AFROTROPICAL *CULICOIDES:* A REDESCRIPTION OF *C. (AVARITIA) IMICOLA* KIEFFER, 1913 (DIPTERA: CERATOPOGONIDAE) WITH DESCRIPTION OF THE CLOSELY ALLIED *C. (A.) BOLITINOS* SP. NOV. REARED FROM THE DUNG OF THE AFRICAN BUFFALO, BLUE WILDEBEEST AND CATTLE IN SOUTH AFRICA

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ABSTRACT

MEISWINKEL, R., 1989. Afrotropical *Culicoides:* A redescription of *C. (Avaritia) imicola* Kieffer, 1913 (Diptera: Ceratopogonidae) with description of the closely allied *C. (A.) bolitinos* sp. nov. reared from the dung of the African buffalo, blue wildebeest and cattle in South Africa. *Onderstepoort Journal of Veterinary Research*, 56, 23–39 (1989).

Culicoides (Avaritia) imicola, Kieffer is redescribed and its current worldwide distribution reviewed. It is compared with the closely allied *C. (A.) bolitinos* sp. nov. Descriptions of both sexes of *C. imicola* and *C. bolitinos* sp. nov. are based entirely on series of reared adults. T-tests were performed on antennal and palpal data to differentiate more clearly these 2 species. The results are tabulated. Short notes are given on the larval habitat of *C. bolitinos* sp. nov. in South Africa, namely the dung of the African buffalo, *Syncerus caffer,* the blue wildebeest, *Connochaetes taurinus,* and cattle, *Bos* races. The existence of *C. bolitinos* in Nigeria, Kenya, Malawi, Zimbabwe, Lesotho and South Africa is established while *C. imicola* is newly recorded from Malawi, Botswana, Namibia and Swaziland. Finally seven references in the literature are shown to refer either to *C. bolitinos* sp. nov. or to closely allied as yet undescribed species.

INTRODUCTION

In the Afrotropical region the single most important species of the *Culicoides* subgenus *Avaritia* is *C. imicola* as it is both a proven and suspected vector of certain viruses in livestock. The most noteworthy are bluetongue in sheep and African horse sickness (Du Toit, 1944). *C. imicola,* mostly recorded under the old name of *C. pallidipennis* Carter, Ingram & Macfie, 1920 occurs both throughout and outside the African continent. Although Egypt, Morocco and Algeria remain the only north African countries from which *C. imicola* has been reported (Macfie, 1943; Nagaty & Morsy, 1959; Szadziewski, 1984) it has also been found on the northern side of the Mediterranean in Spain and Portugal (Mellor, Jennings, Wilkinson & Boorman, 1985), Cyprus and western Turkey (Jennings, Boorman & Ergün, 1983) and on the Greek islands of Lesbos (Boorman & Wilkinson, 1983) and Rhodes (Boorman, 1986). However it remains unrecorded from the central Mediterranean on mainland Italy and Greece (Mellor, Jennings & Boorman, 1984), the Balearic Islands, as also the islands of Sardinia, Corsica, Sicily, Malta and Crete (Boorman, Jennings, Mellor & Wilkinson, 1985).

East of the Mediterranean *C. imicola* occurs in Israel from which 4 bluetongue serotypes have to date been isolated (Braverman, Barzilai, Frish & Rubina, 1985). It also ranges throughout western and southern Asia being recorded from India under the names of *C. minutus* Sen & Dasgupta, 1959 and *C. pseudoturgidus* Dasgupta, 1962, these species synonymized with *C. imicola* by Dyce & Wirth (1983). It has also been recorded from Iraq under the name *iraqensis* (Khalaf, 1957) and from Iran as *C. pallidipennis* (Navai & Mesghali, 1968). Going still further east, beyond the Indian subregion, is the recent record of *C. imicola* from Laos (Howarth, 1985).

Though known from as far afield as Madagascar (De Meillon, 1961; Callot, Krêmer & Brunhes, 1968) and Reunion (Clastrier, 1959), some 2500 km off the east coast of Africa, *C. imicola* still remains unrecorded from many mainland African countries such as Malawi, Mozambique, Zambia, Botswana and Namibia. This is probably due to the paucity of collections as bluetongue or African horse sickness have in recent years been recorded from these countries (Ozawa, 1985). However,

in adjoining countries *C. imicola* is widespread being reported to be the commonest species in Kenya (Khamala, 1971; Khamala & Kettle, 1971; Davies & Walker, 1974; Walker, 1977) and in Nigeria (Dipeolu & Sellers, 1977) the latter study showing that it comprised 38 % of all *Culicoides* collected. In Zimbabwe Phelps, Blackburn & Searle (1982) showed *C. imicola* to comprise 61,7–96,8 % of the biting midges caught near a paddock containing both horses and cattle. Similarly in South Africa *C. imicola* can be said to be ubiquitous in certain situations and can account for up to 94 % of collections made near mules, sheep and cattle (Nevill & Anderson, 1972).

