

Divergence of sex comb phenotypes in the *Drosophila fima* species group and radiation on Afrotropical *Ficus*, including five new species from East Africa and Madagascar (Diptera : Drosophilidae)

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Abstract – The Afrotropical *Drosophila fima* species group is unique with regard to male terminalia morphology and functioning, tarsal structure, sex comb diversity, and to ecology. Five new species, all belonging to the dyula complex on the basis of male terminalia, are described here. Four of them from East Africa provide the usual, albeit remarkable tarsal pattern of the so-called 'tarsus-modified' species, namely *D. longicrinis*, *D. pilacrinis*, *D. stenotrichala* and *D. trichala*. But the fifth new species from Madagascar and the Eastern Arc mountains of Tanzania, *D. inopinata*, provides a new combination of traits unexpected in the *fima* group, that is male terminalia typical of the dyula complex but lacking both tarsal modification and sex combs which were previously thought to characterize also the complex. The co-occurrence of such contrasted tarsal patterns within a 'clade' of closely related species may help understanding how rapidly the sex comb phenotype of males may change. It is argued that the diversity of sex comb phenotypes is related to the adaptive radiation of the *fima* group species on *Ficus*; and that having different sex comb features may be a way for species packing to occur.

Résumé – Divergence des phénotypes 'peignes sexuels' chez les espèces du groupe *Drosophila fima* et radiation sur les *Ficus* afrotropicaux, incluant cinq nouvelles espèces d'Afrique de l'Est et de Madagascar. – Le groupe afrotropical *Drosophila fima* est unique tant par la morphologie et le fonctionnement des terminalias mâles, que par les changements de structure des tarse, la diversité des peignes sexuels ou encore l'écologie. Cinq nouvelles espèces du groupe *fima*, toutes appartenant au complexe dyula, sur la base des terminalias mâles, sont décrites ici. Quatre d'entre elles, d'Afrique orientale, montrent le schéma classique, quoique remarquable, des espèces dites « aux-tarses-modifiés », à savoir *D. longicrinis*, *D. pilacrinis*, *D. stenotrichala* et *D. trichala*. Mais, la cinquième, originaire de Madagascar et des montagnes de l'Arc Oriental de Tanzanie, *D. inopinata*, présente une nouvelle combinaison de traits pour le phénotype 'peignes sexuels' inattendue dans le groupe *fima*, associant des terminalias mâles typiques du complexe dyula avec l'absence des modifications tarsales et des peignes sexuels qui semblaient jusqu'alors caractériser eux aussi le complexe. La coexistence de types tarsaux aussi contrastés au sein d'un 'clade' d'espèces affines peut aider à comprendre à quelle vitesse le phénotype « peignes sexuels » peut changer. Il semble que la divergence des peignes sexuels ait favorisé la radiation adaptative et l'accumulation écologique des espèces sur une même ressource, les *Ficus* afrotropicaux.

In *Drosophila* genetic changes primarily involve spectacular premating sexual behaviour, marked by novel male characters that appear as a result of sexual selection (Carson 1997). Given that it is a dimorphic sexual character, modified tarsal segments on the prothoracic legs is one such evolutionary innovation that is generally thought to have evolved under the driving force of sexual selection. Modified tarsi have evolved independently in a few unrelated taxa within the

family Drosophilidae and sporadically in various families of Diptera like Lauxaniidae and Sarcophagidae (McAlpine 1987: 961, 1183). In a few Hawaiian drosophilids the tarsal segments vary in length, sometimes resulting in compaction. Other species from the rest of the world, like *Stegana tarsalis*, a species of the subfamily Steganinae from West Indies, show modified compacted (t2-4) tarsal segments (Wheeler 1981).

But the most remarkable changes in drosophilids worldwide concern the modifications of the « sex-comb », a row of stout, rounded black bristles ('teeth') on the fore legs (figs. 25-28). Curiously, this remar-

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kable structure, limited to males, is lacking in other Diptera, and within the subfamily Steganinae. Moreover, in the Drosophilinae, it has evolved only in several species groups of the subgenus *Sophophora* but is absent in the large subgenus *Drosophila*. Therefore, the tarsal sex comb probably evolved as a synapomorphic character in the Sophophoran lineage of the genus *Drosophila* after the *Sophophora/Drosophila* split. Indeed, the sex comb is a very peculiar, secondarily evolved structure the function of which is still unclear.

The genetic basis of the sex comb phenotype of males has been studied by Santamaria (1993, 1998). According to this author, the pleiotropic mutant phenotypes of the Polycomb group of genes (PcG) are very similar to the diagnostic characters used in the classification of Diptera. Santamaria (1993, 1998) suggests that spatial modulation of the PcG products may have accompanied speciation.

Worldwide, the sex comb phenotype has evolved solely in species of the *obscura* and *melanogaster* species groups, both belonging to the subgenus *Sophophora*. The earliest offshoot of this subgenus (the *willistoni* species group) includes species that have no sex combs (Powell 1997; Powell & DeSalle 1995). Among the sex comb bearing *Sophophora*, the *obscura* species group, which is thought to have arisen first, invariably has two sex combs on each fore leg regardless of the lineage considered (Palearctic, Nearctic or Afrotropical). In contrast, the *melanogaster* group provides a wide diversity of sex comb phenotypes including sex combs of variable size, structure, and number: one sex comb (e.g., the *melanogaster* subgroup), two (e.g., the bulk of the *montium* subgroup and the *ficuspila* subgroup), or three (e.g., most *ananassae* subgroup species).

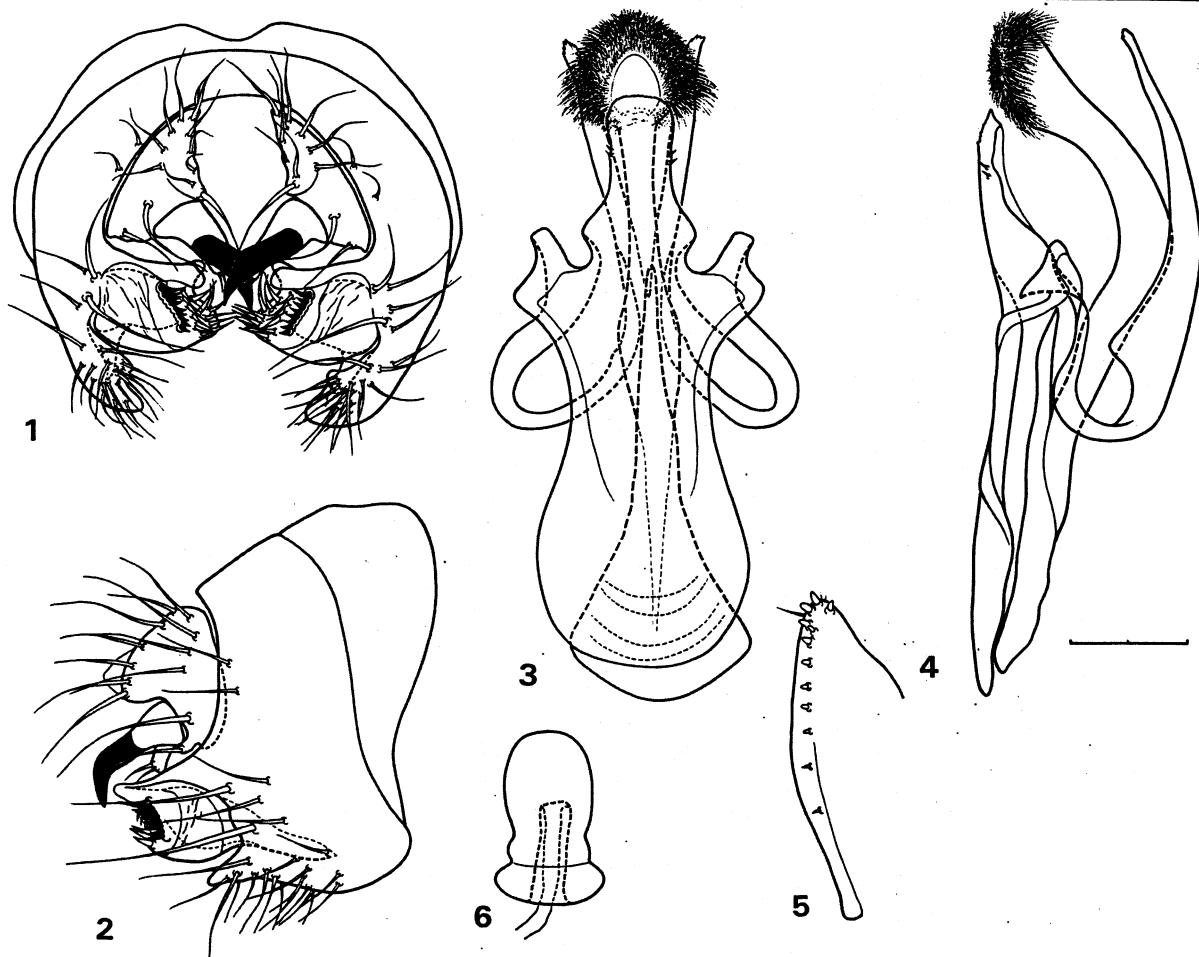
But setting apart the *obscura* and *melanogaster* species groups, only the Afrotropical region harbours additional Sophophoran species groups showing more or less modified tarsal sex combs: the *dentissima* (Tsacas 1980; Lachaise & Chassagnard 2001), and *fima* (Tsacas & Lachaise 1981) species groups, which are both endemic to the Afrotropical region. The two others, the *melanogaster* and *obscura* species groups, are not, but include subgroups (the *melanogaster* species subgroup) or complexes (the *nikananu* species complex within the *montium* species subgroup) for the former group, and subgroups (the *microlabis* subgroup) for the latter, the historical home range of which also was restricted to that biogeographic region.

The *fima* species group was described by Burla (1954) on the basis of morphological and biometrical traits and also on characteristics of larvae and pupae. In 1981, Tsacas & Lachaise stressed that all species of the *D. fima* group can be characterized by a specific

mode of functioning of male terminalia, and hence provided a more accurate definition of the *fima* group. This mode of functioning is unique in *Drosophila* and results from the fusion of anterior and posterior parameres, forming a single structure that operates as a guide for the movement of the aedeagus. There is no structural connection between the phallapodeme and this guide. Unlike most other *Drosophila*, posterior parameres of the *D. fima* species group are thus immovable and do not therefore contribute to propel the aedeagus. The consequence of these morphological peculiarities is that the aedeagus is free and considerably more mobile than in any other *Drosophila*. Indeed, in the rest position, it can retract deeply behind the hypandrium whereas during erection it can protrude significantly further out of the apex of the abdomen. As a result of the special rest position of the aedeagus, the hypandrium is considerably narrowed as a tube, constraining the apex of the abdomen of males to be markedly bent antero-ventrally.

The *fima* species group is also of particular interest since it is comprised of a diversity of markedly different sex comb phenotypes of males. There are species without sex combs, others have four sex combs (arranged in oblique, subtransverse or sublongitudinal alignment with respect to the tarsal axis), and still others have two sex combs, each composed of a transverse row. The rows are comprised of a variable number, ranging from 2 to 18, of black, rounded stout bristles (teeth) depending on the species, the tarsomere, and the position of the row.

