AFROTROPICAL CULICOIDES: C. (AVARITIA) LOXODONTIS SP. NOV., A NEW MEMBER OF THE IMICOLA GROUP (DIPTERA: CERATOPOGONIDAE) ASSOCIATED WITH THE AFRICAN ELEPHANT IN THE KRUGER NATIONAL PARK, SOUTH AFRICA

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ABSTRACT

MEISWINKEL, R., 1992. Afrotropical *Culicoides: C. (Avaritia) loxodontis* sp. nov., a new member of the Imicola group (Diptera: Ceratopogonidae) associated with the African elephant in the Kruger National Park, South Africa. *Onderstepoort Journal of Veterinary Research*, 59, 145–160 (1992)

Culicoides (Avaritia) loxodontis sp. nov., is described and illustrated from both sexes collected in South Africa. It is the 5th species of the Imicola group of the subgenus Avaritia to be described from the Afrotropical Region, and is presently known only from the Kruger National Park where it has been collected in light-traps and reared from the dung of the African elephant (Loxodonta africana) on various occasions. A number of character states, and statistical analyses of antennal and palpal measurements, are used to separate the new species from its taxonomic congeners C. imicola Kieffer, 1913, C. pseudopallidipennis Clastrier, 1958, C. bolitinos Meiswinkel, 1989 and C. miconbo Meiswinkel, 1991. It is suggested that the occurrence of the African elephant is the primary factor that determines the distribution of Culicoides loxodontis sp. nov., and that this close association, coupled with the fact that C. loxodontis sp. nov. can be locally abundant, may result in the cycling of certain arboviruses between this bitting midge and the elephant.

INTRODUCTION

The 1st 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, later shown 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) (Meiswinkel, 1989). Today C. bolitinos is recognised as the species most closely related to the Oriental-Australa-sian-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 4-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 3 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).

Following upon these leads the writer in 1985 continued investigations on the dung-inhabiting *Culicoides* fauna of the large herbivores of the Kruger National Park, and since then has reared 6 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 3, i.e. *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 2 closely related species difficult to identify 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 2 valid but closely related species that need reappraisal both biologically and taxonomically.

The 6th species reared from elephant dung is *C.* (A.) loxodontis sp. nov., which is described below. Unlike the others known from elephant dung, the new species is a member of the Imicola group, which in turn is 1 of at least 6 groups that constitute the subgenus Avaritia in the Afrotropical Region. In Africa 4 species of the Imicola group have thus far been described: *C. imicola, C. pseudopallidipennis, C. bolitinos* and *C. miombo.* Until now *C. bolitinos* was the only one of these known to have its immatures developing in animal dung.

As in previous papers (Meiswinkel, 1989, 1991), some emphasis is placed on a numerical description of *C. loxodontis* sp. nov. so as to differentiate it more clearly from 3 of its taxonomic congeners *C. imicola, C. bolitinos* and *C. miombo.* Although *C. pseudopal-lidipennis* is still too poorly known to be included in detail in the present analysis, 2 character states easily separate it from *C. loxodontis* sp. nov. and these will be discussed.

MATERIALS AND METHODS

Statistical Analysis

Analyses were made by means of the parametric completely random design by Dr Henk van Ark of this institute. The mean measurements of each antennal and palpal segment taken from 25 specimens were utilized. Barlett's test showed most variances

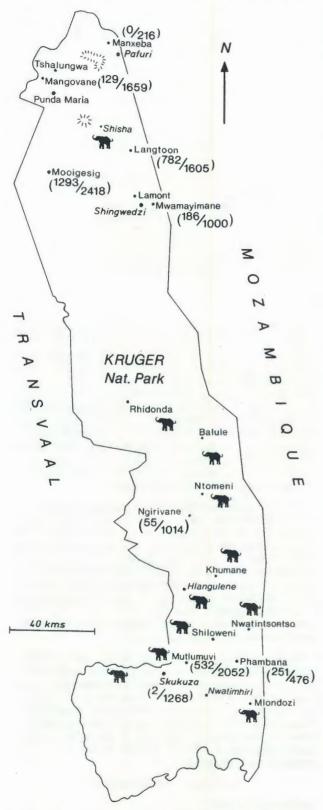


FIG. 1 A map of the Kruger National Park indicating localities where C. (Avaritia) loxodontis sp. nov. was either reared from dung (elephant symbol) or collected in light-traps; in parentheses the number of C. (A.) loxodontis captured is given as a fraction of the total number of Culicoides midges collected

to be homogeneous while comparisons of means were done using Bonferroni's multiple comparison test. However, heterogeneous variances occurred at 10 % in the measurements of the shortest antennal segments IV and V, and therefore a non-parametric Kruskal-Wallis analysis was used to obtain the corrected chi-squared values given in Table 4. For comparison of C. loxodontis with C. imicola, C. bolitinos and C. miombo the relevant numerical data for the last 3 species were drawn from Meiswinkel (1991). Unfortunately no detailed data are yet available to include C. pseudopallidipennis, the 5th member of the Imicola group. Finally, the mean lengths for the antennal and palpal segments given in the tables will be seen to differ fractionally from those in the text; this is because the latter means were obtained from many more specimens (63-80). Similarly the given total lengths of the palp, measured as a single unit in those specimens in which the palps were straight and not bent, will also be seen to differ from the totalled measurements of the individual segments. This is because segments I and II overlap diagonally where they articulate (Fig. 4).