Though it can be said that these numbers reflect a veterinary bias which favours the collection of *C. imicola* on cattle farms and the like it also reveals that man is an important link who maintains and spreads this species. This is also the opinion of Howarth (1985) who in his treatment of the *Culicoides* of Laos said that 'many of the widespread species may have been spread indirectly through human activities. This is especially true for species closely associated with domestic animals, such as . . . *C. imicola* and *C. brevitarsis.* From ancient times to the present, cattle drives have occurred between India and Thailand'. Similarly in Australia the important immigrant *Avaritia* species of *C. brevitarsis, C. brevipalpis* and *C. wadai* only established themselves and spread widely once cattle dung, the only suitable larval habitat for the immatures, became constantly available (Dyce, 1982). Thus the presence of *C. brevitarsis* in near pest proportions in that country today is undoubtedly man-induced. In South Africa a similar picture as regards the abundance of *C. imicola* is emerging, especially in heavily stocked situations, while the converse appears to be true in those places where man has as yet interfered little with the environment. Though little or no quantitative work has been done in the wild areas of the Afrotropical region, recent as yet unpublished studies by the writer in the Kruger National Park, South Africa reveal that of the 10 species of the subgenus *Avaritia* found there, *C. imicola* remains uncommon and localized. This is due not to a lack of suitable hosts, but more because the hosts can roam far and wide thus preventing a buildup of enormous foci of *C. imicola.* Secondly, but equally important, is that larval habitats in such natural areas are subject to the seasonal vagaries of both drought and flood which severely check the numbers of *C. imicola* (personal observations, 1985/86). In

the farmyard situation, however, irrigation is controlled and constant year round and this coupled to the maintenance of large sedentary populations of domesticated animals, exactly suits the needs of *C. imicola* and leads to an escalation in its populations. Studies in recent years have revealed a 2nd member of the *imicola* group, *C. bolitinos* sp. nov., also associated with farming activities in southern Africa (Nevill, Venter, Edwardes, Pajor, Meiswinkel & Van Gas, 1988). It is also 1 of the 10 *Avaritia* species found in the K.N.P. but is the only 1 which will breed in buffalo and cattle dung. This paper will clarify its systematics and briefly indicate its possible veterinary importance.

As to the taxonomy of members of the subgenus *Avaritia* there are 'unfortunately in each region difficult taxonomic problems in the accurate determination of some proven or potential vectors . . . this includes the so-called *imicola* group . . ' . (Wirth & Dyce, 1985). In the Afrotropical region there is increasing evidence that *C. imicola* forms part of a complex of species within the *imicola* group of the subgenus *Avaritia* with new species still to be described. At present *C. pseudopallidipennis* Clastrier (1958) is the only other described member of the group, and though occurring widely in Africa is difficult to identify and appears to be most often rare and localized in its distribution. The male remains unknown. *C. bolitinos* sp. nov. is the 3rd member of the *imicola* group.

It is for 2 reasons that the emphasis of this paper will be on a numerical description of *C. imicola* and *C. bolitinos* sp. nov. Firstly, it is forseeable that members of the *C. imicola* group will soon be subjected to the modern techniques of enzyme and hydrocarbon cuticular analyses. Promising results have recently been obtained on certain European *Culicoides* by Waller, Belliard & Krêmer (1987) who examined 10 species including 3 members of the subgenus *Avaritia* to which *C. imicola* belongs. However, the value of such studies depends strongly upon species being as soundly established taxonomically as possible. For this to be achieved, a population needs to be sampled and significant numbers analysed to assess the range of variation that exists within traditionally used characters and ratios and to establish new parameters. This is best achieved from reared material. Such data are given additional depth by knowledge of the biologies of various species as it is often the habits rather than the morphology that reveals the presence of sibling species, this is especially evident in vector complexes such as *gambiae* in *Anopheles* and *damnosum* in *Simulium*. Indications are that the genus *Culicoides* will be no exception.

Finally, the presence of such cryptic species has obvious implications concerning the mechanisms of disease transmission and until an effort is made to define these species more accurately, both on the biological and taxonomic level, our isolations of viruses from species pools will remain bedevilled by generalities. Furthermore it will preclude any truth being lent to the picture of *Culicoides* dynamics in the important areas of distribution, feeding habits, transmission cycles and vector competence.

MATERIALS AND METHODS

The redescription of *C. imicola* is based entirely on slide mounts of 136 of more than 6000 adults reared under field conditions at Onderstepoort during April and May 1986, using the tent-trap emergence method described by Pajor (1987). The type series material used for the description of *C. bolitinos* sp. nov. comprises 92 of 512 midges that were reared from half of a single African buffalo (*Syncerus caffer*) dung pat. The pat was collected off short grass adjoining a stand of *Phragmites* reeds on the lower banks of the dry Timbavati River near Roodewal in the West-central area of the Kruger National Park. These data are on occasion linked to and supplemented by further information gained from numerous specimens collected by light-trap or reared from cattle, buffalo and blue wildebeest (*Connochaetes taurinus*) dung in various localities of the Transvaal, Orange Free State, Cape and Natal as well as from Zimbabwe and Malawi. The dung collected by the author was always a single or half of a pat placed into a cardboard box and then stored in a fine gauze net to await emergence of *Culicoides* if present. The dung collected by E. M. Nevill, J. E. Randall, G. J. Venter and colleagues always comprised 5–10 pats placed together in a large, black plastic box closed with a ventilated lid. Mounted over a hole made in one side of the box was a white exit cone onto which was fixed a 500 mℓ paper icecream cup. Emerging *Culicoides* attracted to the light make their way through the cone into the paper cup. These midges were removed daily to be identified, counted and sexed. On one occasion both *C. imicola* and *C. bolitinos* sp. nov. were aspirated in equal but low numbers off a darted buffalo in the Skukuza boma, Kruger National Park. Light-trapping was done using a commercially available modified New Jersey-type downdraught trap equipped with an 8-watt U.V. tube.

