Ruwenzori range in Uganda (Tsacas, 1980). The altitudinal range of the *altissima* complex is 1850 to 2750 m, possibly more, making this cluster of taxa a strictly montane species complex, the highest known in the tropical African region.

The *Drosophila* subgenus (i.e., *Drosophila* s. str.*)* provides four other new taxa with restricted geographical ranges within the Eastern Arc mountains, in addition to *D. usambarensis.* These are *D. gata*, *D. neogata*, *D. paragata* and *D. pilocornuta*, which have only been reported from Mount Usambara. Only one of these four species, *D. pilocornuta,* is known to date, like *D. usambarensis*, from West-Usambara, while two other related species, *D. gata* and *D. paragata*, were only recorded from East-Usambara. Uniquely, *D. neogata*, has a distribution that covers all the Usambara mountains. Three of these four new species, *D. gata*, *D. neogata* and *D. paragata*, appear to be closely related on the basis of overall and detailed morphology and we propose to place them in a new cluster of taxa, the *gata* species complex. The assignment of this new species complex to a species group is more questionable (the *gata* species complex is nonetheless tentatively arranged here into the *virilis* section of the subgenus), a difficulty that was stressed formerly for other new complexes (Tsacas & Chassagnard, 1999). If

TABLE 1. Position of the seven new *Drosophila* species in the within-genus classification and their distributions in Tanzanian montane forests. Asterisks indicate new taxa; (-) = no subgroups recognized in the relevant species group; (likely new) = the description of which will be delayed until related taxa shall be found.

Drosophilidae (Drosophilinae), Genus *Drosophila*					Kiliman-jaro	West-Usambara		E-Usambara	Uzungwa
Subgenus	group	subgroup	complex	species	Marangu	Magambo	Mazumbaï	Amani	Mang'ula
Sophophora	*dentissima*	-	*altissima*	*kilimanjarica* *	■				
Sophophora	*dentissima*	-	likely new	*usambarensis**		■	■		
Sophophora	*melanogaster*	*montium*	*megapyga**	*baucipyga**			■	■	■
Drosophila	ungrouped	-	likely new	*pilocornuta**			■		
Drosophila	ungrouped	-	*gata**	*neogata* *			■	■	
Drosophila	ungrouped	-	*gata**	*gata* *				■	
Drosophila	ungrouped	-	*gata**	*paragata**				■	

TABLE 2. Resources on which new *Drosophila* species were recorded in Mt Usambaras, including the fruits of the forest trees of the genera *Parinari* (Chrysobalanaceae), *Syzygium* (Myrtaceae) and *Ficus* (Moraceae). No resources are reported for *D. paragata.*

Drosophila	*usambarensis*	*baucipyga*	*neogata*	*gata*	*pilocornuta*
West-Usambara	*Parinari excelsa* *Syzygium guineense*	*Parinari excelsa*	*Ficus sur*	–	–
East-Usambara	–	*Ficus mucuso*	*Ficus mucuso*	*Ficus mucuso*	*Ficus chirindensis*

relatedness within species complex is unequivocal, the affinities between species complexes of the *Drosophila* subgenus in the Afrotropical region is still a matter of conjecture. Some species complexes might be raised to the species group level in the future. As a result, setting apart the six cosmopolitan or widespread species recorded in the Afrotropical region, 37 of the henceforth 42 strictly Afrotropical representatives of the *Drosophila* subgenus in this biogeographical region remain ungrouped (Tsacas & Chassagnard, 1994, 1999, 2000, and present data).

This new fauna of *Drosophila* contributes further to the great uniqueness of the Tanzanian mountains and suggests a staggering of speciation events depending on the more or less advanced fragmentation and isolation of the covering submontane forests. These new findings provide further evidence that the Usambaras shelter the greatest number of species probably because of their favoured position as a coastal rain-trap (Kingdon, 1990). This author argued that such diversity is primarily due to their being the moistest and most favourable region along the whole eastern seacoast. But the unique richness and diversity of the Usambaras is also reinforced by isolation, the nearest blocks of rain-trapping mountains lying not only 130 km away to the north and south but further inland.

