CHAPTER 3

Morphological comparison of *Culicoides (Avaritia) nudipalpis* Delfinado, 1961 and *C. (A.) imicola* Kieffer, 1913: reappraisal of their separate species status.

3.1 INTRODUCTION

Culicoides nudipalpis was described by Delfinado (1961) from four females collected on the island of Luzon, Philippines. The holotype has apparently been lost (Dyce 1979); Wirth & Hubert (1989) gave further notes on types and synonymy, and described the male for the first time from Sumbawa, Indonesia. To date, *C. nudipalpis* has been recorded only from various islands comprising the Philippines and Indonesia i.e. from Luzon in the north-west to Timor in the south-east. These fall east of Huxley's modification of the Wallace line (Rosen 1988). Except for the record of the type series taken in a carabao-baited trap, nothing is known about the biology of *C. nudipalpis*. Judging from its sparse treatment in the literature, it is either rare and/or seasonal in its presence or is being misidentified as one of the other commoner Oriental/Australasian species of the subgenus *Avaritia*. These would include *C. orientalis* Macfie, 1932, *C. brevitarsis* Kieffer, 1917, *C. flavipunctatus* Kitaoka, 1975 and *C. wadai* Kitaoka, 1980. *Culicoides imicola*, however, is very abundant and widespread, being found through most of Africa into the Mediterranean, and from thence across the Near and Middle East as far as Laos. In distribution *C. imicola* and *C. nudipalpis* are not contiguous as neither has been recorded from peninsular Malaysia, Sumatra, Java, Borneo and the Celebes.

Regarding their status as two species, it is notable that almost the entire redescription of *C. nudipalpis* by Wirth & Hubert (1989) word-for-word duplicates that given by them for *C. imicola*. Not surprisingly, they conclude that *C. nudipalpis* 'is nearly identical with *C. imicola* ... and very similar to *C. brevitarsis* ...'. Furthermore, comparison of Fig. 284 and 287 in Wirth & Hubert (1989) show the wings of *C. imicola* and *C. nudipalpis* to be remarkably similar if not inseparable. The single feature used by these authors to distinguish females of *C. nudipalpis* is 'the virtual absence of the palpal pit; the third palpal segment of *C. nudipalpis* has a round pitlike area on the surface, but it lacks depth'. For *C. imicola* the third segment is described as 'without definite sensory pit but with sensilla grouped in a circular area on surface of segment'. While the wording may differ, the meaning is similar. The same character is used to separate the males. Comparison of their descriptions suggests two further differences between *C. imicola* and *C. nudipalpis*: palpal ratio (PR) 2,3 vs 0,68 and proboscis/head ratio (P/H) 0,88 vs 0,68 respectively. The large difference between the palpal ratios is clearly a lapsus as measurement of Fig. 122b in Wirth & Hubert (1989) gives a PR of 2,25. However, they did not refer to the significant difference in P/H ratios.

This synopsis begs the question as to whether these are indeed two good species. Doubt as to their separate status deepens when one considers that two Indian species, *C. minutus* Sen & Das Gupta, 1959 and *C. pseudoturgidus* Das Gupta, 1962, have already been found to be synonyms of *C. imicola* (Dyce & Wirth 1983). If *C. nudipalpis* is shown to be yet another synonym, it would mean a further extension in the already large geographic range of *C. imicola*, from the southern tip of Africa to the northern doorstep of Australia. This possibility of synonymy is important as *C. imicola* is probably the most important vector of the viruses of bluetongue (BT) and African horsesickness (AHS) known in the Old World.

These questions, and the recent acquisition of five females and two males of *C. nudipalpis*, prompted its present comparison with *C. imicola*. As the sample size of *C. nudipalpis* is too small to attempt a full redescription of *C. nudipalpis*, only key characters are compared.

3.2 MATERIALS AND METHODS

Initial examination of fresh unmounted *C. nudipalpis* females in alcohol indicated the species to be smaller than *C. imicola*, especially as regards relative length of the proboscis. The taxonomic value of this apparent difference was further evaluated in slide-mounted specimens, along with eight other character states. The results are summarized (Table 3.1) and depicted graphically (Fig. 3.1). The graph compares proboscis length against wing-length; unconverted raw data were used. For tabulation the data were converted to μm.

To negate seasonal effects and geographic clines in the *C. imicola* data, 121 individuals representing eight populations from various ecological zones of Africa were randomly chosen, these augmented by three extralimital populations (Spain, Israel and Thailand). They are listed in Table 3.2. Data on males were taken from Meiswinkel (1989). *Culicoides nudipalpis* was represented by four females and two males from Mindoro Island, Philippines, and one female from the island of Timor (Table 3.1). Too few specimens of *C. nudipalpis* were available for a more detailed comparison.

3.2.1 Statistical analyses

Only five females of *C. nudipalpis* were available for analysis. To make fair comparisons, and to have equal representativeness, data on *C. imicola* in Table 3.2 were obtained from five randomly chosen specimens from each of nine populations. These 45 females form part of the 121 used to generate Fig. 3.1. Comparison between populations was done by means of an analysis of variance for a completely random design. Population means were compared by the Bonferroni method.

3.3 RESULTS

Nine character states were examined; the taxonomic value of each is assessed separately:

a. **Wing length**: Fig. 3.1 compares proboscis length against wing length. While separation of *C. imicola* (n = 121; 11 populations) from *C. nudipalpis* (n = 5; 1 population) is clear Bonferroni's analysis of variance revealed wing length to be an unstable character. Although considerable overlap occurred between the populations tested, *C. nudipalpis* did have the shortest wings (Table 3.1). Future scrutiny of a longer series may well prove *C. nudipalpis* to be smaller than *C. imicola*. As regards *C. imicola*, it is notable that little to no overlap exists in wing length between three South African populations, i.e. Ndumu, Upington and Stellenbosch. This result could be interpreted as representing three species, but as these same populations exhibit consistency in proboscis length, and all other

Fig. 3.1

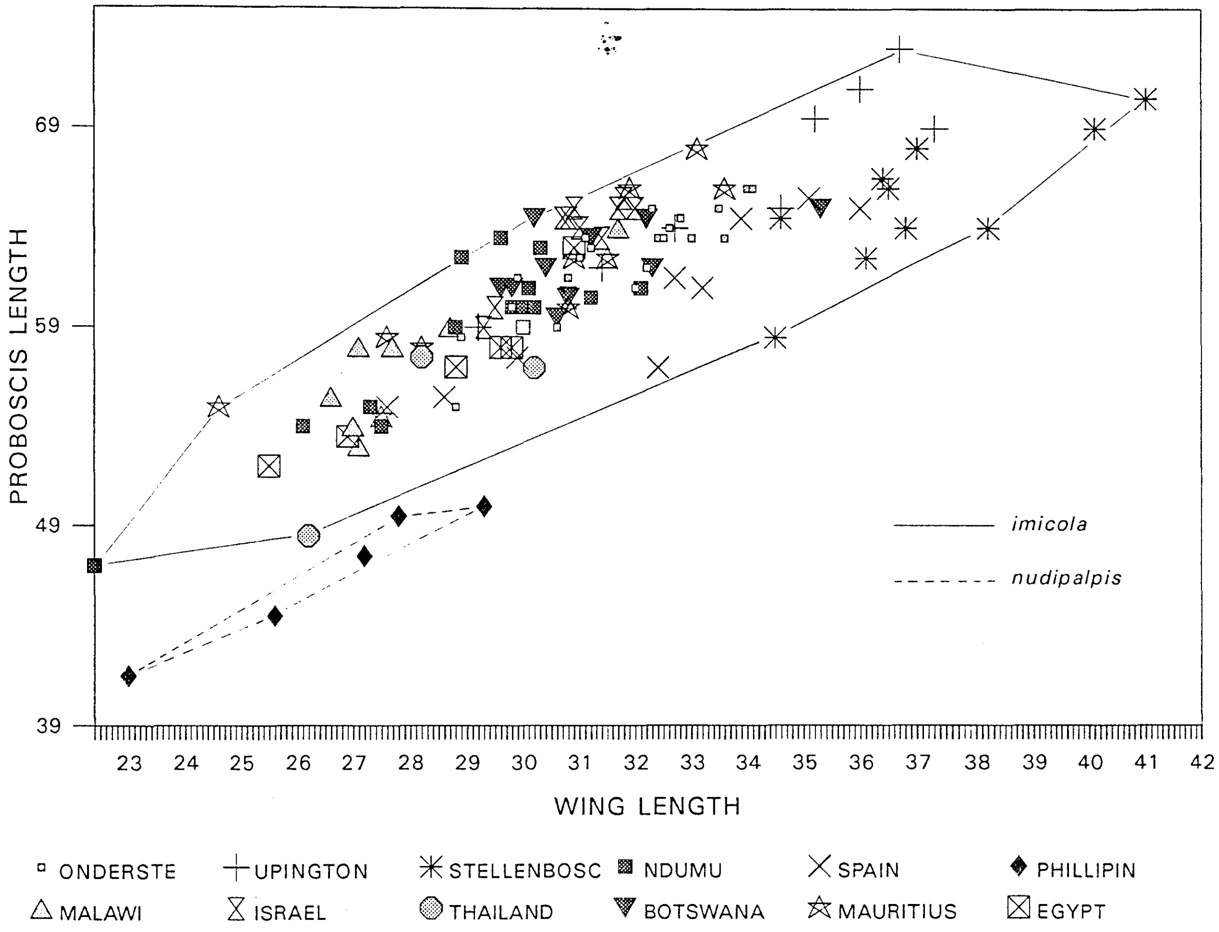


Fig. 3.1 Scatter diagram of proboscis length against wing length: separation of 11 populations of *C. imicola* (n = 121) from one of *C. nudipalpis* (n = 5).

characters, I do not hesitate to classify them as one species. This supports the earlier inference that wing length is unreliable, being more variable under environmental influences, whether nutritional or climatic. Hensley & Atchley (1977), in a study of natural and laboratory populations of the N. American *C. variipennis*, also found that there are 'highly significant differences among temperature groups in continuous body measurements, e.g., wing length and width ...'

b. **Proboscis length**: Table 3.1 and Fig. 3.1 show the proboscis of *C. nudipalpis* to be significantly shorter than that of *C. imicola*. Its usefulness as a distinguishing feature is graphically illustrated in Fig. 3.1: 24 % of the randomly chosen *C. imicola* specimens (representing ten of the 12 populations) have a wing length overlapping that of *C. nudipalpis*, but only 7 % (two specimens) share a similar proboscis length. One of the two *C. imicola* outliers is from northern Thailand and falls so near the *C. nudipalpis* data set in Fig. 3.1 that it could just as easily be identified as *C. nudipalpis*. While its intermediate position is suggestive of a geographic cline, it and the remaining two specimens from Thailand, have the antennal ratio, better defined palpal pit and coeloconica distribution typical of *C. imicola*. Such outliers alert us to the danger of basing identifications and descriptions on single specimens.

c. **P/H ratio**: A short proboscis results in a low proboscis/head (P/H) ratio. The data in Table 3.1 and 3.2 show that the difference in P/H between *C. nudipalpis* (0,66–0,73) and *C. imicola* (0,82–1,02) is highly significant. Indeed I consider this to be the most reliable way of separating these two species. These data support those provided by Wirth & Hubert (1989) for *C. nudipalpis*, and by Boorman (1991) for *C. imicola*.

d. **Antennal length**: Despite its small size the total antennal length of *C. nudipalpis* appears to be inseparable from that of *C. imicola* (Table 3.1). More data are needed to confirm this.

e. **Antennal ratio (AR)**: *Culicoides nudipalpis* has a significantly higher AR than *C. imicola* (n = 167; Onderstepoort population). Fig. 3.1 shows 24 Onderstepoort specimens to fall in the centre of all *C. imicola* populations scored, and thus to be reliably representative of the species.

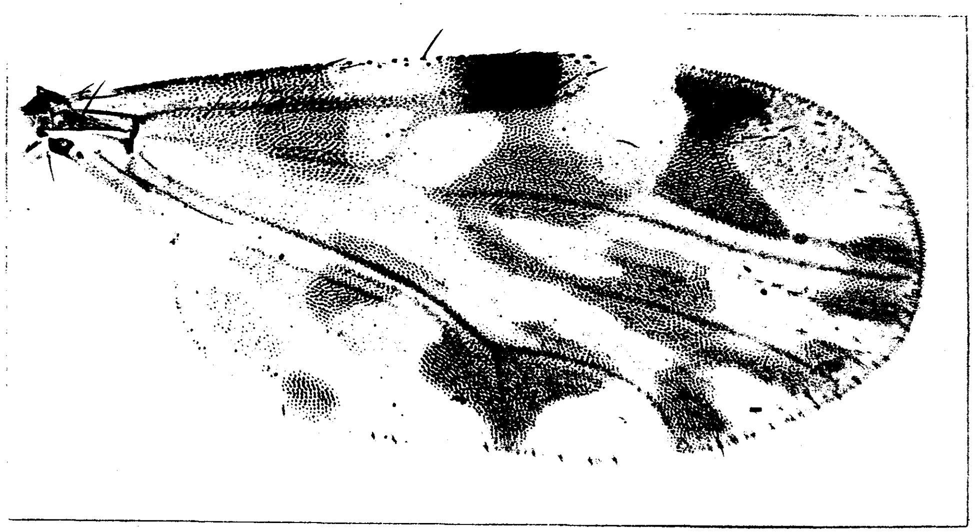
A higher antennal ratio indicates that the combined length of the distal five flagellar segments is longer than that of the basal eight segments. In *C. imicola,* a smaller difference exists between these two measurements resulting in a lower AR. The AR data provided by Delfinado (1961) and Wirth & Hubert (1989) differ from those presented here (Table 3.1). This may be due to mixed series or differing methods of mensuration.

f. **Sensilla coeloconica distribution**: Four of the nine *C. nudipalpis* female antennae examined have a coeloconica distribution of 3, 11–15; the remaining five (56 %) have 3, 12–15. In *C. imicola* only seven (4 %) of 172 antennae examined had a coeloconica on segment 11 (Onderstepoort population). The difference between the two species is significant but unreliable for identification, as more than half of the individuals examined of both species shared the coeloconica distribution of 3, 12–15.

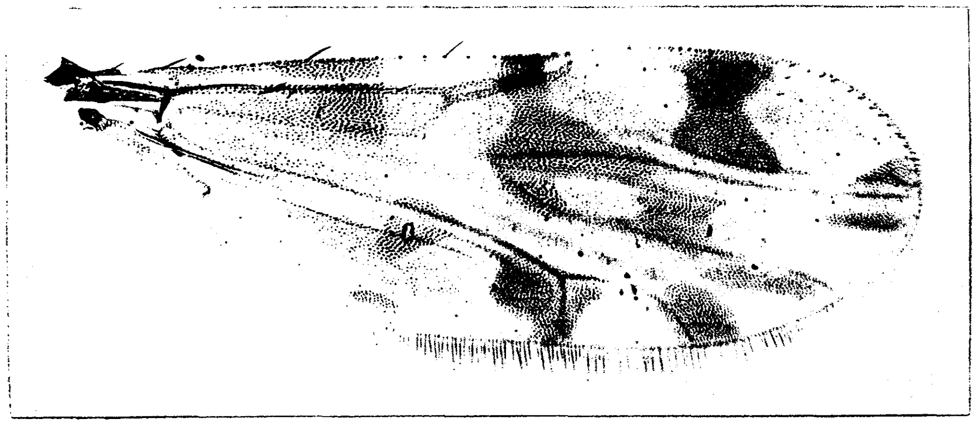
g. **Third palpal segment**: In their key to the south-east Asian *Culicoides*, Wirth & Hubert 1989) separate *C. nudipalpis* and *C. imicola* in that the former has ‘third palpal segment with indistinct pit, the margins not definite’; the latter has the ‘segment with distinct pit with well-defined sunken margins’. While this differentiation is more positive than the vague textual one made by Wirth & Hubert (1989) the key does pinpoint what appears to be an important difference between *C. nudipalpis* and *C. imicola.* Although few specimens of *C. nudipalpis* were examined, the palpal pit conformed with both the Delfinado (1961) and Wirth & Hubert (1989) descriptions. In most of the *C. imicola* material examined the palpal pit was better defined and deeper. However, the palpal pit may be a subjective character as its small size and variable angle of display can make accurate examination difficult. Furthermore, some specimens of *C. imicola* do have a shallow pit with poorly defined margins. To ensure accurate identification, the palpal pit is best used in combination with the P/H ratio.

h. **Wing pattern:** Comparison of Fig. 284 (*C. imicola*) with Fig. 287 (*C. nudipalpis*) in Wirth & Hubert (1989) shows the wing pattern of these two species to be virutally indistinguishable. This is confirmed by comparing two wing photographs of *C. imicola* (Thailand: Fig. 3.2 and 3.3) and two of *C. nudipalpis* (Timor: Fig. 3.4; West Irian: Fig. 3.5). The wing pattern feature

3.2



3.3



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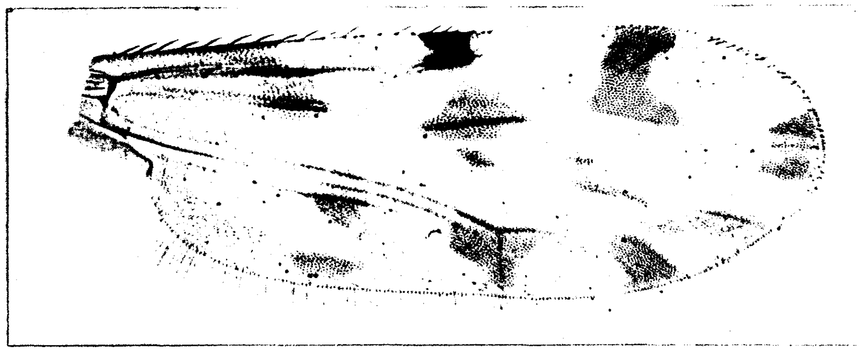

Fig. 3.2 *C. imicola*: Wing, female; Thailand (A.L. Dyce collection).

Fig. 3.3 *C. imicola*. Wing, male; Thailand (A.L. Dyce collection).

Fig. 3.4 *C. nudipalpis*. Wing, female; Timor (A.L. Dyce collection).

Fig. 3.5 *C. nudipalpis*. Wing, male; West Irian (A.L. Dyce collection).

that most reliably separates *C. imicola* from its known congeners *C. brevitarsis, C. pseudopallidipennis, C. bolitinos, C. miombo*, and *C. loxodontis*, is the preapical pale excision on the anterior margin of vein M_1 which leaves the apex of the vein broadly and squarely darkened. The same feature exists in *C. nudipalpis*, even though the preapical excision is inclined to straddle vein M_1 more deeply and broadly, almost separating the dark spot at the apex of the vein from the dark area straddling the same vein medially. However, this is a nicety; there is no doubt that the wings of *C. nudipalpis* and *C. imicola* are more similar to one another than to any other known member of the Imicola group worldwide. This strong similarity, if not representative of one species, at least confirms the two species to be closely related.

i. **Male genitalia**: The two specimens of *C. nudipalpis* had 84 and 112 spicules on the sternital membrane, so are moderately densely spiculate. This is approximately double the mean of 47 found in 50 specimens of *C. imicola* (Meiswinkel 1989). However, the range in *C. imicola* is considerable: 8–145 spicules. This comfortably embraces the number found in *C. nudipalpis*. Otherwise the genitalia of *C. nudipalpis* are very similar to, if not inseparable from, those of *C. imicola*.

3.4 CONCLUSION

Culicoides imicola and *C. nudipalpis* are good species, most easily distinguished in proboscis length and P/H ratio. Characters of secondary significance are body size, antennal length, antennal ratio (AR), sensilla coeloconica distribution, and definition of sensillar pit on the third palpal segment. Current data suggest that *C. imicola* and *C. nudipalpis* occur allopatrically; they are found west and east of the Wallace line respectively. This allopatry is another useful aid to identification. The two species are virtually inseparable in wing pattern and male genitalia. Longer series of both sexes of *C. nudipalpis* need to be examined to more fully quantify species differences.

Taxonomically there seems little doubt that *C. imicola* and *C. nudipalpis* are true sister species; they form a subgroup within the Imicola group of the subgenus *Avaritia*. The Imicola group comprises seven currently known species; five are found in Africa i.e. *C. imicola, C. pseudopallidipennis, C. bolitinos,* *C. miombo* and *C. loxodontis*, the remaining two (*C. nudipalpis* and *C. brevitarsis*) being in the Oriental/Australasian Region. The presently known allopatric distribution pattern of *C. imicola* and *C. nudipalpis*, west and east of the Wallace line respectively, suggests ancient vicariance involving the splitting of an ancestral species into two populations with subsequent speciation. It may be argued that *C. nudipalpis* is a subspecies of *C. imicola*; only studies involving cross-mating and/or enzyme electrophoresis would clarify whether they are indeed genetically isolated, as this morphological study suggests.

In Africa, *C. imicola* predominates in the medium rainfall (300–750 mm/annum) savannas and savanna-woodland areas. It declines rapidly to virtually disappear in the higher-rainfall forested tropics and frost-prone highland regions (Itoua & Cornet 1986; Meiswinkel 1991; Venter & Sweatman 1989; Venter & Meiswinkel 1994). Under optimal conditions, *C. imicola* can become superabundant, especially in situations where man husbands various kinds of livestock and maintains them on sunlit, short-grassed, irrigated pastures. In such locales, *C. imicola* can comprise 96 % of very large *Culicoides* collections made (Nevill 1971). Virtually nothing is known about the host preferences of *C. nudipalpis*, besides the fact that the type series was collected in a carabao-baited trap. In a recent study of *Culicoides* associated with poultry on the island of Luzon, Philippines, not one specimen of *C. nudipalpis* was recorded among >10 000 specimens of 17 species collected (Abella, Manuel, Cariaso & Kamiya 1994). This further suggests that *C. nudipalpis* is strictly mammalophilic.

Where known, the immature stages of *Avaritia* species worldwide thrive in semi-moist habitats such as animal dung, rotting fruits, humus, leaf-litter and fungi. The pupae do not float at the water surface, and are thus prone to drowning in any situation that becomes waterlogged (e.g. ricefields). These realities may help explain why *C. imicola*, and its sister-species *C. nudipalpis*, do not occur in abundance in the higher rainfall tropics of Africa and south-east Asia despite the presence of animal hosts. In this regard it is relevant to note that in a survey of *Culicoides* associated with cattle in Indonesia, the most specimens of *C. nudipalpis* were collected at Kupang on the island of Timor; although this locale experiences a relatively high rainfall (1 250 mm/annum) this is offset by a long eight-month dry season (Sukarsih, Daniels, Sendow & Soleha 1994).

Culicoides imicola is recognized to be one of the most important vectors of bluetongue and African horsesickness known worldwide. It remains to be established whether its congener, *C. nudipalpis*, is equally efficient at vectoring these orbiviruses. It is clear that all aspects of the bionomics of *C. nudipalpis* need further research; these should include studies into its distribution and prevalence, and the factors restricting its abundance.