Measurements are given in μm and were made at 400 × magnification. Ratios used are partly as set out on p. 20 of the Khamala & Kettle treatment of the East African *Culicoides* (1971). The P/H ratio, where the distance from the tip of the proboscis to the tormae is divided by the distance from the tormae to the interocular seta, was only measured in those mounts where the head was entire and in its proper round form i.e. not squashed and distorted by coverslipping. The reverse ratio, H/P, used by Khamala & Kettle (1971) and Boorman & Dipeolu (1979) is not adopted here. A new ratio used is the antennal trichodea ratio (AtR) in which the length of the longest blunt-tipped trichodea on female antennal segment VI (Fig. 1a) is divided by the length of segment VI (Fig. 1b). The antennal ratio (AR) is made from the length of segments XI–XV measured as a single unit divided by
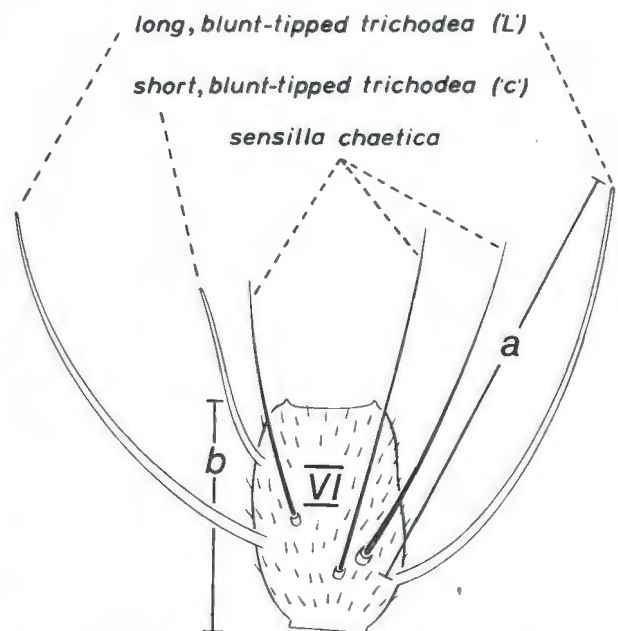

FIG. 1 *C. (Avaritia) imicola.* Antenna, female: segment VI showing the measurement of a long blunt-tipped sensilla trichodea (a) divided by the length of the segment (b) to obtain the antennal trichodea ratio (AtR)
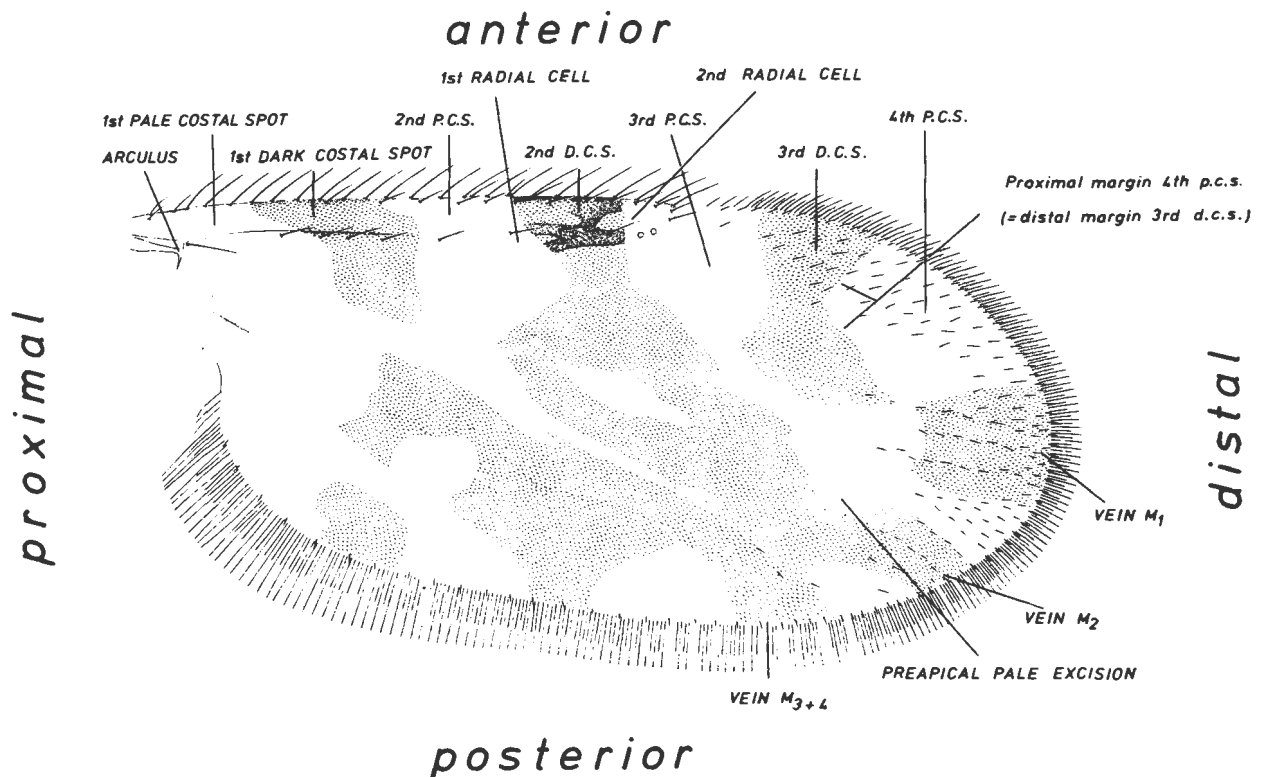
FIG. 2 C. *(Avaritia) imicola*. Wing, female: indicating important diagnostic characters (p.c.s. = pale costal spot; d.c.s.=dark costal spot)
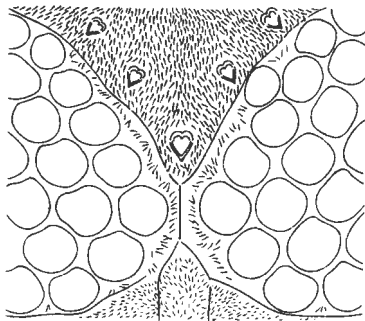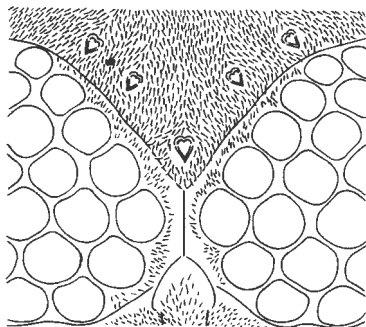