Ecological data may provide further indications about the distribution and diffusion of "montane" *Drosophila* species. The Mazumbaï forest can be seen as 'an island of lower montane rainforest in the West Usambara' (Redhead, 1981). There are four major types of forest at Mazumbaï: *Ocotea/Podocarpus*; *Ocotea/Syzygium*; *Newtonia/Syzygium*; and, *Newtonia/Parinari/Syzygium* (Hall, 1985). The *Newtonia/Parinari/Syzygium* forest appears to be most suitable for *Drosophila*. While the pods of the legume *Newtonia* (Mimosoidea) are unsuitable for *Drosophila*, the fruits of both *Parinari excelsa* Sabine (Chrysobalanaceae) and *Syzygium guineense* (Wild.) DC. (Myrtaceae) yield a great diversity of drosophilid species, including the two new species described here, *D. baucipyga* and *D. usambarensis*. According to Lovett (1993b), *Parinari excelsa* is the most common species of tree in the submontane forest in the West Usambara: it accounts for the greatest number of individuals – (c. 7%) and is the most frequent species, occurring in the greatest number of plots (55%). It is also the species that has the largest basal area (c. 13%). In contrast *Syzygium guineense* is not considered to be among the ten most common and frequent trees in West Usambara in general, although locally abundant at Mazumbaï (Lovett, 1993b). It could still be however among the most preferred host plants for *Drosophila* (Table 2). The findings of Lovett (1993b) indicating that *Parinari excelsa* is more common (c. 20%), frequent (c. 90%) and contributes the greatest basal area (c. 47%) in northern Uzungwa in the Mwanihana Forest Reserve is consistent with this expectation. There, *Syzygium guineense* is also among the ten most common (3%), frequent (34%) and contributive species (2%). *D. baucipyga* was recorded on *P. excelsa* fallen fruits in West-Usambara and also occurs in the Mwanihana Forest Reserve. It is therefore likely that this species is closely associated with these host-plants.

In addition to these species, fig trees are major breeding sites for *Drosophila* in Tanzania in general and more especially in the Usambaras. Of a total 40 species of *Ficus* reported from Tanzania (Berg, 1990; Berg & Wiebes, 1992), 19 were recorded during our 1995–1996 investigations in submontane forest habitats. Sixteen of these species provided figs, of which nine yielded *Drosophila*. Both *Ficus mucuso* Ficalho and *Ficus sur* Forsskål produce huge numbers of syconia (figs) which mature, and hence fall, synchronously. Such resource patches on the soil are very attractive to a diversity of unspecialised *Drosophila* differing ecologically from specialized, strictly fig-breeding drosophilids (Harry et al., 1996, 1998). As a result, three new species were found sympatrically on fallen *F. mucuso* syconia, namely *D. baucipyga*, *D. neogata* and *D. gata* in Amani in East-Usambara. In West-Usambara, *D. neogata* was caught on fallen syconia of *Ficus sur* and *D. pilocornuta* on fallen syconia of *Ficus chirindensis* C.C. Berg, a fig tree restricted to East Africa (Table 2).

The *megapyga* species complex of the *montium* subgroup and the *dentissima* group all attest to the existence of past connections between the forests of the Eastern Arc mountains, the Virunga and Ruwenzori ranges and those of the main western Guinea-Congo forests, particularly those of the Cameroon Volcanic Line. For the *dentissima* group alone, connections extend still further west to the Guinean range (Mt Nimba). The persistent riverine forests of the Congo river may have been a link between the Virunga-Ruwenzori forests and north-eastern Gabon - southern Cameroon region. The genera *Parinari*, *Syzygium* and *Ficus* are widespread along this putative north-Congo migratory pathway and may have been among the host-plants that repeatedly favoured the migration of *Drosophila* during various geological and climatic episodes.

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