3.5 REFERENCES

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Table 3.1 Six character states separating *C. nudipalpis* and *C. imicola*; data according to Delfinado (1961), Wirth & Hubert (1989), and this study

Character	***C. nudipalpis***	**X**	**n**	***C. imicola***	**X**	**n**
Wing length	0,66–0,91	0,82	5	0,92–1,17	1,06	150
Definado	0,77–1,02	0,85	9	-	-	-
Wirth & Hubert	0,80	?	?	0,79–0,86	0,82	5
Proboscis length	103,8–125,0	116,5	5	117,5–177,5	156,8	45
Delfinado	-	-	-	-	-	-
Wirth & Hubert	-	-	-	-	-	-
Proboscis/head ratio (P/H)	0,66–0,73	0,70	5	0,82–1,02	0,90	45
Delfinado	-	-	-	-	-	-
Wirth & Hubert	0,68	-	-	0,88	-	-
Antennal length	428,8–502,5	477,5	5	435,0–494,5	466,0	25
Delfinado	-	-	-	-	-	-
Wirth & Hubert	-	-	-	-	-	-
Antennal ratio (AR)	1,06–1,12	1,07	5	0,95–1,10	1,01	167
Delfinado	1,09–1,18	1,14	4	-	-	-
Wirth & Hubert	1,20	-	-	1,17–1,19	1,18	2
Sensilla coeloconica	3,11–15 (44 %)	-	9	3,11–15 (4 %)	-	172
	3,12–15 (56 %)	-	9	3,12–15 (96 %)	-	172
Delfinado	3,11–15	-	-	-	-	-
Wirth & Hubert	3,11–15 (?)	_	_	3,11–15 (?)	-	-
	3,12–15 (?)	-	-	3,12–15 (?)	-	-

TABLE 3.2 Comparison of means (Bonferroni) of nine populations of *C. imicola* with one of *C. nudipalpis*; means connected by a continuous vertical line are not significantly different at 5 %

Species and population		Proboscis length (μm)		P/H ratio		Wing length (raw data)	
C. nudipalpis	(n = 5):						
	(n = 4)	Philippines	46,600	Philippines	0,700	Philippines	26,580
	(n = 1)	Timor					
C. imicola	(n = 45):						
		Malawi	57,600	Israel	0,858	Malawi	28,320
		Ndumu	57,900	Ndumu	0,880	Ndumu	28,640
		Spain	61,700	Mauritius	0,884	Mauritius	30,360
		Mauritius	61,900	Stellenbosch	0,896	Botswana	30,740
		Botswana	62,600	Upington	0,900	Israel	31,080
		Israel	63,600	Spain	0,904	Onderstepoort	32,420
		Onderstepoort	64,000	Onderstepoort	0,908	Spain	32,740
		Stellenbosch	66,800	Malawi	0,908	Upington	35,180
		Upington	68,200	Botswana	0,976	Stellenbosch	36,920
F-value			13,048		17,590		8,492

CHAPTER 4

Culicoides (Avaritia) miombo Meiswinkel, 1991, a widespread species closely allied to *C. (A.) imicola* Kieffer, 1913 (Diptera: Ceratopogonidae)

4.1 INTRODUCTION

During a study monitoring bluetongue virus (BTV) activity in a Nigerian dairy herd, Herniman, Boorman & Taylor (1983) collected >70 000 *Culicoides* over a 12 month period. They found that only two species, *imicola* and *schultzei*, occurred throughout the wet and dry seasons, and these were thus deemed the most likely to be involved in bluetongue transmission. However, they noted that each species 'may be placed with a few close relatives, distinguishable only with difficulty, into species groups. It was impractical to differentiate species on a project of this scale and accordingly these insects were enumerated in terms of species groups ...; for convenience these species groups are referred to ... as *imicola*, *milnei* or *schultzei*.' Elsewhere they note that the species closely related to *C. imicola* are *C. brosseti*, C. *grahamii* and *C. kibatiensis*, and that they occurred in proportions of 'approximately 2:1:1:0,5', and that these proportions remained much the same throughout the period of their study.

The four last-mentioned species all belong in the subgenus *Avaritia*, which is commonly, but mistakenly, equated in the literature with the Imicola group (Itoua & Cornet 1986; Glick 1990). In fact, these four species belong in four separate species groups; these groupings are recognized by Itoua & Cornet (1986) but are ranked by them as subgroups only. In my assessment, approximately 10 groups represent the 70 species constituting the subgenus *Avaritia* worldwide. Their biologies are diverse, and within each group each species possesses a unique life-cycle. As conceded by Herniman *et al.* (1983), 'the relative importance of individual members of the *imicola* and other groups is unknown but it is clearly possible that differences in feeding habit or vector competence might differentiate between the species.'

In this chapter it will be shown that the species referred to by Herniman *et al.* (1983) as *C. brosseti* is in fact the recently described *C. miombo* Meiswinkel, 1992. Conversion of the Nigerian data show it can achieve some measure of abundance, namely that it represented approximately 6–8 % of all *Culicoides* captured. Although few data are available, those presented in this chapter indicate that *C. miombo* is tropical in its distribution, and in wetter climates can be more common than *C. imicola*. Herniman *et al.* (1983) also state that '*imicola*... showed a clear preference for cattle blood ...' and further reinforced their conclusion that it (or rather the group) is the principal vector of BTV in Nigeria.

As *C. miombo* forms a significant part of this group, and is taxonomically very closely related to *C. imicola* s.s., it may also be playing a role in virus transmission. It follows that the lumping of species with diverse life strategies into groups can detrimentally affect interpretations as regards the epidemiology of a particular disease. The situation can be improved, in part, by refining the taxonomy of Afrotropical *Culicoides*. This, in turn, should promote more detailed investigations into their larval habitats, prevalence, geographic distribution and vector competence. Only then can each species be more reliably linked to, or disassociated from, the presence of a specific orbiviral disease.

The redescription of *C. miombo* is introduced with a brief description of the floristic composition and geographical extent of wetter Zambezian miombo woodland south of the equator, and of drier Guineo-Congolian rainforest and Sudanian woodland north of the equator. This is done to indicate the basic climatic preferences of *C. miombo* and, to initiate the exploration and definition of the ecozone preferences of various *Culicoides* species in Africa. It is the sympatric occurrence of various biota that will produce the patterns needed to elucidate the biogeography of this genus, a subject which has been almost wholly neglected in the region.

4.2 RESULTS

Africa, including Madagascar, is divided into 20 major phytochoria, which are further subdivided into 80 major vegetation units (White 1983). *Culicoides miombo* is for the present recorded from or very near to 14 of these units which fall into six of the major phytochoria; these 14 units form part of forest, forest transitions, woodlands and woodland transition zones. These phytocoria and vegetation zones are listed in Table 4.1 and then briefly discussed in the text to indicate the broad climatic preferences of *C. miombo*. This is followed by a more detailed description of topography, vegetation and climate of the type locality of the new species in Malawi.

4.2.1 Phytochoria with which *C. miombo* is associated

The type locality of *C. miombo* in Malawi is dominated by *Brachystegia* woodland (Leguminosae: Caesalpinioideae), and falls into the mapping unit 25 of White (1983) classified as 'wetter Zambezian miombo woodland'. Wetter miombo, however, is only one of 20 vegetation types comprising the Zambezian regional centre of endemism. For a detailed account see White (1983).

As to climate, almost the entire Zambezian region falls within the tropical summer rainfall zone. There is a single rainy season, chiefly from November to April with rainfall being between 500–1400 mm/annum. Precipitation in general decreases from north to south, but there are pronounced regional variations. Mean and annual temperatures range from 18–24 °C. There are three seasons: 1. Wet season November–April, where rain falls mostly as thunder-showers and heavy showers, with a fair amount of sunshine. 2. Cool season May–August, where day temperatures are moderately high with continuous sunshine; night temperatures are low and ground frosts may occur in sheltered valleys. 3. Hot season September–November, where temperatures and atmospheric humidity progressively increase until the oppressive feeling in the air is relieved by the advent of rains.

On the African mainland south of the equator, *C. miombo* has been positively identified from five other localities i.e. Rekomitjie (16°08'S, 29°24'E), north-western Zimbabwe; Maun (20°01'S, 23°25'E), northern Botswana; Ndumu (26°55'S, 32°15'E), northern Natal, South Africa; Skukuza (24°58'S, 31°36E) north-eastern Transvaal, and Tiwi (4°14S, 39°34'E) south-eastern Kenya. The records of *C. brosseti* from Dundo (9°46'S, 14°42'E), north-western Angola by Kremer (1972) and the species labelled as A–1 and A–10 by Kitaoka & Zulu (1990) from Chilanga (15°54'S, 28°35'E), Zambia in all probability refer to *C. miombo* (Fig. 4.1).

North of the equator *C. miombo* has been recorded as *C. imicola* from Ife, Nigeria (Kitaoka, Kaneko & Shinonaga 1984), and as *C. brosseti* Vattier & Adam, 1966 from Ibadan and Vom, Nigeria (Boorman & Dipeolu 1979). The record of *C. brosseti* from Simousso, Burkina Faso (Cornet 1969) quite likely also refers to *C. miombo*. It is now recorded for the first time from five localities in the Ivory Coast, i.e. Parhadi (8°27'N, 3°29'W), Ganse (8°35'N, 3°54'W), Korhogo (9°27'N, 5°39'W), Yamoussoukro (6°49'N, 5°15'W) and Biankouma (7°45'N, 7°18'W).

There are important parallels between the Sudanian phytochorion north of the equator and the Zambezian one south of the equator. Their climates are broadly similar, especially with regard to rainfall. In the Sudanian, however, temperatures are appreciably higher (24–28 °C) and nearly constant year-round, while frost is unknown; the dry season is more severe. Floristically, Sudanian *Isoberlinia* woodland (units 27, 30 and 32) can be regarded as an impoverished variant of miombo woodland.

Off the African mainland, the single record of *C. brosseti* (Kremer & Brunhes 1972) from Manakara, Madagascar, is quite likely a misidentification of *C. miombo*. Manakara (22°06'S, 48°00'E) is on the eastern coast, an area that falls into White's major phytochoria XIX (the East Malagasy regional centre of endemism) and in vegetation unit 11b, a mosaic of lowland rainforest and secondary grassland.

Table 4.1 lists all these localities and briefly indicates the vegetation unit, altitude, mean annual temperature, rainfall and incidence of frost at these localities in western and southern Africa. Fig. 4.1 and 4.2 map the localities and the phytochoria they occupy. Localities accompanied by a question mark are those from which I have not seen specimens of *C. miombo*.

4.2.2 **Type locality (Fig. 4.3)**

Description of the lakeshore plains of Malawi

Malawi is a small landlocked country that lies partially in the southernmost extension of the great African Rift Valley. Where the rift runs through Malawi it is 40–90 km wide, but much of it is under Lake Malawi (570 km long x 80 km wide). Broadly speaking, Malawi comprises five major landscape types (Fig. 4.3a).

The type series of *C. miombo* consists of 142 specimens (74 ♀♀ 68 ♂♂) collected at Kawalazi (11°37'S, 34°06'E) and Limphasa (11°38'S, 34°13'E) in north-eastern Malawi (Fig 4.3b). These locales are 12 km apart and lie 600–700 m a.s.l. between the towns of higher-lying Mzuzu (1 235 m; 11°27'S, 34°01'E) and lower-lying Nkhata Bay (481 m; 11°36'S, 34°18'E). This hot lowland area with a mean maximum temperature in November of 35 °C, lies in the Rift Valley trough, known as the lakeshore plains; the trough runs along most of the central length of Malawi. The plains, in which isolated hills

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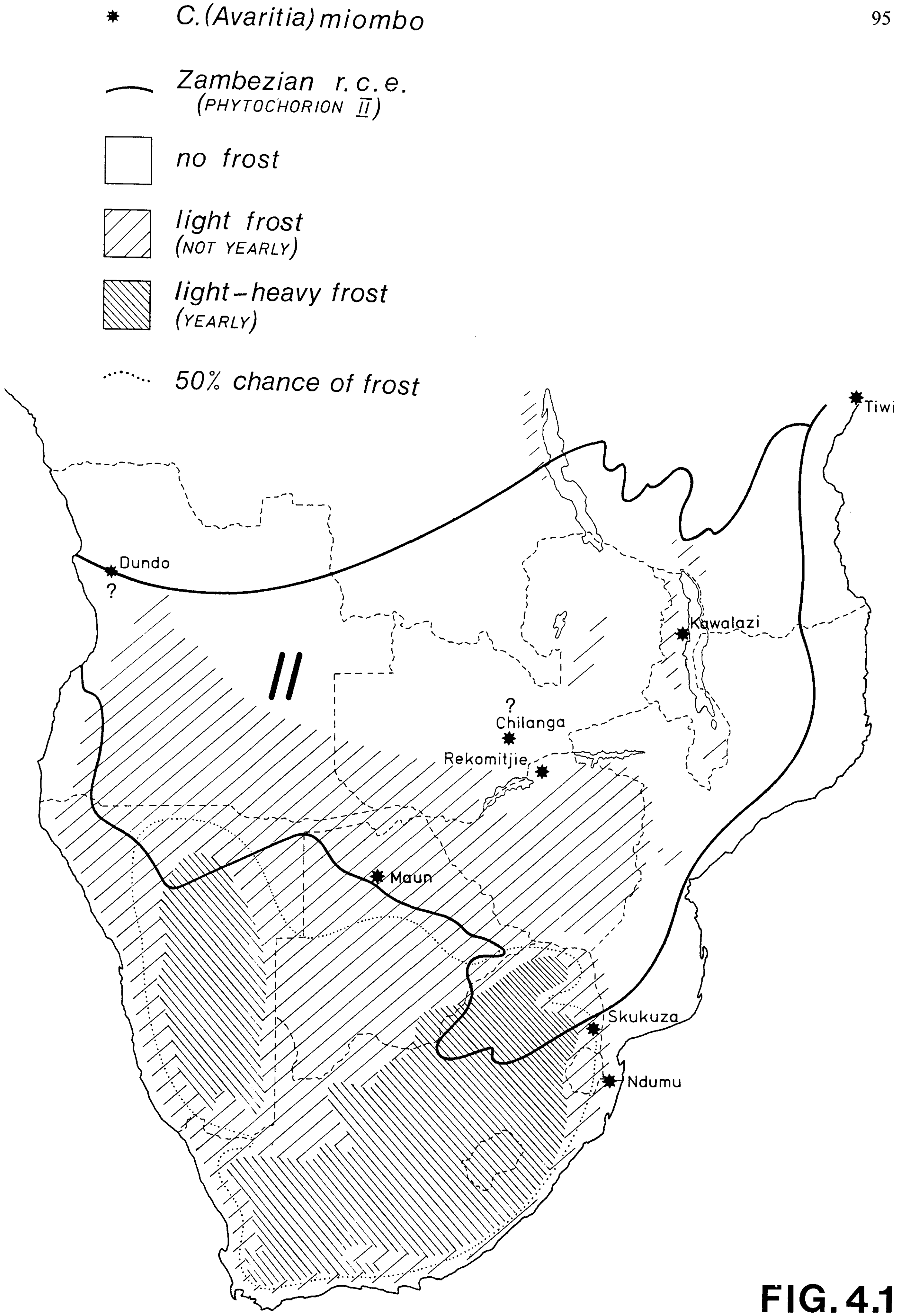


FIG. 4.1

Fig. 4.1 Map of southern Africa detailing the extent of the Zambezian regional centre of endemism (r.c.e.) (phytochorion II), the prevalence of frost, and the localities where *C. (Avaritia) miombo* has been collected.

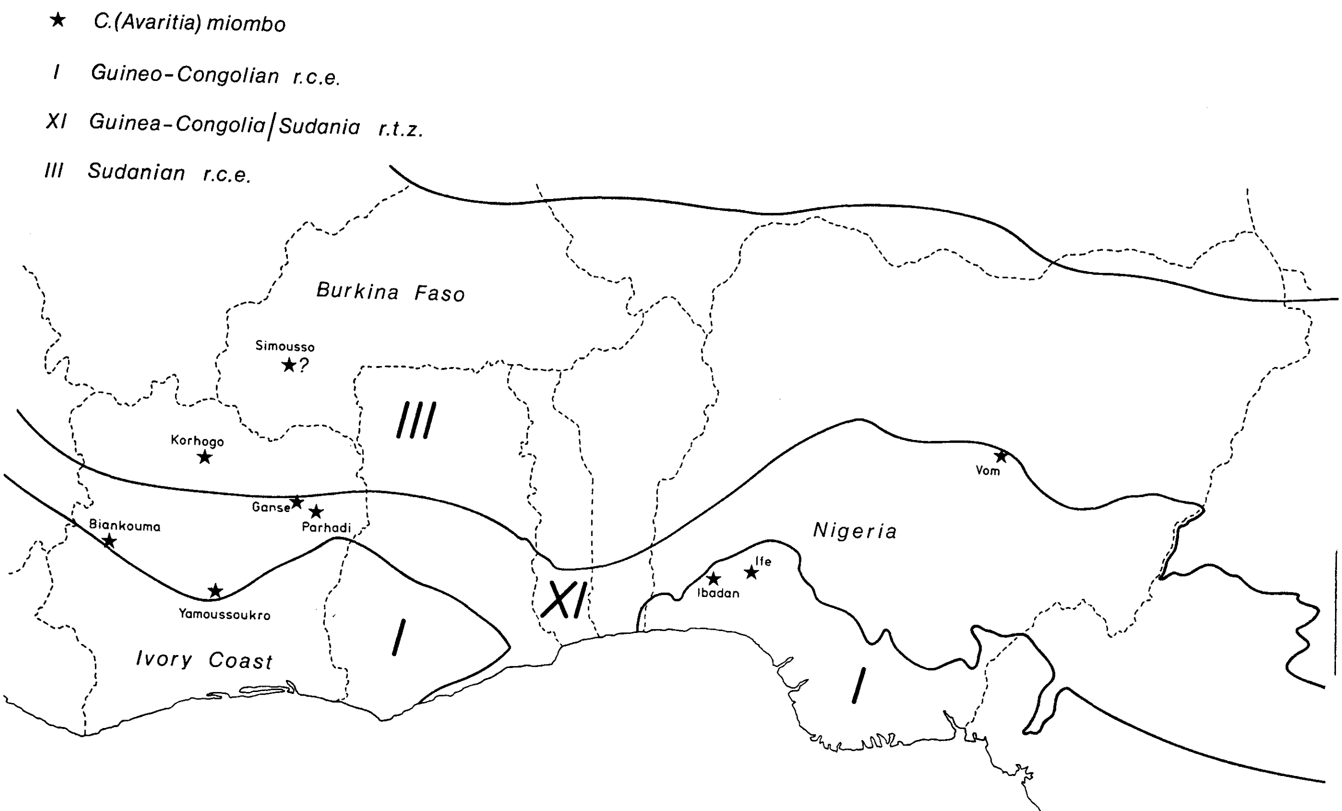


Fig.4.2

Fig. 4.2 Map of western Africa detailing the extent of the Guineo-Congolian and the Sudanian regional centres of endemism (phytocorion I and III); the Guinea-Congolia/Sudanian regional transition zone (r.t.z.) (phytochorion XI), and the localities where *C. (Avaritia) miombo* has been collected.

frequently arise, vary in extent but may be as wide as 25 km. In these wider sections, such as between Kawalazi and Nkhata Bay, the natural vegetation is lowland woodland with large and small swampy areas fed by numerous streams and rivers; these waters originate in the jumble of hills and ridges that make up the western escarpment. The fertile red alluvial soils of the plains have been developed for large-scale agricultural projects, as well as subsistence agriculture. The escarpment, which forms the western border of the lakeshore plains, consists of a series of low terraces which represents old shorelines of the lake; most of these slopes are covered in *Brachystegia* woodland and are generally not highly populated. Rainfall and temperature data for Kawalazi are not available, but during the years 1963–1977 higher-lying Mzuzu had a mean annual rainfall of 1 218 mm, a mean minimum temperature of 11,7 °C, and a mean maximum of 17,8 °C. For the years 1955–1977, lower-lying Nkhata Bay had corresponding figures of 1 695 mm, 18,8 °C and 27,8 °C. The data for Kawalazi would be most similar to that of Nkhata Bay, except for rainfall averaging nearer 1 400 mm per annum (Piet Verster, Kawalazi Estates, personal communication 1990).

At Kawalazi the *Brachystegia* woodlands (miombo) are not in a pristine state, but are under some pressure from man. Much of the area between Mzuzu and Nkhata Bay is cultivated, with large tracts planted to *Hevea* rubber (Vizara estate), tea and coffee (Chombe and Kawalazi estates) and eucalyptus. Besides such corporate investments, Malawians also clear smaller areas for fruit, cassava and grain crops. Because their protein intake comprises largely fish, not many cattle or other domesticated breeds are kept in this area. Between the cultivated sectors, however, fairly sizeable tracts of *Brachystegia* woodland still exist. At Kawalazi the light-trap was operated on the western slope of the Mphezi hills (Fig. 4.3b), in largely undisturbed *Brachystegia* woodlands with a moderate amount of foliage between the sparse field layer and the lower canopy at 5–8 m. A shaded, moist, and well-vegetated depression was located 100 m away from the light-trap and was fed by a small, constantly-running stream. No domesticated stock occurred in the immediate vicinity; game consisted of a small troop of baboons, smaller mammals and birds. Kawalazi was randomly monitored by light-trap over most months starting October 1987 through to April 1989; this revealed *C. miombo* to be entirely absent during the drier months of October and November. It was only after rains had commenced that *C. miombo* appeared but always in low numbers, for example in April 1989 only 54 specimens (0,9 %) of a total of 6 043 *Culicoides* collected were of this species.

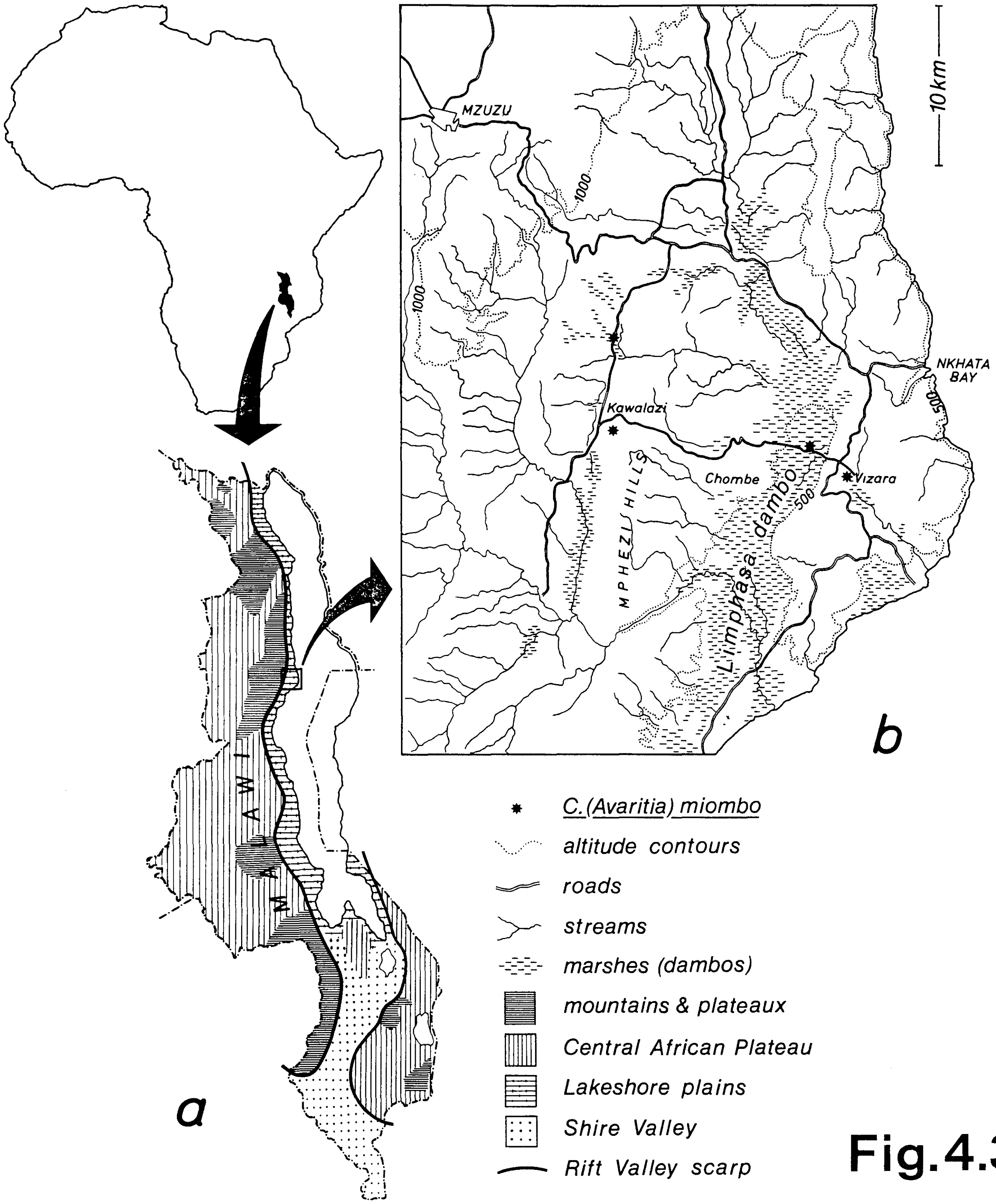


Fig.4.3

Fig. 4.3 (a) Map of Malawi showing five major landscape types, and (b) in greater detail, the topography of the type locality of *C. (Avaritia) miombo*.