FIG. 3 C. *(Avaritia) imicola*. Eyes, female

FIG. 4 C. *(Avaritia) bolitinos* sp. nov. Eyes, female

the length of III–X also measured as a unit; elsewhere the antennal segments were individually measured (as in Lane, 1981; 1984), i.e. omitting the membranous intersegmental connectant. The measurement of the entire palp will also be seen to differ from the totalled measurements of the individual segments. This is because segments I and II diagonally overlap where they articulate (Fig. 7,8). In Tables 1 and 3 the chaetica counted on the female and male antennae do not include the single chaetica always found apically on segment XV in all species of *Culicoides;* these counts concern themselves

only with those chaetica found at the base of a segment. In the male the individual segments comprising the antenna were only measured in 1 specimen of each species as the segments may on occasion be incompletely fused. Greater emphasis was placed on measuring the female segments as it is this sex which is primarily encountered in collections. The wing photographs were prepared from slide-mounted specimens by Mr Ian Roper (22 Langer ave., Dolans Bay, New South Wales 2229, Australia). Fig. 2 is a drawing of the female wing of C. *imicola* labelled to clarify the terminology used in the present study. Illustrations of the male genitalia have the left basimere showing dorsal setation and spiculation, with the right basimere representing the ventral view. Illustrations of the antennae have those sensilla occurring ventrally drawn with broken lines. T-tests (two-tailed) were performed only on the female palpal and antennal measurements data to establish where the most significant differences existed between the 2 species.

RESULTS

Culicoides (Avaritia) imicola Kieffer 1913
(Fig. 1–3, 5, 7, 9, 11, 13, 15, 17, 19; Table 1–7)

Culicoides imicola Kieffer 1913: 11. Kenya.

Culicoides pallidipennis Carter, Ingram & Macfie 1920: 265. Ghana.

Culicoides pallidipennis Carter, Ingram & Macfie; Fiedler, 1951: 30. South Africa.

Culicoides iraqensis Khalaf 1957: 343. Iraq.

Culicoides pallidipennis Carter, Ingram & Macfie; Clastrier, 1958: 194. Senegal.

Culicoides pallidipennis Carter, Ingram & Macfie; Nagaty & Morsy, 1959: 71. Egypt.

Culicoides minutus Sen & Das Gupta 1959: 622: Dyce & Wirth, 1983: 221. India.

Culicoides pallidipennis Carter, Ingram & Macfie; Caeiro, 1961: 230. Angola.
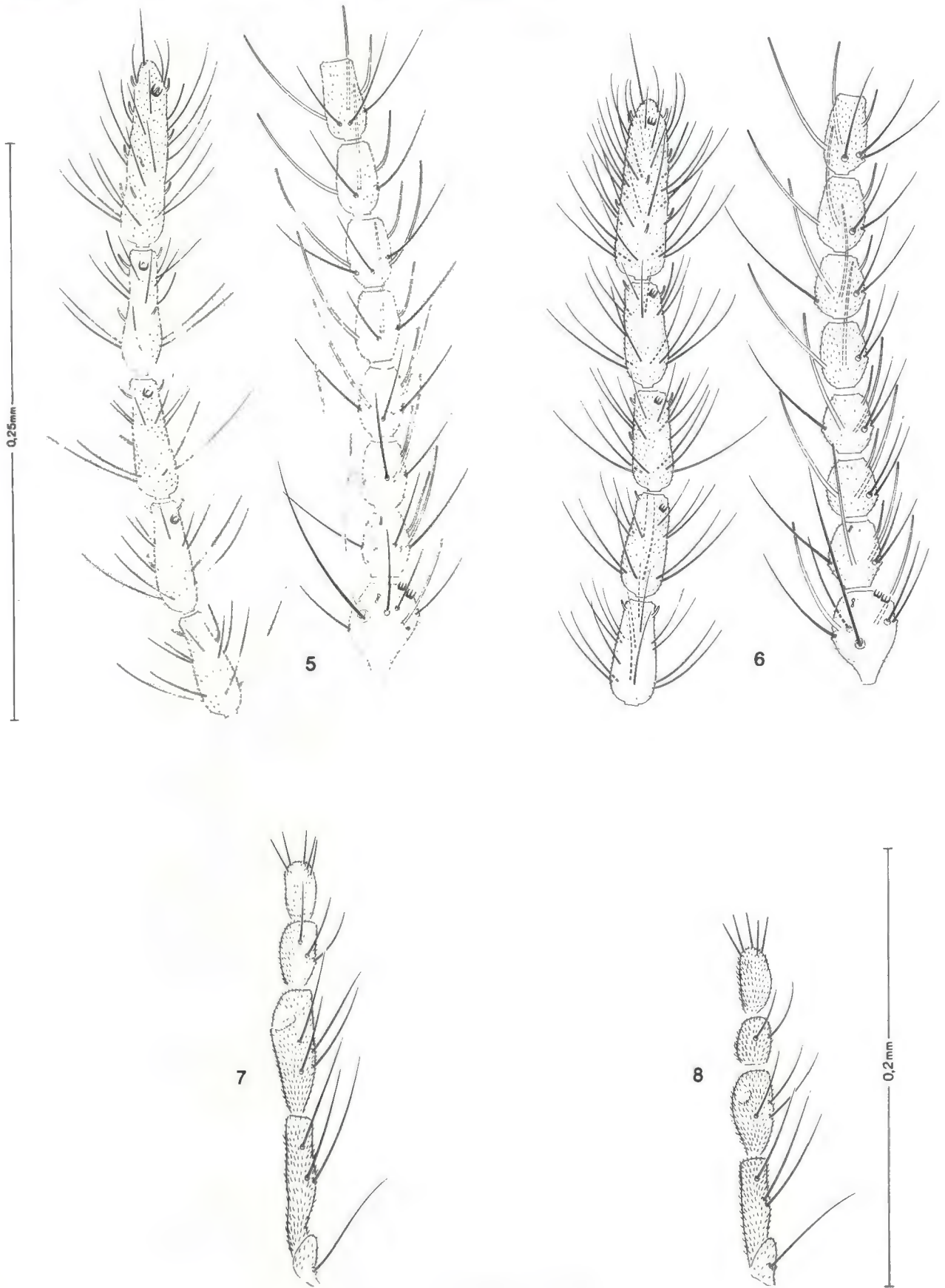
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FIG. 5 *C. (Avaritia) imicola.* Antenna, female: segments XI–XV on left, segments III–X on right