However, modification of the tarsal segments *per se* additionally to the differentiation of sex combs is rare and has so far been observed only in the *Drosophila fima* species group and more especially in the *dyula* complex. This species complex ("der *dyula*-Formenkomplex") was defined by Burla (1954) to include *D. dyula* Burla and two undescribed forms ("abweichende Form A"; "abweichende Form B") which he thought were distinct species. These were later described as *D. aloma* Tsacas (A) and *D. sycophila* Tsacas (B) together with six other new species of the *dyula* complex, namely *D. dimitra*, *D. microralis*, *D. petita*, *D. sycophaga*, *D. sycovora*, and *D. tychaea* in Tsacas & Lachaise (1981). These *fore-tarsus modified* species are closely related on the basis of the affinities of the male terminalia (Tsacas & Lachaise 1981) but molecular evidence of their relatedness is still lacking. The change of the fore legs in the *dyula* species complex is characterised by an apical and dorsal extension bearing a short (3-4 teeth) sex comb on the first two tarsomeres. The width of the dorsal extension is generally half as short as the remaining tarsus and its rela-



Figures 1-6

Drosophila (Sophophora) pilacrinis n. sp. – 1, epandrium and associated structures, caudal view. – 2, *idem*, lateral view. – 3, aedeagus and associated structures, ventral view. – 4, *idem*, lateral view. – 5, ovipositor. – 6, spermatheca. (Scale: 0.1 mm)

tive length (with respect to the tarsus length) varies depending on the species. The tarsus-bearing extension of the first tarsomere (basitarsus) overlaps the basal part of the second, and the extension of the second tarsomere overlaps the third.

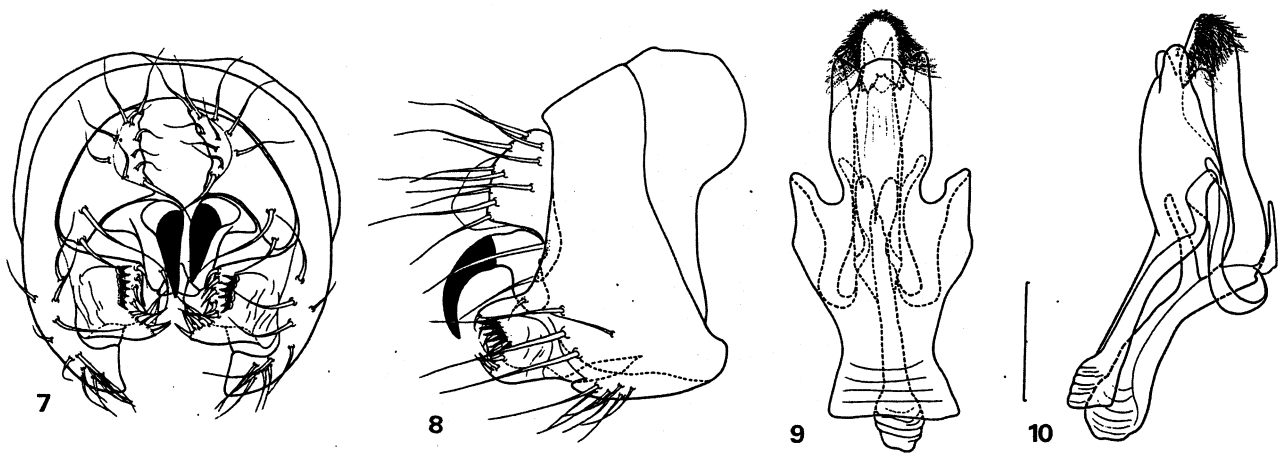
Here, we describe five new species of the *dyula* complex including four tarsus-modified and one intriguing non-modified species, and discuss their importance in the evolution of the sex comb phenotype in males. We present a summary of knowledge on the radiation of the *fima* species group, including the new taxa on *Ficus* (Moraceae) in the Afrotropical region, and discuss the idea that ecology and sex comb diversity must have some relevance to speciation and to species accumulation.

TAXONOMY

SUBGENUS *Sophophora*
fima group
dyula species complex

Drosophila (Sophophora) pilacrinis n. sp.
(figs. 1-6, 25)

Type material – Holotype ♂, Tanzania: Mazumbaï, West-Usambara, alt. 1400 m, 20.ii.95, on *Ficus sur* (Moraceae). Paratypes: 9♂♂, 7♀♀, *idem* but 19.iii.96; 13♂♂, *idem* but Soni, alt. 1270-1280 m, 17.ii.95; 11♂♂, 2♀♀, *idem* but Mgwashi, 21.iii.96, on *Ficus thonningii*; 3♂♂, 1♀, *idem* but 18-21.iii.96,



Figures 7-10

Drosophila (Sophophora) trichala n. sp. – 7, epandrium and associated structures, caudal view. – 8, *idem*, lateral view. – 9, aedeagus and associated structures, ventral view. – 10, *idem*, lateral view. (Scale: 0.1 mm)

swept on fallen decaying fruits of *Parinari excelsa* (Chrysobalanaceae); 2♂♂, 2♀♀, *idem* but 21.iii.96, on *Syzygium guineense* (Myrtaceae); 1♀, Mt Magambo, Juniper forest, Gologolo, alt. 1955m, 26.iii.96; 38♂♂, 19♀♀, East-Usambara, Amani, alt. 914 m, on fallen figs of *Ficus mucoso*, 25.ii.95; 1♀, *idem* but Usa River, Mt Meru alt. 1350 m, on fallen figs of *Ficus vallis-choudae*, 30.iii.96; 1♂, Mt Meru, 1350m, *Grevillea robusta* (Proteaceae), 8.iv.96 (*D. Lachaise, M. Harry*) (MNHN).

Diagnosis – Closely related to *D. dimitra* Tsacas, differs from it by having the tip of the medial extension of novasternum truncate and serrate, the posterior paramere narrower in lateral view, and the ventral edge of the epandrium tapering posteriorly.

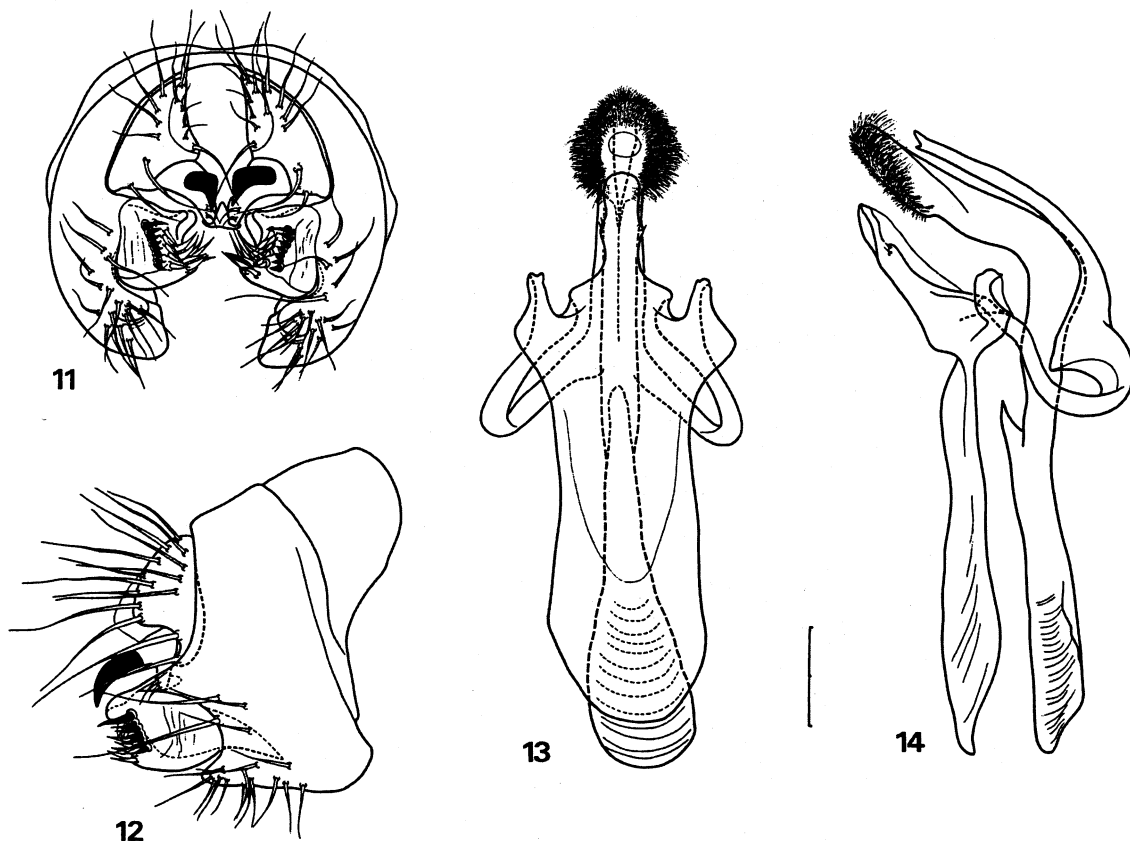
Description – **Male/Female.** *Head.* Frons yellowish-brown between orbital plates, pale yellow anteriorly to orbital plates, yellow area extending by narrow medial stripe reaching ocellar triangle, frons width/frons height = holotype 1.4 (paratypes, males 1.21-1.45, females 1.20-1.44), frons width/head width (fw/fh) = 0.52, 0.50-0.52; 0.49-0.51; Fronto-orbital plates glossy and dark brown, proclinate orbital seta *or1* close to posterior reclinate (*or3*), anterior reclinate (*or2*) minute arising very close to and positioned externally from *or3*; proclinate orbital/posterior reclinate orbital (*or1/or3*) = 1 (0.94-1; 0.84-0.95), anterior reclinate orbital/posterior reclinate orbital (*or2/or3*) = 0.3 (0.29-0.32; 0.26-0.35). Ocellar triangle same colour as orbital plates,

ocellar setae long and divergent. Face: glossy, greyish white; carina and peristoma whitish, carina very narrow, linear, short, hardly prominent. Antenna yellow-brown, darker dorsally, arista with 5 dorsal and 3 ventral rays plus terminal fork. One vibrissa followed by two shorter setae posteriorly. Gena narrow, same colour as face, greatest diameter of eye: genal width in line of greatest diameter of eye (*g/e*) = 0.10 (0.09-0.11; 0.09-0.11).

Thorax. Entirely glossy; scutum yellow brown bearing at edge of scutellum a dark brown triangle tapering forward. Acrostichal setulae in 6 rows, posterior dorsocentral setae very long. Scutellum dark brown, *b/a* (basal scutellar seta: apical scutellar seta) = 0.78 (0.82-0.89; 0.88-0.93). Pleura brown, darker than scutum; anterior/posterior katepisternal setae (*a/p*) = 0.45 (0.48-0.58; 0.46-0.53). Legs yellowish. In males, first and second tarsomeres with short transverse sex comb comprised of 3 teeth apically, modified part of second tarsomere overlapping third tarsomere. Wing width: wing length (*ww/wl*) = 0.39 (0.38-0.43; 0.36-0.38), *C* = costal index = length ratio (*a/b*) of first to second costal section = 1.6 (1.56-1.7; 1.47-1.63), *C3* fringe = 0.61 (0.56-0.73; 0.6-0.66).

Abdomen. Glossy dark brown, same colour as scutellum, slightly paler anteriorly.

Male terminalia. Epandrium dark brown, posterior margin with distinct lobe pointing posteroventrally below surstylus. Surstylus broader than high, bearing row of 8-9 short pointed teeth, with two rows of 4-5 and 3-4 inner setae, respectively, cluster of 4-6 setae at ventral innermost corner of surstylus. Medial extension of hypandrium truncate and



Figures 11-14

Drosophila (Sophophora) longicrinis n. sp. – 11, epandrium and associated structures, caudal view. – 12, *idem*, lateral view. – 13, aedeagus and associated structures, ventral view. – 14, *idem*, lateral view. (Scale: 0.1 mm)

serrate on posterior margin and posteroventral end. Posterior parameres narrower and more regular in lateral view, accordion-pleated at tip. Secondary forceps below cercus bearing stout, elbowed tooth.