All material of C. loxodontis sp. nov. examined was collected in the Kruger National Park, either by light-trap or reared from elephant dung. Light-trapping was done using a commercially available modified New Jersey-type downdraught trap equipped with an 8-watt U.V. tube. Elephant 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 2 age categories. Either it was (i) a discrete round bolus or boli only a few hours old, or (ii) was a 1-2 day-old subsample of 1-5 boli that had been flattened by the workings of various dung-beetle (Scarabaeoidea) species into a large (\pm 1 m diameter) 30-50 mm high amorphous mass. All dung was collected off hard ground, 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 originally evacuated by the elephant itself. Of the more than 200 specimens that were used for the present description of C. loxodontis sp. nov. only 1 female and 24 males reared from elephant dung plus 1 associated pupal exuvia are included in the type series. Under field conditions it proved difficult to keep such tiny insects alive for more than 48 h in order to have specimens sufficiently mature for mounting in Canada balsam.

The descriptive format, style of illustration and ratios used are almost exactly as set out in Meiswinkel (1989, 1991). The only difference is that the range in number and mean number of sensilla coeloconica and chaetica on the antennae of both sexes are now given to provide the descriptions with greater detail.

It is important to note that the female antennal ratio (AR) is not derived in the manner traditionally employed in the taxonomic study of the genus *Culicoides* worldwide, i.e. where each individual flagellar segment is measured and the resultant sum of segments XI–XV then divided by the sum of segments III–X. In this series of papers on the subgenus *Avari*-

TABLE 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 sp. nov.

		Antennal segments												
	111	IV	V	VI	VII	VIII	IX	x	XI	XII	XIII	XIV	xv	Total and mean total
Female: (n = 80–81) Sens. coeloconica:														
range/segment mean No./segment	2-3	0	0	0	0	0	0	0	0-1 0,05	0-1 0,98	1,00	1,00	0–1 0,98	6–8 6,93
Sens. chaetica:	2,31	0	"	"	0	0	0	0	0,03	0,30	1,00	1,00	0,90	0,33
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								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	63,6	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 Sens. chaetica:	2	0	0	0	U	0	0	0	0	0	0,96	1,77	1,92	6,65
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	ő	0	0	0	3,42			10,15
Sens. trichodea (blunt-tipped)	ILL	LLC	LLC	LLC	Lc	Lc	Lc	C	0	0	0,42	2,00	0	10,13
Mean lengths of segments	72,6		LLO		8.8 -		0		. 0	→	75,2	63,1	85,8	635,4

tia the writer will continue to derive the AR differently, i.e. by measuring segments XI-XV and III-X as single units, i.e. the intersegmental membranous connectant is included in the calculations. If the two methods are used on the same antenna the resultant AR's differ by a factor of 0,05. For those who wish to know the 'traditional' AR in the present series of papers, the mean lengths of each flagellar segment can be extracted from the descriptive text and the AR re-calculated. In the case of C. loxodontis the 2 mean AR's are 0,99 and 1,04 (traditional). It needs to be said that the measuring of these individual antennal segments at 400 x magnification demands accuracy. For this reason the writer separates the antennae away from the head and mounts them flat and straight in a thin film of phenolbalsam, and they are not allowed to be squashed during coverslipping. Measurements are therefore derived from antennae in their natural shape and resting on a flat plane. Most researchers leave the antennae in position near the top of the well-rounded head from where the antennae droop downwards, and as they settle randomly in the mountant, facing either inwards or outwards, they will assume an irregularly bent or spiralled position. Unless the head is completely squashed during coverslipping, surements made from such antennae suffer from an error of parallax. This error is further compounded when it is taken into account that 26 individual segments may be measured per adult specimen over 10 or more specimens; the resultant antennal ratios derived from such material will contain an error factor difficult to predict or calculate. This is critical when we are dealing with complexes of closely related species such as the Imicola group.

RESULTS

Culicoides (Avaritia) loxodontis sp. nov. (Fig. 2-15; Table 1-6)

FEMALE (Fig. 2-7, 13-15; Table 1-6)

Head. Eyes (Fig. 2); bare, contiguous over a distance equal approximately to the diameters of be-

tween 1 and 2 adjacent facets. Antenna (Fig. 3, 14; Table 1-4) slender, basal segments IV-X barrelshaped, 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-(n=80); total length of antenna: 63,5 μm 428,8-516,3 μm, mean 453,1 μm (n=80); widths of antennal III-XV: 28,8-22,5-20,0segments 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 2 for deviations from the norm; antenna with a total of 6-8 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 3 for deviations from the norm; blunt-tipped sensilla trichodea distribution of the LLc type, i.e. each of segments IV-X with 2 long and 1 short sensilla trichodea, segment III with only 2 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

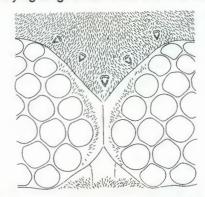


FIG. 2 *C.* (Avaritia) loxodontis sp. nov. Eyes, female (paratype Pafuri 6)