Twelve km to the east of Kawalazi, near Vizara, is found the extremely large Limphasa dambo (Fig. 4.3b) or marsh that is some 30 km long and 0,5–3 km wide. It is thickly vegetated with 1 m high grasses and herbage, is saturated underfoot, and fed by quietly flowing, meandering streams. Occasionally very large palms and associated bush trace an eccentric line through the dambo. Elsewhere, small parts of the dambo are planted to rice. A number of small scattered villages have arisen on the low banks of the dambo; here some cattle are kept and spend their days grazing the drier parts of the marsh.

The collecting of *Culicoides* at Limphasa was done on two occasions, once only during each of the hot, dry months of October and November, 1987, by truck-trapping on a slightly elevated road that transected the dambo. On these two occasions a total of four females and more than 100 males of *C. miombo* was caught at dusk. The presence of so many males could have been the result of a mating swarm being captured which in turn suggests that the larval habitat of *C. miombo* was in close proximity.

One other site was sampled once by light-trap in November 1987, this was the cattle-kraal at the Vizara rubber estate 4 km east of Limphasa. Here only two ♀♀ of *C. miombo* were caught amongst 359 *C. imicola* and 71 *C. bolitinos*.

4.2.3 ***Culicoides (Avaritia) miombo*** **(Fig. 4.4–4.14; Table 4.2–4.7)**

Culicoides brosseti Vattier & Adam: Boorman & Dipeolu 1979: 17. Nigeria (misident.).
Culicoides imicola Kieffer: Kitaoka, Kaneko & Shinonaga 1984: 458. Nigeria (misident.).

Female (Fig. 4.4–4.8, 4.13, 4.14; Table 4.2–4.7)

Head. Eyes (Fig. 4.4); seemingly bare but mostly sparsely to moderately hairy, with hairs absent from a transverse band formed by the median three to eight rows of facets; eyes contiguous for a distance of between one and two facets. Antenna (Fig. 4.5, 4.13; Table 4.2–4.5) slender, basal segments IV–IX barrel-shaped, distal segments X–XIV faintly vasiform narrowing perceptibly subapically, XV nearly parallel-sided only narrowing apically; mean lengths of antennal segments III–XV: 36,8–23,3–23,6–25,7–28,1–27,3–28,2–32,7–44,6–46,0–48,4–49,5–83,3 µm (n = 68); total length of antenna: 470,0–537,5 mean 505,2 µm (n = 36); widths of antennal segments III–XV:

28,1–20,0–17,5–16,3–15,0–15,6–15,6–15,0–14,4–14,4–14,4–13,7–15,0 μm (n = 1); AR 1,09–1,25, mean 1,15 (n = 66); sensilla coeloconica present on segments III, XII–XV in 97 % of antennae examined (n = 70), see Table 4.3 for deviations from the norm; sensilla chaetica distribution on segments III–XV was 5–3–2–3–2–3–2–3–0 (n = 70) in 97,5 % of antennae examined, see Table 4.4 for deviations from the norm; sensilla trichodea distribution of the LLc type i.e. each of segments IV–X with two long and one short blunt-tipped trichodea, segment III with only two long blunt-tipped trichodea (n = 70); AtR 1,27–1,76, mean 1,54 (n = 68); segments XI–XIV each with 8–12 sharp-tipped sensilla trichodea of varying lengths and thicknesses distributed in a basal and subapical whorl; XV with two times as many trichodea these distributed in a basal, median and subapical whorl (Fig. 4.5); similarly the short blunt-tipped basiconica range from 2–7 on each of the distal flagellar segments XI–XV (Fig. 4.5); all antennal segments uniformly clothed throughout with fine spiculae.

The distributions of sensilla coeloconica, chaetica and trichodea are given in Table 4.2. Palp (Fig. 4.6, 4.14; Table 4.6): of a moderate length, slender, light brown throughout, mean lengths of palpal segments I–V: 19,85–49,77–45,90–25,60–26,8 μm (n = 70); total length 147,5–177,5 μm, mean 162,6 μm (n = 70); palpal segment I with only one rather long chaetica (n = 70), II with two to four rather short chaetica mean 3,06 (91 % with three chaetica; n = 70); III moderately long and slender carrying only one to four rather short chaetica, mean 2,87 (75 % with three chaetica; n = 70), with a small, round and shallow subapical pit with opening about half the width of segment in diameter, margin of pit smooth but well-defined, IV with one to four chaetica, mean 2,44 (44 % with three chaetica; n = 70), V with no chaetica on median portion of segment but does always bear five short erect bristles apically; these bristles appear to be different in form and function to those chaetica found on the basal segments and are thus dealt with separately; PR 2,44–3,00, mean 2,80 (n = 70); P/H ratio 0,87–0,96, mean 0,91 (n = 20); mandible with 13–18 fine teeth, mean 15 (n = 64).

Thorax. Legs: brown with all femora narrowly pale basally and with fore and middle femora indistinctly pale apically. All tibiae with a narrow well-defined basal pale band; remainder of fore and middle tibiae brown while apices of hind tibiae are pale, TR 1,51–1,84, mean 1,66 (n = 70); comb on apex of hind tibia with five spines, the first being the longest and only slightly longer than the second (n = 70). Wing (Fig. 4.8): length 0,83–1,01 mm, mean 0,94 mm (n = 66); breadth 0,41–0,51 mm, mean 0,46 (n = 66),

Fig. 4.4

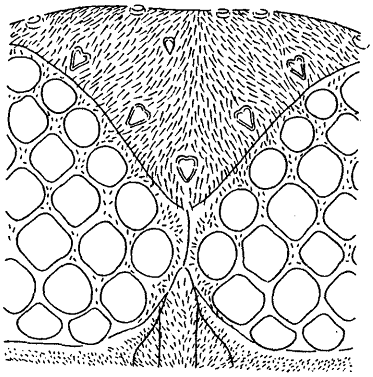


Fig. 4.4 *Culicoides (Avaritia) miombo*. Eyes, female (paratype Malawi 825).

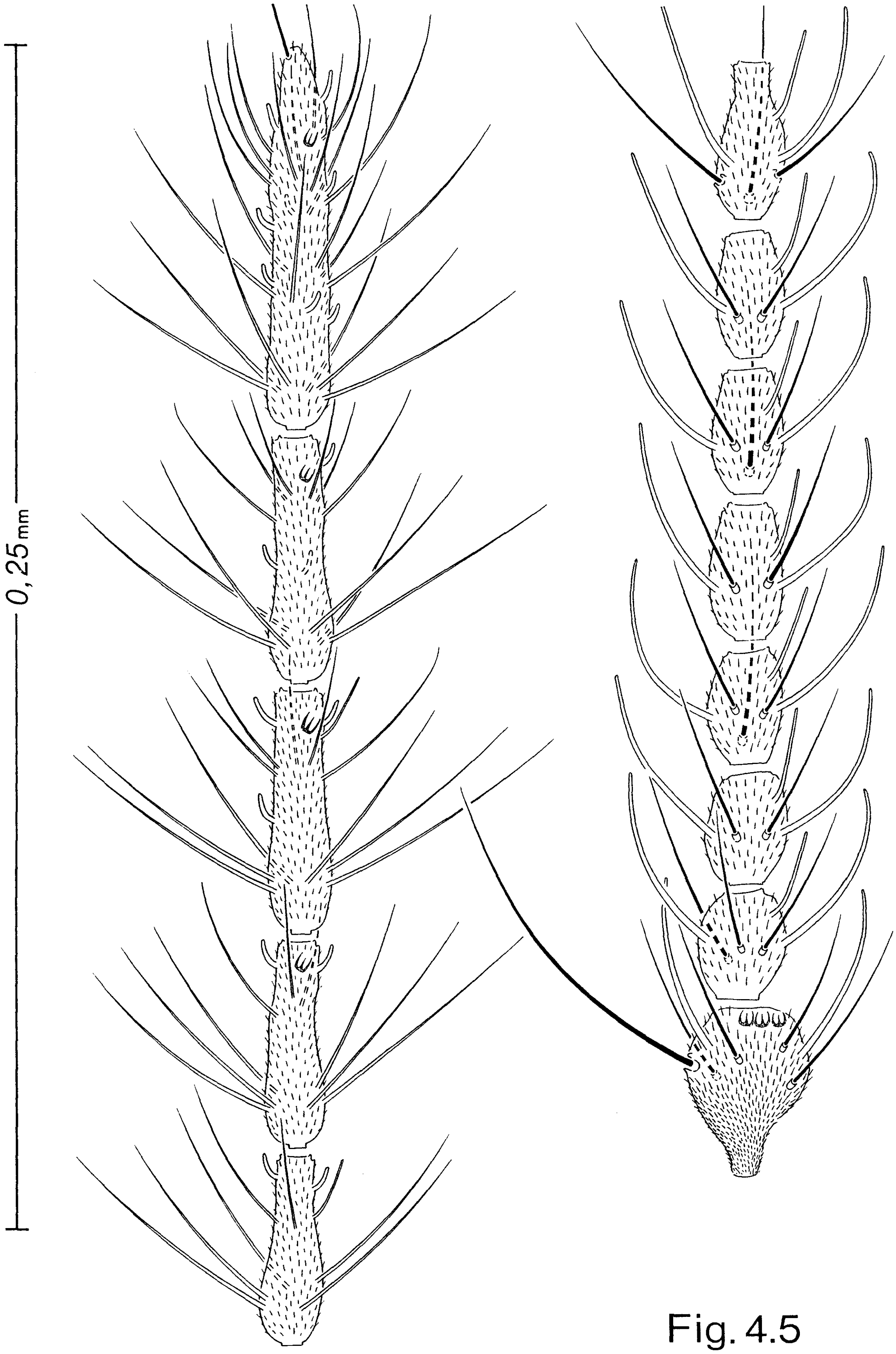
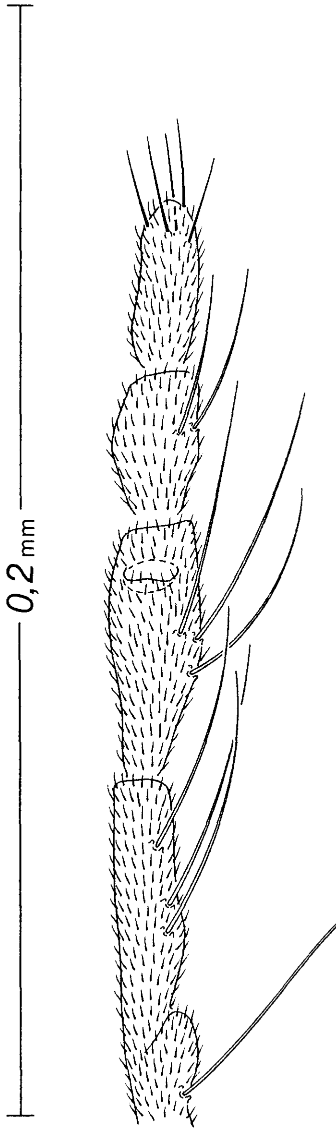


Fig. 4.5

Fig. 4.5 *Culicoides (Avaritia) miombo*. Antenna, female: segments XI–XV on left, segments III–X on right (paratype Malawi 822).



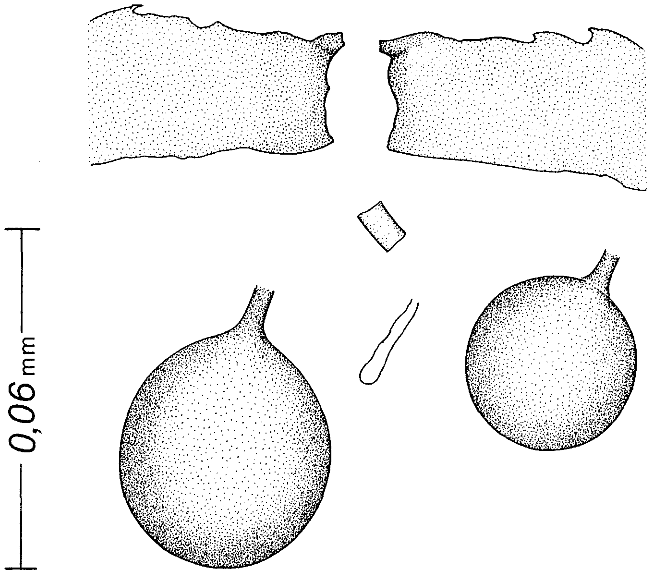


FIG. 4.7

FIG. 4.6

Fig. 4.6 *Culicoides (Avaritia) miombo*. Palp, female (paratype Malawi 813).

Fig. 4.7 *Culicoides (Avaritia) miombo*. Genitalia, female: spermathecae and sclerotization surrounding gonopore (paratype Malawi 809).

Fig.4.8

Fig.4.9

Fig. 4.8 *Culicoides (Avaritia) miombo*. Wing, female (holotype Malawi 820).

Fig. 4.9 *Culicoides (Avaritia) miombo*. Wing, male (holotype Malawi 951).

CR 0,56–0,60, mean 0,58 (n = 66); macrotrichia scanty, confined to distal third of wing in cells R_5, M_1 and M_2 only; microtrichia dense and coarse.

Dark pattern of wing greyish-brown, pale areas faint yellowish, fairly well defined but irregularly shaped; two radial cells, proximal half of first and distal third of second cell, pale. The wing of *C. miombo* is clearly darker than that of its congeners *C. imicola, C. pseudopallidipennis* and *C. bolitinos* as a result of the general reduction in the size of the pale areas. The most distinctive feature of the wing pattern is the elongate dark smudge which arises at the proximal base of the anal cell, cuts diagonally across the cell to terminate at the posterior wing margin well proximad of the apex of vein Cu_1. It is important to note that this smudge is divided into two by a fairly broad pale interruption subapically. Only in rare instances will these 2 dark areas be indistinctly and narrowly fused; only the smaller distal dark area is found in *C. imicola, C. bolitinos* and *C. pseudopallidipennis*. Other important species-specific wing pattern characters are: (i) pale costal spot two that straddles the r–m crossvein is reduced in size, slightly waisted medially, but expands to fairly broadly abut the anterior wing margin; (ii) distal or fourth pale costal spot in cell R_5 abuts wing margin, but in many specimens this spot is both reduced in size and isolated by a narrow dark strip that runs along the antero-distal wing margin; in rare dark forms this distal pale spot in cell R_5 almost disappears; (iii) proximal margin of this 4th pale costal spot rounded rather than sharply pointed; (iv) median third of anterior margin of vein M_1 never entirely pale but brownish; (v) vein M_2 has both margins very broadly darkened for most of its length, does not have a preapical excision on the anterior margin only but instead can be fairly abruptly tapered on both margins near its apex; however, this tapering still leaves both margins at the apex of vein M_2 dark, while in some darker specimens the tapering may again flare into a more broadly brown apex. Scutum brown in alcohol but strikingly adorned with two fairly large, yellow, very narrowly separated admedian vittae, scutellum narrowly brown medially, lateral margins broadly yellow; bearing one median bristle and one shorter bristle on each corner in 36/37 specimens, remaining specimen different in having two median bristles. Haltere knobs distinctly brown.

Abdomen (Fig. 4.7): Two moderately sclerotized, slightly unequal spermathecae present, measuring 40–50 x 35–41 μm and 34–44 x 29–35 μm (n = 20); both round and devoid of small hyaline punctations, with moderately long, narrow, pigmented necks; rather small, narrow, rudimentary third

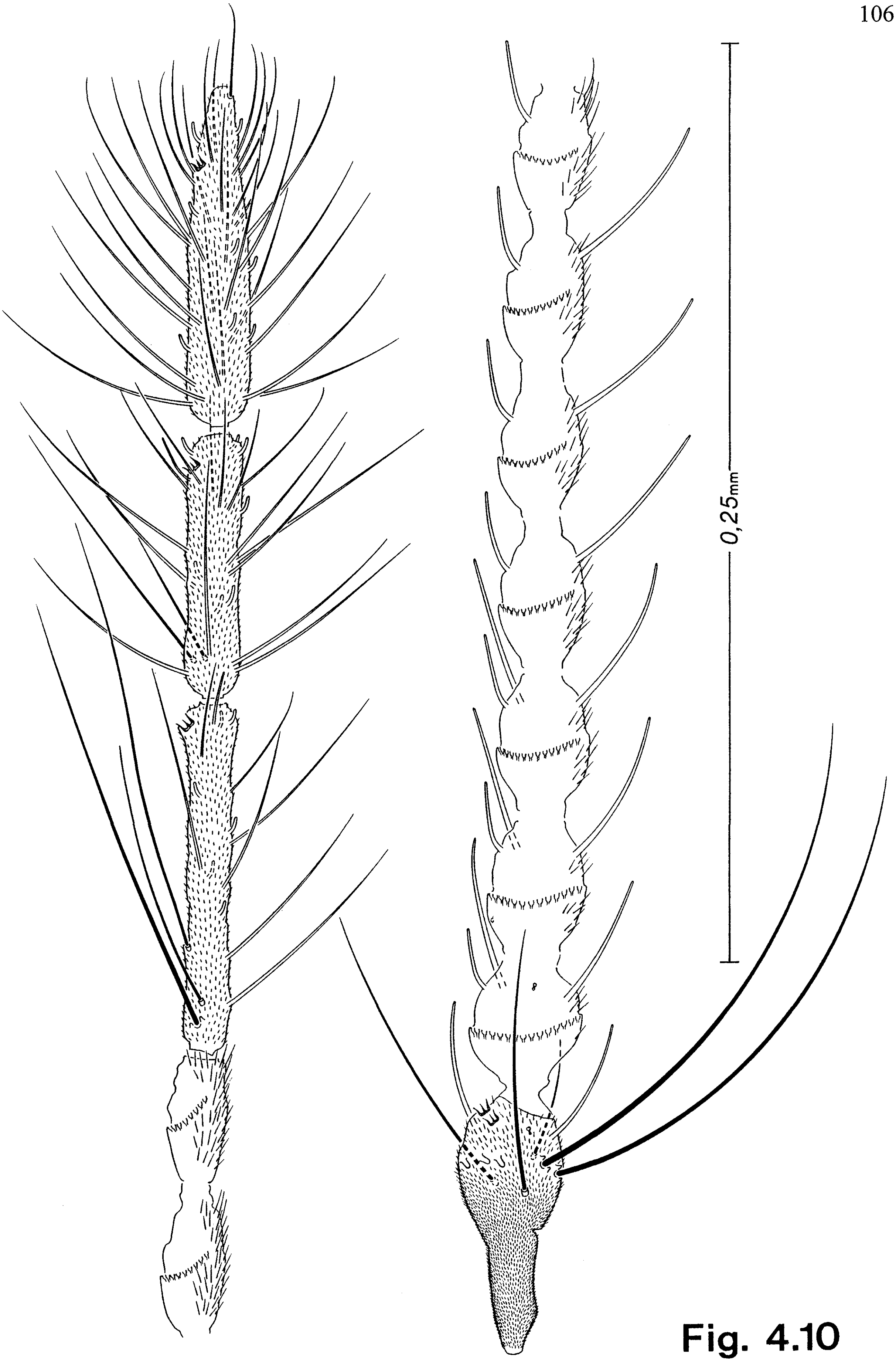


Fig. 4.10

Fig. 4.10 *Culicoides (Avaritia) miombo*. Antenna, male: segments XI-XV on left, segments III-X on right (paratype Malawi 834).

spermatheca present measuring 14–21 x 4 μm; small sclerotized ring on common spermathecal duct cylindrical, smooth and parallel-sided, a little longer than broad, and about half the length of the rudimentary spermatheca; sclerotization surrounding the gonopore as shown in Fig. 4.7.

Male (Fig. 4.9–4.12; Table 4.2, 4.7)

Head. Eyes sparsely hairy between most facets. Antenna (Fig. 4.10, Table 4.2): plume rather sparse, fibrillae light brown, almost completely encircling medially each of segments IV–XII in a regular whorl; these segments with very few spiculae, distal segments XIII–XV densely and evenly clothed with spiculae; lengths of segments III–XV: 71,3–36,3–37,5–37,5–37,5–37,5–37,5–37,6–37,5–36,3–96,3,75,0–92,5 μm (n = 1); sensilla coeloconica distribution: 100 % with two on segment III, 100 % with one on XIII, 100 % with one on XIV and 92 % with two and 8 % with one on XV (n = 25); sensilla chaetica distribution: five of varying lengths and thicknesses on III, two basally (first long and robust, second shorter and weaker) and one medially (being very slender and 1,5 x longer than segment) on XIII, two basally (both very slender but of different lengths, the one a little shorter than segment the other fractionally longer than segment) on XIV, none basally on XV only one apically (n = 25); sensilla trichodea distribution on segment III–XII: III with two long blunt-tipped trichodea, segments IV–VI with two long and one short blunt-tipped trichodea, segments VII–IX with one long and one short blunt-tipped trichodea, segment X with one short blunt-tipped trichodea only, segments XI and XII lacking trichodea (n = 25). The only deviation from the norm noted was an additional long blunt-tipped trichodea in two antennae on segment VII; this extra trichodea was shorter than normal and obviously aberrant. The distributions of the sensilla coeloconica, chaetica and trichodea are identical to those found in *C. imicola* and *C. bolitinos* and appear in Table 4.2.