Female terminalia. Ovipositor robust and brownish, similar to that of *D. dimitra*, differing by apex being more pointed and bearing a single row of 8 teeth, only the first tooth behind the apical bristle being accompanied by a second tooth. Spermatheca, (unknown in *D. dimitra*), resembling a nipple shield.

Male. Body length: 2.02 (2.03-2.1) mm; wing length: 2.29 (2.10-2.45) mm.

Female. Body length: 2.50-2.53 mm; wing length: 2.45-2.63 mm.

Etymology – From the Latin *pila* (=ball) and *crinis* (=hair), alluding to the rounded and hairy end of the distiphallus.

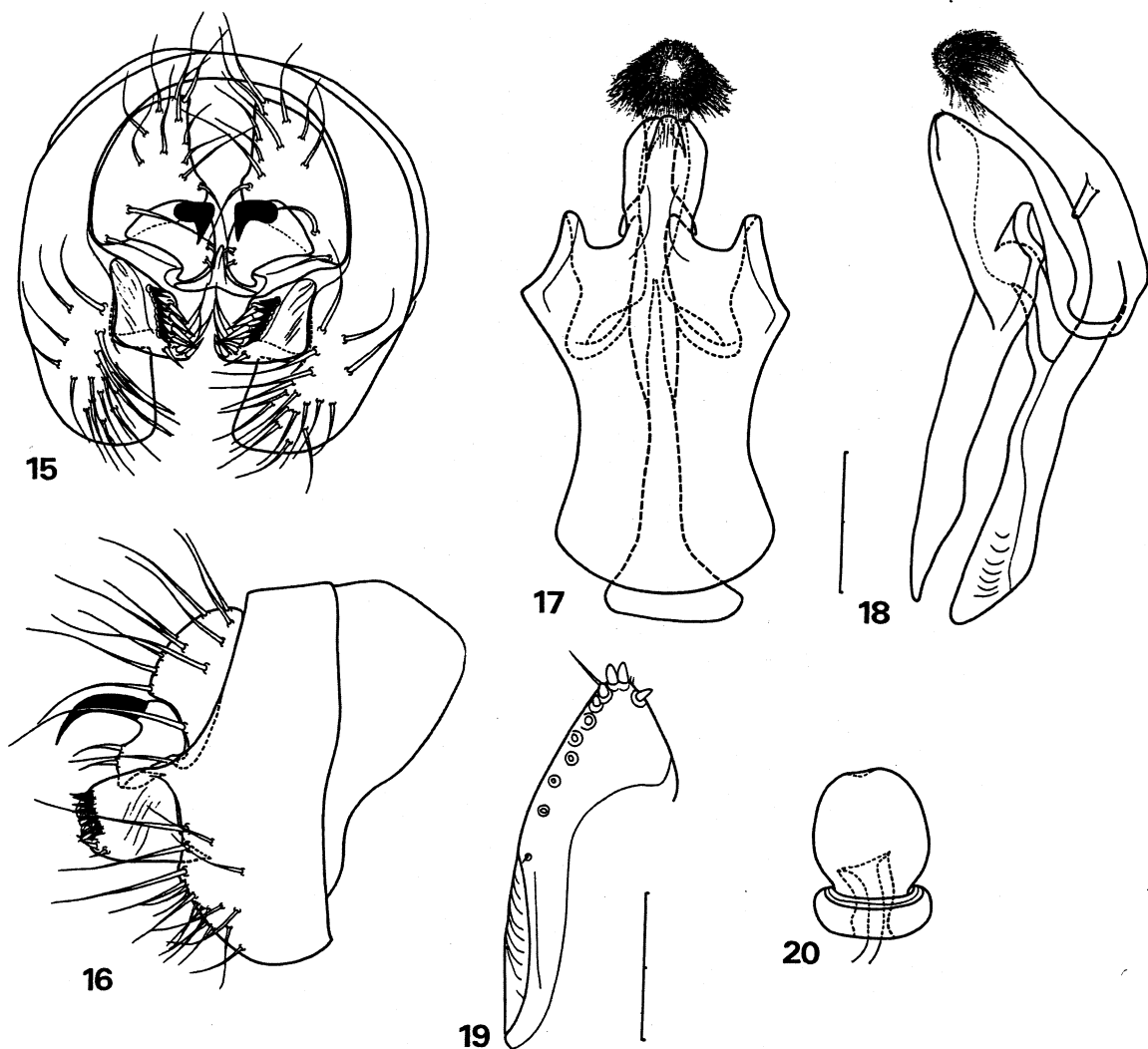
Distribution – Tanzania.

Drosophila (Sophophora) trichala n. sp.
(figs. 7-10, 26)

Type material – Holotype ♂, Tanzania: Amani, East-Usambara, alt. 914 m, 25.ii.95, on fallen figs of *Ficus mucoso* (Moraceae). Paratypes: 1 ♂, *idem*; 1 ♂, Mt Meru, Arusha (Ngota) National Park, alt. 1700 m, 10-12.iii.95, Juniper (*Juniperus procera*) forest, on fallen fruits of *Trichilia* (Meliaceae) (*D. Lachaise, M. Harry*) (MNHN).

Differential diagnosis – Closely related to *D. sycovora* Tsacas, differing by the scutum and pleura being paler, the medial extension of the novasternum significantly longer with the apex more markedly trilobate, the posterior paramere shorter, and the distiphallus very different.

Description – Male. **Head.** Frons rusty brown between orbital plates, becoming paler before orbital plates, fw: hw = 0.5 (0.5), fw: fh = 1.2 (1.19-1.25). Fronto-orbital plates



Figures 15-20

Drosophila (Sophophora) stenotrichala n. sp. – 15, epandrium and associated structures, caudal view. – 16, *idem*, lateral view. – 17, aedeagus and associated structures, ventral view. – 18, *idem*, lateral view. – 19, ovipositor. – 20, spermatheca. (Scale: 0.1 mm)

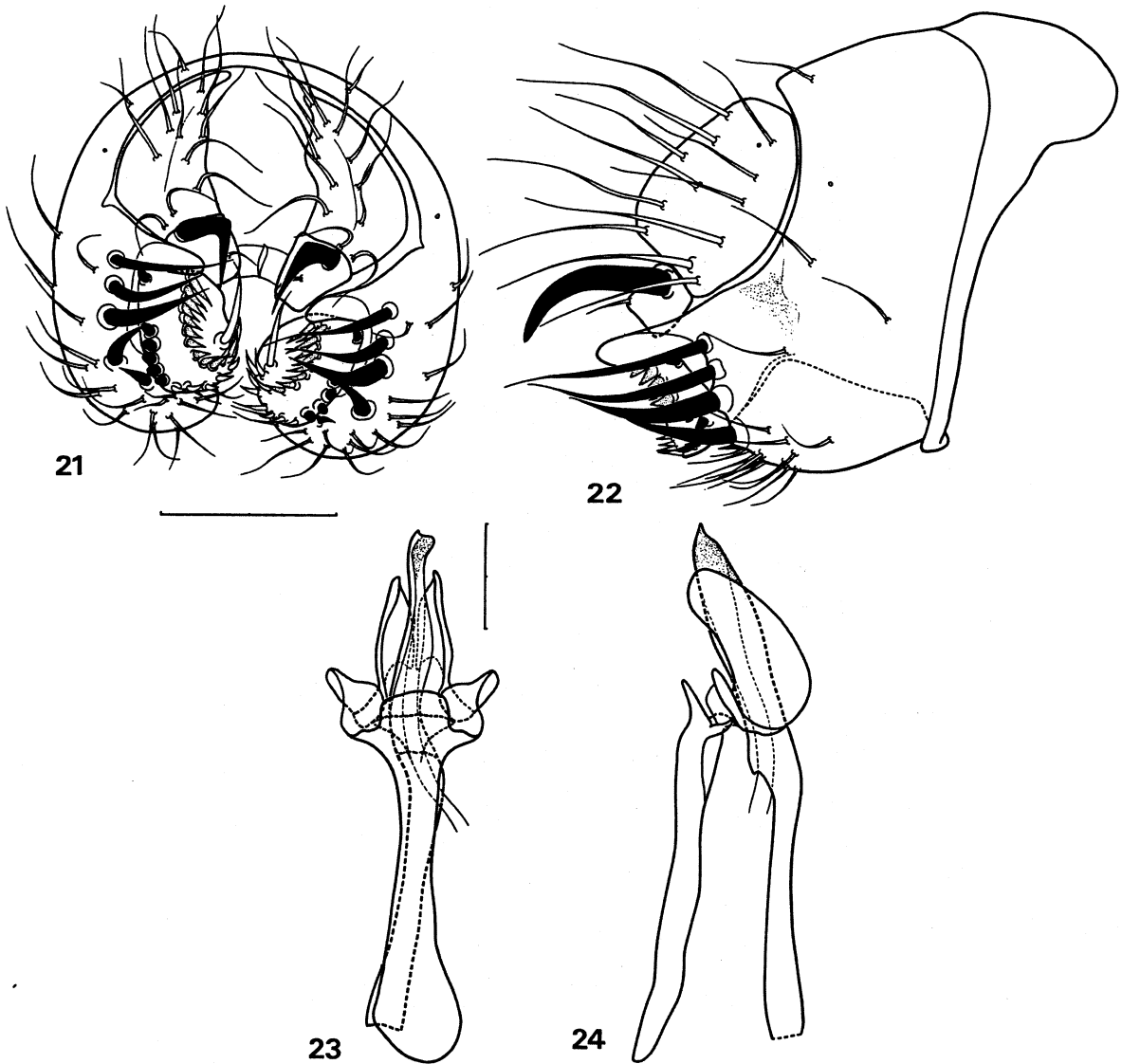
glossy and dark brown, *or1* and *or3* closely set, *or2* reduced to a cilium, at the same level but external to *or1*, $or1/or3 = 0.94$ (0.94-1), $or2/or3 = 0.29$ (0.31). Ocellar triangle same colour as orbital plates, ocellar setae long and divergent. Face, carina and peristoma greyish yellow, carina very narrow, linear, short, hardly protruding. Antenna yellow brown, flagellomere (third antennal segment) darkened, arista with 5 dorsal and 2-3 ventral rays plus terminal bifurcation. 2 vibrissae, ventral one shorter and thinner. Gena narrow, same colour as face, $g/e = 0.10$ (0.09).

Thorax. Glossy; scutum yellow brown, in the holotype a depression on the scutum appears darker, 6 rows of acrostichal setulae, posterior dorsocentral setae very long. Scutellum dark brown, $b/a = 0.84$ (0.85-0.9). Pleura same

colour as scutum, $a/p = 0.55$ (0.53). Legs yellowish. In males first and second tarsomeres with short transverse sex comb comprised of 3 teeth apically, modified part of second tarsomere overlapping the third one. Wing width: wing length (ww/wl) = 0.38 (0.36-0.38), $C = 1.43$ (1.56-1.59), $C3$ fringe = 0.61 (0.63).

Abdomen. Glossy, dark brown, same colour as scutellum, slightly paler on anterior edge.