FIG. 6 *C. (Avaritia) bolitinos* sp. nov. Antenna, female: segments XI–XV on left, segments III–X on right

FIG. 7 *C. (Avaritia) imicola.* Palp, female.

FIG. 8 *C. (Avaritia) bolitinos* sp. nov. Palp, female

Culicoides pseudoturgidus Das Gupta 1962: 538; Dyce & Wirth, 1983: 223. India.

Culicoides pallidipennis Carter, Ingram & Macfie; Khamala & Kettle, 1971: 41. Kenya, Uganda and Tanzania.

Culicoides imicola Kieffer; Krêmer, 1972: 648. Redescription.

Culicoides imicola Kieffer; Boorman & Dipeolu, 1979: 31. Nigeria.

Female (Fig. 1–3, 5, 7, 9, 13; Table 1–7)

Head. Eyes (Fig. 3); bare, contiguous for a distance of between 1 and 2 facets. Antenna (Fig. 5, Table 1, 2, 3, 4, 5 and 7) slender, basal segments IV–X barrel-shaped, distal segments XI–XIV faintly vasiform narrowing perceptibly subapically, XV nearly parallel-sided only narrowing apically; lengths of antennal segments III–XV: 37,4–24,4–24,2–25,9–27,1–26,9–27,3–29,8–41,3–43, 4–44,1–44,3–70,8 μm (n=25); total length of antenna: 435,0–494,5 mean 466,0 μm (n=25); widths of antennal segments III–XV: 27,6–21,6–18,0–18,0–16,8–16,8–15,6–15,6–16,8–16,8–16,8–16,8–18,0 μm (n=1); AR 0,95–1,10, mean 1,01 (n=167); sensilla coeloconica present on segments III, XII–XV in 92,5 % of antennae examined (n=172), see Table 2 for deviations from the norm; sensilla chaetica distribution on segments III–XV was 5–3–2–3–2–3–2–3–0–0–0–0–0 (n=172) in 95 % of antennae examined, see Table 3 for deviations from the norm; sensilla trichodea distribution of the LLc type i.e. each of segments IV–X with 2 long and 1 short blunt-tipped trichodea, segment III with only 2 long blunt-tipped trichodea (n=172); AtR 1,59–2,27, mean 1,86 (n=173); segments XI–XV each with 9–23 sharp-tipped sensilla trichodea of varying lengths and thicknesses as also 1–9 short blunt-tipped basiconica per segment; each antennal segment is uniformly clothed throughout with fine spiculae. The distributions of the sensilla coeloconica, chaetica and trichodea appear in Table 1. Palp (Fig. 7; Table 6): of a moderate length, slender, light brown throughout, lengths of palpal segments I–V: 18,96–54,24–46,85–30,64–26,97 (n=160); total length 165,6–182,4 μm, mean 176,06 μm (n=25); III moderately long and slender carrying only 3–4 rather short chaetica, with a small, round and shallow subapical pit with opening about half the width of segment in diameter, margin of pit smooth; PR 2,40–3,38, mean 2,86 (n=172); P/H ratio 1,01–1,22, mean 1,07 (n=20); mandible with 12–16 fine teeth (n=42). Legs brown with fore and middle femora narrowly pale basally and subapically; hind femora brown, only narrowly pale basally; all tibiae brown with a distinct narrow subbasal pale band, only hind tarsi also narrowly pale apically; TR 1,52–1,76, mean 1,64 (n=100); comb on apex of hind tibia with 5 spines, the 1st being the longest and only slightly longer than the 2nd. Wing: (Fig. 2,9): length 0,92–1,17 mm, mean 1,06 (n=150); breadth 0,43–0,61 mm, mean 0,52 mm (n=100); CR 0,54–0,59, mean 0,56 (n=100); macrotrichia scanty, confined to distal 3rd of wing in cells R_5, M_1 and M_2 only; microtrichia dense and coarse. Dark pattern of wing grey, pale areas white to yellowish well-defined but irregularly shaped; 2 radial cells, proximal ½ of 1st and distal ½–2/3 of 2nd cell pale. The more important species-specific wing pattern characters are: (i) pale costal spots 2 and 3, those that cover the r–m crossvein and distal ½ of 2nd radial cell respectively, are rather broadly separated by a dark area below the radial cells, (ii) distal or 4th pale costal spot in cell R_5 broadly abuts wing margin and always has its proximal margin moderately to fairly strongly pointed, and (iii) entire posterior margin of vein M_2 dark, anterior margin is dark for proximal 2/3 but