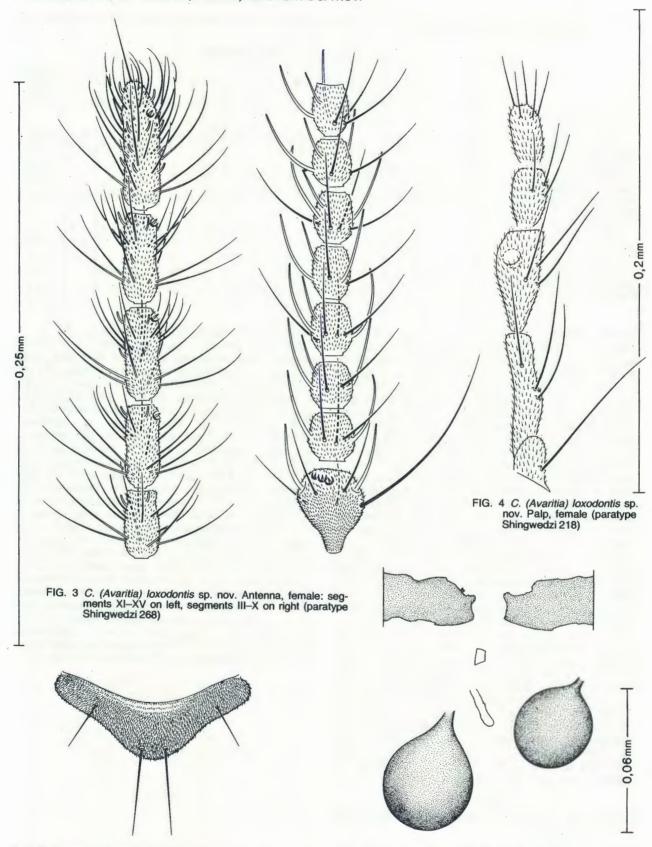


FIG. 5 C. (Avaritia) loxodontis sp. nov. Scutellum, female (paratype Shingwedzi 232)

FIG. 6 C. (Avaritia) loxodontis sp. nov. Genitalia, female: spermathecae and sclerotization surrounding gonopore (paratype Shingwedzi 37)

TABLE 2 Number and frequency of coeloconica present on each of female antennal segments III-XV of C. (Avaritia) loxodontis sp. nov.

No. of coeloconica per segment	Antennal segments								
No. of coeloconica per segment of C. loxodontis	Ш	IV-IX	Х	XI	XII	XIII	XIV	XV	
0	_	81	81	77	1	-	_	1	
1	_	_	_	4	80	81	81	80	
2	7	_	_	_		-	- 1	_	
3	74	-	-	-	-	-	-	_	
o. of antennae examined	81	81	81	81	81	81	81	81	

a basal and subapical whorl; XV with approximately twice as many trichodea, these distributed almost throughout segment (Fig. 3); similarly the short blunt-tipped basiconica range from 2-9 on each of the distal flagellar segments XI-XV (Fig. 3); all antennal segments uniformly clothed throughout with fine spiculae (Fig. 3). The range and mean number of sensilla coeloconica, chaetica and blunt-tipped trichodea are given in Table 1. Palp (Fig. 4, 15; Table 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 μ m, mean 163,3 μ m (n=63); palpal segment I with 1–2 rather long chaetica, mean 1,01 (n=77), II with 2-4 rather short chaetica, mean 3,00 (97 % with 3 chaetica; n=77); III of a moderate length, slightly swollen and carrying 3-5 rather short chaetica, mean 3,07 (93 % with 3 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 1-4 short chaetica, mean 2,66 (45 % with 3 chaetica; (n=77), V with no chaetica on median portion of segment but always bears 5 short erect PR 2,07-2,92, mean 2,53 bristles apically; (n=80); P/H ratio 0,82-0,99, mean 0,89 (n=35); 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 5 spines, the 1st being the longest and only slightly longer than the 2nd (n=81). Wing: (Fig. 7,13); 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

3rd of cell R5 with very few at the apex of cells M1 and M2 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; 2 short radial cells equal in length, proximal 1/2 of 1st and distal 1/2-2/3 of 2nd 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 spot in cell R5 to be more strongly pointed than found in its taxonomic congeners; occasionally this pointed margin may even fuse narrowly with the distal margin of the 3rd pale costal spot that covers the tip of the 2nd radial cell (Fig. 13). Other important specific wingpattern characters are:

- (i) The distal margin of the pale costal spot 2 that straddles the r-m crossvein is expanded medially and tends almost to fuse, under the radial cells, with the 3rd pale costal spot whose proximal margin is expanded medially;
- (ii) posterior margin of vein M2 entirely darkened but anterior margin broadly excised to leave the apex of vein M2 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) entirely brown, bearing 2 long median bristles and 1 shorter bristle on each corner (n=41). Haltere knobs pale. Abdomen: (Fig. 6): 2 moderately sclero-

TABLE 3 Number and frequency of chaetica present on each of female antennal segments III-XV of C. (Avaritia) loxodontis sp. nov.