Male terminalia. Epandrium dark brown, closely related to *D. sycovora*. Posterior edge of epandrium with truncate lobe below surstylus, dorsal half of epandrium bare. Surstylus height greater than width, bearing row of 6-7 short pointed teeth, with a single row of 4-5 short inner setae, cluster of 6-7 longer setae at ventral, innermost corner



Figures 21-24

Drosophila (Sophophora) inopinata n. sp. – 21 epandrium and associated structures, caudal view. – 22, *idem*, lateral view. – 23, aedeagus and associated structures, ventral view. – 24, *idem*, lateral view. (Scale: 0.1 mm)

of surstylus. Secondary forceps below cercus bearing a stout claw-like tooth. Apex of long medial extension of novasternum wide and trilobate, each lateral lobe bearing two minute spinules. Parameres very short and narrow. Aedeagus and aedeagal apodeme making a marked angle, distiphallus with a double-beaked end, serrate laterally, sub-terminal end of aedeagus with a typical 'mop of hair'.

Female. Unknown.

Male. Body length: 2.42 mm; wing length: 2.24 mm.

Etymology – From the Greek τριχάλοσ-α (= three tips), alluding to the trilobate shape of the apex of the long medial extension of the novasternum.

Distribution. – Tanzania (Mt Meru, Mt East-Usambara).

Drosophila (Sophophora) longicrinis n. sp.
(figs. 11-14, 28)

Type material – Holotype ♂, Kenya, Mt Elgon, alt. 2290 m, km 2 from main gate, site 7, on fallen figs of *Ficus thonningii* (fig tree 3: Kikuyu name 'mgumu'; Kiswahili name 'Mfumu') mission Kenya, September 1984. Paratype: 1 ♂, *idem*, 4.ix.84 (D. Lachaise, M.L. Cariou, M. Ashburner) (MNHN).

Table 1 – Origin of the five new species of *Drosophila* of the *fima* group from the Eastern Arc mountain forests (West-Usambara Mts, East-Usambara Mts, Uzungwa Mts) and Mt Meru in Tanzania, from Mt Elgon in Kenya and from Madagascar. Habitat resource indicates where the species was found as imago.

<i>Drosophila</i>	location	Mt	country	alt.	date	habitat/resource
<i>D. pilacrinis</i> sp.n.	Mazumbai	West-Usambara	Tanzania	1450m	Feb.-March	<i>Ficus sur</i>
	Mazumbai	West-Usambara	Tanzania	1450m	March	<i>Parinari excelsa</i>
	Mazumbai	West-Usambara	Tanzania	1450m	March	<i>Syzygium guineense</i>
	Soni	West-Usambara	Tanzania	1270m	February	<i>Ficus sur</i>
	Mgwashi	West-Usambara	Tanzania		March	<i>Ficus thonningii</i>
	Gologolo	Magambo, W-Usamb.	Tanzania	1955m	March	Juniper forest
	Amani	East-Usambara	Tanzania	800m	February	<i>Ficus mucuso</i>
	Usa River	Meru	Tanzania	1350m	March	<i>Ficus vallis-choudae</i>
Usa Nursery	Meru	Tanzania	1350m	March	<i>Grevillea robusta</i>	
<i>D. trichala</i> sp.n.	Amani	East-Usambara	Tanzania	800m	February	<i>Ficus mucuso</i>
	Meru	Meru	Tanzania	1700m	February	<i>Trichilia</i> sp.
<i>D. longicrinis</i> sp.n.	Site 7	Elgon	Kenya	2290m	September	<i>Ficus thonningii</i>
<i>D. stenotrichala</i> sp.n.	Gologolo	Magambo, W-Usamb.	Tanzania	1955m	March	Juniper forest
<i>D. inopinata</i> sp.n.	Amani	East-Usambara	Tanzania	800m	February	<i>Ficus mucuso</i>
	Amani	East-Usambara	Tanzania	800m	Feb.-March	<i>Terminalia catappa</i>
	Mang'ula	Uzungwa	Tanzania	300m	March	
	Ranomafana		Madagascar		Oct.-Nov.	

Diagnosis – Closely related to *D. pilacrinis* n. sp., differing by the medial extension of the novasternum being narrower, with a non-serrate apex, and the distiphallus with the aspect of a lampbrush.

Description – Male. *Head*. Frons yellowish brown between orbital plates, pale yellow before orbital plates, FW: HW = 0.5 (0.45), FW: FH = 1.35 (1.4). Fronto-orbital plates glossy, dark brown; *or1* and *or3* closely set, *or2* reduced to a cilium, at the same level but external to *or1*, *or1/or3* = 0.94 (0.94-1), *or2/or3* = 0.33 (0.37). Ocellar triangle same colour as orbital plates, ocellar setae long and divergent. Face and peristoma glossy, greyish white; carina very narrow, linear, short, hardly protruding. Antenna slightly darker than frons, arista with 5 dorsal and 3 (rarely 2) ventral rays plus terminal bifurcation. 1 vibrissa. Gena narrow and same colour as peristoma, *g/e* = 0.09 (0.10).

Thorax. Glossy; scutum, scutellum and pleura brownish, 6 rows of acrostichal setulae, dorsocentral setae very long, *b/a* = 0.83 (0.87). *a/p* = 0.55 (0.52). Legs brownish. In males, first and second tarsomeres with short transverse sex comb comprised of 3 teeth apically, modified part of second tarsomere overlapping the third. Wing width: wing length (*ww/wl*) = 0.39 (0.36-0.39), *C* = 1.43 (1.56-1.59), *C3* fringe = 0.60 (0.67).

Abdomen. Glossy and brownish.

Male terminalia. Epandrium brown, very similar to that of *D. pilacrinis* n. sp., but upper part bare. Apex of long medial extension of novasternum narrower with non-serrate apex, posterior parameres similarly long and narrow but

ending as in an elephant trump. Aedeagus and aedeagal apodeme markedly bent ventrally, distiphallus appearing as a lampbrush.

Female. Unknown.

Male. Body length. - 2.3 (2.37) mm; wing length: 2.4 (2.4) mm.

Etymology – From the Latin *longus* (=long) and *crinis* (=hair), alluding to the shape of the distiphallus.

Distribution – Kenya (Mt Elgon).

Drosophila (Sophophora) stenotrichala n. sp.
(figs. 15-20, 27)

Type material – Holotype ♂, Tanzania, West-Usambara, Mt Magambo, Gologolo, alt. 1955m, Juniper forest, 26.iii.96. Paratypes: 2♂♂, 1♀, *idem* (Lachaise, Harry) (MNHN).

Diagnosis – Closely related to *D. trichala*, differing by the apex of the medial extension of the novasternum being markedly trilobate but narrower, parameres lacking, and the distiphallus very different.

Description – Male/Female. *Head*. Frons rusty brown between orbital plates, paler before orbital plates, *fw: hw* = 0.51 (0.5-0.52; 0.57), *fw: hw* = 1.96 (1.94-2; 1.76). Fronto-orbital plates glossy, dark brown; *or1* and *or3* closely set; *or2*

Table 2 – Distribution of the *Drosophila fima* group species in Kenya, Tanzania, Zaïre, Malawian Highlands, Natal, and Madagascar.

<i>Drosophila</i>	Mt Elgon	Mt Meru	Mt Magamb o	Mazumbai W-Usamb.	Amani E-Usamb.	Mt Uzungwa	SE Zaire	Burundi	Viphya Plateau	Zomba Plateau	Natal S.Africa	Rano. Mada
<i>D. abron</i>	■	■		■	■	■						
<i>D. akai</i>				■	■	■						
<i>D. alladian</i>						■						■
<i>D. dimitra</i>							■	■				
<i>D. dimitroides</i>										■	■	
<i>D. dyula</i>							■					
<i>D. fima</i>									■	■	■	■
<i>D. inopinata</i>						■						■
<i>D. iroko</i>				■	■							
<i>D. kulango</i>				■	■							
<i>D. longicrinis</i>	■	■										
<i>D. neomitra</i>										■	■	
<i>D. pilacrinis</i>		■	■	■	■							
<i>D. stenotrichila</i>		■	■	■	■							
<i>D. trichala</i>		■	■		■	■						

reduced to a cilium, at the same level but external to *or1*, $or1/or3 = 1.08$ (1.08-1.14; 0.95), $or2/or3 = 0.33$ (0.33-0.35; 0.31). Ocellar triangle same colour as orbital plates; ocellar setae long, divergent. Face, carina, and peristoma greyish yellow; carina very narrow, linear, short, hardly prominent. Antenna yellow brown, flagellomere darkened, arista with 5 dorsal and 3 (or 2) ventral rays plus terminal bifurcation. 2 vibrissae, ventral one shorter and thinner. Gena narrow, same colour as face, $g/e = 0.1$ (0.09-0.11; 0.09).

Thorax. Glossy; scutum yellow brown, 6 rows of acrostichal setulae, posterior dorsocentral setae very long. Scutellum dark brown, $b/a = -$ (0.87-0.88; 0.85). Pleura slightly lighter than scutum, $a/p = 0.50$ (0.53-0.54; 0.54). Legs same colour as pleura. In males, first and second tarsomeres with short transverse sex comb comprised of 3 teeth apically, modified part of second tarsomere overlapping the third. Wing width: wing length (ww/wl) = 0.39 (0.36-0.39; 0.39), $C = 1.56$ (1.60-1.69; 1.86), $C3$ fringe = 0.63 (0.62-0.63; 0.62).

Abdomen. Glossy and brown.

Male terminalia. Epandrium brown, closely related to *D. trichala* n. sp., upper half of epandrium similarly bare, differing by ventral lobe being twice as broad albeit showing a similarly truncate shape, surstylus oblique, bearing row of 8-9 short pointed teeth, with a single row of 5 longer inner setae, cluster of 4-5 setae, the two innermost longer and at ventral, innermost corner of surstylus. Secondary forceps below cercus bearing claw-like tooth, large yet nearly half the size as in *D. trichala*. Medial extension of novasternum shorter and narrower, apex markedly trilobate, the three lobes overlapping one another, parameres lacking. Aedeagus and aedeagal apodeme markedly bent ventrally, aedeagus

bearing on each side a short lateral fin, distiphallus simple, beak-less and hairy.

Female terminalia. Ovipositor robust, similar to that of *D. dimitra*, differing by two apical-most teeth being more stout, and lack of second tooth accompanying row of 8 teeth. Spermatheca rounded.

Male. Body length: 2.24 (2.11-2.24) mm; wing length: 2.24 (2.26-2.37) mm.

Female. Body length: 2.37 mm; wing length: 2.76 mm.

Etymology – From the Greek στενός (= narrow), τριχάλος-α (= three tips), alluding to the narrow, trilobate apex of the medial extension of the novasternum.

Distribution – Tanzania (W-Usambara).

Drosophila (Sophophora) inopinata n. sp.
(figs. 21-24)

Type material – Holotype ♂, Tanzania, East-Usambara, Amani, on fallen figs of *Ficus mucoso*, 25.ii.95. **Paratypes:** 2♂♂, *idem*; 1♂, *idem* but on decaying flowers of *Terminalia catappa* (Combretaceae), 26.ii.95; 1♂, *idem*, 8.iii.96; 1♂, *idem* but Mang'ula forest, Uzungwa, alt. 300m, 5-7.iii.95 (*Lachaise, Harry*). **Other material examined:** 3♂♂, Madagascar, Ranomafana, ca. 21°S, 47°E, 31.x.-3.xi.87, registered specimens S.F. McEvey 5471, 5485, 5486 (*McEvey, Aulard*) (MNHN).

Diagnosis – Unequivocally related to the *dyula*-like species but the fore tarsi not modified and tarsal sex combs lacking.