Wing: (Fig. 4.9). Genitalia (Fig. 4.11, 4.12), tergum nine (Fig. 4.11) almost square, fractionally waisted transversely at midlength, finely spiculate throughout except for narrow strips of the anterior and posterior margins being bare, bearing 14–17 chaetica of different lengths, mean 15 (n = 25); apicolateral processes replaced by thin, hyaline flanges lacking tiny spiculae but each carrying a single fine, rather short straight chaetica issuing from the interface that comprises the base of the flange and the adjoining spiculate fringe where the concave body of the tergum commences, posterior margin of tergum which separates these flanges gently concave, lacking marked indentation or infuscation; two well-developed

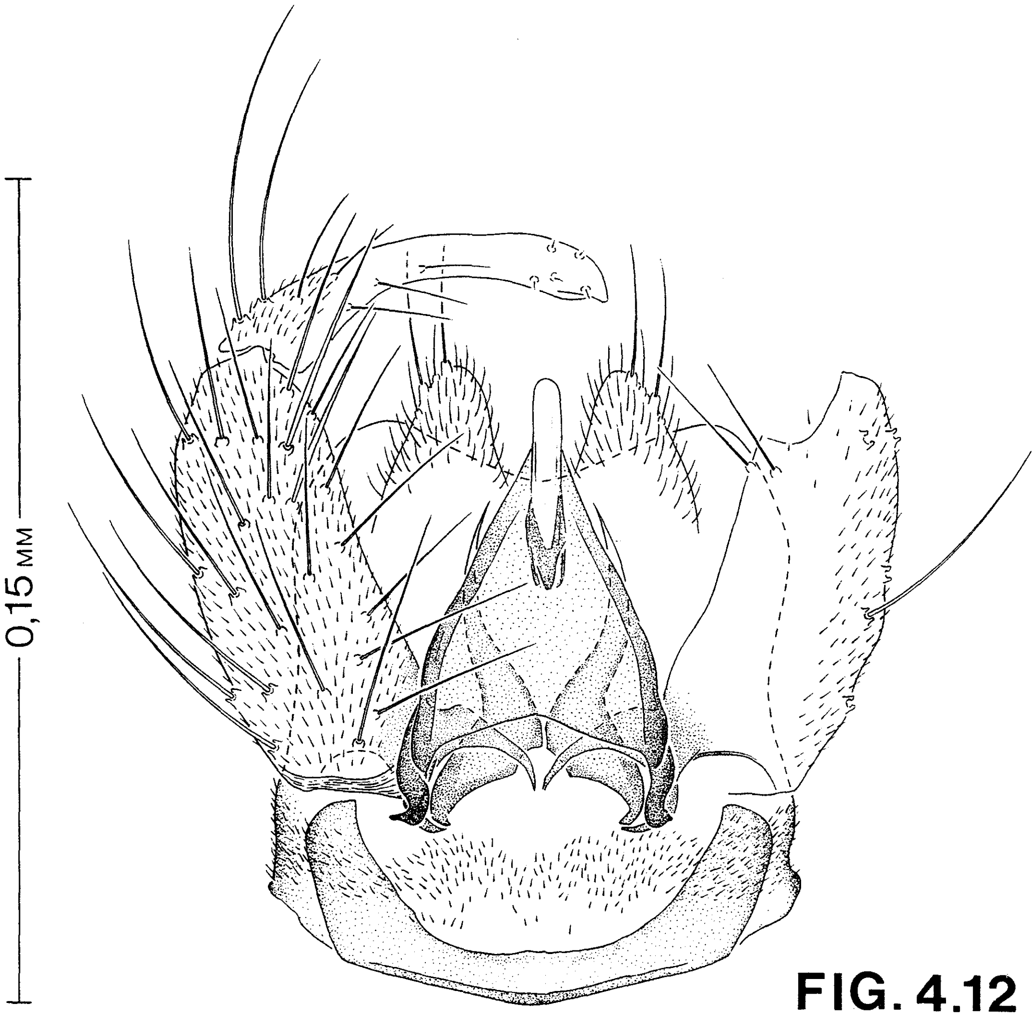


FIG. 4.12

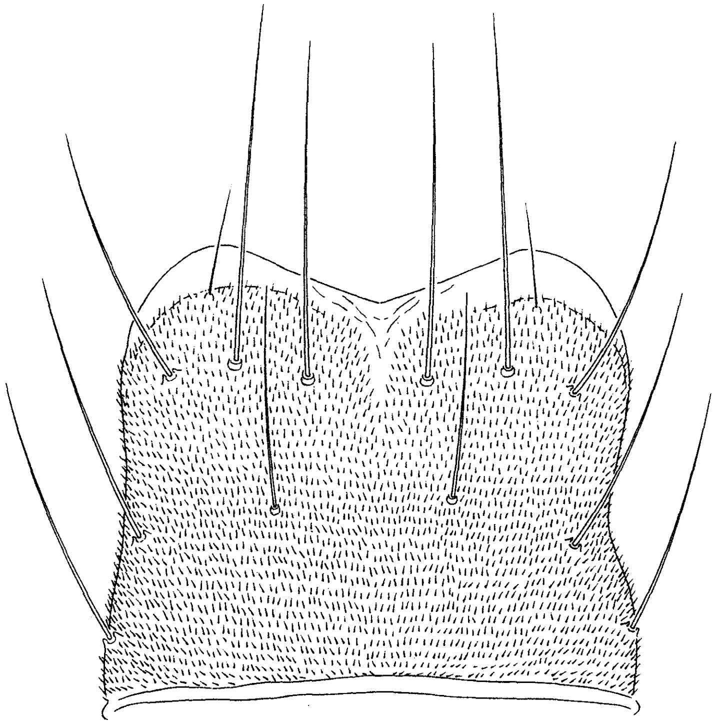


FIG. 4.11

Fig. 4.11 *Culicoides (Avaritia) miombo*. Genitalia, male: tergum IX (paratype Malawi 161).

Fig. 4.12 *Culicoides (Avaritia) miombo*. Genitalia, male (paratype Malawi 161).

FIG. 4.13

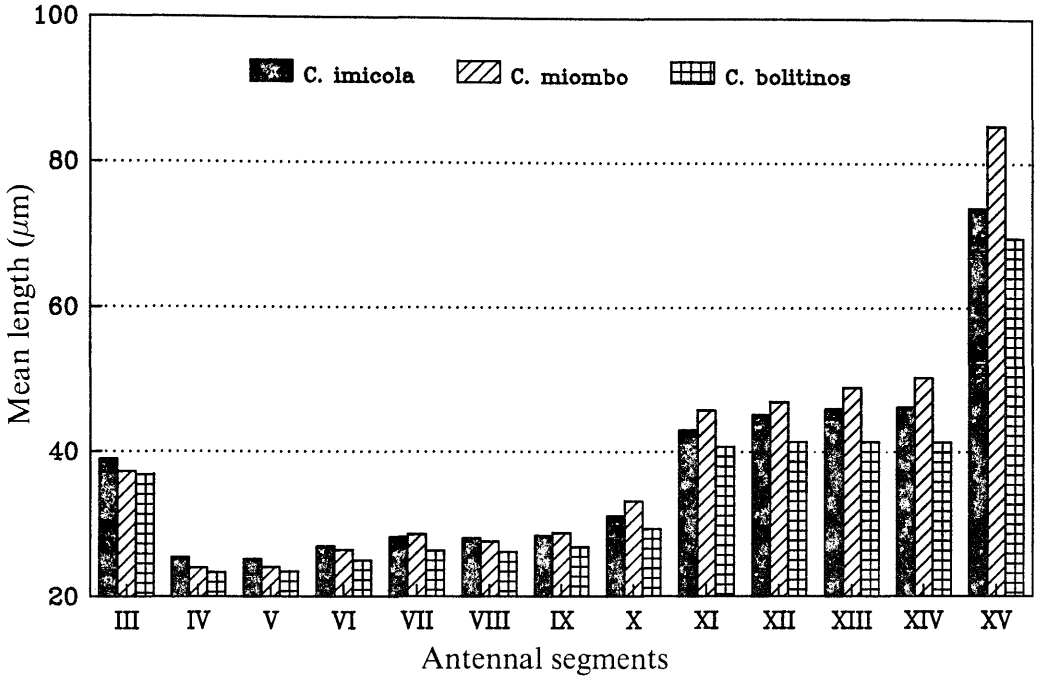


FIG. 4.14

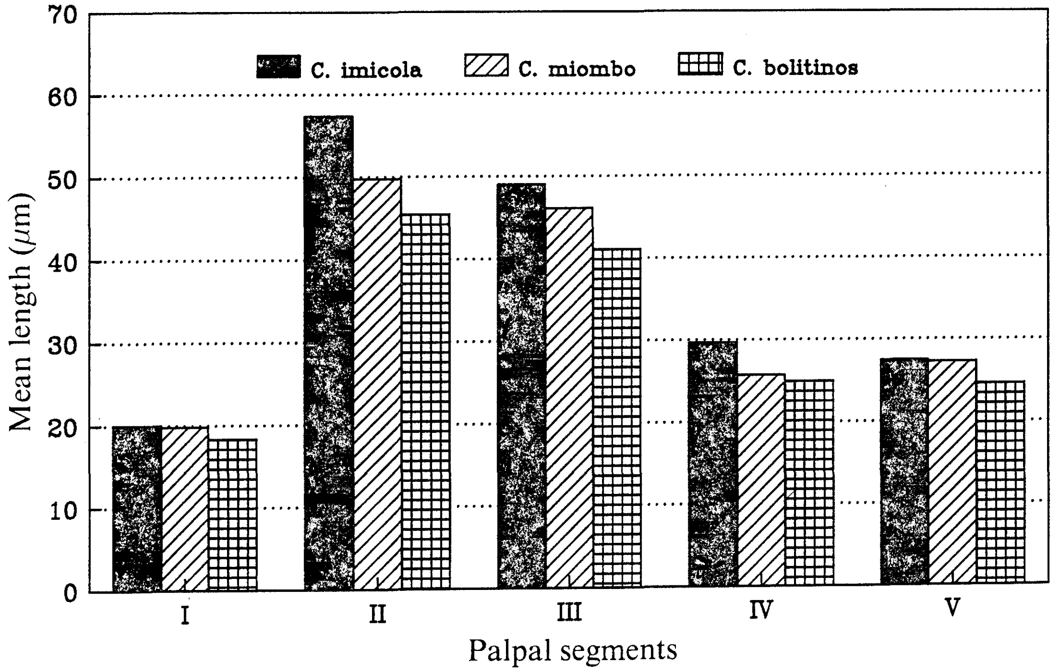


Fig. 4.13 Comparison of mean lengths (µm) of each of female antennal segments III-XV of *C. (Avaritia) imicola, C. (A.) miombo* and *C. (A.) bolitinos.*

Fig. 4.14 Comparison of mean lengths (µm) of each of female palpal segments I-V of *C. (Avaritia) imicola, C. (A.) miombo* and *C. (A.) bolitinos.*

cerci (Fig. 4.12), each bearing with long spiculae and two long and two short chaetica apically; cerci protruding well beyond posterior margin of tergum; sternum nine (Fig. 4.12) with a rather deep excavation, membrane within the excavated area always densely spiculate, bearing 80–280 spiculae, mean 170 (n = 16), basimere with dorsal and ventral spiculae and chaetica as illustrated (Fig. 4.12), basimere 2,6 x as long as broad with basal infuscate collar and well-developed dorsal and ventral roots of the form typical for the subgenus *Avaritia.* Distimere 0,8 x length of basimere, rather stout, gently curved and broadly blunt-tipped; basal half spiculate carrying six to seven bristles of varying lengths and thicknesses, extreme apex with about five very short fine tactile sensilla. Aedeagus (Fig. 4.12) subtriangular, slender, almost equal in length to the basimere; basal arch concave, only fractionally infuscate on lateral margins, distal margin of 4arch reaching to nearly 0,3 x length of aedeagus; lateral margins of aedeagus smooth and gently convex, darkly but narrowly infuscate and converging distad to end in a hyaline, round-tipped, parallel-sided terminal projection whose base projects anteriorly into median area of aedeagus in the form of a raggedly infuscate peg. Parameres (Fig. 4.12) separate, nearly touching medially from where they diverge anteriad and posteriad at 45 °, posterior halves as two convex almost hyaline blades initially stout but tapering smoothly to sharp, simple, erect tips.

Etymology. In southern Africa the widespread *Brachystegia* woodland is locally known as ‘miombo’. Its distribution correlates strongly with that of the new species. All biota in these areas are sensitive to temperate conditions.

Type material

MALAWI: Holotype ♀ (Slide Malawi 820), Kawalazi (11°37’S, 34°06’E) 20 km south-east of Mzuzu, northern Malawi, IV.1989, P. & K. Verster, blacklight at homestead in *Brachystegia* woodland.

73 ♀♀ 68 ♂♂	paratypes, slides labelled and numbered to sex, the collection data as follows:
4 ♀♀	(slides Malawi 153–155, 166), Limphasa dambo, 8 km south-west of Nkhata Bay, 15.XI.1987, R. Meiswinkel truck-trap dusk.
10 ♂♂	(slides Malawi 156–165), Limphasa dambo, 8 km south-west of Nkhata Bay, 15.XI.1987, R. Meiswinkel, truck-trap, dusk.
5 ♀♀	(slides Malawi 208–212), Kawalazi, 20 km south-east of Mzuzu, northern Malawi,

	14.II.1988, P. & K. Verster, blacklight at homestead in *Brachystegia* woodland.
47 ♂♂	(slides Malawi 243–254, 267–270, 917–947), Limphasa dambo, 8 km south-west of Nkhata Bay, 26.X.1987, R. Meiswinkel, truck-trap, dusk 17:00–18:00.
1 ♂	(slide Malawi 60), Kawalaz, 20 km south-east of Mzuzu, northern Malawi, 14.XI.1987, R. Meiswinkel, truck-trap in marshy and wooded area five km north of woodland light-trapping site, dusk.
14 ♀♀	(slides Malawi 854–856, 902, 904–907, 909–914), Kawalazi, 20 km south-east of Mzuzu, northern Malawi, II.1989, P. & K. Verster, blacklight at homestead in *Brachystegia* woodland.
2 ♂♂	(slides Malawi 857, 915), Kawalazi, 20 km south-east of Mzuzu, northern Malawi, II.1989, P. & K. Verster, blacklight at homestead in *Brachystegia* woodland.
6 ♀♀	(slides Malawi 837–842), Kawalazi, 20 km south-east of Mzuzu, northern Malawi, III.1989, P. & K. Verster, blacklight at homestead in *Brachystega* woodland.
1 ♂	(slide Malawi 858), Kawalazi, 20 km south-east of Mzuzu, northern Malawi, III.1989. P. & K. Verster, blacklight at homestead in *Brachystegia* woodland.
44 ♀♀	(slides Malawi 801–819, 821–833, 843–853, 953), Kawalazi, 20 km south-east of Mzuzu, northern Malawi, IV.1989, P. & K. Verster, blacklight at homestead in *Brachystegia* woodland.
7 ♂♂	(slides Malawi 834–836, 950–952, 976), Kawalazi, 20 km south-east of Mzuzu, northern Malawi, IV.1989, P. & K. Verster, blacklight at homestead in *Brachystegia* woodland.

Paratype slides from this type series will be deposited in the following Museums:

1 ♂ 1 ♀;	The Natural History Museum, London.
1 ♂ 1 ♀;	United States National Museum, Washington, D.C.
1 ♂ 1 ♀;	Museum National d'Histoire naturelle, Paris.
1 ♀ 1 ♂;	Australian National Insect Collection, Canberra.

Holotype ♀ and remaining paratype ♀♀ and ♂♂ in the Onderstepoort collection.

Other slide material examined but not forming part of type series:

ZIMBABWE:

20 ♀♀ 10 ♂♂ (slides Zimbabwe 113–142), Rekomitjie Research Station (16°08’S, 29°24’E), north-western Zimbabwe, 16.III.1988, R.J. Phelps, light-trap, warthog pen.

SOUTH AFRICA:

1 ♀ (slide Ndumu 11), Ndumu Game Reserve (26°55’S, 32°15’E), northern KwaZulu, Natal, 6.VI.1988, R. & P. Meiswinkel, blacklight in camp.

1 ♂ (slide Renosterkoppies 85), 20 km s of Skukuza, Kruger National Park, 18.XI.1992, R. Meiswinkel, blacklight in veld.

BOTSWANA:

5 ♀♀ (slides Botswana 1–5), Mamalakwe river near Maun (20°01’S, 23°25’E), northern Botswana, 6.VI.1988, H.V. de V. Clarke, light trap.

IVORY COAST:

5 ♀♀ 8 ♂♂ (slides Ivory Coast 1–13), Parhadi (8°27’N, 3°29’W), north-eastern Ivory Coast, 25.IX.1990. R. Meiswinkel & J.C. Koffauth, blacklight at 15 cattle on edge of village in disturbed forest.

NIGERIA:

1 ♀ 1 ♂ Vom (9°45’N, 8°46’E), north-eastern Nigeria, 31.VIII.1975, W. Taylor, at light.

Unmounted material examined

IVORY COAST:

125 ♀♀ 1 ♂ Yamoussoukro (6°49’N, 5°16’W), central Ivory Coast, 13.IX.1990, R. Meiswinkel & L.E.O. Braack, blacklight at cattle kraal.

24 ♀♀ Ganse (8°35’N, 3°54’W), north-eastern Ivory Coast, 24.IX.1990, R. Meiswinkel & G.J. Venter, blacklight at sheep and goats in village.

1 ♀ Biankouma (7°45’N, 7°18’W), western Ivory Coast, 28.IX.1990, R. Meiswinkel & J.C. Koffauth, blacklight at four cattle in dense forest.

15 ♀♀	Parhadi (8°27'N, 3°29'W), north-eastern Ivory Coast, 25.IX.1990, R. Meiswinkel & J.C. Koffauth, blacklight at 15 cattle on edge of village in disturbed forest.
23 ♀♀	Korhogo (9°27'N, 5°39'W), northern Ivory Coast 26.IX.1990, R. Meiswinkel & J.C. Koffauth, blacklight at 40 cattle in cultivated area adjoining ricefields.

KENYA:

19♀♀ 3♂♂	Tiwi, 20 km south of Mombasa, 12.VIII.1994, R. & P. Meiswinkel, blacklight at 33 goats.

SOUTH AFRICA:

4 ♀♀	Kruger National Park, 10 km east of Lower Sabie, 28.VIII.1991, R. Meiswinkel, blacklight 500 m from the heavily reeded and treed confluence of the Mlondozi and Sabie rivers.
1 ♀	Kruger National park, 10 km east of Lower Sabie, 28.VIII.1991, R. Meiswinkel, blacklight on the banks of the Mlondozi river 1 km north of where it joins the Sabie river.
1 ♀	Kruger National Park, 10 km east of Lower Sabie, 17.IX.1991, R. Meiswinkel, blacklight on banks of Mlondozi river.
1 ♀	Kruger National Park, Skukuza, 19.II.1992, R. Meiswinkel, blacklight in research camp on margins of reeded bed of Nwaswitshaka river.
1 ♀	Kruger National park, Skukuza, 16.XI.1992, R. Meiswinkel, blacklight at buffalo boma.
1 ♀	Kruger National Park, 8 km east of Lower Sabie, 9.XII.1992, R. Meiswinkel & C. Kiss, blacklight in open veld 2 km north of Sabie river.
1 ♀	Kruger National Park, Skukuza, 13.I.1993, R. Meiswinkel, blacklight at buffalo boma.
3 ♀♀	Kruger National Park, Skukuza, 23.III.1993, R. Meiswinkel, blacklight at empty elephant and rhinoceros bomas 1 km south of Sabie river.
1 ♀	Kruger National Park, Manzimahle, 19.V.1993, R. Meiswinkel, blacklight at water-filled clay dam 20 km north-east of Skukuza.
2 ♀♀	Kruger National Park, Mutlumuvi, 20.V.1993, R. Meiswinkel, blacklight in dense thicket at confluence of Mutlumuvi and Sand rivers 12 km n.e. of Skukuza.
1 ♀	Kruger National Park, Skukuza, 22.VI.1993, R. Meiswinkel, blacklight at horse stables.
1 ♂	Kruger National Park, ± 3 km east of Skukuza, 4.III.1993, H.A. Standfast & A.L. Dyce, 5-watt

light-trap on edge of dense forests fringing Sabie river, 01:18–02:18; collection no. KNP 93.141/H.

4.3 DISCUSSION

4.3.1 Taxonomy

Culicoides (Avaritia) miombo appears to have been included six times previously in studies on Afrotropical *Culicoides.* Boorman & Dipeolu (1979) identified a Nigerian series as belonging to *C. (A.) brosseti* Vattier & Adam 'on account of the very prominent and extensive yellow markings on the anterior half of the mesonotum'. They did, however, note that their specimens differed in having a higher palpal ratio and lower costal ratio than were described for *C. brosseti* by the original authors Vattier & Adam (1966). I have examined a slide-mounted male and female of the Boorman & Dipeolu (1979) series collected at Vom and consider them to be *C. miombo.* Their photograph of the female wing of *C. brosseti* is inseparable from the one figured above; especially characteristic is the dark streak at the extreme base of the anal cell. Boorman & Dipeolu erroneously described the male genitalia as having the 'tergite without lateral processes, posterior margin almost straight' and the membrane of sternum nine as 'bare'. *Culicoides miombo* in fact has a very densely spiculate membrane and moderately developed apicolateral flanges, exactly as in the Vom male before me. *Culicoides brosseti* appears to be the only truly cavernicolous species of *Culicoides* currently known from the Afrotropical Region. However, *C. brosseti* is not a member of the Imicola group, but, as pointed out by Itoua & Cornet (1986), belongs to the Trifasciellus group which contains a third species, *C. dubitatus* Kremer, Rebholtz-Hirtzel & Delecolle, 1976. The Trifasciellus group differs from the Imicola group in a number of morphological features, involving the male genitalia and the distribution pattern of the long and short blunt-tipped sensilla trichodea on the antennae of both sexes. *C. brosseti,* like *C. miombo,* possesses prominent yellow admedian vittae on the anterior half of the mesonotum, and this is likely the reason why *C. miombo* has been mistakenly identified as *C. brosseti* for the last 20 years.

The second reference to *C. miombo is* one made by Kitaoka, Kaneko & Shinonaga (1984). Their wing photograph of a specimen of *C. imicola* from Ife, Nigeria is clearly that of *C. miombo,* the dark streak at the base of the anal cell once again being highly diagnostic.

The third reference is that of Cornet (1969) who recorded a single female from Simousso, Burkina Faso. It is likely that he was dealing with *C. miombo* and not *C. brosseti.*

The fourth reference is that of Kremer (1972) who recorded 'trés nombreux... femelles et mâles' of *C. brosseti* from Dundo, Angola. Though no taxonomic data were given, it is likely that he too had *C. miombo* before him.

The fifth reference is the record of 16 ♀♀ and 1 ♂ *C. brosseti* from Manakara, Madagascar (Kremer & Brunhes 1972). As in the Angolan series, no taxonomic data were given, but as the two studies were published by Kremer in the same year the material examined may have been conspecific.

The final reference (Kitaoka & Zulu 1990) deals with two unnamed species of *Culicoides* from Chilanga, Zambia, provisionally labelled as C. A–1 and C. A–10. These authors note that they are 'members of the *brosseti* subgroup of the subgenus *Avaritia* . . . which have two yellowish vittae on the thorax', and that together they comprised only 4 % of nearly 10 000 *Culicoides* collected around a guinea-pig run. It is certain that these represent *C. miombo* and that their rarer C. A–10 is simply an abnormally dark variant.

I have not seen the material detailed above in the last four references; their identification is thus tentative, and for this reason a question mark is placed next to these records in Fig. 4.1 and 4.2.

4.3.2 **Differential diagnosis**

Fifteen character states that easily separate the two species *C. imicola* and *C. miombo* are summarized in Table 4.7. To differentiate *C. miombo* not only from *C. imicola* but also from *C. bolitinos,* statistical analyses were conducted on the antennal and palpal measurements of the three species. The mean measurement of each antennal and palpal segment, taken from 25 specimens of each species, was first tabulated and then tested for significant differences (Table 4.5, 4.6). It was found that *C. bolitinos* and *C. miombo* showed no difference in measurements between antennal segment III–V and palpal segment IV, while in turn a comparison of *C. imicola* and *C. miombo* showed antennal segments VI–IX and palpal segments I and V to be inseparable. It must be noted that heterogeneous variances occurred in the measurements of antennal segments IV and V but these were accepted as homogeneous mainly because the small size of these segments may have affected the accuracy of their measurements in all three species. Table 4.5 and Fig. 4.13 show that as a trio the three species are most easily separated by significant differences in the relative lengths of antennal segments X–XV. The same separation can be obtained using palpal segments II and III (Table 4.6, Fig. 4.14). Of the 15 character states that separate *C. miombo* and *C. imicola,* six are discussed in detail below. Three characters are very reliable for separating *C. miombo* and *C. imicola* under the dissecting microscope: The former has (a) prominent, pale yellow, admedian vittae on the scutum, (b) haltere knobs brown, and (c) the prominent dark smudge at the base of the anal cell of the wing. These and five other character states are discussed in further detail below; where data are available these two species are also differentiated from *C. bolitinos* and *C. pseudopallidipennis.*

1. Female. Wing: The wing of *C. miombo* is distinctly darker than that of *C. imicola, C. pseudopallidipennis* or *C. bolitinos.* The following wing characters more clearly define *C. miombo* as a good species:

    a. The second pale costal spot is round where it straddles the r–m crossvein, is rather strongly waisted medially only to expand and broadly abut the anterior wing margin. This spot is more quadrate and not waisted medially in the remaining three species of the Afrotropical Imicola group.

    b. The shape of the distal pale spot in the apex of cell R_5: its proximal margin is weakly pointed to rounded; this spot is quite often, especially in darker specimens, indistinctly separated or isolated from the wing apex by a narrow dark strip that runs along the antero-distal wing margin; in still darker specimens the pale spot may almost vanish. In *C. imicola, C. pseudopallidipennis* and *C. bolitinos*, this pale spot always broadly abuts the wing margin and is never isolated from the wing margin.

    c. The median third of the anterior margin of vein M_1 is more brown than pale; predominantly to entirely pale in *C. imicola, C. pseudopallidipennis* and *C. bolitinos.*

    d. Vein M_2 is broadly darkened for most of its length and does not have the very obvious preapical excision seen on the anterior margin in *C. imicola.* In *C. miombo* vein M_2

is near its apex moderately to fairly abruptly tapered on both margins; however, this tapering still leaves both margins of vein M_2 at the apex narrowly dark and never entirely pale as in *C. bolitinos.* Furthermore, in the majority of specimens of *C. miombo,* this preapical tapering once again expands leaving the extreme apex of vein M_2 more broadly dark.

e. Extreme base of anal cell with a prominent, long, dark smudge; in *C. imicola, C. pseudopallidipennis* and *C. bolitinos* this area is entirely pale.