No. of chaetica per segment of C. loxodoritis	Antennal segments												
	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII	XIV	X۷
0	_	_	_	_	_				77	81	81	81	81
1	_		- 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	_	-		-	-	-	-	_	-	-	_	-
o. of antennae	81	81	81	81	81	81	81	81	81	81	81	81	81

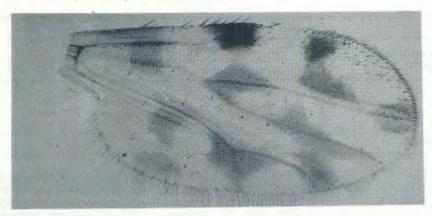


FIG. 7 C. (Avaritia) loxodontis sp. nov. Wing, female (paratype Pafuri 7)

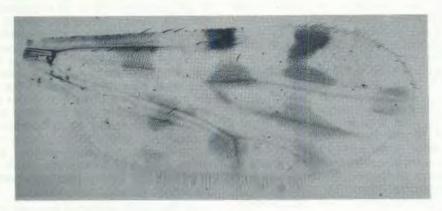


FIG. 8 C. (Avaritia) loxodontis sp. nov. Wing, male (paratype Pafuri 8)

tized slightly unequal spermathecae present, measuring 47,5–56,3 \times 35,0–42,5 μ m, mean 52,8 \times 41,0 μ m and 42,5–43,8 \times 30,0–35,0 μ m, mean 40,3 \times 32,3 μ m (n=20); both round and devoid of small hyaline punctations, with moderately long narrow pigmented necks; a rather small and narrow rudimentary 3rd spermathecae present measuring 11,3–22,5 \times 3,1–8,8 μ m mean 16,8 \times 4,3 μ m (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 spermathecae; sclerotization surrounding the oviduct as shown in Fig. 6.

MALE: (Fig. 8-12; Table 1).

Head. Eyes bare. Antenna (Fig. 9; Table 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 1 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 length 635,4 μm (n=24); sensilla coeloconica distribution: segment III with 2 (n=26); XIII with 0–1, mean 0,96 (96 % with 1 coeloconica; n=26); XIV with 1–2, mean 1,77 (87 % with 2 coeloconica; n=26); XV with 1–2, mean 1,92 (92 % with 2 coeloconica; n=26); antenna with a total of 5–7 coeloconica.

mean 6,65 (n=26); sensilla chaetica distribution: 5 of varying lengths and thicknesses on III; 2 (sometimes 3) basally (1st long and robust, 2nd shorter and weaker) and 1 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 5 antennae, while 1 antenna had the long mediallyoccurring sensilla chaetica absent); 2 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 1 apically (n=26); blunt-tipped sensilla trichodea distribution on segment III-XII: III with 2 long sensilla trichodea, segments IV-VI each with 2 long and 1 short sensilla trichodea, segments VII-IX with 1 long and 1 short sensilla trichodea, segment X with 1 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 1 antenna on segment V, and a short blunt-tipped trichodea in 1 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 1. Those of C. pseudopallidipennis remain unknown. Thorax: Scutellum with 2 median bristles

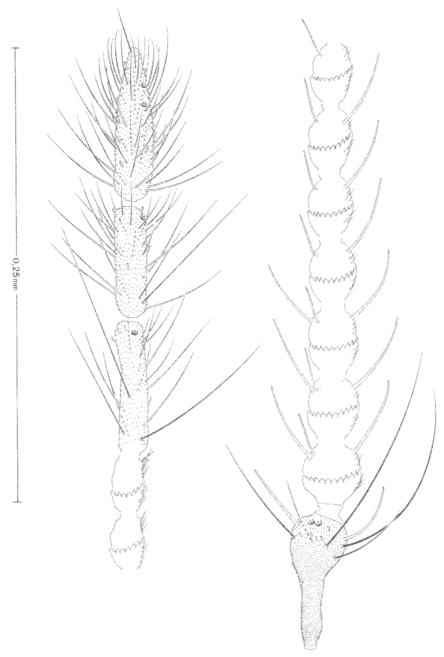


FIG. 9 C. (Avarita) loxodontis sp. nov. Antenna, male: segments XI-XV on left, segments III-X on right (paratype Shingwedzi 283)

and no lateral bristles (n=47). Wing: (Fig. 8). Genitalia: (Fig. 10–12) tergum 9 (Fig. 10, 11) square, slightly waisted medially, finely spiculate throughout except for narrow strips of the anterior and 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. 11, to moderately but very rarely deeply concave as in Fig. 10; median area not infuscate but bearing a number of striations (Fig. 10); 2 well-developed cerci (Fig. 11), each adorned with long spi-

culae and 2 long and 2 short chaetica; cerci protruding well beyond posterior margin of tergum; sternum 9 (Fig. 11) with a rather deep and wide excavation, membrane within the excavated area with 0-3 spiculae, mean 0,21 (n=80), of these 87,5 % had no spiculae; basimere with dorsal and ventral spiculae and chaetica as illustrated (Fig. 11), basimere 2,4 × 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. 11) 0,88 × length of basimere (n=7), rather stout, gently curved and broadly blunt-tipped; basal half spiculate, carrying 6-7 bristles of varying lengths and thicknesses, extreme apex with

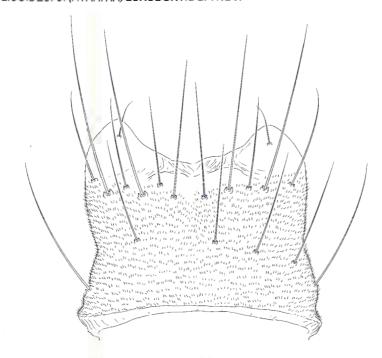


FIG. 10 C. (Avaritia) loxodontis sp. nov. Genitalia, male: tergum IX (paratype Hlangulene 16)