Description – **Male.** *Head.* Frons pale rusty brown between orbital plates, peristoma yellowish extending to ocellar triangle by concolorous medial narrow stripe, fw: hw = 0.47 (0.51-0.54), fw: hw = 1.4 (1.4-1.5). Fronto-orbital plates wide, glossy and hardly darkened; *or1* and *or3* closely set; *or2* reduced to a cilium, at the same level but external to *or1*; *or1/or3* = 0.76 (0.72-0.74); *or2/or3* = 0.29 (0.28-0.30). Ocellar triangle small, dark brown, contrasting with orbital plates; ocellar setae long and divergent. Face, carina, and peristoma greyish yellow; carina narrow, slightly more prominent than in the four species described above. Antenna same colour as peristoma but flagellomere slightly darkened, arista with 5 (rarely 4) dorsal and 3 ventral rays plus terminal bifurcation and 3-4 inner rays unusually developed. 2 vibrissae, ventral one shorter and thinner. Gena narrow linear and same colour as face, *g/e* = 0.05 (0.05-0.08).

Thorax. Scutum glossy; pale rusty brown anteriorly, becoming a dark brown trident-like pattern posteriorly; 6 rows of acrostichal setulae; posterior dorsocentral setae very long, although shorter the anterior dorsocentral setae are unusually long. Scutellum dark velvet brown, *b/a* = - (0.95-0.97). Pleura slightly glossy, slightly darkened compared to anterior part of scutum; *a/p* = 0.6 (0.52). Legs whitish. In males, first and second tarsomeres of fore tarsus not modified and tarsal sex combs lacking. Wing width: wing length (*ww/wl*) = 0.38 (0.36-0.39), *C* = 1.55 (1.41-1.5), *C3* fringe = 0.6 (0.6-0.68).

Abdomen. Glossy and brown.

Male terminalia. Epandrium brown, closely related to *D. dyula* and *D. petitae* Tsacas.

Female. Unknown.

Male. Body length: 1.74 (1.84) mm; wing length: 1.71 (1.68-1.76) mm.

Distribution – Tanzania (East-Usambara, Uzungwa), Madagascar.

Etymology – From the Latin *inopinatus* (*a*) (= unexpected), evoking the new combination of traits, that is tarsus not modified combined with male terminalia, characterizing the tarsus-modified *dyula*-like species.

Biogeography and ecology of the new species

Table 1 summarizes the origin of the five new species of *Drosophila* of the *fima* group from the Eastern Arc mountain forests (West-Usambara Mts, East-Usambara Mts, Uzungwa Mts), Mt Meru in Tanzania, Mt Elgon in Kenya, and from Madagascar. Table 2

gives the distribution of the *Drosophila fima* group species including the new species in Kenyan, Tanzanian, Zaïrian and Malawian Highlands, Natal and Madagascar.

Four of the five new species (*D. pilacrinis*, *D. trichala*, *D. stenotrichala*, *D. inopinata*) originate mostly from the fragmented submontane rainforests of the Eastern Arc mountains, a NE-SW mainland 'archipelago' that includes ancient, Tertiary crystalline mountains, most notably Mounts Usambara, Mt Guru, Mt Uluguru and Mt Uzungwa (Lovett 1993; Lovett & Wasser 1993). The strictly montane fauna of the Eastern Arc *Drosophila* is most speciose and attest to past connection between eastern and western African mountains (Lachaise & Chassagnard 2001). Two of the new species (*D. pilacrinis* and *D. trichala*) originate from the northeastern-most part of the Eastern Arc and from Mt Meru, a far more recent, Pleistocene volcanic mountain, assumed to be less than 1 My old (Wilkinson *et al.* 1986; Griffiths 1993). Accordingly, the passage of *dyula* relatives from the Eastern Arc mountain forests to forests of young volcanoes occurred within the last million years. One species (*D. longicrinis*) is reported only from Mt Elgon, a Miocene volcanic mountain.

New records of the *fima* species group

Additional to the new species from East Africa and Madagascar, a new series of records of *fima* group species from the Gulf of Guinea in West Africa are reported here. They include records from the Gulf of Guinea islands (São Tomé and Príncipe Islands) and from the neighbouring mainland (Cameroon). This is the first time that *Drosophila* are recorded from Príncipe Island, and species of the *fima* group are clearly identified from São Tomé island. Also, one record of *D. alladian* in NE. Madagascar represents the first time that the species is reported from the great island. All specimens mentioned below are kept in absolute alcohol for DNA extraction at CNRS-Gif.

– *D. abron* Burla, 1954. 1♀, N'simi forest, south of Yaoundé, Cameroon 02-17.xi.95 (*M. Harry*)

– *D. akai* Burla, 1954. 1♀, N'simi forest, south of Yaoundé, Cameroon 02-17.xi.95 (*M. Harry*)

– *D. alladian* Burla, 1954. 1♂, N'simi forest, south of Yaoundé, Cameroon 02-17.xi.95 (*M. Harry*); 5♂, 2♀, NE. Madagascar, Masoa, Naora, on fallen figs of *Ficus* sp., x.2000 (*M. Veuille*, *A. Sarovy*); 101♂, 28♀, São Tomé, Obo forest Reserve, 12-25.ii.2001 (except when indicated otherwise), including: 17♂, 9♀, 1440m; 1♂, *Ficus thonningii*, 1300m, 13.iii.98; 1♂, 1235m; 74♂, 19♀, 1200m, *Ficus chlamydocarpa* fer-

Table 3 – Altitudinal ranges of the 24 species (including *D. sp. aff. petitae*) of the *Drosophila fima* group in Western and Eastern Africa. Species are ranked according to highest elevations. Black indicates actual records, grey, expectations. Asterisks indicate the species belonging to the *dyula* complex.

<i>Drosophila</i> spp.		Altitudinal range											
		0-200	201-400	401-600	601-800	801-1000	1001-1200	1201-1400	1401-1600	1601-1800	1801-2000	2001-2200	2201-2400
<i>D. abure</i>	West												
<i>D. sycophaga</i> *	West												
<i>D. sycovora</i> *	West												
<i>D. aloma</i> *	West												
<i>D. petitae</i> *	West												
<i>D. sycophila</i> *	West												
<i>D. dimitroides</i> *	East												
<i>D. neomitra</i> *	East												
<i>D. dyula</i> *	West												
<i>D. inopinata</i> *	East												
<i>D. alladian</i>	West												
	East												
<i>D. akai</i>	West												
	East												
<i>D. iroko</i>	West												
	East												
<i>D. fima</i>	West												
	East												
<i>D. kulango</i>	West												
	East												
<i>D. tychaea</i> *	West												
<i>D. trichila</i> *	East												
<i>D. microralis</i> *	West												
<i>D. sp. aff. petitae</i> *	West												
<i>D. dimitra</i> *	West												
<i>D. pilacrinis</i> *	East												
<i>D. stenotrichila</i> *	East												
<i>D. abron</i>	West												
	East												
<i>D. longicrinis</i> *	East												

nandesiana; 3♂, Bom Successo, 1153m, 1♂, 1000m, 1♂, Monte Café, 650m, 3♂, São Tomé city, 0-10m (*D. Lachaise, M. Harry*); 4♂, 3♀, Príncipe Island, São Joaquim, *Ficus sur*, mona shelter, 17-19.ii.2001 (*D. Lachaise, M. Harry*).

– *D. fima* Burla, 1954. 1♂, São Tomé Island, Obo forest Reserve, 12-25.ii.2001, Bom Successo, 1153m, 1♂, 1♀, SE. São Tomé, São João dos Angolares (*D. Lachaise, M. Harry*); 1♀, SW. São Tomé, Praia Xixi, 0-10m (*C. Claude, L. Primo*); 15♂, 19♀, Príncipe Island, São Joaquim, *Ficus sur*, mona shelter, 19.ii.2001; 10♂, 12♀, reared from fallen figs of *F. sur* (*D. Lachaise, M. Harry*).

– *D. kulango* Burla 1954. 1♀, São Tomé, Monte Café, cacao plantation, 650m, 12-25.ii.2001 (*D. Lachaise, M. Harry*); 1♀, SW. São Tomé, Praia Xixi, 0-10m (*C. Claude, L. Primo*); 1♀, Príncipe Island, São Joaquim, *Artocarpus*, 17.ii.2001 (*D. Lachaise, M. Harry*).

In view of these new species and records the composition and geographic distribution of the *D. fima* species group can be summarized as follows:

The *fima* species group

– *D. abron* Burla, 1954: Ivory Coast; Cameroon (new record), Kenya, Mt Elgon (new record), Tanzania,

Table 4 – Distribution of the 23 species (*plus D. sp. aff. petitae*) of the *Drosophila fima* group species in West Africa (Guinea, Ivory Coast, Nigeria), West-central Africa (Central Africa, Cameroon, Gabon, Congo), East Africa (Kenya, Tanzania, Burundi, Malawi, Zimbabwe), Southern Africa to the south of the Limpopo River (Natal, South Africa), and Madagascar. Host-plant without brackets means (the *Drosophila* species has been reared from fallen figs of); with brackets means (the *Drosophila* species has been swept above fallen figs of). None = caught but not reported in association with any host-plant. *Drosophila* species of the *fima* group are ordered according to biogeographic affinities. Asterisks indicate the species belonging to the *dyula* complex. The names of fig trees are given according to Berg's revision of *Ficus* (Berg, 1990) and Berg & Wiebes (1992).

<i>Drosophila</i>	West Africa	West-central Africa	East Africa	Southern Africa Madagascar
<i>D. abure</i>	(<i>Ficus kamerunensis</i>) <i>Ficus lyrata</i> <i>Ficus mucoso</i> <i>Ficus ovata</i> <i>Ficus recurvata</i> <i>F. sansibarica macrosperma</i>			
<i>D. sycophaga</i> *	<i>Ficus kamerunensis</i> (<i>F. sansibarica macrosperma</i>)			
<i>D. sycovora</i> *	<i>Ficus vogeliana</i>			
<i>D. alladian</i>	<i>F. chlamydocarpa fernandesiana</i> (<i>Ficus kamerunensis</i>) (<i>Ficus lyrata</i>) <i>Ficus mucoso</i> <i>Ficus ovata</i> <i>F. sansibarica macrosperma</i> <i>Ficus saussureana</i> <i>Ficus sur</i> <i>Ficus vogeliana</i> (<i>Pentadesma butyracea</i>)	<i>Ficus wildemaniana</i>		<i>Ficus sp.*</i>
<i>D. aloma</i> *	<i>Ficus kamerunensis</i> (<i>Ficus lyrata</i>) (<i>Ficus mucoso</i>) (<i>Ficus recurvata</i>) (<i>F. sansibarica macrosperma</i>) (<i>Ficus saussureana</i>) (<i>Ficus sur</i>) <i>Ficus vogeliana</i> (<i>Berlinia sp.</i>) (<i>Pentadesma butyracea</i>) (<i>Parinari excelsa</i>)	(<i>Ficus mucoso</i>) <i>Ficus wildemaniana</i> (<i>Theobroma cacao</i>)		
<i>D. dyula</i> *	(<i>Ficus kamerunensis</i>) (<i>Ficus lyrata</i>) <i>Ficus mucoso</i> (<i>Ficus recurvata</i>) (<i>F. sansibarica macrosperma</i>) <i>Ficus saussureana</i> <i>Ficus sur</i> <i>Ficus vogeliana</i> (<i>Berlinia sp.</i>) (<i>Parinari excelsa</i>)	(<i>Ficus mucoso</i>)		
<i>D. petitae</i> *	(<i>Ficus lyrata</i>) (<i>F. sansibarica macrosperma</i>)	<i>Ficus wildemaniana</i> (<i>Ficus sp.</i>)		
<i>D. sycophila</i> *	(<i>Ficus lyrata</i>) (<i>Ficus mucoso</i>) (<i>Ficus recurvata</i>) (<i>Ficus sur</i>)	(<i>Ficus mucoso</i>) <i>Ficus wildemaniana</i>		