2. Female. Eyes: The extent of hairiness of the eyes in *C. miombo* is a deceptive character state that shows considerable variation. Firstly, the areas between the facets are at most only sparsely adorned with short hairs. These hairs will not be seen in specimens whose eyes are poorly cleared of dark pigment. Secondly, the median transverse band of three to eight rows of facets is usually devoid of hairs with only the more lateral, and thus obscured, interfacetal areas weakly haired. The eyes of *C. miombo* therefore need to be carefully examined in material which is properly prepared. *Culicoides miombo* appears to be the only member of the Imicola group worldwide that possesses hairy eyes.

3. Female. Palps: The mean length of the entire palp in *C. miombo* (mean 169,8 µm; n = 25) is almost exactly intermediate between that of *C. imicola* (mean 183,6 µm, n = 25) and *C. bolitinos* (mean 154,6 µm, n = 25) as shown in Fig. 4.14. This is because the three species are quite easily separable on the mean lengths of palpal segments II and III.

   In *C. pseudopallidipennis* the mean length of the palp is 175,3 µm, i.e. very similar to *C. imicola* and *C. miombo*. However, *C. pseudopallidipennis* differs in that it has a swollen third palpal segment.

4. Female. Antennae: As to the length of the entire antenna the converse is true; that of *C. miombo* is the longest (mean 506,0 µm; n = 25); with *C. imicola* intermediate (mean 485,5 µm; n = 25) and that of *C. bolitinos* again shortest (mean 451,9 µm; n = 25). As shown in Table 5 and Fig. 4.13 the three species are easily separable on the mean lengths of antennal segments X–XV.

Those segments with statistically non-significant differences in length are underlined in Table 4.5.

5. Female. Antennae: The antennal trichodea ratio (AtR) gives an equally interesting result in that, despite having the longest antennae of the three species, *C. miombo* carries the shortest long blunt-tipped trichodea on antennal segment VI. These trichodea are longer but more or less equal in size in *C. imicola* and *C. bolitinos.* As illustrated by Clastrier (1958), these trichodea are rather short and unusually swollen in *C. pseudopallidipennis*.

6. Male. The males of the three species differ most significantly in the extent of spiculation on the membrane of sternum nine of the genitalia. In *C. miombo* it is moderately to densely spiculate (80–280 spiculae, mean 170; n = 16), in *C. imicola* it is sparsely to moderately spiculate (8–145 spiculae, mean 47; n = 50) whereas in *C. bolitinos* it is normally bare, occasionally carrying a few spiculae (0–18 spiculae, mean 2,56; n = 50); this membrane is also bare in *C. pseudopallidipennis.* There are subtle differences between the former three species in the shape of the posterior margin of tergum nine, but these are difficult to quantify.

4.3.3 **Larval habitat**

Unknown; suspected to be in well-vegetated marshy areas. The dung of cattle or any other large herbivore is thought not to be the larval habitat of *C. miombo* as none of nearly 400 specimens examined had the phoretic deutronymph stage of *Myianoetus* mites attached to its abdomen, an association that is commonly found amongst the adults of those *Avaritia* species whose immatures develop exclusively in animal dung.

4.3.4 **Vector status**

Unknown; however, one needs to re-examine the findings of Lee (1979) who assayed 270 000 *Culicoides* caught during the years 1967–1970 at the dairy herd of the University of Ibadan, Nigeria. Seventy isolates of 16 arboviruses belonging to seven groups were made either from single *Culicoides* species pools or from multiple species pools that comprised at least 14 species. These quite likely included *C. miombo* sp. nov., as Lee reported *C. imicola* to be one of the four most abundant species taken during the study. The likelihood that *C. miombo* formed part of Lee's collection is supported by the statement made by Boorman & Dipeolu (1979) that *C. brosseti* (misidentification for *C. miombo)* was taken 'in large numbers with *C. imicola'* at Ibadan.

4.3.5 **Distribution**

In discussing biota that are strictly tropical in their occurrence (a subject admirably explored for certain sections of the southern African fauna by Stuckenberg 1969) it is worthwhile to recall the words of Nix (1983) '. . . the available evidence indicates that the 20 °C isotherm encloses virtually all occurrences of tropical savanna on all continents' where 'annual mean rainfall ranges between 1 000 and 1 500 mm, annual mean air temperature exceeds 24 °C and mean minimum temperature of the coldest month is between 13–18 °C. However, significant occurrences of tropical savannas are also found between the 8 °C and 13 °C isotherm for the coldest month and the absence of freezing temperatures', while the 8 °C isotherm 'coincides very approximately with the 50 % probability of a freezing temperature occurring in any one year'. Importantly, Nix also notes that frost is a very '... meaningful boundary condition for living organisms'.

This definition fits *C. miombo*, as in Table 4.1 it can be seen that it is largely restricted to those parts of Africa below 1 000 m in altitude, where frost is absent or rare, and where the rainfall is relatively high (700–1 500 mm/annum), especially if this rainfall is distributed through all or most months of the year. It thus seems reasonable to predict that these ecological preferences will preclude *C. miombo* from ever becoming established in the more arid or cooler, more temperate areas of southern Africa, and likely explain why it occurs in such low numbers in Ndumu, South Africa; Maun, Botswana; Rekomitjie, Zimbabwe and Kawalazi, Malawi. All these localities are marginally embraced by the 8 °C minimum isotherm and thus experience frost occasionally (Fig. 4.1) and furthermore will have four to six months of the year hot and dry. For example at Kawalazi, Malawi, during the hot dry months of October and November, *C. miombo* was rarely collected and then only near marshy areas. It was only found more widely once rains had commenced but even so remained uncommon, representing only 0,9 % of 6 043 *Culicoides* collected in the rainy month of April, 1989 (van Ark & Meiswinkel 1992).

In light of *C. miombo*'s apparent need for fairly high temperatures and a high average rainfall, it is pertinent to look north of the equator and repeat Boorman and Dipeolu's 1979 observation that *C. brosseti* (= *C. miombo*) occurred in large numbers in Nigeria. Here the minimum temperature of the coldest month is in the region of 18–22 °C, considerably higher than the 8 °C found in areas sampled for *C. miombo* in southern Africa. Similarly, in the Ivory Coast *C. miombo* was always present in collections made in the northern half of the country (R. Meiswinkel, unpublished data 1990), where at least some rain falls in each month of the year and frost is absent. Only once, however, was *C. miombo* the most abundant species in the Ivory Coast, comprising 26,2 % of a subsample of 500 *Culicoides* caught at zebu cattle on the outskirts of Yamoussoukro. In the same collection *C. imicola* only constituted 0,8 % of the catch (R. Meiswinkel, unpublished data 1990). It is important to note that not a single specimen of *C. miombo* was found amongst ± 10 000 *Culicoides* collected at four sites in the wetter southern half of the Ivory Coast. Although there is a paucity of data, this suggests that *C. miombo* is virtually absent from the very high rainfall forested regions of equatorial Africa. When this is linked to the fact that no specimens of *C. miombo* have been collected in 30 years in the semi-arid and warm-temperate regions of South Africa, the implication is strong that *C. miombo* evolved in the tropical woodlands immediately adjacent to the wetter rainforest block of equatorial Africa.

4.4 CONCLUSIONS

Culicoides miombo is a new member of the Imicola group; it is widespread and can be common in the tropical woodlands of Africa. Because of its preference for high temperatures, good rainfall and frost-free regimes, it is unlikely that *C. miombo* will ever become established in the more arid or temperate parts of southern Africa. It has until now been confused taxonomically with *C. brosseti* and *C. imicola*, and as a result little is known about its host preferences, seasonal abundance and prevalence. Its larval habitat also remains undiscovered. Finally, *C. miombo* deserves mention as a potential vector of cattle viruses.

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TABLE 4.1 List of 18 localities from which *C. (Avaritia) miombo* has been recorded in Africa and Madagascar with details of associated major phytochorion, vegetation unit, altitude, mean annual temperature, rainfall and incidence of frost

Locality	Co-ordinates	Altitude (a.s.l.)	Major phytochorion (after White, 1983)	Vegetation unit	Mean annual temperature	Rainfall (mm per annum)	Frost/ no frost
Ibadan **NIGERIA**	7°17'N, 3°30'E	< 500m	Transition between Guineo-Congolian regional centre of endemism (I) and the Sudanian regional centre of endemism (III)	2	26° C	1200	no frost
Ife, NIGERIA	7°28'N, 4°34'E	< 500m		2 11a,12			
Vom, NIGERIA	9°45'N, 8°46'E	1220 m	(III)	27, 29a, 32	24–28° C	1400	no frost
Simousso, BURKINA FASO	11°01'N, 4°03'W	< 500m	(III)	27, 29a,	24–28° C	1400	no frost
Parhadi, IVORY COAST	8°27'N, 3°29'W	300–400 m	(III)	11a	25,5° C	1100	no frost
Ganse, IVORY COAST	8°35'N, 3°54'W	100–200 m	(III)	11a	25,5° C	1100	no frost
Korhogo, IVORY COAST	9°27'N, 5°39'W	300–400 m	(III)	27	26° C	1300–1400	no frost
Yamoussoukro, IVORY COAST	6°49'N, 5°16'W	200–300 m	Guinea-Congolia/Sudania regional transition zone XI	2, 11a	25,5° C	1100–1200	no frost
Biankouma, IVORY COAST	7°45'N, 7°18'W	500–700 m	(XI)	11a	24,5° C	1400–1500	no frost

Dundo, ANGOLA	9°46'S, 14°42'E	< 500 m	Guineao-Congolia/Zambezian regional transition zone (X)	29c	21° C	700–900	no frost
Kawalazi & Limphasa, MALAWI	11°37'S, 34°06'E	600–700 m	Zambezian regional centre of endemism (II)	25	18–24° C	1400	frost localized to above 1200m altitude and in depressions
Rekomitjie, ZIMBABWE	16°08'S, 29°24'E	500–1000 m	(II)	26, 28	18–24° C	1400	frost localized to above 1200m altitude and in depressions
Maun, BOTSWANA	20°01'S 23°25'E	500–1000 m	(II)	28, 35a	18–24° C	1400	frost localized to above 1200m altitude and in depressions
Ndumu, SOUTH AFRICA	26°55'S, 32°15'E	0–100 m	Tongoland-Pondoland regional mosaic (XV) of undifferentiated woodland in transition to bushland: 20 % of woody plants are Zambezian linking species	29e, 16c	22° C	600–1000	no frost
Manakara, MADAGASCAR	22°06'S, 48°00'E	0–100 m	East Malagasy regional centre of endemism (XIX) of lowland rain forest and secondary grassland	11b	23–25° C	2000–3000	no frost
Masai-Mara G.R., KENYA	1°30'S, 35°05'E	1700-1900 m	The Somalia-Masai regional centre of endernism (IV)	45	25-30° C	500-1000	no frost
Tiwi, KENYA	4°14'S, 39°34'E	0-200 m	The Zanzibar-Inhambane regional mosaic (XIII)	16a	26° C	800-1200	no frost
Skukuza, SOUTH AFRICA	24°58'S, 31°36'E	230 m	Tongoland-Pondoland regional mosaic (XV)	29e	22° C	500	frost very rare

TABLE 4.2 Mean lengths (μm) of segments and mean distribution of sensillae on the female and male antennae of *C. (A.) miombo*

C. miombo	**Antennal segments**												
	III	**IV**	**V**	**VI**	**VII**	**VIII**	**IX**	**X**	**XI**	**XII**	**XIII**	**XIV**	**XV**
Female:													
Sens. coeloconica	3	0	0	0	0	0	0	0	0	1	1	1	1
Sens. chaetica	5	3	2	3	2	3	2	3	0	0	0	0	0
Sens. trichodea (blunt-tipped	LL	LLc	LLc	LLc	LLc	LLc	LLc	LLc	–	–	–	–	–
Lengths of segments	36,8	23,3	23,6	25,7	28,1	27,3	28,2	32,7	44,6	46,0	48,4	49,5	83,3
Male:													
Sens. coeloconica	2	0	0	0	0	0	0	0	0	0	1	1	2
Sens. chaetica	5	0	0	0	0	0	0	0	0	0	3	2	0
Sens. trichodea (blunt-tipped)	LL	LLc	LLc	LLc	Lc	Lc	Lc	c	–	–	–	–	–
Lengths of segments	71,3	36,3	37,5	37,5	37,5	37,5	37,5	37,6	37,5	36,3	96,3	75,0	92,5

TABLE 4.3 Number and frequency of coeloconica present on each of female antennal segments III–XV of *C. (Avaritia) miombo*

No. of coeloconica per segment of *C. miombo*	**Antennal segments**							
	III	**IV-IX**	**X**	**XI**	**XII**	**XIII**	**XIV**	**XV**
0	–	70	70	69	–	–	1	1
1	–	–	–	1	70	70	68	69
2	–	–	–	–	–	–	1	–
3	69	–	–	–	–	–	–	–
4	1	–	–	–	–	–	–	–
No. of antennae examined	**70**	**70**	**70**	**70**	**70**	**70**	**70**	**70**

TABLE 4.4 Number and frequency of chaetica on each of female antennal segments III–XV of *C. (Avaritia) miombo*

No. of chaetica per segment *C. miombo*	**Antennal segments**												
	III	**IV**	**V**	**VI**	**VII**	**VIII**	**IX**	**X**	**XI**	**XII**	**XIII**	**XIV**	**XV**
0	–	–	–	–	–	–	–	–	68	70	70	70	70
1	–	–	1	–	1	–	–	–	2	–	–	–	–
2	–	–	69	–	69	4	70	3	–	–	–	–	–
3	–	69	–	69	–	64	–	66	–	–	–	–	–
4	–	1	–	1	–	2	–	1	–	–	–	–	–
5	70	–	–	–	–	–	–	–	–	–	–	–	–
No. of antennae examined	**70**	**70**	**70**	**70**	**70**	**70**	**70**	**70**	**70**	**70**	**70**	**70**	**70**

TABLE 4.5 Comparison of mean lengths (μm) of female antennal segments III–XV of 3 *Culicoides* species*

Antennal segment	**Species**			**F. value**
	C. imicola **μm**	***C. miombo*** **μm**	***C. bolitinos*** **μm**	
III	39,00	37,30	36,85	11,171
IV	25,45	24,00	23,35	20,261
V	25,20	24,08	23,45	12,500
VI	26,95	26,45	25,00	11,641
VII	28,23	28,63	26,35	14,755
VIII	28,08	27,63	26,18	9,656
IX	28,43	28,80	26,85	13,085
X	31,10	33,20	29,33	32,047
XI	43,00	45,75	40,75	26,595
XII	45,20	46,95	41,40	40,739
XIII	45,98	48,95	41,43	58,127
XIV	46,20	50,30	41,35	56,764
XV	73,78	85,25	69,60	63,220
Total	485,48	506,0 μ	451,85	40,346

All F-values are significant at 5 %; means underlined are not significantly different at 5 %; n = 25 for each species

TABLE 4.6 Comparison of mean lengths (mm) of female palpal segments I–V of 3 *Culicoides* species*

Palpal segment	**Species**			**F-Value**
	C. imicola	***C. miombo***	***C. bolitinos***	
I	20,05	19,85	18,35	6,333
II	57,40	49,80	45,45	96,885
III	49,05	46,15	41,10	45,363
IV	29,65	25,70	24,90	54,368
V	27,45	27,25	24,55	14,207
Total	**183,6**	**169,75**	**154,55**	**118,044**

* All F-values are significant at 5 %; means underlined are not significantly different at 5 %; n = 25 for each species

TABLE 4.7 Fourteen morphological character states used to separate *C. imicola* from *C. miombo*

	C. imicola		***C. miombo***
♀	thorax entirely brown in alcohol	-	thorax with two prominent yellow admedian vittae
-	scutellum entirely brown	-	scutellum narrowly brown medially and broadly yellow laterally
-	base of anal cell entirely pale	-	base of anal cell with a prominent brown streak
-	anterior margin of second pale costal spot straddling the r–m crossvein straight	-	anterior margin strongly indented medially
-	proximal margin of distal pale spot in cell R_5 pointed	-	this margin weakly pointed to rounded
-	median third of anterior margin of vein M_1 pale	-	this area brownish
-	apex of vein M_2 broadly dark on both margins this preceded by a broad, pale and rather deep preapical excision on the anterior margin only; this excision usually touches and sometimes straddles M_2	-	apex of vein M_2 narrowly dark on both margins, this preceded by only a small, pale and indistinctly shallow preapical excision on both the anterior and posterior margins; these excisions do not touch or straddle vein M_2
-	haltere knobs pale	-	haltere knobs brown
-	palp slightly longer: 165,6–182,4 μm mean 176,1 μm (n = 25)	-	palp slightly shorter: 147,5–177,5 μm mean 162,6 μm (n = 70)
-	antennal segments X–XV shorter (see Table 4.4)	-	these segments longer (see Table 4.4)
-	AR 0,95–1,10 mean 1,01 (n = 167)	-	AR 1,09–1,25 mean 1,15 (n = 66)
-	AtR 1,59–2,27 mean 1,86 (n = 173)	-	AtR 1,27–1,76 mean 1,54 (n = 68)
-	eyes bare	-	eyes sparsely to moderately hairy
♂	membrane of sternum nine with eight to 145 spiculae, mean 47 (n = 50)	-	membrane with 80–280 spiculae, mean 170 (n = 16)

CHAPTER 5

Culicoides (Avaritia) loxodontis Meiswinkel, 1992, a member of the Imicola group (Diptera: Ceratopogonidae) associated with the African elephant in the Kruger National Park, South Africa

5.1 INTRODUCTION

The first species of Afrotropical *Culicoides* found to inhabit large herbivore dung was reported by Nevill (1968) to be *C. pallidipennis* Carter, Ingram & Macfie, 1920 (= *C. imicola*) which he had reared from cattle dung in the Transvaal, South Africa. This record was, however, shown by Meiswinkel (1989) to refer not to *C. imicola* but to the previously unknown species *C. bolitinos,* a species that has since been repeatedly reared from cattle dung as well as from the dung of the African buffalo *(Syncerus caffer)* and the blue wildebeest *(Connochaetes taurinus)*. Today *C. bolitinos* is recognised as the species most closely related to the Oriental-Australasian-eastern Palaearctic *C. brevitarsis* Kieffer, the immatures of which also develop exclusively in the dung of Bovidae such as the water buffalo *(Bubalus bubalis)* and cattle (Dyce 1982).

Subsequent to the record by Nevill (1968), Mr. Alan Dyce of Sydney, Australia, during a four-month visit to Onderstepoort in 1973/74, also reared *C. bolitinos* from the dung of the African buffalo and cattle in South Africa. In addition, he made the discovery that three other *Culicoides* species of the subgenus *Avaritia* lived in the dung of the African elephant and the plains zebra *(Equus burchellii).* The *Culicoides* species reared were identified as *C. gulbenkiani* Caeiro, 1959, C. sp. # 54 and C. sp. # 50. None of these is a member of the Imicola group. These findings were made in the Kruger National Park and were reported upon in a short communication (Dyce & Marshall 1989).

In 1985, following upon these leads, I continued investigations on the dung-inhabiting *Culicoides* fauna of the large herbivores of the Kruger National Park, and since then have reared six species of the subgenus *Avaritia* from elephant dung alone. One of these, *C. (A.) kanagai* Khamala & Kettle, 1971, has been reported upon (Meiswinkel 1987). A further three, *C. tororoensis* Khamala & Kettle, 1971, C. sp. # 54 and C. sp. # 50, in large measure support the findings of Dyce & Marshall (1989), the only discrepancies being that their record of *C. gulbenkiani* is most likely a misidentification of *C. tororoensis* and that C. sp. # 54 consists of two closely related species difficult to separate in the adult stage. As regards the taxonomic status of *C. gulbenkiani* and *C. tororoensis*, I disagree with Glick (1990) who stated the latter to be a synonym of the former. These are two valid but closely similar species that need reappraisal both biologically and taxonomically.

The sixth species reared from elephant dung is *C. (A.) loxodontis* which is redescribed below. Unlike the others known from elephant dung, it is a member of the Imicola group, which in turn is one of at least six groups that constitute the subgenus *Avaritia* in the Afrotropical Region. In Africa five species of the Imicola group have thus far been described: *C. imicola, C. pseudopallidipennis, C. bolitinos, C. miombo* and *C. loxodontis*. Only *C. bolitinos* and *C. loxodontis* have their immatures developing in animal dung.

As in previous chapters, some emphasis is placed on a numerical description of *C. loxodontis* so as to differentiate it more clearly from three of its taxonomic congeners *C. imicola, C. bolitinos* and *C. miombo*. While *C. pseudopallidipennis* will be redescribed in Chapter 6, two character states easily separate it from *C. loxodontis* and these will be discussed.

5.2 MATERIALS AND METHODS

The type material of *C. loxodontis* was collected in the Kruger National Park, either by light-trap or reared from elephant dung. The dung was randomly collected, and placed in a cardboard box, and then stored in a fine gauze net to await emergence of *Culicoides*, if present. The dung belonged to two age categories. Either it was (i) a discrete round bolus or boli only a few hours old, or (ii) was a one to two day-old subsample of one to five boli that had been flattened by

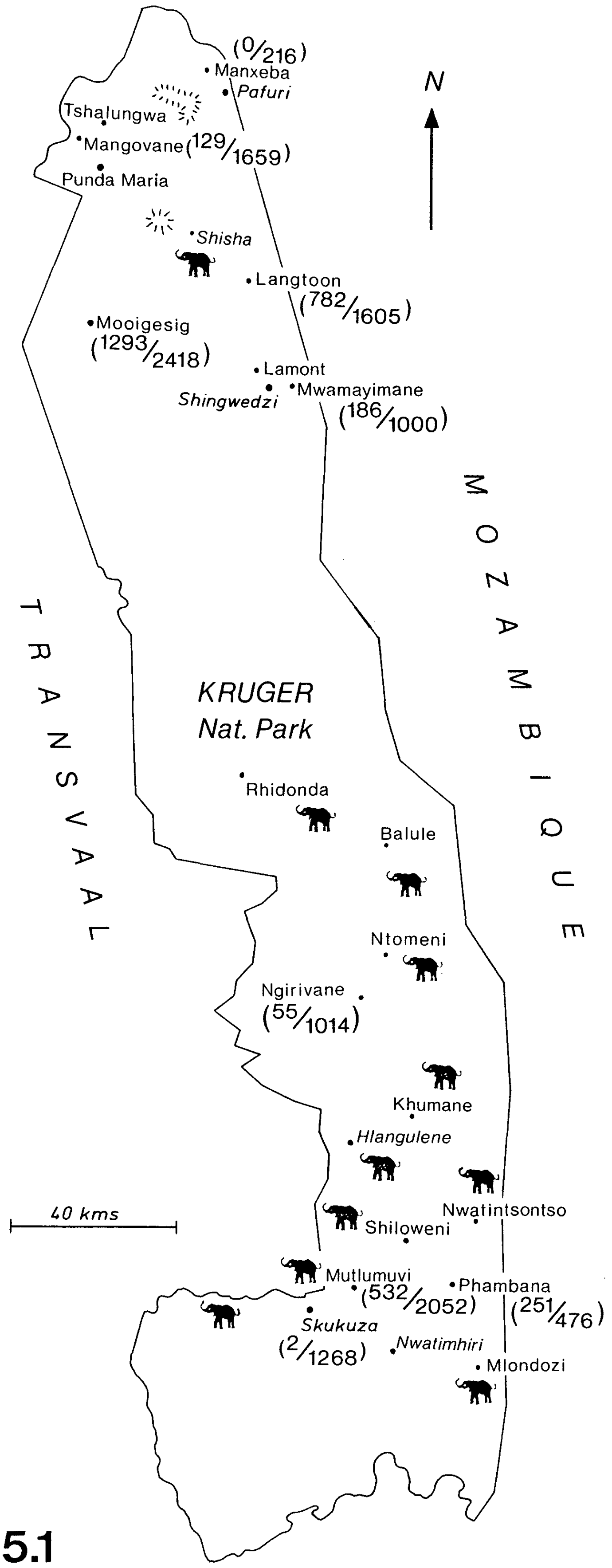


Fig. 5.1

Fig. 5.1 A map of the Kruger National Park indicating localities where *C. (Avaritia) loxodontis* was either reared from elephant dung (elephant symbols) or collected in light-traps; in parentheses the number of *C. (A.) loxodontis* captured is given as a fraction of the total number of *Culicoides* midges collected.

the workings of various dung-beetle (Scarabaeoidea) species into a large (± 1 m diameter) 30–50 mm high amorphous mass. All dung was collected off hard substrates, mostly tarred or sand roads, or from similarly bare unvegetated patches away from roads. None of the samples included soil, water or vegetation that was not evacuated by the elephant itself. Of the more than 200 specimens used for the description of *C. loxodontis*, only one female, 24 males and one associated pupal exuvia reared from elephant dung, are included in the type series. Under field conditions it proved difficult to keep such tiny insects alive for more than 48 hours in order to have specimens sufficiently mature for mounting in Canada balsam.