FIG. 11 C. (Avaritia) loxodontis sp. nov. Genitalia, male (paratype Shingwedzi 117)

TABLE 4 Comparison of mean lengths (μm) of female antennal segments III–XV of 4 Culicoides species of the Imicola group (n = 25)

F-value		mean lengths	Species and r		Antennal segment
10,245	loxodontis 39,05	imicola 39,00	miombo 37,30	bolitinos 36,85	111
$\chi^2 = 26,464$	imicola 25,45	loxodontis 24,65	miombo 24,00	bolitinos 23,35	IV
$\chi^2 = 19,705$	imicola 25,20	miombo 24,08	loxodontis 23,95	bolitinos 23,45	V
7,878	imicola 26,95	miombo 26,45	loxodontis 26,15	bolitinos 25,00	VI
19,329	miombo 28,63	imicola 28,23	bolitinos 26,35	loxodontis 25,85	VII
19,755	imicola 28,08	miombo 27,63	bolitinos 26,18	loxodontis 25,15	VIII
20,800	miombo 28,80	imicola 28,43	bolitinos 26,85	loxodontis 25,75	IX
49,212	miombo 33,20	imicola 31,10	bolitinos 29,33	loxodontis 27,85	Х
48,404	miombo 45,75	imicola 43,00	bolitinos 40,83	loxodontis 37,65	XI
41,128	miombo 46,95	imicola 45,20	bolitinos 41,40	loxodontis 40,80	XII
44,926	miombo 48,95	imicola 45,98	loxodontis 42,70	bolitinos 41,43	XIII
51,949	miombo 50,30	imicola 46,20	loxodontis 42,15	bolitinos 41,35	XIV
85,413	miombo 85,25 miombo	imicola 73,78 imicola	bolitinos 69,60 loxodontis	loxodontis 63,30 bolitinos	XV
42,611	506,00	485,48	445,00	451,85	Olai

about 6 very short fine sensilla. Aedeagus (Fig. 11, 12) shield-shaped, slender, 0,9 × length of basimere (n=7); basal margin concave, only narrowly and lightly infuscate towards lateral margins, distal margin of arch reaching to 0,18–0,26 × 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 5–8 tiny sclerotized papillae (Fig. 11,12); base of this terminal projection inserts anteriorly into median

area of aedeagus in the form of a raggedly infuscate "peg" (Fig. 11). Parameres (Fig. 11) separate, nearly touching medially from where they diverge anteriad and posteriad at approximately 45°, posterior halves as 2 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.

TABLE 5 Comparison of mean lengths (µm) of female palpal segments I-V of 4 Culicoides species of the Imicola group (n=25)

Antennal segment		Species and	mean lengths		F-value
1	bolitinos 18,35	miombo 19,85	imicola 20,05	loxodontis 22,65	11,985
II	bolitinos 45,45	miombo 49,80	loxodontis 54,43	imicola 57,40	64,934
III	bolitinos 41,10	loxodontis 44,95	miombo 46,15	imicola 49,05	31,806
IV	bolitinos 24,90	loxodontis 25,75	miombo 25,70	imicola 29,65	37,672
V	bolitinos 24,55	loxodontis 25,73	miombo 27,25	imicola 27,45	12,810
otal	bolitinos 154,55	loxodontis 163,30	miombo 169,75	imicola 183,60	88,541

TABLE 6 Twelve morphological and biological character states used to separate *C. imicola* from *C. loxodontis* sp. nov.