Ficus chlamydocarpa fernandesiana (HUtch.) C.C. Berg (Moraceae)
Ficus elasticoides De Wildeman (Moraceae)
Ficus kamerunensis Mildbraed & Burret (Moraceae)
Ficus lyrata Warburg (Moraceae)
Ficus mucoso Ficalho (Moraceae)
Ficus ovata Vahl (Moraceae)
Ficus recurvata De Wildeman (Moraceae)
Ficus sansibarica ssp. *macrosperma* (Mildbraed & Burret) C.C. Berg
Ficus saussureana De Candolle (Moraceae)

Ficus sur Forsskål (Moraceae)
Ficus sycomorus Linnaeus (Moraceae)
Ficus thonningii Blume (Moraceae)
Ficus vallis-choudae Delile (Moraceae)
Ficus vogeliana (Miquel) (Moraceae)
Ficus wildemaniana De Wildeman & T. Durand (Moraceae)
Ficus sp. unidentified (but one of the endemic Malagassy species)*
Artocarpus communis J.R. & G. Forst. (Moraceae)
Berlinia confusa Hoyle (Caesalpinaceae)

Table 4. (Continued)

<i>D. iroko</i>	<i>F. sansibarica macrosperma</i> (<i>Tieghemella heckelii</i>)		none
<i>D. abron</i>	<i>Ficus elasticoides</i> (<i>Ficus kamerunensis</i>) <i>Ficus lyrata</i> <i>Ficus mucuso</i> <i>Ficus ovata</i> <i>Ficus recurvata</i> <i>F. sansibarica macrosperma</i> <i>Ficus saussureana</i> <i>Ficus sur</i> <i>Ficus vogeliana</i> (<i>Parinari excelsa</i>) (<i>Pentadesma butyracea</i>)	(<i>Ficus mucuso</i>) <i>Ficus wildemaniana</i>	(<i>Ficus mucuso</i>) (<i>Ficus sur</i>) (<i>Ficus thonningii</i>)
<i>D. akai</i>	<i>Ficus elasticoides</i> (<i>Ficus kamerunensis</i>) <i>Ficus lyrata</i> <i>F. sansibarica macrosperma</i> <i>Ficus mucuso</i> <i>Ficus ovata</i> <i>Ficus recurvata</i> <i>Ficus saussureana</i> <i>Ficus sur</i> <i>Ficus vogeliana</i>	<i>Ficus wildemaniana</i>	none
<i>D. kulango</i>	<i>Ficus lyrata</i> (<i>Ficus mucuso</i>) (<i>F. sansibarica macrosperma</i>) (<i>Ficus vogeliana</i>) <i>Treculia africana</i>	<i>Ficus wildemaniana</i>	none
<i>D. fima</i>	<i>F. chlamydocarpa fernandesiana</i> <i>Ficus elasticoides</i> (<i>Ficus kamerunensis</i>) <i>Ficus lyrata</i> <i>Ficus mucuso</i> <i>F. sansibarica macrosperma</i> <i>Ficus saussureana</i> <i>Ficus sur</i> <i>Ficus vogeliana</i> <i>Artocarpus</i> (<i>Berlinia confusa</i>) (<i>Hirtella</i> sp.) <i>Nauclea pobeguini</i> (<i>Parinari excelsa</i>) (<i>Tieghemella heckelii</i>)	(<i>Ficus mucuso</i>) <i>Ficus wildemaniana</i>	(<i>Ficus sycomorus</i>) (<i>Ficus thonningii</i>) none
<i>D. microralis</i> *		none	
<i>D. sp. aff. petitae</i> *		none	
<i>D. tychaea</i> *		none	
<i>D. dimitra</i> *		<i>Coffea</i> pulp	none
<i>D. dimitroides</i> *			(<i>Ficus thonningii</i>)
<i>D. longicrinis</i> *			(<i>Ficus thonningii</i>)
<i>D. neomitra</i> *			(<i>Ficus thonningii</i>)
<i>D. pilacrinis</i> *			(<i>Ficus mucuso</i>) (<i>Ficus sur</i>) (<i>Ficus thonningii</i>) (<i>Ficus vallis-choudae</i>) (<i>Grevillea robusta</i>) (<i>Parinari excelsa</i>) (<i>Syzygium guineense</i>)
<i>D. stenotrichila</i> *			none
<i>D. trichala</i> *			(<i>Ficus mucuso</i>) (<i>Trichilia</i> sp.)
<i>D. inopinata</i> *			(<i>Ficus mucuso</i>) none (<i>Terminalia catappa</i>)

Coffea sp. (Rubiaceae)*Grevillea robusta* A. Cunn. (Proteaceae)*Hirtella* sp. (Rosaceae)*Nauclea pobeguini* (Hua ex Pob.) Merrill (Rubiaceae)*Parinari excelsa* Sabine (Chrysobalanaceae)*Pentadesma butyracea* Sabine (Chrysobalanaceae)*Syzygium guineense* (Willd.) De Candolle (Myrtaceae)*Terminalia catappa* Linnaeus (Combretaceae)*Theobroma cacao* Linnaeus (Sterculiaceae)*Tieghemella heckelii* Pierre & A. Chev. (Sapotaceae)*Treculia africana* Decaisne (Moraceae)*Trichilia* sp. (Meliaceae)

E. Usambara Mts and Uzungwa Mts (new record)

- *D. abure* Burla, 1954: Ivory Coast
- *D. akai* Burla, 1954: Ivory Coast ; Cameroon (new record), Gabon; Tanzania, W-Usambara Mts, E. Usambara Mts (new record)
- *D. alladian* Burla, 1954: Ivory Coast ; Cameroon (new record), Gabon; São Tomé (new record), Tanzania, E. Usambara Mts (new record) and Uzungwa Mts (new record); Madagascar (new record).
- *D. aloma* Tsacas (in Tsacas & Lachaise 1981): Centrafrica; Ivory Coast, Cameroon, Gabon, Republic of Congo.
- *D. dimitra* Tsacas (in Tsacas & Lachaise 1981): Cameroon ; Burundi, SE. Zaïre (Lubumbashi).
- *D. dimitroides* Chassagnard & Tsacas (in Chassagnard *et al.* 1997): Malawi.
- *D. dyula* Burla, 1954: Ivory Coast, Cameroon, Central Africa, Zaïre.
- *D. fima* Burla, 1954: Ivory Coast; Nigeria, Cameroon, Gabon, São Tomé, Príncipe (new record), Central Africa, Gabon, Congo, Burundi, Tanzania, South Africa (Natal).
- *D. inopinata* n. sp. Lachaise & Chassagnard (this work): Tanzania, Madagascar.
- *D. iroko* Burla, 1954: Ivory Coast; Tanzania, W. Usambara Mts (new record).
- *D. kulango* Burla, 1954: Ivory Coast ; Gabon; São Tomé, Tanzania, W. Usambara Mts, E. Usambara Mts (new record).
- *D. longicrinis* n. sp. Lachaise & Chassagnard (this work): Kenya (Mt Elgon).
- *D. microralis* Tsacas (in Tsacas & Lachaise 1981): Nigeria (Mambilla Plateau); Cameroon (Mt Cameroon).
- *D. neomitra* Chassagnard & Tsacas (in Chassagnard *et al.* 1997): Malawi.
- *D. petitae* Tsacas (in Tsacas & Lachaise 1981): Ivory Coast ; Cameroon, Gabon.
- *D. pilacrinis* n. sp. Lachaise & Chassagnard (this work): Tanzania.
- *D. stenotrichala* n. sp. Lachaise & Chassagnard (this work): Tanzania.
- *D. sycophaga* Tsacas (in Tsacas & Lachaise 1981): Ivory Coast.
- *D. sycophila* Tsacas (in Tsacas & Lachaise 1981): Ivory Coast ; Cameroon, Central Africa, Gabon.
- *D. sycovora* Tsacas (in Tsacas & Lachaise 1981): Ivory Coast (Taï).
- *D. trichala* n. sp. Lachaise & Chassagnard (this work): Tanzania.
- *D. tychaea* Tsacas (in Tsacas & Lachaise 1981): Cameroon (Mt Cameroon).

- *D. sp.* undescribed aff. *petitae* Tsacas (in Tsacas & Lachaise 1981): Nigeria (Mambilla Plateau), Cameroon (Mt Cameroon).

Geographic distribution

Of the 23 *fima* group species described (except *D. sp.* aff. *petitae*), 16 have restricted geographic ranges in western or eastern Africa:

- West Africa (west of the Dahomey gap): *D. abure*, *D. sycophaga*, *D. sycovora*.

- West Africa (east of the Dahomey gap): *D. microralis*, *D. tychaea*.

- West-west central Africa (Guineo-congolian forest block): *D. aloma*, *D. dimitra*, *D. petitae*, *D. sycophila*.

- East Africa: *D. dimitroides*, *D. inopinata*, *D. longicrinis*, *D. neomitra*, *D. pilacrinis*, *D. stenotrichala*, *D. trichala*.

Widespread west-east and north-south (within latitudes 8° north and 30° south): *D. alladian*, *D. fima*. Widespread west-east (but restricted within latitudes 8 north and 5 south): *D. abron*, *D. akai*, *D. dyula*, *D. iroko*. Among these six widespread species, there are very contrasting abundance patterns. Three are common: *D. fima*, *D. abron*, *D. alladian*, and three are rare: *D. akai*, *D. dyula*, *D. iroko*.

No related species has as yet been reported beyond latitude 10° north, that is in the Sahelian area. To the South, if two species (*D. dimitroides* and *D. neomitra*) are only known from the Zomba Plateau in Malawi so far (Chassagnard *et al.* 1997), no species of the group are restricted to Southern Africa to the south of the Limpopo River, a classic biogeographic barrier. Only the ubiquitous *D. fima* extends to Natal (Dhlinza Forest, Eshowe, Zululand) in South Africa (Tsacas 1990).

These data clearly suggest that the historical home range of the *fima* species group is the Afrotropical mainland with two speciation spots on each side of the Rift, one in the Guineo-congolian forest block (9 endemic species), the other in East African forests (7 endemic species). Almost all (15 of 16) species with restricted geographical ranges belong to the *dyula* complex, which therefore appears to have two (western/eastern) centres of speciation. Only *D. abure*, reported only from the Ivory Coast, so far does not belong to this complex.

The finding of *D. inopinata* n. sp. in the Ranomafana forest in central Madagascar, and the record of *D. alladian* Burla at Masoa in northeastern Madagascar, indicate that the *fima* group passed over the Mozambique channel to colonize Madagascar.

Table 5 – Diversity of the sex comb phenotypes of males among *fima*-group members associated with Afrotropical *Ficus* (Moraceae). *Drosophila* species without brackets means reared from fallen figs; with brackets means swept above fallen figs.