5.3 RESULTS

5.3.1 ***Culicoides (Avaritia) loxodontis*** (Fig. 5.2–5.15; Table 5.1–5.6)

Female (Fig. 5.2-5.7, 5.13–5.15; Table 5.1–5.6)

Head. Eyes (Fig. 5.2); bare, contiguous over a distance equal approximately to the diameters of between one and two adjacent facets. Antenna (Fig. 5.3, 5.14; Table 5.1–5.4) slender, basal segments IV–X barrel-shaped distal segments XI–XIV more or less parallel-sided only narrowing fractionally medially, XV parallel-sided only narrowing apically; mean lengths of antennal segments III–XV: 39,6–25,2–24,5–26,6–26,3–25,8–26,2–28,5–38,6–42,1–43,9–42,6–63,5 μm (n = 80); total length of antenna: 428,8–516,3 μm, mean 453,1 μm (n = 80); widths of antennal segments III–XV: 28,8–22,5–20,0–19,4–18,8–18,8–17,5–17,5–16,3–16,9–16,3–16,9–18,1 (n = 1); AR 0,92–1,08, mean 0,99 (n = 80); sensilla coeloconica present on segments III, XII–XV in 92,5 % of antennae examined (n = 81), see Table 5.2 for deviations from the norm; antenna with a total of six to eight coeloconica, mean 6,93 (n = 81); mean sensilla chaetica distribution on segments III–XV is 5,00–3,52–2,15–4,04–2,06–4,00–2,04–3,02–0,05–0–0–0–0 (n = 81), see Table 5.3 for deviations from the norm; blunt-tipped sensilla trichodea distribution of the LLc type, i.e. each of segments IV–X with two long and one short sensilla trichodea, segment III with only two long sensilla trichodea (n = 81); AtR 1,35–1,67 mean 1,47 (n = 42); segments XI–XIV each with 13–17 sharp-tipped sensilla trichodea of varying lengths and thicknesses distributed in a basal and subapical whorl, XV with approximately

Fig. 5.2

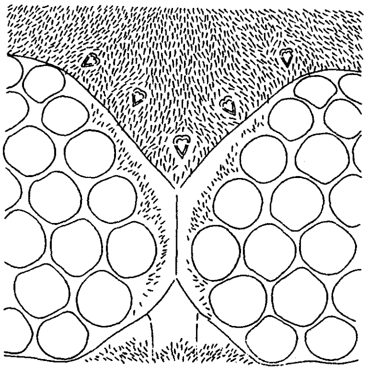


Fig. 5.2 *Culicoides (Avaritia) loxodontis*. Eyes, female (paratype Pafuri 6).

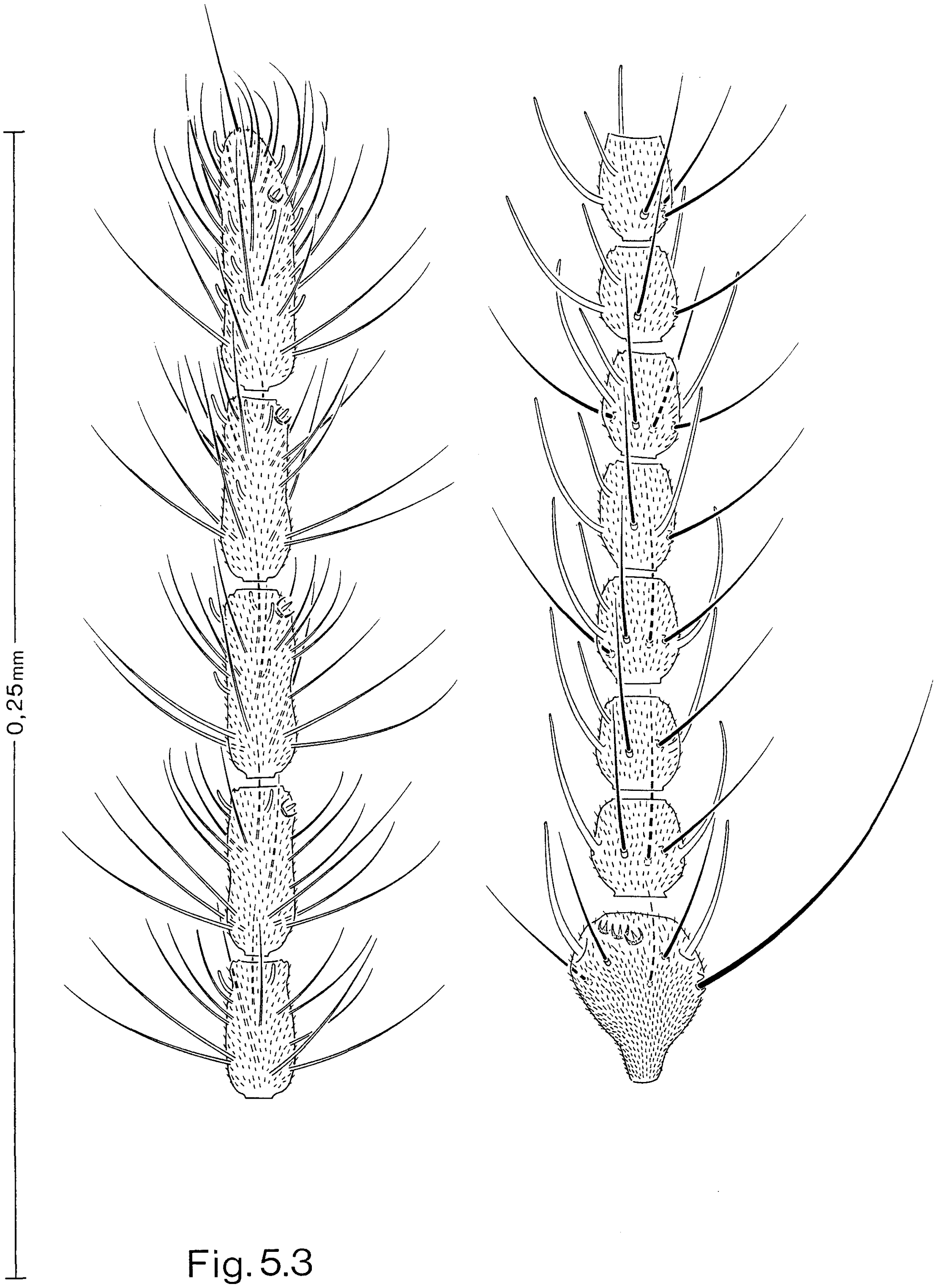


Fig. 5.3

Fig. 5.3 *Culicodes (Avaritia) loxodontis*. Antenna, female: segments XI–XV on left, segments III–X on right (paratype Shingwedzi 268).

twice as many trichodea, these distributed almost throughout segment (Fig. 5.3); similarly the short blunt-tipped basiconica range from two to nine on each of the distal flagellar segments XI–XV (Fig. 5.3); all antennal segments uniformly clothed throughout with fine spiculae (Fig. 5.3). The range and mean number of sensilla coeloconica, chaetica and blunt-tipped trichodea are given in Table 5.1. Palp (Fig. 5.4, 5.15; Table 5.5); of a moderate length, slender, light brown throughout mean length of palpal segments I–V; 22,65–54,43–44,95–25,75–25,73 μm (n = 63); total length 147,5–175,0 μm, mean 163,3 μm (n = 63); palpal segment I with one to two rather long chaetica, mean 1,01 (n = 77), II with two to four rather short chaetica, mean 3,00 (97 % with three chaetica; n = 77); III of a moderate length, slightly swollen and carrying three to five rather short chaetica, mean 3,07 (93 % with three chaetica, n = 70), with a small, round and shallow subapical pit with diameter of opening 35–50 % the width of segment, margin of pit smooth but well defined; IV with one to four short chaetica, mean 2,66 (45 % with three chaetica; n = 77); V with no chaetica on median portion of segment but always bears five short erect bristles apically; PR 2,07–2,92, mean 2,53 (n = 80); P/H ratio 0,80–0,89, mean 0,84 (n = 20); mandible with 12–16 teeth, mean 13,2 (n = 75).

Thorax. Legs: brown, with all femora narrowly pale basally, and with fore and middle femora indistinctly pale apically. All tibiae with a narrow, well-defined subbasal pale band; remainder of fore and middle tibiae brown while apices of hind tibiae are indistinctly paler; TR 1,44–1,75, mean 1,68 (n = 40); comb on apex of hind tibia with five spines, the first being the longest and only slightly longer than the second (n = 81). Wing: (Fig. 5.7, 5.13), length 0,77–0,96 mm, mean 0,88 mm (n = 80), breadth 0,38–0,48 mm, mean 0,44 mm (n = 80), CR 0,55–0,59, mean 0,57 (n = 80); macrotrichia scanty, confined to distal third of cell R_5 with very few at the apex of cells M_1 and M_2 only; microtrichia dense and coarse. Dark areas of wing pattern greyish-brown, pale areas whitish with microtrichia, and macrotrichia yellowish; pale areas of wing extensive, fairly well defined but irregularly shaped; two short radial cells equal in length, proximal half of first and distal half to two-thirds of second cell pale. As a result of the general increase in the size of the pale areas and concomitant reduction of the dark areas, the wing of *C. loxodontis* is paler than that of *C. imicola, C. bolitinos* and *C. miombo,* but comes closest to that of *C. pseudopallidipennis.* The most distinctive feature of the wing pattern in the majority of specimens is for the proximal margin of the distal pale

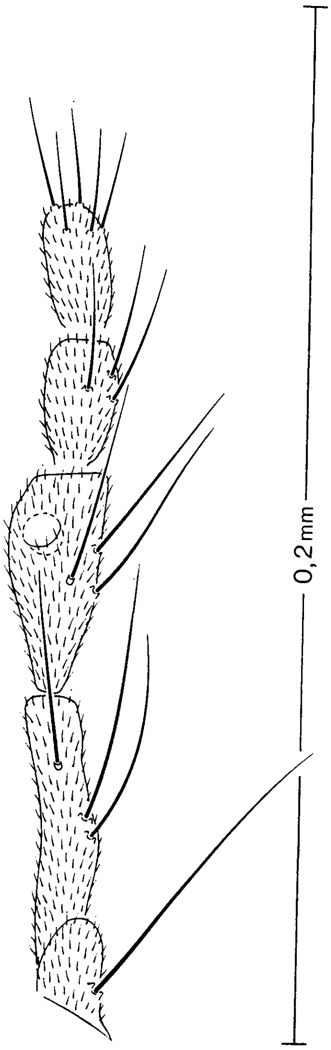


Fig. 5.4

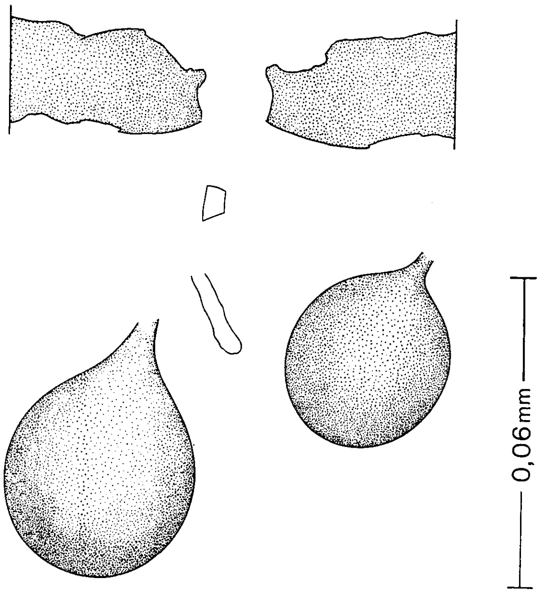


Fig. 5.5

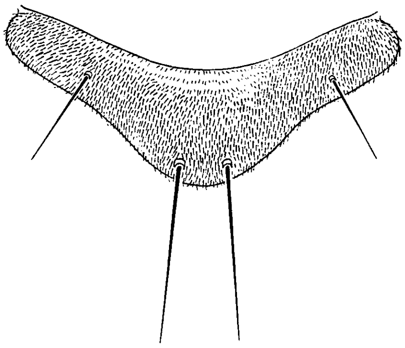


Fig. 5.6

Fig. 5.4 *Culicoides (Avaritia) loxodontis*. Palp, female (paratype Shingwedzi 218).

Fig. 5.5 *Culicoides (Avaritia) loxodontis*. Genitalia, female: spermathecae and sclerotization surrounding gonopore (paratype Shingwedzi 37).

Fig. 5.6 *Culicoides (Avaritia) loxodontis*. Scutellum, female (paratype Shingwedzi 232).

spot in cell R_5 to be more strongly pointed than is found in its taxonomic congeners; occasionally this pointed margin may even fuse narrowly with the distal margin of the third pale costal spot that covers the tip of the second radial cell (Fig. 5.13). Other important specific wing pattern characters are:

(i) The distal margin of the second pale costal spot that straddles the r–m crossvein is expanded medially and tends almost to fuse, under the radial cells, with the third pale costal spot whose proximal margin is expanded medially;

(ii) posterior margin of vein M_2 entirely darkened but anterior margin broadly excised to leave the apex of vein M_2 pale or only narrowly and indistinctly darkened on both margins; this preapical excision is broader than, but not nearly as clearly defined as, that seen in *C. imicola*;

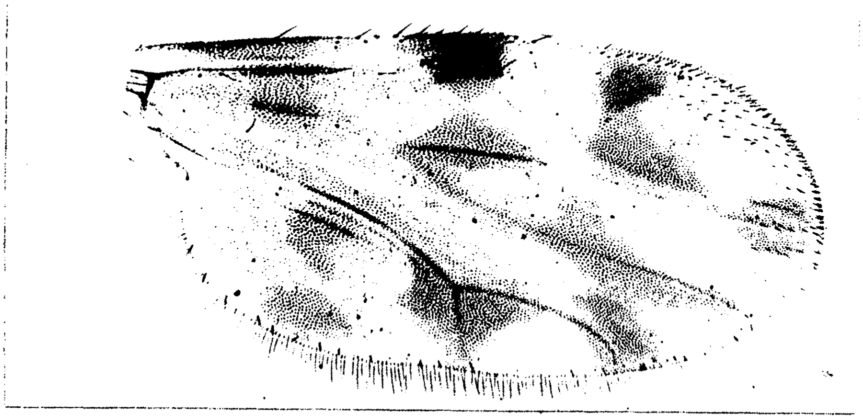
(iii) proximal base of anal angle pale.

Scutum entirely brown in alcohol; scutellum (Fig. 5.5) entirely brown, bearing two long median bristles and one shorter bristle on each corner (n = 41). Haltere knobs pale. Abdomen (Fig. 5.6): two moderately sclerotized slightly unequal spermathecae present, measuring 47,5–56,3 x 35,0– 42,5 μm, mean 52,8 x 41,0 μm and 42,5–43,8 x 30,0–35,0 μm, mean 40,3 x 32,3 μm (n = 20), both round and devoid of small hyaline punctations, with moderately long narrow rudimentary third spermatheca present measuring 11,3–22,5 x 3,1–8,8 μm mean 16,8 x 4,3 μm (n = 27), small sclerotized ring on common spermathecal duct cylindrical, smooth and parallel-sided, a little longer than broad, and about half the length of the rudimentary spermatheca; sclerotization surrounding the oviduct as shown in Fig. 5.6.

Male (Fig. 5.8–5.12; Table 5.1).

Head. Eyes bare. Antenna (Fig. 5.9; Table 5.1): plume rather sparse, fibrillae light brown, almost completely encircling medially each of segments IV–XII in a regular whorl; these segments with very few spiculae which are on one face only; distal segments XIII–XV densely and evenly clothed with spiculae; mean lengths of segment III: 72,6, IV–XII: 338,8, XIII–XV: 75,2–63,1–85,8; total mean

5.7



5.8

Fig. 5.7 *Culicoides (Avaritia) loxodontis*. Wing, female (paratype Pafuri 7).

Fig. 5.8 *Culicoides (Avaritia) loxodontis*. Wing, male (paratype Pafuri 8).

length 635,4 µm (n = 24); sensilla coeloconica distribution: segment III with two (n = 26); XIII with nought to one, mean 0,96 (96 % with one coeloconica, n = 26), XIV with one to two, mean 1,77 (87 % with two coeloconica, n = 26), XV with two coeloconica (n = 26); antenna with a total of five to seven coeloconica, mean 6,65 (n = 26); sensilla chaetica distribution: five of varying lengths and thicknesses on III; two (sometimes three) basally (first long and robust, second shorter and weaker) and one medially (being very slender and 1,5 times longer than segment) on XIII (the deviations from the norm were an additional long and robust sensilla chaetica basally on segment XIII in five antennae, while one antenna had the long medially-occurring sensilla chaetica absent); two basally (both very slender but of different lengths, the one a little shorter than segment, the other fractionally longer than segment) on XIV; none basally on XV, only one apically (n = 26); blunt-tipped sensilla trichodea distribution on segment III–XII: III with two long sensilla trichodea, segments IV–VI each with two long and one short sensilla trichodea, segments VII–IX with one long and one short sensilla trichodea, segment X with one short sensilla trichodea only, segments XI and XII lacking sensilla trichodea (n = 26), the only deviation from the norm noted was an additional long blunt-tipped sensilla trichodea in one antenna on segment V, and a short blunt-tipped trichodea in one antenna on segment XI; these additional trichodea were shorter than normal and obviously aberrant. The distributions of the sensilla coeloconica, chaetica and trichodea are identical to those of *C. imicola, C. bolitinos* and *C. miombo,* and appear in Table 5.1. Those of *C. pseudopallidipennis* differ to some degee and are detailed in Chapter 6 (Table 6.3). Thorax: Scutellum with two median bristles and no lateral bristles (n = 47). Wing: (Fig. 5.8). Genitalia: (Fig. 5.10–5.12) tergum nine (Fig. 5.10, 5.11) square, slightly waisted medially, finely spiculate throughout except for a narrow strip of the anterior and a broad strip of the posterior margins being bare, bearing 12–23 chaetica of different lengths, mean 16,7 (n = 63); apicolateral processes replaced by thin, hyaline flanges lacking spiculae but each carrying a single fine, rather short sensilla chaetica; posterior margin of tergum which separates these flanges most often straight as in Fig. 5.11, to moderately but very rarely deeply concave as in Fig. 5.10; median area not infuscate but bearing a number of striations (Fig. 5.10); two well-developed cerci (Fig. 5.11), each adorned with long spiculae and two long and two short chaetica; cerci protruding well beyond posterior margin of tergum; sternum nine (Fig. 5.11) with a rather deep and wide excavated area with nought to three spiculae, mean 0,21 (n = 80), of these 87,5 % had no spiculae; basimere with dorsal and

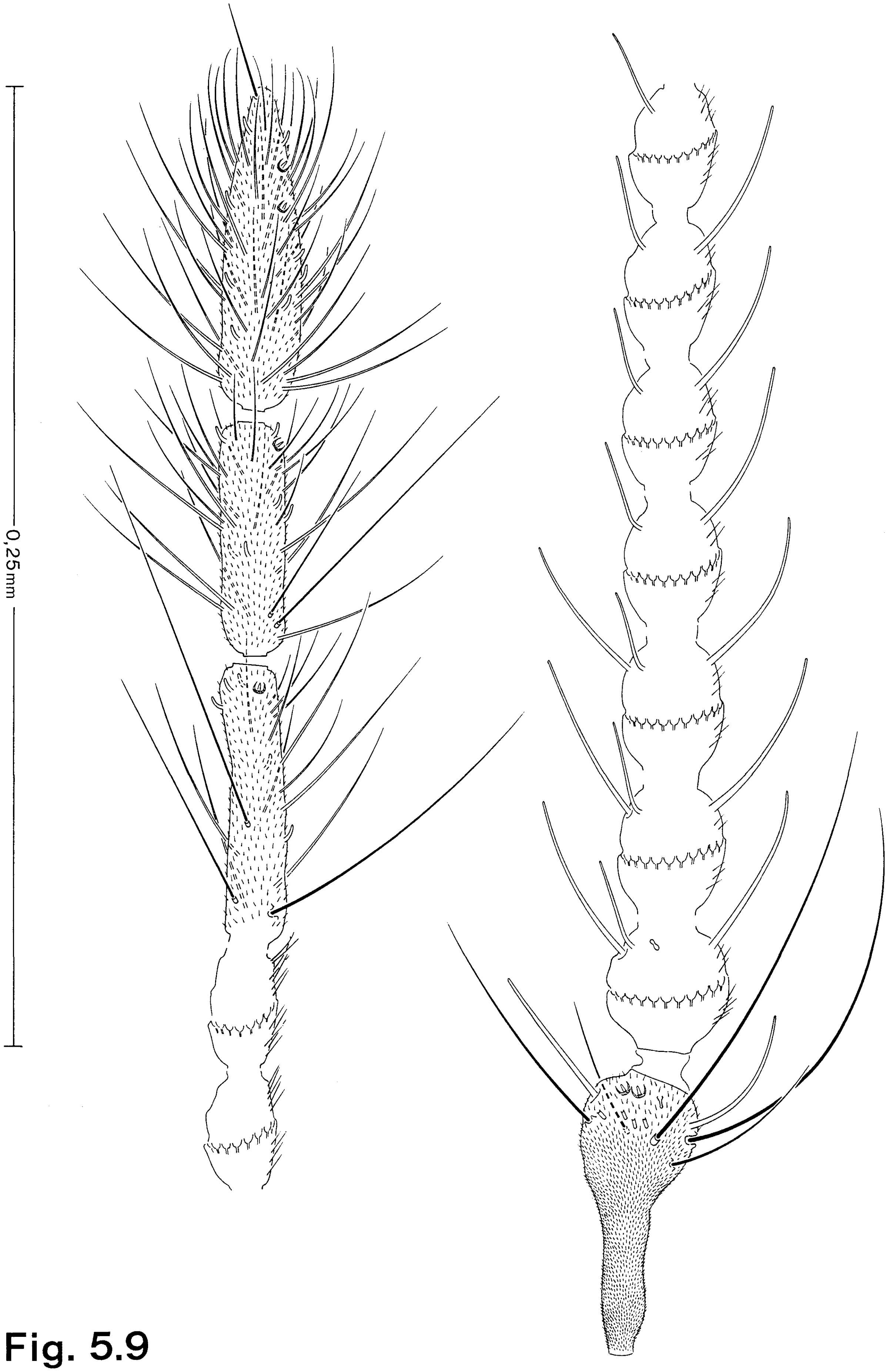


Fig. 5.9

Fig. 5.9 *Culicoides (Avaritia) loxodontis*. Antenna, male: segments XI–XV on left, segments III–X on right (paratype Shingwedzi 283).