The state of the s	C. imicola	C. loxodontis						
Morphological								
	m with 1 median bristle ($n = 87$)	 Scutellum 	with 2 median bristles $(n = 41)$					
spot in	nerally darker with proximal margin of distal pale cell R5 moderately pointed; this point never fuses 3rd pale costal spot covering radial cells	 wing paler with this margin moderately or strongly pointed this point occasionally fuses narrowly with the 3rd pale costal spot 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 M2 palp shorter; 147,5–175,0 mean 163,3 μm (n = 63) proboscis shorter: P/H ratio 0,82–0,99, mean 0,89 (n = 35) 						
	vein M2 broadly dark on both margins this preceded I-defined excision							
- palp long	ger; 165,6–182,4 mean 176,1 μm (n = 25)							
20)	is longer: P/H ratio 1,01-1,22, mean 0,07 (n =							
— antenna 4)	I segments IV, V, VII–XV significantly longer (Table	— these segr	ments shorter (Table 4)					
- AtR 1,59	9-2,27, mean 1,86 (n = 173)	- AtR 1,35-	1,67, mean 1,47 (n = 42)					
basally i	Il segments VI and VIII with 3 sensilla chaetica n 90-94 % of specimens (n = 172)	(n = 81)	ments with 4 or 5 chaetica in 98 % of specimens					
∂ — membra= 50)	ne of sternum 9 with 8-145 spiculae, mean 47 (n	- membrane	e with $0-3$ spiculae, mean $0,21$ (n = 80)					
extreme	apex of aedeagus hyaline, round-tipped, smooth m with 1 median bristle (n = 38)		smooth but serrated by 5–8 tiny chitinised papillae with 2 median bristles ($n = 41$)					
Biological								
	abitat in short-grassed, moist kikuyu pastures and of organically enriched drainage furrows and	immature stages found exclusively in the dung of the Africal elephant						
South A	al FRICA: Holotype ♀ (slide Shingwedzi ont windmill (23° 06′ S, 31° 24′ E)	24 ♂ ♂	(slides Shingwedzi 160–165, 177, 234–250), (collection data as above).					
on banks o Shingwedzi Park, 20. II.	f Mphongolo river 6 km north-west of rest camp, northern Kruger National 1990, R. Meiswinkel and L.E.O. Braack, 8h00–22h00.	94 ਹੋ ਹੋ	(slides Shingwedzi 276–295, 373–466), Mooigesig dam area, 45 km w of Shingwedzi rest camp, northern K.N.P., 25. IV. 1990, R. Meis-					
	♂ paratypes, slides labelled and numbered to sex, the collection data as follows:		winkel, L.E.O. Braack & D. de Klerk, blacklight in <i>Colophospermum mopane/Acacia nigrescens</i> savanna, 17h00–22h00.					
6 9 9	(slides Shingwedzi 37, 45, 48, 54, 64, 68), Shingwedzi rest camp, northern K.N.P., 1 .IX. 1979, B. de Meillon and R. Meiswinkel, blacklight.	28 ਹੋ ਹੈ	(slides Shingwedzi 301–328) Langtoon dam area, 30 km n. o Shingwedzi rest camp, northerr K.N.P., 24. IV. 1990, R. Meiswinkel L.E.O. Braack & D. de Klerk, black					
3 ठै ठै	(slides Shingwedzi 43, 57, 66), (collection data as above).		light in Colophospermum mopane shrub-veld, 17h00-22h00.					
6 ♀ ♀	(slides Shingwedzi 82 – 84, 86, 90, 113), Shingwedzi rest camp, northern K.N.P., 19. IV. 1983, R. Meiswinkel, blacklight.	1 ♀	(slide Pafuri 7), Pafuri anthrax camp on banks of Luvuvhu river, northern K.N.P., 15. IV. 1986, R. Meiswinkel & L.E.O. Braack, black-					
233	(slides Shingwedzi 100, 117), (collection data as above).		light 13 m up Acacia albida tree, 18h00-23h00.					
1 ♀	(slide Shingwedzi 78), Shingwedzi rest camp, northern K.N.P., 7. IX. 1984, R. Meiswinkel, blacklight.	1 ♂ 1 ♀	(slide Pafuri 8), (collection data as above). (slide Skukuza 18), Skukuza resi					
40 ♀ ♀	(slides Shingwedzi 167-171, 173-175, 210-223, 225-233, 261-269), Lamont windmill on banks of Mphongolo river, 6 km		camp, southern K.N.P., 11. III. 1984, R. Meiswinkel & L.E.O. Braack, blacklight on banks of Sa- bie river.					
	n.w. of Shingwedzi rest camp, northern K.N.P., 20. II. 1990, R. Meiswinkel & L.E.O. Braack, black- light 18h00–22h00.	1 3	(slide Skukuza 122), Skukuza rest camp, southern K.N.P., 15. I. 1985, R. Meiswinkel & L.E.O. Braack, blacklight on banks of Sabie river.					

1 9 (slide Hlangulene 10), 50 km n. of Skukuza rest camp, southern K.N.P., 26. II. 1986, R. & P. Meiswinkel, reared from elephant dung. 23 3 3 (slides Hlangulene 1-9, 11-16, 19, 22, 25-30), (collection data as above). 1 9 (slide Tshalungwa 13), 18 km n. of Punda Maria rest camp n.w. K.N.P., 10. IV. 1986, R. Meiswinkel & L.E.O. Braack, blacklight 18h30-21h00. 1 3 (slide Tshalungwa 14), (collection data as above). 3 9 9 (slides Phambana 1-3), 28 km e. of Skukuza rest camp, southern K.N.P., 8. V. 1990, D. de Klerk, blacklight 17h00-22h00. 1 3 + pupal exuvia (slide Skukuza 351), ex elephant dung on sand

Unmounted light-trap material examined

248 ♀♀ 3 ♂ Phambana, 28 km e. of Skukuza rest camp, southern K.N.P., 8. V. 1990, D. de Klerk, blacklight 17h00–22h00.

1991, H. Nevill.

road 20 km w. of Skukuza rest

camp, southern K.N.P., 14. V.

- 74 ♀♀ 55 ♂ Mangovane spring, 10 km n. of Punda Maria rest camp, northern K.N.P., 3. III. 1991, R. Meiswinkel, L. E. O. Braack, Alan L. Dyce & M. Swanepoel, blacklight 18h30–20h15.
- 157 ♀♀ 29 ♂♂ Mwamayimane windmill, 6 km e. of Shingwedzi rest camp, northern K.N.P., 20. II. 1990, R. Meiswinkel & L. E. O. Braack, blacklight 17h30–24h00.
- 1161 ♀♀ 39 ♂ Mooigesig dam area, 45 km w. of Shingwedzi rest camp, northern K.N.P., 25. IV. 1990, R. Meiswinkel, L. E. O. Braack & D. de Klerk, blacklight in Colophospermum mopane/Acacia nigrescens savanna, 17h00–22h00.
- 728 ♀ ♀ Langtoon dam area, 30 km n. of Shingwedzi rest camp, northern K.N.P., 24. IV. 1990, R. Meiswinkel, L. E. O. Braack & D. de Klerk, blacklight in *Colophospermum mopane* shrubveld, 17h00–22h00.
- 50 ♀♀ 5 ♂ Ngirivane windmill, 12 km w. of Satara rest camp, central K.N.P., 18. IX. 1991, R. Meiswinkel, H. van Ark & M. Swanepoel, blacklight 18h00–24h00.
- 14 ♀♀ 1 ♂ At confluence of Mutlumuvi and Sand rivers, 12 km n.e. of Skukuza rest camp, southern K.N.P., 19. IX. 1991, R. Meiswinkel, H. van Ark & M. Swanepoel, black-

light in dry thickets, 18h00-24h00.