Sex comb number per fore leg	0	2	4
<i>Ficus chlamydocarpa</i> ssp. <i>fernandesiana</i>	<i>D. fima</i>	<i>D. sp.n.</i> (undescribed)	<i>D. alladian</i>
<i>Ficus elasticoides</i>	<i>D. abron</i> <i>D. fima</i>		<i>D. akai</i>
<i>Ficus kamerunensis</i> :	(<i>D. abron</i>) (<i>D. abure</i>) (<i>D. fima</i>)	<i>D. aloma</i> (<i>D. dyula</i>) <i>D. sycophaga</i>	(<i>D. akai</i>) (<i>D. alladian</i>)
<i>Ficus lyrata</i>	<i>D. abron</i> <i>D. abure</i> <i>D. fima</i> <i>D. kulango</i>	(<i>D. aloma</i>) (<i>D. dyula</i>) (<i>D. petitae</i>) (<i>D. sycophila</i>)	<i>D. akai</i> (<i>D. alladian</i>)
<i>Ficus mucoso</i>	<i>D. abron</i> <i>D. abure</i> <i>D. fima</i> (<i>D. inopinata</i>) (<i>D. kulango</i>)	(<i>D. aloma</i>) <i>D. dyula</i> (<i>D. pilacrinis</i>) (<i>D. sycophila</i>) (<i>D. trichala</i>)	<i>D. akai</i> <i>D. alladian</i>
<i>Ficus ovata</i>	<i>D. abron</i> <i>D. abure</i>		<i>D. akai</i> <i>D. alladian</i>
<i>Ficus recurvata</i>	<i>D. abron</i> <i>D. abure</i>	(<i>D. aloma</i>) (<i>D. dyula</i>) (<i>D. sycophila</i>)	<i>D. akai</i>
<i>Ficus sansibarica</i> ssp. <i>macrosperma</i>	<i>D. abron</i> <i>D. abure</i> <i>D. fima</i> <i>D. iroko</i> (<i>D. kulango</i>)	(<i>D. aloma</i>) (<i>D. dyula</i>) (<i>D. petitae</i>) (<i>D. sycophaga</i>)	<i>D. akai</i> <i>D. alladian</i>
<i>Ficus saussureana</i>	<i>D. abron</i> <i>D. fima</i>	(<i>D. aloma</i>) <i>D. dyula</i>	<i>D. akai</i> <i>D. alladian</i>
<i>Ficus sur</i>	<i>D. abron</i> <i>D. fima</i>	(<i>D. aloma</i>) <i>D. dyula</i> (<i>D. pilacrinis</i>) (<i>D. sycophila</i>)	<i>D. akai</i> <i>D. alladian</i>
<i>Ficus sycomorus</i>	(<i>D. fima</i>)		
<i>Ficus thonningii</i>	(<i>D. abron</i>) (<i>D. fima</i>)	<i>D. dimitroides</i> (<i>D. longicrinis</i>) (<i>D. neomitra</i>) (<i>D. pilacrinis</i>)	
<i>Ficus vallis-choudae</i>	(<i>D. pilacrinis</i>)		
<i>Ficus vogeliana</i>	<i>D. abron</i> <i>D. fima</i> (<i>D. kulango</i>)	<i>D. aloma</i> <i>D. dyula</i> <i>D. sycovora</i>	<i>D. akai</i> <i>D. alladian</i>
<i>Ficus wildemanianna</i>	<i>D. abron</i> <i>D. aloma</i> <i>D. fima</i> <i>D. kulango</i>	<i>D. petitae</i> <i>D. sycophila</i>	<i>D. akai</i> <i>D. alladian</i>

That *D. inopinata* was found there on fallen figs indicates that the great diversity of *Ficus* species present on Madagascar likely has favoured the colonization of the *fima* group members. However, *D. inopinata* was recorded also in the Eastern Arc mountain forests of Tanzania (Mts Usambara and Uzungwa) suggesting that the species differentiation most likely occurred on continental Africa. Consistent with this assumption, there is no member of the *fima* group endemic to Madagascar and hence no evidence of speciation events of the group in the great island.

Intriguingly, the altitudinal ranges of the *fima* relatives reflect their geographic ranges. That is, the more confined they are geographically, the more restricted they are altitudinally, and vice versa (tab. 3). Thus, some western species like *D. abure*, *D. sycophaga*, and *D. sycovora* are strictly lowland inhabitants, while others like the eastern *D. stenotrichala* and *D. longicrinis* are seemingly confined to relatively high elevations between 1800–2000 and 2200–2400 m, respectively. In between, there is a diversity of species with increasing upper limits. It is worth noting that if

there is no lowland-restricted species sensu-stricto in East Africa, there are several taxa from West-central Africa (like *D. tychaea* from Mt Cameroon and *D. microralis* from Mt Cameroon and the Nigerian Mambilla Plateau) which live only at 1400-1600 m for the former and 1400-1800 m for the latter. Such altitudes are quite significant for Western Africa and rule out the null hypothesis that the altitudinal ranges of the *fima* group species follows the West-East altitudinal increase of the plateau.

Radiation on *Ficus*

Of the 23 described species of the *fima* group, 19 have been found in association with *Ficus* (Moraceae), breeding in early or late decaying syconia (fig receptacles). The four others (*D. dimitra*, *D. microralis*, *D. stenotrichala* and *D. tychaea*) are rare and their ecology is poorly known. Each of these 19 fig-associated *Drosophila* were found on a variable number (from 1 to 15) of *Ficus*, not necessarily sympatric (tab. 4). All over the Afrotropical region 16 species of *Ficus* have hitherto been shown to harbour a variable number (from 1 to 12) of *D. fima* related species, again not necessarily sympatric (tab. 5). Thus, despite specialization on figs there is clear evidence that among the *fima* relatives some are more specialized than others. For example, the strict association of *D. sycovora* with the most peculiar fig-tree *F. vogeliana* in the Taï rainforest at the southwesternmost part of the Ivory Coast contrasts markedly with the widespread *D. alladian* or *D. fima* which can be found on a great diversity of *Ficus* over a wide geographic area. Moreover, the greater the number of host-figs, the more frequently are the extra-resources visited occasionally. These latter are clearly secondary resources and do not conflict with the assumption that the specialization on figs is a synapomorphic character that most likely appeared in the primeval ancestral population from which all extant species of the *fima* group arose.

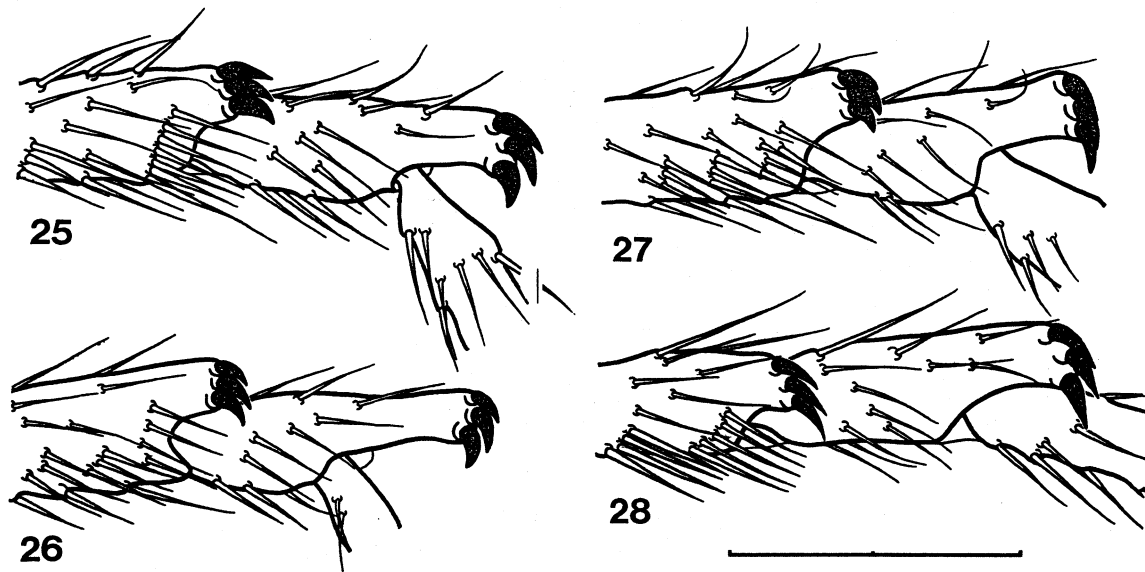
DISCUSSION

A new combination of traits for the sex comb phenotype in the *fima* group – Within the genus *Drosophila*, the Afrotropical *fima* species group is unique with regard to the morphology and functioning of male terminalia, the modification of the tarsal structure, the sex comb phenotype diversity, and to their ecology. Five new species of the *fima* group, all belonging to the *dyula* complex on the basis of male terminalia, are described in this work. They all display the special mode

of functioning unique in *Drosophila* resulting from the fusion of anterior and posterior parameres and from a tubular hypandrium. Four of them from East Africa provide the usual, albeit remarkable, tarsal pattern of the so-called 'tarsus-modified' species, namely *D. longicrinis*, *D. pilacrinis*, *D. stenotrichala* and *D. trichala*. But the fifth new species from the Eastern Arc mountains of Tanzania (Mts Usambara, Mts Uzungwa) and Madagascar, *D. inopinata*, provides a new combination of traits that was unexpected in the *fima* group, that is male terminalia typical of the *dyula* complex but lacking both tarsal modification and sex combs, which were thought also to characterize the complex.

The phylogenetic placement of the *fima* species group – Little attention has so far been given to the genetics and molecular biology of the *fima* species group, probably because most species are so specialized that they cannot be bred easily. Only the widespread *D. abron* and *D. fima* could be bred successfully on standard *Drosophila* medium over a few generations. It was nonetheless shown that the amylase electromorphic patterns differ markedly between the *fima* (*D. fima*) and the other species groups, notably the *melanogaster* and *obscura* groups (Prigent 1997). The phylogenetic placement of the *fima* species group remains poorly defined. There is only evidence from ribosomal RNA sequence (Pélandakis & Solignac 1993) that it is a member of the subgenus *Sophophora* and that it is grouped with the *ananassae* 'subgroup'. The *fima* and *ananassae* 'groups' are clustered together with the *obscura* group and distinct from the *melanogaster* group. It should be noted incidentally that these rRNA data, together with morphological data, suggest that the *ananassae* species cluster should be removed from the *melanogaster* group and ranked at the group level. Interestingly, the *fima* and *ananassae* lineages are among those groups showing the widest diversity of sex comb phenotypes in the subgenus *Sophophora*.

Current and missing sex comb phenotypes in the *fima* group – Noticeably, none of the *fima* group species so far has been reported with only one sex comb on the first tarsus as it is invariably the case in, for example, all species of the *melanogaster* subgroup. Moreover, unlike species of the *dentissima* species group, the other strictly Afrotropical species group of *Drosophila* (Tsacas 1980; Lachaise & Chassagnard 2001), the sex comb phenotype with longitudinal alignment is virtually unknown in the *fima* species group (but see *D. akai* below). In contrast, there are a diversity of species the sex comb phenotypes of which exhibit either oblique or transverse rows of generally three-



Figures 25-28

First and second tarsomeres with sex-combs. – 25, *Drosophila (Sophophora) pilacrinis* n. sp. – 26, *Drosophila (Sophophora) trichala* n. sp. – 27, *Drosophila (Sophophora) stenotrichala* n. sp. – 28, *Drosophila (Sophophora) longicrinis* n. sp.

four teeth, as those tarsus-modified species described in this work. Also, there are various species of the *fima* group without sex combs, like *D. abron*, *D. abure*, *D. fima*, *D. iroko*, and *D. kulango*. Others, have four sex combs, two on the first, and two on the second fore tarsus: four short in *D. alladian*, and three short and one long in *D. akai*. Considering the phylogenetic placement of the *fima* and *obscura* groups, it can be assumed, in agreement with Santamaria (1998), that the character “only one sex comb” is a synapomorphy in the *melanogaster* subgroup (Lachaise *et al.* 2000), with respect to a more plesiomorphic “two sex combs”.