distal 1/3 is more or less equally divided into a pale preapical section which touches and occasionally straddles vein M_2, followed by an equally broad dark distal section which always leaves the apex of veing M_2 broadly dark. Abdomen (Fig. 13): 2 moderately sclerotized slightly unequal spermathecae present, measuring 50 × 39 μm and 39 × 34 μm; both are round and entirely devoid of small hyaline punctations, with short narrow pigmented necks; rather small narrow rudimentary 3rd spermatheca present measuring 18 × 8 μm; sclerotized ring on common spermathecal duct cylindrical, smooth end parallel-sided, a little longer than broad, less than half the length of the rudimentary spermatheca; sclerotization surrounding the oviduct as shown in Fig 13. Thorax light brown in alcohol; scutellum with 1 median bristle and 1 shorter bristle on each corner in 85/87 specimens, remaining 2 specimens differed in having 2 median bristles.

Male (Fig. 11, 15, 17, 19; Table 1 & 7)

Head. Eyes bare. Antenna (Fig. 15, Table 1): plume rather sparse, appressed, plume fibrillae light brown, almost completely encircle medianally 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: 62,4–36,0–36,0–38,4–38,4–38,4–38,4–38,4–36,0–33,6–88,8–67,2–91,2 μm (n=1); sensilla coeloconica distribution: 96 % with 2 on segment III, 98 % with 1 on XIII, 98 % with 1 on XIV and 96 % with 2 on XV (n=50); sensilla chaetica distribution: 5 of varying lengths and thicknesses on III, 2 (rarely 3) basally (1st long and robust, 2nd shorter and weaker) and 1 medianally (though very slender is 1½ × longer than segment) on XIII, 2 basally (both weak but of different lengths) on XIV, none basally on XV only 1 apically; sensilla trichodea distribution on segments III–XII: III with 2 long blunt-tipped trichodea, segments IV–VI with 2 long and 1 short blunt-tipped trichodea; segments VII–IX with 1 long and 1 short blunt-tipped trichodea, segment X with 1 short blunt-tipped trichodea only, segments XI and XII lacking trichodea (n=25). The distributions of the sensilla coeloconica, chaetica and trichodea appear in Table 1. Wing: (Fig. 11). Abdomen. Genitalia (Fig. 17, 19): tergum 9 (Fig. 17) square, fractionally waisted medianally, finely spiculate throughout except for narrow strips of the anterior and posterior margins being bare, bearing 11–19 chaetica of different lengths, mean 15 (n=45); apicolateral processes are replaced by thin, hyaline flanges these lacking spiculae but each carrying a single fine, rather short 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; the posterior margin of tergum which separates these flanges is gently concave and without median indentation or infuscation; 2 well-developed cerci (Fig. 19), each adorned with long spiculae and 2 long and 2 short setae apically, protrude well beyond posterior margin of tergum (Fig. 19); sternum 9 (Fig. 19) with moderately deep excavation, membrane within the excavated area can be sparsely to rather strongly spiculate the excavated area bearing from 8–145 spiculae, mean 47 (n=50); basimere with dorsal and ventral spiculae and chaeticae as illustrated (Fig. 19), basimere 2,4 × 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 × length of basimere, rather stout, gently curved and broadly blunt-tipped; basal half spiculate and carrying 6 bristles of varying lengths and thicknesses, extreme apex with about 5 very short, fine tactile sensilla. Aedeagus (Fig. 19) narrow shield-shaped, slender and 0,9 × length of

TABLE 1 Lengths (μm) of segments and mean distributions of sensillae on the male and female antennae of *C. (Avaritia) imicola* and *C. (A) bolitinos* sp. nov.

	Antennal segments												
	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII	XIV	XV
C. imicola													
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	LL	LLc	LLc	LLc	LLc	LLc	LLc	LLc	—	—	—	—	—
Lengths of segments	37,4	24,4	24,2	25,9	27,1	26,9	27,3	29,8	41,3	43,4	44,1	44,3	70,8
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	LL	LLc	LLc	LLc	Lc	Lc	Lc	c	—	—	—	—	—
Lengths of segments	62,4	36,0	36,0	38,4	38,4	38,4	38,4	38,4	36,0	33,6	88,8	67,2	91,2
C. bolitinos													
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	LL	LLc	LLc	LLc	LLc	LLc	LLc	LLc	—	—	—	—	—
Lengths of segments	35,4	22,4	22,5	24,0	25,3	25,1	25,8	28,1	39,2	39,7	39,8	39,7	66,8
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	LL	LLc	LLc	LLc	Lc	Lc	Lc	c	—	—	—	—	—
Lengths of segments	55,2	31,2	31,2	31,2	31,2	31,2	31,2	28,8	28,8	28,8	72,0	62,4	76,8

TABLE 2 Number and frequency of coeloconica present on each of female antennal segments III–XV of *C. (Avaritia) imicola* and *C. (A.) bolitinos* sp. nov.

No. of coeloconica per segment *C. imicola*	Antennal segments							
	III	IV–IX	X	XI	XII	XIII	XIV	XV
0	—	172	171	165	8	—	—	—
1	—	—	1	7	164	172	172	170
2	1	—	—	—	—	—	—	2
3	169	—	—	—	—	—	—	—
4	2	—	—	—	—	—	—	—
No. of antennae examined	172	172	172	172	172	172	172	172
C. bolitinos								
0	—	56	56	55	—	—	—	—
1	—	—	—	1	56	56	56	55
2	—	—	—	—	—	—	—	1
3	56	—	—	—	—	—	—	—
4	—	—	—	—	—	—	—	—
No. of antennae examined	56	56	56	56	56	56	56	56

TABLE 3 Number and frequency of chaetica present on each of female antennal segments III–XV of *C. (Avaritia) imicola* and *C. (A.) bolitinos* sp. nov.