454 ♀♀ 78 ♂ At confluence of Mutlumuvi and Sand rivers, 12 km n.e. of Skukuza rest camp, southern K.N.P., 22. I. 1992, R. Meiswinkel, blacklight in dry thickets, 18h45–24h00.

Unmounted reared material examined

- 42 ♀♀ 68 ♂ Rhidonda windmill, 23 km w. of Letaba rest camp, central K.N.P., 16, XI. 1979, R. Meiswinkel.
- 30 ♀♀ 45 ♂ Shiloweni dam, 38 km n.e. of Skukuza, southern K.N.P., 22. I. 1991, L. E. O. Braack.
- 163 ♀♀ 323 ♂ ♂ Khumane dam, 67 km n.e. of Skukuza, southern K.N.P. 22. I. 1991, L. E. O. Braack.
- 57 ♀♀ 87 ♂ Nwatintsontso, 50 km n.e. of Skukuza, southern K.N.P., 22. I. 1991, L. E. O. Braack.
- 30 ♀♀ 18 ♂♂ Mlondozi, 6 km e. of Lower Sabie rest camp, south-eastern K.N.P., emerged 16–17. IX. 1991 from dung evacuated by ± 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 K.N.P., 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 K.N.P., 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 K.N.P., emerged 6. II. 1992 from dung evacuated 29. I. 1992, R. Meiswinkel.
- 82 ♀♀ 230 ♂♂ Ntomeni windmill, 15 km n. of Satara rest camp, central K.N.P., emerged 6. II. 1992 from dung evacuated by large elephant bull 29. I. 1992, R. Meiswinkel.

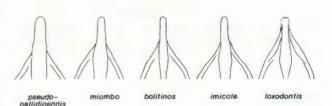


FIG. 12 Genitalia male: comparison of the apices of the aedeagi of 5 species of the Imicola group

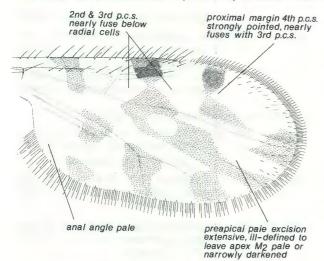


FIG. 13 C. (Avaritia) loxodontis sp. nov. Wing, female: diagnostic features

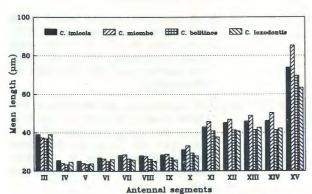


FIG. 14 Comparison of mean lengths (μm) of each of the female antennal segments III–XV of C. (Avaritia) imicola, C. (A.) miombo, C. (A.) bolitinos and C. (A.) loxodontis sp. nov.

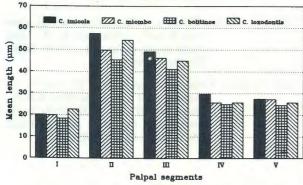


FIG. 15 Comparison of mean lengths (μm) of each of female palpal segments I–V of C. (Avaritia) imicola, C. (A.) miombo, C. (A.) bolitinos and C. (A.) loxodontis sp. nov.

DISCUSSION

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.

Differential diagnosis

The 12 character states that separate *C. imicola* and *C. loxodontis* are summarized in Table 6 and are discussed in further detail below. Where data are available these 2 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 R5 strongly pointed, (b) has the preapical pale excision on the anterior margin of vein M2 more extensive and ill-defined leaving the apex of M2 pale or only slightly and indistinctly darkened, and (c) has 2 median bristles on the scutellum in both sexes; these bristles are, however, difficult to detect under the dissecting microscope, especially if 1 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 2 subpopulations of C. loxodontis captured in light-traps at Mooigesig and Langtoon (Fig. 1) showed that at the former site 186 of 697 (26,7 %) carried between 1-13 mites/midge, while at the latter site 84 of 728 (11,5 %) had between 1-9 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 very 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 3rd palpal segment which can quite easily be seen under the dissecting microscope, thus differentiating it from the slender 3rd 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 4 taxonomic congeners more easily:

- Female. Wing: The wing of C. loxodontis is distinctly paler than that of C. imicola, C. bolitinos or C. miombo, but most closely resembles that of C. pseudopallidipennis. The next 4 wing characters more clearly define C. loxodontis as a good species and are labelled in Fig. 13:
 - (a) The shape of the distal pale spot in the apex of cell R5: its proximal margin usually