Recurrent evolution of varying sex comb phenotypes within a clade – In the *dyula* complex the various tarsal patterns observed provide evidence that the sex comb present/sex comb absent alternative and the transverse/oblique rotation occurred within a limited clade of closely related species. The sex comb phenotype of males also was shown to be very heterogeneous within species subgroups in the *melanogaster* group. For example, in the *suzukii* subgroup, the sex comb may be longitudinal, transverse or absent depending on the species (Lemeunier *et al.* 1986). Also, in the *montium* species subgroup where most species have two sex combs, there is one species complex, the *nikanunu* complex, the members of which have only one sex comb very similar (for some species) to that of the *melanogaster* complex species. The co-occurrence of

such contrasting tarsal patterns within a putative ‘clade’ of closely related species may help understanding how rapidly the sex comb phenotype of males may change. The parallel evolution (probably convergences) observed in a number of unrelated species groups also suggests that the sex comb character is prone to homoplasy. Accordingly, sex comb phenotype alone should not be used without corroboration from other evidence for inferring species complex or species group boundaries. As a result, even though the direction of change remains conjectural, such a diversity indicates that the shift from one sex comb phenotype of males to another (including the shift from sex comb present as opposed to sex comb absent, or vice versa) is probably rapid in evolutionary terms. These data support the view that rapid phenotypic divergence must be driven by disruptive selection (Schluter 2001).

Alignment and rotation of sex combs varying as a function of their length – The case of *D. akai* and *D. alladian* is quite remarkable in this respect. Both species have two sex combs (3-6 teeth) on the first tarsomere and two on the second tarsomere. They differ mostly by the first sex comb of the second tarsomere being significantly longer (10-13 teeth) in *D. akai* than in *D. alladian* (5-8 teeth). The second sex comb of the second tarsomere, that is the apical-most one, varies the other way round, being shorter in *D. akai*

(2-3 teeth) than in *D. alladian* (3-4 teeth). Remarkably, in both species the alignments of short and long sex combs vary in the same way as a function of the sex comb length. The longer the sex comb, the more longitudinal is the alignment; and the shorter the sex comb, the more transverse it is. It turns out that the alignment could be predicted in view of the sex comb length. Also, this correlation supports the view that it is probably a great advantage for males to have longer sex combs in terms of sexual selection, but that this evolutionary trend (longer sex comb) is dramatically constrained by the space limiting structure of the tarsus.

Also, the striking correlation between length (number of teeth) and alignment (c. 45° rotation) in the first two sex combs of the first tarsomere in both species suggests that their rotation occurred concomitantly. In that respect, it is of interest to stress that the mutant sex comb curved (*scc*) of *Drosophila subobscura* was shown to prevent the rotation and suppress the differentiation of the first tarsal sex comb (Pascual & Mestres 1995; Santamaria 1998). Furthermore, the tarsal patterns observed in *D. akai* and *D. alladian* suggest that the rotation of the two sex combs of the second tarsomere (exhibiting sublongitudinal and subtransverse alignments respectively) rotate independently from one another and from the pair on the basal tarsomere.

The one-sex comb versus two-sex comb alternative – Most *Sophophora* species have two sex combs, one on the first tarsus (or, basitarsus) and another on the second. Some of them have also a sex comb on the third tarsus, others have only one sex comb on the first tarsus as is the case in all species of the *melanogaster* subgroup. Others do not have a sex comb as is the case in the neotropical *saltans* and *willistoni* species groups. Among the four other groups, the *obscura* group, with two sex combs is considered to be the most early offshoot of the Sophophoran radiation (Powell & DeSalle 1995; Powell 1997). All these data support Santamaria's (1998) assumption that the longitudinal alignment is a synapomorphy derived from the transverse row of more primitive species group in the genus *Drosophila*. It was suggested that the last two rows turn nearly 90° to take up their present position in *D. melanogaster* relatives.

How many genes are responsible for the sex comb differentiation? – The presence of a sex comb on the fore leg in the X0 male half of bipartite gynandromorphs in *D. melanogaster* (Sinnott *et al.* 1950) and *D. teissieri* (D. Lachaise, unpublished) indicates that the Y chromosome is not needed for the sex comb of males

to differentiate. Recently, emphasis has been given to the number of genes involved in ordinary phenotypic differences and their relationship with the genetics of reproductive isolation (Orr 2001). More than two genes account for the difference in sex comb tooth number between *D. simulans* and *D. mauritiana* (True *et al.* 1997), and four between *D. simulans* and *D. sechellia* (Macdonald & Goldstein 1999). Otherwise, it was shown that basically, many mutations of *D. melanogaster* cause the differentiation of two sex combs. Two groups of genes are responsible for the differentiation of two sex combs in *D. melanogaster* mutants (see Santamaria 1998 for review). The occurrence of two sex combs and the dorsal position at the apical end of the first and second tarsomeres of the sex comb of *D. longicrinis*, *D. pilacrinis*, *D. stenotrichala*, *D. trichala* and the other modified-tarsus species evoke the pattern observed in a diversity of *D. melanogaster* mutants from either the Polycomb group of genes (Santamaria 1993; Santamaria & Randsholt 1995), or a more heterogeneous group of genes including notably sex comb distal '*scd*' (Lindsley & Zimm 1992) and bric a brac '*bab*' (Godt *et al.* 1993). It is of interest to stress that regulatory changes at the *bab* locus were thought to play a key role in the evolution of sexual dimorphism, and that sexual selection has contributed to the evolution of *bab* regulation (Kopp *et al.* 2000). After Santamaria (1998), the occurrence of convergent phenotypes in mutants suggests that the capability to develop a sex comb on the second tarsus exists in wild-type *Drosophila melanogaster*, but is repressed in normal development. It can be expressed again should various genetic alterations bring back the ancestral pattern, for instance by loss of function of *bab* or *scd*. In the *dyula* species complex, the two-sex combs on modified tarsus is a synapomorphous character and the absence of sex comb in *D. inopinata* most probably is an example of how reversible adaptive evolution can be in sexual populations (see discussion in Teotónio & Rose 2000).

Sexual selection and radiation on *Ficus* – There is no evidence in any *Drosophila* of a polymorphic population with some males having and others lacking sex combs. However, the different patterns exhibited by closely related species (e.g., *D. inopinata* compared to *D. trichala*), and the reiteration of varying tarsus-modified patterns in unrelated groups (homoplasy) suggests adaptive evolution which generally implies a transitional polymorphic state. The varying species specific features of the new species described here support Santamaria's (1998) assumption that the evolutionary innovations of the sex comb phenotype in males is somehow relevant to the speciation process. In

view of the sexual dimorphism of the fore leg structure in the *fima* species group, it can be assumed that changes of this phenotype result from sexual selection, and there is growing evidence that sexual selection may be a major driving force of speciation in animals because it has a direct impact on reproductive isolation, and may be associated with a range of adaptive radiations (Eberhard 1985; Coyne 1992; Wu & Hollocher 1998). Therefore, it can be hypothesized that the diversity of sex comb phenotypes in the *fima* group species is somehow relevant to the adaptive radiation of the *fima* group species on *Ficus* in the Afrotropical region.

Of these 23 *fima* group species, 19 (including *D. inopinata*, *D. longicrinis*, *D. pilacrinis*, and *D. trichala* described here) have so far been recorded on fallen figs of 16 species of Afrotropical *Ficus*. The presence in the Afrotropical region of *fima* relatives on decaying figs can be predicted with great confidence. Therefore the association with figs is likely a synapomorphous ecological trait for the *fima* group species.

This *Drosophila-Ficus* association is fully independent from the *Lissocephala-Ficus* association in the same biogeographic region (Harry *et al.* 1996, 1998). The *Lissocephala* species evolved on green figs, the *Drosophila fima* relatives on red-black figs (Lachaise & Tsacas 1983). The strikingly different adaptive evolutions of two genera of drosophilids on figs in the Afrotropical region indicate the crucial role of fig trees as key resource in that region and more generally of host-plant in ecological speciation. Both specialized groups of drosophilids have presumably evolved under the driving force of sexual selection but in different ways. Unlike *Lissocephala*, which are highly territorial species (*D.* Lachaise, unpublished) –exhibiting what could be seen more or less as a lek behaviour (see Shelly & Whittier 1997, for review on lek behavior in insects)– but have no tarsal sex combs in males, *D. fima* group members do not appear similarly territorial but have evolved remarkable innovations of the sex combs.

The *fima* species group has experienced a burst of speciation on figs and presumably rapid phenotypic evolution of sex combs. What is amazing is that the *fima* burst occurred on a single type of resource. Some *Ficus* species may harbour up to 12 *Drosophila fima* group species but which display a diversity of sex comb phenotypes (tab. 5). Locally, there are generally four to five *fima* relatives that can coexist on a resource (a fallen fig patch) at a given time. They most generally include a mix of species including some without sex combs and others with two and four sex combs. Moreover, whenever two species have large population

densities, they invariably include two species with contrasted sex comb phenotypes (e.g., without sex combs against four sex combs). As a corollary, two overdominant species with similar sex comb patterns are generally exclusive on a fig patch. This is commonly observed in eastern and western Africa in the widespread pairs of taxa, namely *D. abron* versus *D. fima* (sex comb absent), and *D. akai* versus *D. alladian* (four sex combs). For example, on figs of *Ficus mucuso* at Amani in Eastern Usambara, and on figs of *Ficus sur* at Mazumbai and Soni in Western Usambara, *D. abron* and *D. akai* are most abundant, whereas *D. fima* and *D. alladian* are absent. In contrast, on figs of *Ficus chlamydocarpa fernandesiana* in São Tomé island, for instance, *D. fima* and *D. alladian* are most abundant, whereas *D. abron* and *D. akai* are absent. It appears that having different sex comb features seems a way for species packing and resource partitioning to occur, as if the 'adaptive landscape' could be primarily a *sexual adaptive landscape*.

However, setting apart *D. inopinata*, the species of the *dyula* complex display a very similar two sex-comb phenotype (see figs. 25-28) but most of them are geographically confined, occur on a limited number of *Ficus*, and have small population sizes. Thus, six *dyula* relatives were reported only from East Africa (*D. dimitroides*, *D. longicrinis*, *D. neomitra*, *D. pilacrinis*, *D. trichala*, and *D. stenotrichala*), and seven only from West Africa (*D. aloma*, *D. dimitra*, *D. microralis*, *D. petitae*, *D. sycophaga*, *D. sycovora*, and *D. tychaea*). Clearly, these two biogeographic species groups evolved in allopatry. When living in sympatry, the two-sex-comb species do not generally co-occur or co-occur at very low frequencies on the same fig patch. It is rare to record more than two *dyula* relatives coexisting at a time on a resource. In that respect it is worth noting that when three such relatives co-occur, like *D. pilacrinis*, *D. trichala* and *D. inopinata* on *Ficus mucuso* in Amani in the Eastern Usambara Mts, one of them (*D. inopinata*) has a contrasted sex comb phenotype (sex comb absent).

Unlike what is shown in most adaptive radiations (Schluter 1998, 2001), the *fima* group species are not highly differentiated ecologically. In contrast, the sex comb phenotypes are strongly divergent between sympatric species. Sex comb divergence may have rendered closely related specialized species capable of co-occurring syntopically on a fig patch. We suggest here that divergent selection on sex combs might be responsible for accumulation of species on a resource (*Ficus* spp.). Although the function of sex combs is still unclear, sex comb patterns may contribute to promote mate recognition and hence may be relevant to the ecological

causes of speciation. However, it was argued that sexual selection by itself is unlikely to lead to speciation in sympatry but can easily produce species in allopatry (Turelli *et al.* 2001). The West (7 species)/East (6 species) partitioning of *dyula* relatives would support this view. Thus, the *fima* species group appears as a good model that deserves being studied further to understand how ecological processes and sexual selection drive speciation.

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