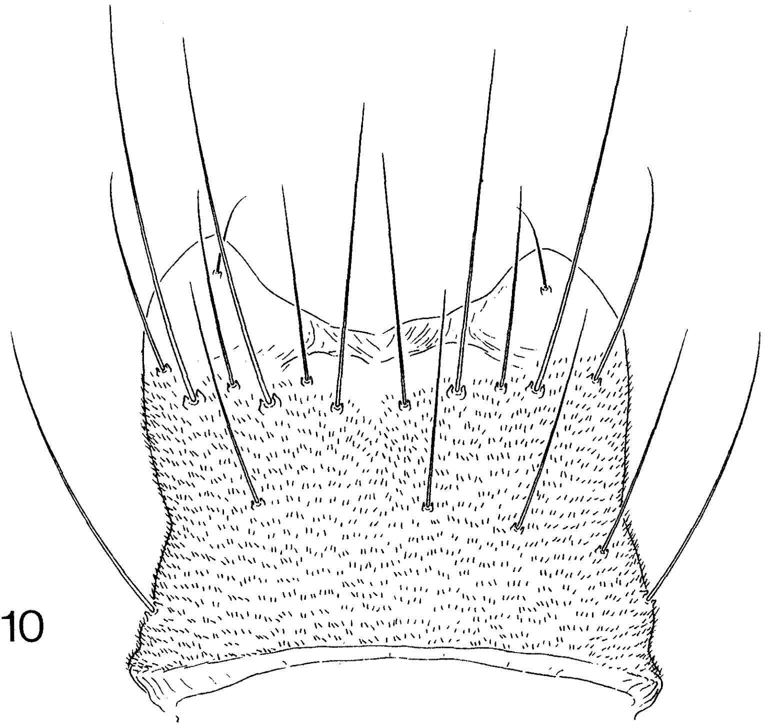


Fig. 5.10

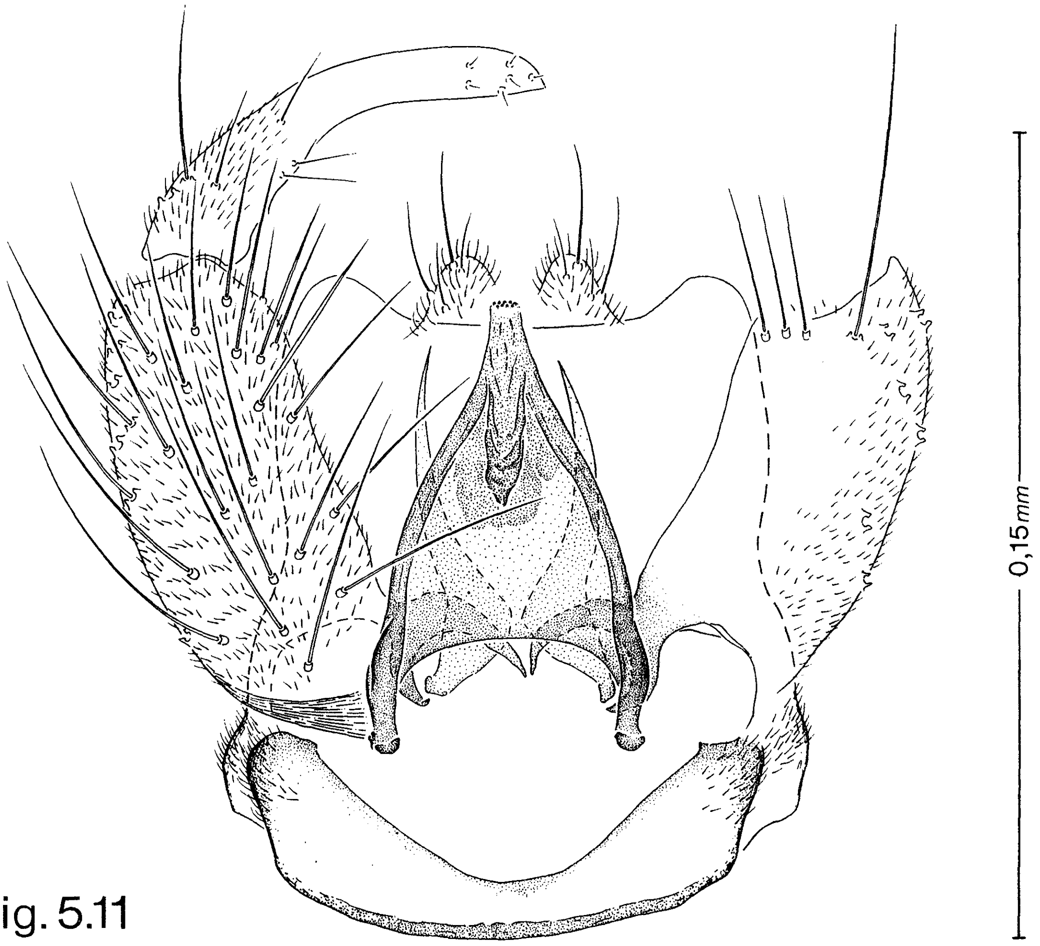


Fig. 5.11

Fig. 5.10 *Culicoides (Avaritia) loxodontis*. Genitalia, male: tergum IX (paratype Hlangulene 16).

Fig. 5.11 *Culicoides (Avaritia) loxodontis*. Genitalia, male (paratype Shingwedzi 117).

ventral spiculae and chaetica as illustrated (Fig. 5.11), basimere 2,4 times as long as broad with basal infuscate collar and well-developed dorsal and ventral roots of the form typical of the subgenus *Avaritia.* Distimere (Fig. 5.11) 0,88 x length of basimere (n = 7), rather stout, gently curved and broadly blunt-tipped, basal half spiculate, carrying six to seven bristles of varying lengths and thicknesses, extreme apex with about six very short fine sensillae. Aedeagus (Fig. 5.11, 5.12) shield-shaped, slender, 1,63–1,86, mean 1,71 x longer than wide (n = 25) and 0,9 x length of basimere (n = 7); basal margin convex, only narrowly and lightly infuscate towards lateral margins, distal margin of arch reaching to 0,18–0,26 x length of aedeagus (n = 7); lateral margins of the aedeagus smooth and gently convex, darkly but narrowly infuscate and converging distad to end in a hyaline, rather short parallel-sided terminal projection whose extreme apex is not smooth but serrated with five to eight tiny sclerotized papillae (Fig. 5.11, 5.12); base of this terminal projection inserts anteriorly into median area of aedeagus in the form of a raggedly infuscate 'peg' (Fig. 5.11). Parameres (Fig. 5.11) separate, nearly touching medially from where they diverge anteriad and posteriad at approximately 45°, posterior halves as two convex almost hyaline blades, basally stout but tapering smoothly to sharp, simple, erect tips.

Etymology. The distribution pattern of the new species correlates with that of the African elephant *Loxodonta africana* in the KNP; in addition, its immatures appear to develop exclusively in elephant dung, further evidence of a close association.

Type material

SOUTH AFRICA: Holotype ♀ (slide Shingwedzi 224), Lamont windmill (23°06'S, 31°24'E) on banks of Mphongolo river six km north-west of Shingwedzi rest camp, northern Kruger National Park, 20.11.1990, R. Meiswinkel and L.E.O. Braack, blacklight 18:00–22:00.

60 ♀♀ 178 ♂♂	paratypes, slides labelled and numbered to sex, the collection as follows:
6 ♀♀	(slides Shingwedzi 37, 45, 48, 54, 64, 68), Shingwedzi rest camp, northern KNP, 1.IX.1979, B. de Meillon and R. Meiswinkel, blacklight.
3 ♂♂	(slides Shingwedzi 43, 57, 66), (collection data as above).

6 ♀♀ (slides Shingwedzi 82–84, 86, 90, 113), Shingwedzi rest camp, northern KNP, 19.IV.1983, R. Meiswinkel, blacklight.

2 ♂♂ (slides Shingwedzi 100, 117), (collection data as above).

1 ♀ (slide Shingwedzi 78), Shingwedzi rest camp, northern KNP, 7.IX.1984, R.Meiswinkel, blacklight.

40 ♀♀ (slides Shingwedzi 167–171, 173–175, 210–223, 225–233, 261–269), Lamont windmill on banks of Mphongolo river, six km n.w. of Shingwedzi rest camp, northern KNP, 20.II.1990, R. Meiswinkel & L.E.O. Braack, blacklight 18:00–22:00.

24 ♂♂ (slides Shingwedzi 160–165, 177, 234–250), (collection data as above).

94 ♂♂ (slides Shingwedzi 276–295, 373–466), Mooigesig dam area, 45 km w. of Shingwedzi rest camp, northern KNP, 25.IV.1990, R. Meiswinkel, L.E.O. Braack & D. de Klerk, blacklight in *Colophospermum mopane*/*Acacia nigrescens* savanna, 17:00–22:00.

28 ♂♂ (slides Shingwedzi 301–328), Langtoon dam area, 30 km n. of Shingwedzi rest camp, northern KNP, 24.IV.1990, R. Meiswinkel, L.E.O. Braack & D. de Klerk, blacklight in *Colophospermum mopane* shrub-veld, 17:00–22:00.

1 ♀ (slide Pafuri 7), Pafuri anthrax camp on banks of Luvuvhu river, northern KNP, 15.IV.1986, R. Meiswinkel & L.E.O. Braack, blacklight 13 m up *Acacia albida* tree, 18:00–23:00.

1 ♂ (slide Pafuri 8), (collection data as above).

1 ♀ (slide Skukuza 18), Skukuza rest camp, southern KNP, 11.III.1984, R. Meiswinkel & L.E.O. Braack, blacklight on banks of Sabie river.

1 ♂ (slide Skukuza 122), Skukuza rest camp, southern KNP, 15.I.1985, R. Meiswinkel & L.E.O. Braack, blacklight on banks of Sabie river.

1 ♀ (slide Hlangulene 10), 50 km n. of Skukuza rest camp, southern KNP 26.II.1986, R. & P. Meiswinkel, reared from elephant dung.

23 ♂♂ (slides Hlangulene 1–9, 11–16, 19, 22, 25–30), (collection data as above).

1 ♀	(slide Tshalungwa 13), 18 km n. of Punda Maria rest camp n.w. KNP, 10.IV.1986, R. Meiswinkel & L.E.O. Braack, blacklight 18:30–21:00.
1 ♂	(slide Tshalungwa 14), (collection data as above).
3 ♀♀	(slides Phambana 1–3), 28 km e. of Skukuza rest camp, southern KNP, 8.V.1990, D. de Klerk, blacklight 17:00–22:00.
1 ♂	+ pupal exuvia (slide Skukuza 351), ex elephant dung on sand road 20 km w. of Skukuza rest camp, southern KNP, 14.V.1991, H. Nevill.

Unmounted light-trap material examined

248 ♀♀ 3 ♂♂	Phambana, 28 km e. of Skukuza rest camp, southern KNP, 8.V.1990, D. de Klerk, blacklight 17:00–22:00.
74 ♀♀ 55 ♂	Mangovane spring, 10 km n. of Punda Maria rest camp, northern KNP, 3.III.1991, R. Meiswinkel, L.E.O. Braack, Alan L. Dyce & M. Swanepoel, blacklight 18:30–20:15.
157 ♀♀ 29 ♂♂	Mwamayimane windmill, six km e. of Shingwedzi rest camp, northern KNP, 20.II.1990, R. Meiswinkel & L.E.O. Braack, blacklight 17:30–24:00.
1161 ♀♀ 39 ♂♂	Mooigesig dam area, 45 km w. of Shingwedzi rest camp, northern KNP, 25.IV.1990, R. Meiswinkel, L.E.O. Braack & D. de Klerk blacklight in *Colophospermum mopane*/*Acacia nigrescens* savanna, 17:00–22:00.
728 ♀♀	Langtoon dam area, 30 km n. of Shingwedzi rest camp, northern KNP, 24.IV.1990, R. Meiswinkel, L.E.O. Braack & D. de Klerk, blacklight in *Colophospermum mopane* shrubveld, 17:00–22:00.
50 ♀♀ 5 ♂♂	Ngirivane windmill, 12 km w. of Satara rest camp, central KNP, 18.IX.1991, R. Meiswinkel, H. van Ark & M. Swanepoel, blacklight 18:00–24:00.
14 ♀♀ 1 ♂	At confluence of Mutlumuvi and Sand rivers, 12 km n.e. of Skukuza rest camp, southern KNP, 19.IX.1991, R. Meiswinkel, H. van Ark & M. Swanepoel, blacklight in dry thickets, 18:00–24:00.
454 ♀♀ 78 ♂♂	At confluence of Mutlumuvi and Sand rivers, 12 km n.e. of Skukuza rest camp, southern KNP, 22.I.1992, R. Meiswinkel, blacklight in dry thickets, 18:45–24:00

Unmounted reared material examined

42 ♀♀ 68 ♂♂	Rhidonda windmill, 23 km w. of Letaba rest camp, central KNP, 16.XI.1979, R. Meiswinkel.
30 ♀♀ 45 ♂♂	Shilolweni dam, 38 km n.e. of Skukuza, southern KNP, 22.I.1991, L.E.O. Braack.
163 ♀♀ 323 ♂♂	Khumane dam, 67 km n.e. of Skukuza, southern KNP 22.I.1991, L.E.O. Braack.
57 ♀♀ 87 ♂♂	Nwatintsontso, 50 km n.e. Skukuza, southern KNP, 22.I.1991, L.E.O. Braack.
30 ♀♀ 18 ♂♂	Mlondozi, six km e. of Lower-Sabie rest camp, south-eastern KNP, emerged 16–17.IX.1991 from dung evacuated ± 45 year-old elephant bull 29.VIII.1991, R. Meiswinkel.
14 ♀♀ 26 ♂♂	At confluence of Mutlumuvi and Sand rivers, 12 km n.e. of Skukuza rest camp, southern KNP, emerged 30.IX–4.X.1991 from dung evacuated by ± 12 year-old male 19.IX.1991, R. Meiswinkel.
1 ♀ 9 ♂♂	12 km e. of Skukuza rest camp, southern KNP, emerged 25–26.X.1991 from dung evacuated by ± 35 year-old elephant bull 16.X.1991, R. Meiswinkel, G. J. Venter & E.M. Nevill.
56 ♀♀ 77 ♂♂	13 km s. of Balule rest camp, central KNP, emerged 6.II.1992, from dung evacuated 29.I.1992, R. Meiswinkel.
82 ♀♀ 230 ♂♂	Ntomeni windmill, 15 km n. of Satara rest camp, central KNP, emerged 6.II.1992 from dung evacuated by large elephant bull 29.I.1992, R. Meiswinkel.

5.4 DISCUSSION

5.4.1 *Taxonomy*

Culicoides (Avaritia) loxodontis does not appear to have been dealt with previously in studies on Afrotropical biting midges. Since its discovery in 1979, I have referred to it as C. sp. # 71 in unpublished reports and correspondence.

5.4.2 *Differential diagnosis*

The 12 character states that separate *C. imicola* and *C. loxodontis* are summarized in Table 5.6 and are discussed in further detail below. Where data are available, these two species are also differentiated from *C. bolitinos, C. miombo* and *C. pseudopallidipennis.*

Three character states reliably separate *C. loxodontis* from *C. imicola* under the dissecting microscope. The former has (a) a generally paler wing, with the proximal margin of the distal pale spot in cell R_5 strongly pointed, (b) has the preapical pale excision on the anterior margin of vein M_2 more extensive and ill-defined, leaving the apex of M_2 pale or only slightly and indistinctly darkened, and (c) has two median bristles on the scutellum in both sexes; these bristles are, however, difficult to detect under the dissecting microscope, especially if one or both have been knocked off during capture. The fact that *C. loxodontis* appears to be exclusively associated with the African elephant means that it will only be captured in the presence or territory of these animals, whereas *C. imicola* will also be widespread where man husbands livestock. Finally, because the immature stages of *C. loxodontis* develop exclusively in the dung of elephants, the adults, during eclosion, become infested with phoretic *Myianoetus* mites. Counts made of the number of mites carried by the females of two subpopulations of *C. loxodontis* captured in light-traps at Mooigesig and Langtoon (Fig. 5.1) showed that at the former site 186 of 697 (26,7 %) carried from one to 13 mites/midge, while at the latter site 84 of 728 (11,5 %) had from one to nine mites. Recently emerged nulliparous females have the highest infestation rate (22 % at Langtoon, 46 % at Mooigesig) (R. Meiswinkel & L.E.O. Braack, unpublished observations 1990). The presence of these mites on *C. loxodontis is* therefore a useful aid to identification as *C. imicola,* a species whose immatures do not live in dung, is entirely free of them.

Based on wing pattern, it is rather difficult to separate *C. loxodontis* from *C. pseudopallidipennis* as both species have predominantly pale wings. However, *C. pseudopallidipennis* has a swollen third palpal segment which can quite easily be seen under the dissecting microscope, thus differentiating it from the slender third segment seen in *C. imicola, C. bolitinos, C. miombo* and *C. loxodontis.*

In slide-mounted specimens, the following 11 character states facilitate the identification and separation of *C. loxodontis* from its four taxonomic congeners quite easily:

1. Female. Wing: The wing of *C. loxodontis* is distinctly paler than that of *C. imicola, C. bolitinos* or *C. miombo*, but closely resembles that of *C. pseudopallidipennis*. The next four wing characters more clearly define *C. loxodontis* as a good species and are labelled in Fig. 5.13.

   (a) The shape of the distal pale spot in the apex of cell R_5: its proximal margin usually strongly pointed (Fig. 5.13). In some specimens this point narrowly fuses with the distal margin of the third pale costal spot covering the tip of the second radial cell. In *C. imicola, C. bolitinos, C. miombo* and *C. pseudopallidipennis*, the proximal margin is moderately pointed to nearly straight.

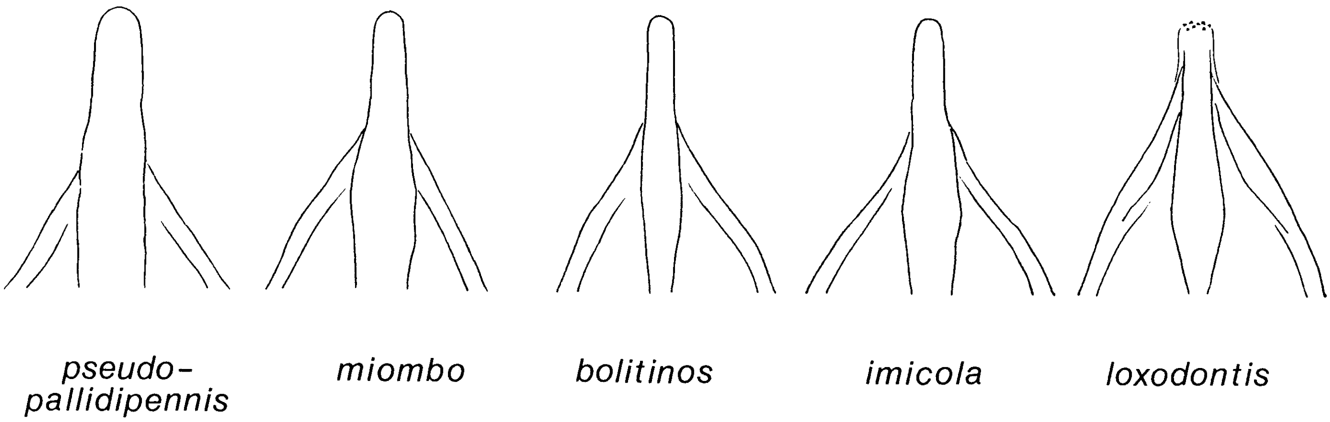
   (b) In *C. loxodontis* and *C. pseudopallidipennis* the second and third pale costal spots nearly fuse under the radial cells (Fig. 5.7, 5.13). In the remaining species these pale spots are well separated from one another by a dark area.

   (c) In *C. loxodontis* vein M_2 has an extensive and ill-defined pale excision on its anterior margin. This leaves the apex of the vein either pale or only narrowly and indistinctly darkened (Fig. 5.7, 5.13). This is again very similar to the configuration seen in *C. pseudopallidipennis* and in part also *C. bolitinos* and *C. miombo. C. imicola is* distinctive in that it has a clearly defined preapical excision that leaves the apex of vein M_2 broadly and obviously darkened.

   (d) As in *C.imicola, C.bolitinos* and *C.pseudopallidipennis*, the extreme base of the anal cell of *C. loxodontis* is pale (Fig. 5.13); in *C. miombo* there is a highly diagnostic, prominent, long, dark smudge.

2. Female. Palps: A low P/H ratio (mean 0,84; n = 20) indicates that *C. loxodontis* has a short proboscis which in turn indicates short palps. As can be seen in Table 5.5 and Fig. 5.15, *C. loxodontis* comes close to *C. bolitinos* in total palpal length while *C. miombo* and *C. imicola* have longer palps. Glick (1990) describes the proboscis of *C. pseudopallidipennis* as ‘long’. Clastrier (1958) gives the measurements of segments II–V of *C. pseudopallidipennis* which indicates that the palps are about as long as those of *C. imicola.* Furthermore, *C. pseudopallidipennis* has a swollen third palpal segment as opposed to the slender one found

Fig. 5.12



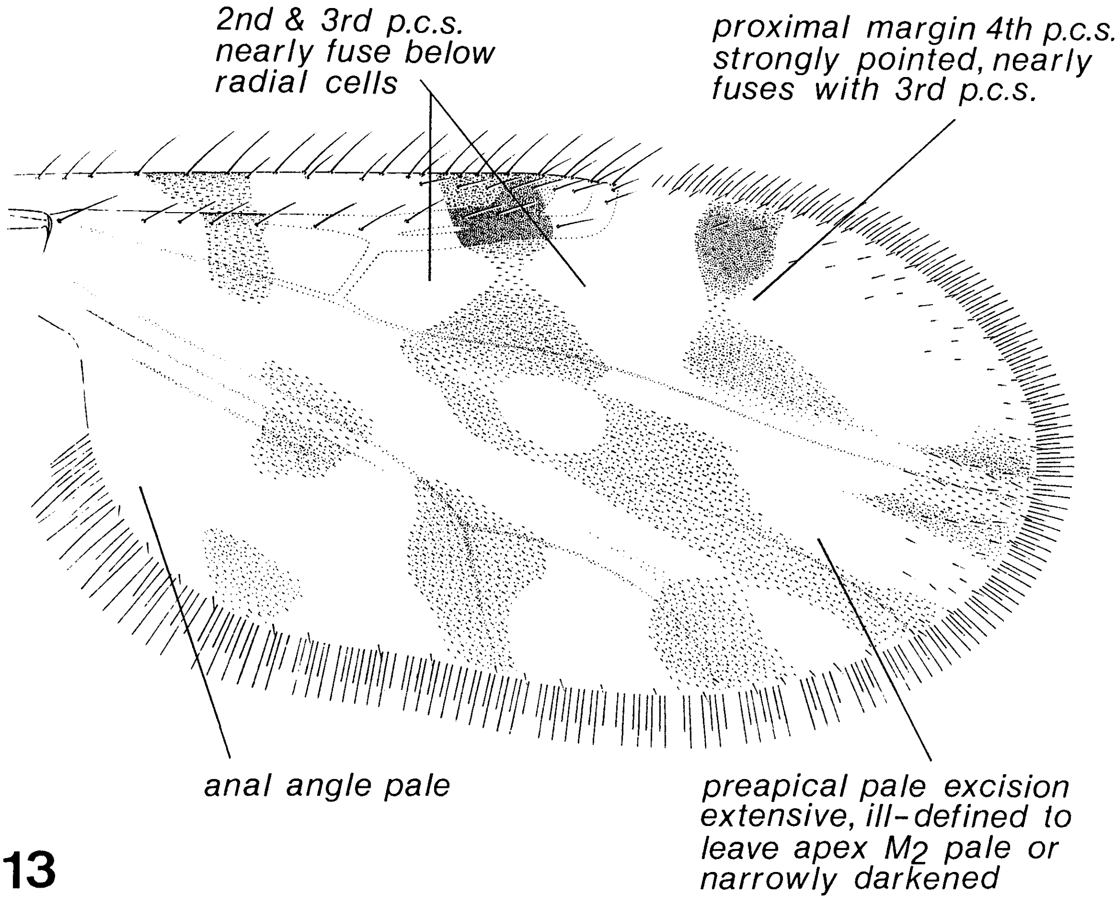


Fig. 5.13

Fig. 5.12 Genitalia male: comparison of the apices of the aedeagi of five species of the Imicola group.