- strongly pointed (Fig. 13). In some specimens this point narrowly fuses with the distal margin of the 3rd pale costal spot covering the tip of the 2nd 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 2nd and 3rd pale costal spots nearly fuse under the radial cells (Fig. 7, 13). In the remaining species these pale spots are well separated from one another by a dark area.
- (c) In C. loxodontis vein M2 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. 7, 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 very clearly defined preapical excision that leaves the apex of vein M2 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. 13); in C. miombo there is a highly diagnostic prominent long dark smudge.
- 2. Female. Palps: A low P/H ratio (mean 0,89; n = 35) indicates that C. loxodontis has a short proboscis which in turn indicates short palps. As can be seen in Table 5 and Fig. 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 indicate that the palps are about as long as those of C. imicola. Furthermore, C. pseudopallidipennis has a swollen 3rd palpal segment as opposed to the slender one found in its 4 taxonomic congeners.
- 3. Female. Antennae: As can be seen in Table 4 and Fig. 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 4 species C. loxodontis, C. imicola, C. bolitinos and C. miombo, are all separable on the mean lengths of antennal segments X, XI and XV, the last-named being the most significant (Table 4). The data provided for C. pseudopallidipennis by Clastrier (1958) come very near that for C. loxodontis except that segment III of the former is given as only 2/3 the length of the 4 species listed in Table 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 2 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 3 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 4 sensilla chaetica basally (Fig. 3 and Table 3), whereas in the other 3 species 3 chaetica are the norm. No data are available for *C. pseudopallidipennis*.
- 6. Female. Scutellum: C. loxodontis (n = 41) always carries 2 long bristles medially (Fig. 5); C. imicola (n = 87), C. bolitinos (n = 20), and C. miombo (n = 37) each have only 1 bristle medially. Clastrier (1958) recorded 1 bristle medially for C. pseudopallidipennis. This consistent presence of 2 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 1 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 9 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. Glick (1990) recorded this membrane bare in a single male of C. pseudopallidipennis that he examined.
- 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 4 taxonomic congeners but is distinctly roughened or serrated by 5–8 tiny, darkly pigmented papillae (Fig. 11, 12). The apex of the aedeagus of *C. loxodontis* is also shorter than in its 4 congeners which all have it a little longer and largely inseparable in shape (Fig. 12).

Larval habitat

C. 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. 1. Despite my persistent efforts during the past 7 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 (R.M. unpublished observations, 1985–1991).

As mentioned earlier, 6 species of the subgenus *Avaritia* have been found to inhabit the dung of *Loxodonta*, the commonest of these being 2 species provisionally labelled C. sp. # 54 pale form and C. sp. # 54 dark form (R. Meiswinkel & H. Nevill, unpublished observations, 1985–1991). *C. loxodontis* is 3rd in abundance; up to 500 specimens have been reared from 2,5 kg of wet elephant dung. In the height of summer the 1st individuals of *C. loxondon-*

tis will emerge after 8–10 days from dung collected when only a few hours old.

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

Distribution

C. (A.) loxondontis sp. nov. is still known only from the Kruger National Park, South Africa. Fig. 1 shows the holotype locality (Lamont windmill, Shingwedzi), and paratype locales (Parfuri, Tshalungwa, Mangovane spring, Langtoon dam, Mooigesig dam, Hlangulene, Phambana and Skukuza) from which the new species has been commonly collected either in lighttraps or reared from elephant dung. As noted earlier, only 1 ♀ and 23 ♂ ♂ reared from elephant dung collected at Hlangulene, and 1 3 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 slidemounted in Canada balsam.

On occasion *C. loxodontis* has been found to be the dominant species in certain areas of the K.N.P. and can comprise up to 52 % of 500–2500 *Culicoides* collected in light-traps operated during the 1st 4–6 h following nightfall. The light-trap data for 9 locales are indicated by the number in parentheses in Fig. 1; rather than providing percentages the actual numbers of *C. loxodontis* out of the total number of *Culicoides* captured are given. At 4 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 2 specimens out of more than 1000 Culicoides collected on the banks of the Sabie river in Skukuza. Manxeba Pan falls into that far northern part of the K.N.P. 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 1 such site, i.e. Mutlumuvi 12 km north-east of Skukuza, C. loxodontis is 1 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 herds 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 \pm 7 500 individuals in the K.N.P. (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 the writer 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 9 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 other dung-inhabiting Avaritia species have been collected at these sites but not a single specimen of C. loxodontis. In South Africa there are 8 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 K.N.P., 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 of extremes such as hot and dry semi-deserts (Namibia), cooler higher-lying plateaux (eastern Zaïre; western Uganda) and the wetter, more humid tropical forests (Zaïre; 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 4 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 K.N.P.) proclaimed 5 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 ± 7500 elephant, the maximum number the vegetation in this 20 000 km² reserve can support without being degraded.

It remains a matter of speculation whether Culicoides loxodontis had enjoyed a similarly widespread distribution in South Africa. However, 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 i.e., utilize the dung of any other herbivore. The writer therefore believes that the dominance of C. loxodontis in parts of the K.N.P. 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.

Conclusions

Culicoides loxodontis is the 5th 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 K.N.P., and it has on a number of occasions been reared only from elephant dung.

Taxonomically, *C. loxodontis* can be confused with *C. imicola* and, especially, *C. pseudopallidipennis*. The separation of these 2 species from *C. loxodontis* depends primarily upon the examination of slide-mounted material, as all 3 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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