No. of chaetica per segment *C. imicola*	Antennal segments												
	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII	XIV	XV
0	—	—	—	—	—	—	—	—	168	172	171	172	172
1	—	—	1	—	—	—	1	—	1	—	1	—	—
2	—	—	160	—	168	—	167	5	—	—	—	—	—
3	—	152	11	161	4	155	4	157	—	—	—	—	—
4	3	17	—	11	—	16	—	10	—	—	—	—	—
5	154	3	—	—	—	1	—	—	—	—	—	—	—
6	14	—	—	—	—	—	—	—	—	—	—	—	—
7	1	—	—	—	—	—	—	—	—	—	—	—	—
No. of antennae examined	172	172	172	172	172	172	172	172	172	172	172	172	172
C. bolitinos													
0	—	—	—	—	—	—	—	—	58	59	59	59	59
1	—	—	1	—	—	—	—	—	1	—	—	—	—
2	—	1	58	—	59	—	58	1	—	—	—	—	—
3	—	56	—	59	—	59	1	58	—	—	—	—	—
4	2	1	—	—	—	—	—	—	—	—	—	—	—
5	54	1	—	—	—	—	—	—	—	—	—	—	—
6	3	—	—	—	—	—	—	—	—	—	—	—	—
No. of antennae examined	59	59	59	59	59	59	59	59	59	59	59	59	59

basimere; basal arch convex with only lateral margins slightly infuscate, distal margin of arch reaching to nearly 0,25 × length of aedeagus; lateral margins smooth and convex, darkly but narrowly infuscate and converging distad to end in a hyaline, round-tipped, parallel-sided terminal projection the base of which projects anteriorly into median area of aedeagus in the form of a raggedly infuscate "peg". Parameres (Fig. 19) separate, nearly touching medianally from where they diverge anteriad and posteriad at 45°, posterior halves are as 2 convex almost hyaline blades initially stout but tapering smoothly to sharp, simple, erect tips.

Slide material used in redescription

South Africa: 83 ♀♀ 53 ♂♂, Onderstepoort, Transvaal. April–May 1986, I.T.P. Pajor, reared from drainage furrow overgrown with Kikuyu grass using in situ tent-type emergence trap.

Additional slide material examined

Transvaal: 5 ♀♀ 27 ♂♂, Honeydew, northern Johannesburg, M. Wasserthal, black light, dates as follows: 3

♀♀ 20 ♂♂ 8. II. 1984; 1 ♂ 14. II. 1984; 2 ♀♀ 6 ♂♂ 25. III. 1984.

1 ♀ 1 ♂, farm Krugerspan, Sentrum, north-western Transvaal, ♀ 21. IV. 1987, ♂ 13. V. 1987, M. Ras, black light.

1 ♂, farm Apél, Sekhukhuneland, central Transvaal, 6. III. 1979, R. Meiswinkel & K. Newberry, white light on edge of sand river.

2 ♀♀ 1 ♂, Makonde, Vendaland, northern Transvaal, 23. IX. 1980, R. Meiswinkel, black light on edge of vlei.

1 ♂, Eiland mineral baths, north-eastern Transvaal, 2. III. 1984, R. Meiswinkel, black light on edge of vlei.

1 ♂, Bergpan saltworks, Soutpansberg district, northern Transvaal, 5. IX. 1984, R. Meiswinkel, black light.

2 ♂♂, Tshipese mineral baths, northern Transvaal, 4. III. 1984, R. Meiswinkel & J. E. Randall, black light on edge of vlei.

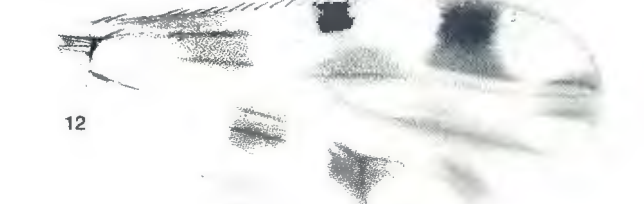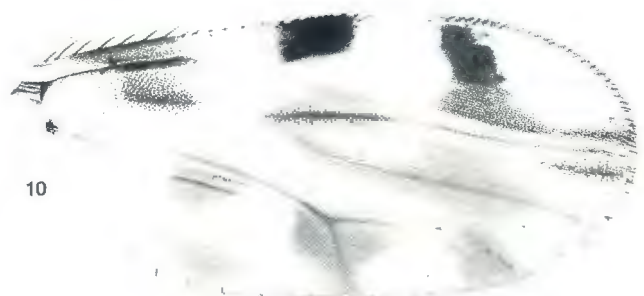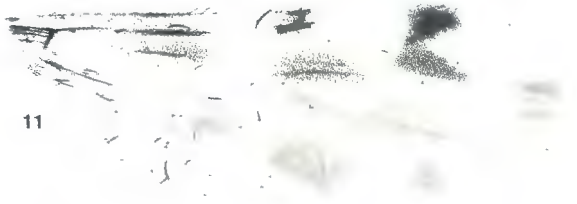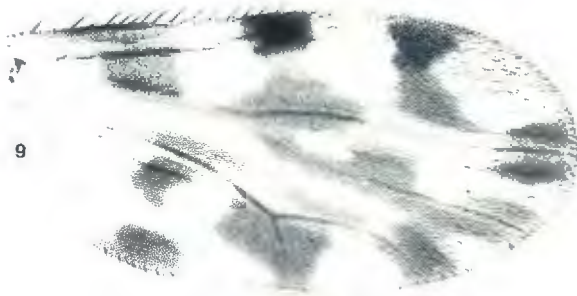1 ♀, Mooketsi, northern Transvaal, 10. II. 1980, R. Meiswinkel, black light.