Fig. 5.13 *Culicoides (Avaritia) loxodontis.* Wing, female: diagnostic features.

Fig. 5.14

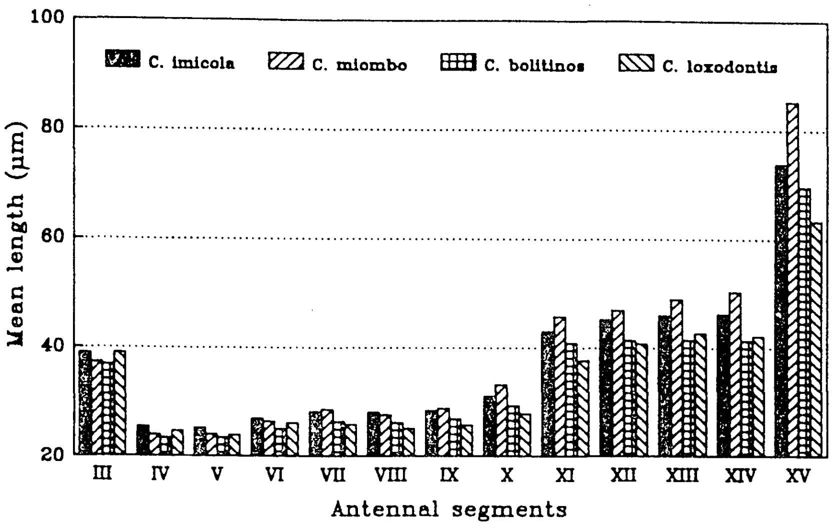


Fig. 5.15

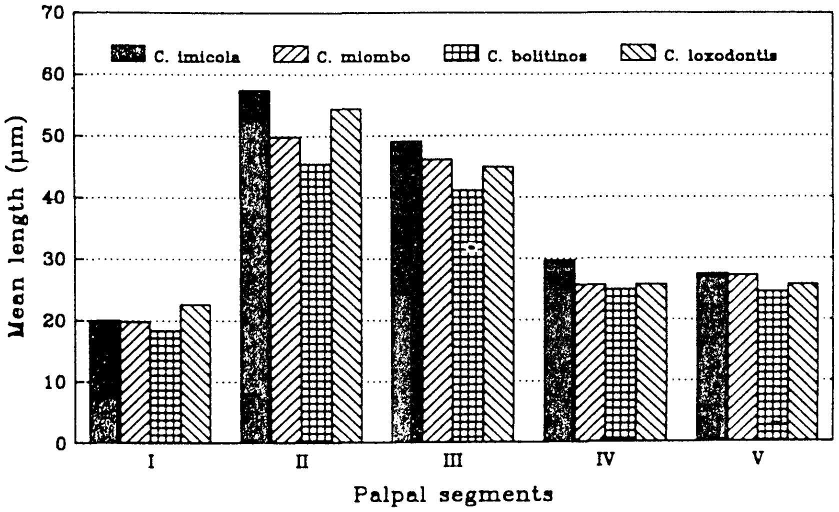


Fig. 5.14 Comparison of mean lengths (μm) of each of the female antennal segments III-XV of *C. (Avaritia) imicola, C. (A.) miombo, C. (A.) bolitinos* and *C. (A.) loxodontis*.

Fig. 5.15 Comparison of mean lengths (μm) of each of female segments I-V of *C. (Avaritia) imicola, C. (A.) miombo, C. (A.) bolitinos* and *C. (A.) loxodontis*.

in its four taxonomic congeners.

3. Female. Antennae: As can be seen in Table 5.4 and Fig. 5.14, *C. loxodontis* has the longest antennal segment III but has the shortest segments VII–XII and XV. Once again it comes closest to *C. bolitinos* in total antennal length. The four species *C. loxodontis, C. imicola, C. bolitinos* and *C. miombo*, are all separable on the mean lengths of antennal segments X, Xl and XV the last-named being the most significant (Table 5.4). The data provided for *C. pseudopallidipennis* by Clastrier (1958) come near that for *C. loxodontis*, except that segment III of the former is given as only two-thirds the length of the four species listed in Table 5.4.

4. Female. Antennae: *C. loxodontis* and *C. miombo* both have the long blunt-tipped sensilla trichodea on antennal segment VI rather short, and as a result share a low antennal trichodea ratio (AtR): mean 1,47 in the former vs 1,54 in the latter, while *C. bolitinos* (mean 1,85) and *C. imicola* (mean 1,86) have longer trichodea and share a higher AtR ratio. As illustrated by Clastrier (1958), these trichodea are rather short and unusually swollen in *C. pseudopallidipennis*, and its AtR ratio will in all likelihood cluster with that of *C. loxodontis* and *C. miombo*. In the latter two species, however, the blunt-tipped trichodea are not swollen.

5. Female. Antennae: One of the most striking and reliable taxonomic differences between *C. loxodontis* (n = 81) and its three congeners *C. imicola* (n = 172), *C. bolitinos* (n = 59) and *C. miombo* (n = 70), is that in *C. loxodontis* antennal segments VI and VIII always bear four sensilla chaetica basally (Fig. 5.3 and Table 5.3), whereas in the other three species three chaetica are the norm. The number of chaetica in *C. pseudopallidipennis* are variable as shown in Chapter 6 (Table 6.3).

6. Female. Scutellum: *C. loxodontis* (n = 41) always carries two long bristles medially (Fig. 5.5); *C. imicola* (n = 87), *C. bolitinos* (n = 20), and *C. miombo* (n = 37) each have only one bristle medially. Clastrier (1958) recorded one bristle medially for *C. pseudopallidipennis.* This consistent presence of two median bristles on the scutellum I have found to be the easiest and most reliable way of identifying a slide-mounted specimen of *C. loxodontis*. Even if one or

both bristles have been lost during capture, their insertion sockets or alveoli remain visible.

7. Male. The extent of spiculation on the membrane of sternum nine of the genitalia once again groups *C. loxodontis* with *C. bolitinos*, and *C. imicola* with *C. miombo*; in the former pair the membrane is mostly bare or occasionally adorned with a few spicules, whereas in the latter pair the membrane is seldom sparsely but mostly moderately to densely spiculate. This membrane bare in *C. pseudopallidipennis.*

8. Male. The most diagnostic feature of the genitalia of *C. loxodontis* is that the extreme apex of the aedeagus is not smoothly rounded and hyaline as in its four taxonomic congeners, but is distinctly roughened or serrated by five to eight tiny, darkly pigmented papillae (Fig. 5.11, 5.12). The apex of the aedeagus of *C. loxodontis* is also shorter than in its four congeners which all have it a little longer and largely inseparable in shape (Fig. 5.12).

5.4.3 ***Larval habitat***

Culicoides loxodontis has on a number of occasions been reared from the dung of the African elephant in the Kruger National Park, these records represented by the symbol of an elephant in Fig. 5.1. Despite my persistent efforts during the past seven years, it has never been reared from the dung of either the white or black rhinoceros, zebra, wildebeest, buffalo, cattle or horse, either within or outside the Kruger National Park.

As mentioned earlier, six species of the subgenus *Avaritia* have been found to inhabit the dung of *Loxodonta*, the commonest of these being two species provisionally labelled C. sp. # 54 pale form and C. sp. # 54 dark form (R. Meiswinkel & H. Nevill, unpublished observations 1985–1991). *Culicoides loxodontis* is third in abundance; up to 500 specimens have been reared from 2,5 kg of wet elephant dung. In the height of summer, the first individuals of *C. loxodontis* will emerge after eight to ten days from dung collected when only a few hours old.

The recently discovered pupa of *C. loxodontis* is quite remarkable and is included in the type series. It will be described elsewhere (H. Nevill, personal communication 1991).

5.4.4 *Distribution*

Culicoides (A.) loxodontis is known only from the Kruger National Park, South Africa, and a single record from Ol Doinyo Sabachi, central Kenya. Fig. 5.1 shows the holotype locality (Lamont windmill, Shingwedzi), and paratype locales (Pafuri, Tshalungwa, Mangovane spring, Langtoon dam, Mooigesig dam, Hlangulene, Phambana and Skukuza) from which the new species has been commonly collected, either in light-traps or reared from elephant dung. As noted earlier, only one ♀ and 23 ♂♂ reared from elephant dung collected at Hlangulene, and one ♂ and its associated pupal exuvia retrieved from elephant dung found 20 km west of Skukuza, form part of the type series of *C. loxodontis*. Rearings made from dung collected at Khumane dam, Shiloweni dam, Nwatintsontso, Rhidonda and Shisha were too teneral to be slide-mounted in Canada balsam.

On occasion, *C. loxodontis* has been found to be the dominant species in certain areas of the KNP and can comprise up to 52 % of 500–2500 *Culicoides* collected in light-traps operated during the first four to six hours following nightfall. The light-trap data for nine locales are indicated by the numbers in parentheses in Fig. 5.1; rather than providing percentages, the actual numbers of *C. loxodontis* out of the total number of *Culicoides* captured are given. At four of these sites *C. loxodontis* was the dominant *Culicoides* of 16–24 species collected (R. Meiswinkel & L.E.O. Braack, unpublished data 1987–1990).

Conversely, *C. loxodontis* can be either absent or rare in light-trap catches, as shown by the nil result for Manxeba Pan and the presence of only two specimens out of more than 1 000 *Culicoides* collected on the banks of the Sabie river in Skukuza. Manxeba Pan falls into that far northern part of the KNP that is visited only by lone elephant bulls and small bachelor herds at certain times of the year. These are culled during the winter months to protect the rare vegetation. The virtual absence of elephants is paralleled by the absence of *C. loxodontis* in light-trap collections. A similar situation prevails in the immediate surrounds of Skukuza, where the presence of larger groups of elephants is sporadic as this is an area generally used only by bachelor bulls in the dry season. Just 5–15 km north, south and east of Skukuza, however, large herds of elephants are to be found at certain times of the year, but are too far distant for their attendant dung-inhabiting *Culicoides* to be captured in a light-trap operated in Skukuza. At one such site, i.e. Mutlumuvi 12 km north-east of Skukuza, *C. loxodontis* is one of the most abundant *Culicoides* species present, especially during the hotter, wetter months.

These statistics imply strongly that *C. loxodontis* will only be sampled in abundance in areas directly frequented by large numbers of elephant. This appears to be borne out by its dominance at Mooigesig, Langtoon, Mwamayimane, Mutlumuvi and Phambana, all locales that were sampled on the same day that large groups of elephants were sighted, and known to carry large elephant herds year after year (van Wyk & Fairall 1969).

Although more precise comparative data need to be assembled, it seems that the ebb and flow in the distribution and abundance of *C. loxodontis* reflects strongly the dynamics of elephant herd as regards their daily food and water requirements, clan ranges, reproductive strategies and seasonal movements. Furthermore, it is likely that the breeding herds, which make up approximately 85 % of the entire elephant population of ± 7 500 individuals in the KNP (A. Hall-Martin & I. Whyte, unpublished data 1973–1990), are most pivotal to the spread and abundance of *C. loxodontis*, as these herds, each numbering from 50–300 individuals, would provide large amounts of dung for the immature stages of *C. loxodontis* and would likely also provide bloodmeals for the adult females. To conclude: not only can *C. loxodontis* be abundant, but it is also found widely in areas inhabited by elephants irrespective of vegetation or landscape type.

Since I first became aware in 1979 of its status as a good species, subsequent collections made randomly in the animal husbandry areas of South Africa have failed to yield a single specimen of *C. loxodontis*. It has also not been found on nine game parks, reserves or hunting lodges sampled in the provinces of Transvaal and Natal, all of which harboured dung-producing herbivores such as the white rhinoceros *(Ceratotherium simum)*, the black rhinoceros *(Diceros bicornis)*, buffalo, zebra and wildebeest. A number of dung-inhabiting *Avaritia* species have been collected at these sites but no specimen of *C. loxodontis*. In South Africa there are eight locales besides the Kruger National Park and adjoining game reserves that carry small populations of mostly introduced elephants. None of these reserves has been sampled for *C. loxodontis*.

The failure, during 12 years of collecting, to find *C. loxodontis* outside the KNP, in areas where elephants do not occur, is further reason for now asserting that the distribution of *C. loxodontis* is tightly linked to that of the African elephant. As regards this association and the resultant distribution of *C. loxodontis*, there are some deeper issues that still need to be researched. Elephants, in being both grazers and browsers, 'are catholic in their habitat requirements' (Smithers 1983) and thus widespread in Africa where man allows them to be. Although it seems safe to assume that *C. loxodontis* will be similarly widespread in the savanna woodland areas of eastern and southern Africa, it is premature to conclude that *C. loxodontis*, despite its dependence on elephant dung, will be as tolerant as the elephant of changes in vegetation and climate in the rest of Africa. In South Africa it will be difficult to assess whether *C. loxodontis* has any ecozone preferences, as its present pattern of occurrence is, in great measure, artificial, the elephant having been eliminated from most of its former range. Therefore, if any vegetational or climatic constraints are exerted on the distribution of *C. loxodontis*, their unravelling will depend on collections still to be made throughout Africa, especially in areas such as hot and dry semi-deserts (Namibia), cooler higher-lying plateaux (eastern Zaire; western Uganda) and the wetter, more humid tropical forests (Zaire; Gabon; Cameroun).

As regards the historical distribution of elephants in South Africa, it is interesting to note that at the end of the 15th century elephants were reported as far south as Mossel Bay on the Cape coast (Smithers 1983). For the next four centuries, their extermination was ferociously pursued to the point where Stevenson-Hamilton (1903) reported that elephants were locally extinct in the Transvaal, even in the Sabi Game Reserve (now the KNP) proclaimed five years previously. However, two years later, the first 10 elephants were recorded in this reserve, having entered from Mozambique (Stevenson-Hamilton 1905). Their numbers slowly increased to stand at 131 in 1931 (Van Wyk & Fairall 1969); today the Kruger National Park is home to ± 7 500 elephant, the maximum number the vegetation in this 20 000 km^2 reserve can support without being degraded.

It remains a matter of speculation whether *Culicoides loxodontis* had enjoyed a similarly widespread distribution in South Africa. Its dependence on elephant dung as a larval habitat does imply that this biting midge species must have receded, along with the elephant, from some areas of its range, as there is still no evidence that *C. loxodontis* will switch resources and utilize the dung of any other herbivore. I therefore believe that the dominance of *C. loxodontis* in parts of the KNP today is directly the result of the spectacular rebound in elephant numbers in the same area over the last 90 years. The abrupt absence of *C. loxodontis* outside the western Park boundaries seems to bear this out, as no concomitant changes in rainfall or vegetation could account for this marked break in distribution.

If it is true that *C. loxodontis* re-entered the Transvaal with elephants from Mozambique, it is likely that it occurs throughout the remainder of southern and eastern Africa and may eventually be found westwards north and south of the equator in the savanna woodland zones encircling the equatorial forest block.

5.5 CONCLUSION

Culicoides loxodontis is the fifth member of the Imicola group of the subgenus *Avaritia* to be described from the Afrotropical Region. It appears to be exclusively associated with the African elephant as the distribution of *C. loxodontis* parallels that of the elephant in the KNP, and it has been reared only from elephant dung.

Taxonomically, *C. loxodontis* can be confused with *C. imicola* and, especially, *C. pseudopallidipennis*. The separation of these two species from *C. loxodontis* depends primarily upon the examination of slide-mounted material, as all three species may occur in ‘elephant country’. Judging from light-trap catches made at a number of sites in the Kruger National Park, *C. loxodontis* can be quite abundant. Because of its abundance and its close association with elephants, *C. loxodontis* deserves attention as a potential vector of orbiviruses to an animal that has been suggested as being a possible reservoir host for African horsesickness (Davies & Otieno 1977).

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TABLE 5.1: Mean lengths (μm) of segments, range in number, mean number and distribution of sensillae on the female and male antennae of *C. (A.) loxodontis*

		Antennal segments													**Total and mean total**
		III	**IV**	**V**	**VI**	**VII**	**VIII**	**VIX**	**X**	**XI**	**XII**	**XIII**	**XIV**	**XV**	
Female: (n = 80–81)															
Sens. coeloconica:	range/segment	2–3	0	0	0	0	0	0	0	0–1	0–1	1	1	0–1	6–8
	mean no./segment	2,91	0	0	0	0	0	0	0	0,05	0,98	1,00	1,00	0,98	6,93
Sens. chaetica:	range/segment	4–7	3–5	2–3	4–5	2–3	3–5	1–3	2–4	0–1	0	0	0	0	24–29
	mean no./segment	5,00	3,25	2,15	4,04	2,06	4,00	2,04	3,02	0,05	0	0	0	0	25,89
Sens. trichodea (blunt-tipped)		LL	LLc	LLc	LLc	LLc	LLc	LLc	LLc	–	–	–	–	–	
Mean lengths of segments		39,6	25,2	24,5	26,6	26,3	25,8	26,2	28,5	38,6	42,1	43,9	42,6	63,5	453,1
Male: (n = 24–26)															
Sens. coeloconica:	range/segment	2	0	0	0	0	0	0	0	0	0	0–1	1–2	1–2	5–7
	mean no./segment	2	0	0	0	0	0	0	0	0	0	0,96	1,92	1,92	6,65
Sens. chaetica:	range/segment	5	0	0	0	0	0	0	0	0	0	2–4	2	0	9–11
	mean no./segment	5	0	0	0	0	0	0	0	0	0	3,42	2,00	0	10,15
Sens. trichodea (blunt-tipped)		LL	LLc	LLc	LLc	Lc	Lc	Lc	c	0	0				
Mean lengths of segments		72,6	<------------------------------------ 338,8 ------------------------------------>									75,2	63,1	85,8	635,5

TABLE 5.2: Number and frequency of coeloconica present on each of female antennal segments III–XV of *C. (Avaritia) loxodontis*

No. of coeloconica per segment of *C. loxodontis*	**Antennal segments**							
	III	**IV–IX**	**X**	**XI**	**XII**	**XIII**	**XIV**	**XV**
0	–	81	81	77	1	–	–	1
1	–	-	–	4	80	81	81	80
2	7	–	–	–	–	–	–	–
3	74	–	–	–	–	–	–	–
4	–	–	–	–	–	–	–	–
No. of antennae examined	81	81	81	81	81	81	81	81

TABLE 5.3: Number and frequency of chaetica present on each of female antennal segments III–XV of *C. (Avaritia) loxodontis*

No. of chaetica per segment *C. loxodontis*	**Antennal segments**												
	III	**IV**	**V**	**VI**	**VII**	**VIII**	**IX**	**X**	**XI**	**XII**	**XIII**	**XIV**	**XV**
0	–	–	–	–	–	–	–	–	77	81	81	81	81
1	–	–	–	–	–	–	1	–	4	–	–	–	–
2	–	–	69	–	76	–	76	1	–	–	–	–	–
3	–	42	12	–	5	2	4	77	–	–	–	–	–
4	2	36	–	78	–	76	–	3	–	–	–	–	–
5	78	3	–	3	–	3	–	–	–	–	–	–	–
6	–	–	–	–	–	–	–	–	–	–	–	–	–
7	1	–	–	–	–	–	–	–	–	–	–	–	–
No. of antennae examined	81	81	81	81	81	81	81	81	81	81	81	81	81

TABLE 5.4: Comparison of mean lengths (μm) of female antennal segments III–XV of four *Culicoides* species of the Imicola group (n = 25)

Antennal segment	Species and mean lengths				F-value
III	*bolitinos*	*miombo*	*imicola*	*loxodontis*	10,245
	36,85	37,30	39,00	39,05	
IV	*bolitinos*	*miombo*	*loxodontis*	*imicola*	x^2 = 26,464
	23,35	24,00	24,65	25,45	
V	*bolitinos*	*loxodontis*	*miombo*	*imicola*	x^2 = 19,705
	23,45	23,93	24,08	25,20	
VI	*bolitinos*	*loxodontis*	*miombo*	*imicola*	7,878
	25,0	26,15	26,45	26,95	
VII	*loxodontis*	*bolitinos*	*imicola*	*miombo*	19,329
	25,85	26,35	28,23	28,63	
VIII	*loxodontis*	*bolitinos*	*miombo*	*imicola*	19,755
	25,15	26,18	27,63	28,08	
IX	*loxodontis*	*bolitinos*	*imicola*	*miombo*	20,800
	25,75	26,85	28,43	28,80	
X	*loxodontis*	*bolitinos*	*imicola*	*miombo*	49,212
	27,85	29,33	31,10	33,20	
XI	*loxodontis*	*bolitinos*	*imicola*	*miombo*	48,404
	37,65	40,83	43,00	45,75	
XII	*loxodontis*	*bolitinos*	*imicola*	*miombo*	41,128
	40,80	41,10	45,20	46,95	
XIII	*bolitinos*	*loxodontis*	*imicola*	*miombo*	44,926
	41,43	42,70	45,98	48,95	
XIV	*bolitinos*	*loxodontis*	*imicola*	*miombo*	51,949
	41,35	42,15	46,20	50,30	
XV	*loxodontis*	*bolitinos*	*imicola*	*miombo*	85,413
	63,30	69,60	73,78	85,25	
TOTAL	*bolitinos*	*loxodontis*	*imicola*	*miombo*	42,611
	451,85	445,00	485,48	506,00	

TABLE 5.5: Comparison of mean lengths (raw data) of female palpal segments I–V of four *Culicoides* species of the Imicola group (n = 25)

Antennal segment	**Species and mean lengths**				**F-value**
I	*bolitinos*	*miombo*	*imicola*	*loxodontis*	
	7,34	7,94	8,02	8,68	11,985
II	*bolitinos*	*miombo*	*loxodontis*	*imicola*	
	18,18	19,92	20,94	22,96	64,934
III	*bolitinos*	*loxodontis*	*miombo*	*imicola*	
	16,44	17,88	18,46	19,62	31,806
IV	*bolitinos*	*loxodontis*	*miombo*	*imicola*	
	9,96	10,24	10,28	11,86	37,672
V	*bolitinos*	*loxodontis*	*miombo*	*imicola*	
	9,82	10,08	10,90	10,98	12,810
TOTAL	*bolitinos*	*loxodontis*	*miombo*	*imicola*	
	61,82	63,94	67,90	73,44	88,541

TABLE 5.6: Twelve morphological and biological character states used to separate *C. imicola* from *C. loxodontis*

	C. imicola		***C. loxodontis***
Morphological			
♀	scutellum with one median bristle (n = 87)	-	scutellum with two median bristles (n = 41)
-	wing generally darker with proximal margin of distal pale spot in cell R_5 moderately pointed; this point never fuses with the third pale costal spot covering radial cells	-	wing paler with this margin moderately or strongly pointed; this point occasionally fuses narrowly with the third pale costal spot
-	apex of vein M_2 broadly dark on both margins, this preceded by a well-defined excision	-	apex either pale or only narrowly dark on both margins; this is a result of the pale excision almost entirely eliminating anterior dark areas at apex of M_2
-	palp longer; 165,6–182,4, mean 176,1 μm (n = 25)	-	palp shorter; 147,5–175,0, mean 163,3 (μm) (n = 63)
-	proboscis longer; P/H ratio 0,82–1,02, mean 0,90 (n = 45)	-	proboscis shorter; P/H ratio 0,80–0,89, mean 0,84 (n = 20)
-	antennal segments IV, V, VII–XV significantly longer (Table 5.4)	-	these segments shorter (Table 5.4)
-	AtR 1,59–2,27, mean 1,86 (n = 173)	-	AtR 1,35–1,67, mean 1,47 (n = 42)
-	antennal segments VI and VIII with three sensilla chaetica basally in 90-94 % of specimens (n = 172)	-	these segments with four or five chaetica in 98 % of specimens (n = 81)
♂	membrane of sternum nine with eight to 145 spiculae, mean 47 (n = 50)	-	membrane with nought to three spiculae, mean 0,21 (n = 80)
-	extreme apex of aedeagus hyaline, round-tipped, smooth	-	apex not smooth but serrated by five to eight tiny sclerotised papillae
-	scutellum with one median bristle (n = 38)	-	scutellum with two median bristles (n = 41)
Biological			
-	larval habitat in short-grassed, moist pastures and margins of organically enriched drainage furrows and swamps	-	immature stages found exclusively in the dung of the African elephant