FIG. 9 *C. (Avaritia) imicola*. Wing, female
FIG. 10 *C. (Avaritia) bolitinos* sp. nov. Wing, female

FIG. 11 *C. (Avaritia) imicola*. Wing, male
FIG. 12 *C. (Avaritia) bolitinos* sp. nov. Wing, male

10 ♀♀ 11 ♂♂, farm Jaffray ± 15 km east of Tzaneen, northern Transvaal, 14. 1. 1984, R. Meiswinkel, black light in sheep pen.

1 ♀ 3 ♂♂, Skukuza, Kruger National Park, eastern Transvaal, 11. III. 1984, R. Meiswinkel & L. E. O. Braack, black light on edge of Sabie river.

Natal: 2 ♀♀, Ngome Tea estate, northern Natal, 3. I. 1981, R. Meiswinkel, black light.

4 ♀♀ 6 ♂♂, Mfomoti, False Bay, northern Natal, 24. IX. 1983, R. Bagnall, black light.

19 ♀♀ 18 ♂♂, Ndumu Game Reserve, northern Natal, 6. VI. 1988, R. Meiswinkel, black light at main camp.

Cape: 8 ♀♀, farm Welgevallen, Stellenbosch, 1 ♀ 7. IX. 1983; 7 ♀♀ 20. VI. 1984, A. Kriel, black light.

2 ♀♀ 5 ♂♂, Verlorenvlei near Redelinghuys, western Cape, 3. V. 1987, G. v. Eeden, black light.

10 ♀♀ 2 ♂♂, farm Veekos near Upington, northern Cape, 1 ♀ 1 ♂ 21. XII. 1983; 1 ♂ 15. XII. 1983; 4 ♀♀ 1. IX. 1986; 2 ♀♀ 4. IX. 1986; 3 ♀♀ 14. X. 1986, L. Jordaan, black light.

2 ♀♀, Augrabies National Park, northern Cape, 23. IX. 1987, M. Edwardes, black light in main camp.

1 ♂ Grootfontein Agricultural College, Middelburg, Cape, 7. II. 1984, J. C. van Straaten, black light.

Namibia: 920 ♀♀, farm Bergvlug ± 30 km east of Windhoek, central Namibia, XI–XII. 1978, H. C. Biggs, light trap.

Botswana: 10 ♀♀, Mamalakwe river near Maun, northern Botswana, 6. VI. 1988, H. V. de V. Clarke, light trap.

Swaziland: 31 ♀♀ 4 ♂♂, High Hope riding School, Manzini, 31. VIII. 1988, G. v. Eeden, black light.

Malawi: 7 ♀♀ 1 ♂, Kawalazi estate ± 30 km east of Mzuzu, northern Malawi, 2 ♀♀ 23. X. 1987; 1 ♂ 24. X. 1987; 5 ♀♀ 14. II. 1988, K. Verster, black light in *Brachystegia* woodland.

1 ♀ 1 ♂, Vizara Rubber Estate near Nkhata Bay, northern Malawi, 14–15. XI. 1987, R. Meiswinkel, black light near cattle kraal.

Iraq: 1 ♂ *C. iraqensis* (holotype), Baghdad, Iraq, 24. V. 1954, K. T. Khalaf, light trap.

Unmounted light-trap material examined

South Africa: Transvaal.

371 ♀♀ 2 ♂♂, Skukuza buffalo boma K.N.P., 14. IV. 1988, L. E. O. Braack & R. Meiswinkel, black light.

153 ♀♀ 14 ♂♂, Skukuza, K.N.P., 12. IV. 1988, P. J. Meiswinkel, black light on banks of Sabie river.

33 ♀♀, Shingwidzi, K.N.P., 10. IV. 1988, L. E. O. Braack & R. Meiswinkel, black light on banks of Shingwidzi river, 18h30–21h00.

16 ♀♀ 18 ♂♂, Manxeba Pan near Pafuri, K.N.P., 12. IV. 1988, L. E. O. Braack & R. Meiswinkel, black light on edge of swamp plain 18h30–21h00.

51 ♀♀ 14 ♂♂, Tshalungwa springs north of Punda Maria, K.N.P. 7. XI. 1985, L. E. O. Braack & R. Meiswinkel, black light 18h30–20h00.

131 ♀♀ 15 ♂♂, Bergpan saltworks, Soutpansberg district, northern Transvaal, 30. XI. 1984, R. Meiswinkel & G. J. Venter, black light at cattle kraal.

Malawi: 348 ♀♀ (202 nulliparous, 146 parous) 11 ♂♂, Vizara Rubber Estate near Nkhata Bay, northern Malawi, 14–15. XI. 1987, R. Meiswinkel, black light near cattle kraal.
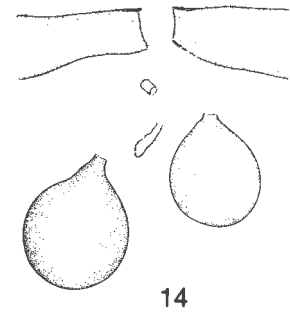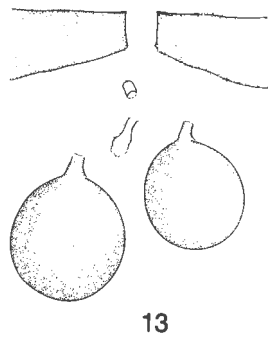
Unmounted host material examined

South Africa: 8 ♀♀, Skukuza, K.N.P., 13. VII. 1985, L. E. O. Braack, aspirated off darted buffalo in boma.
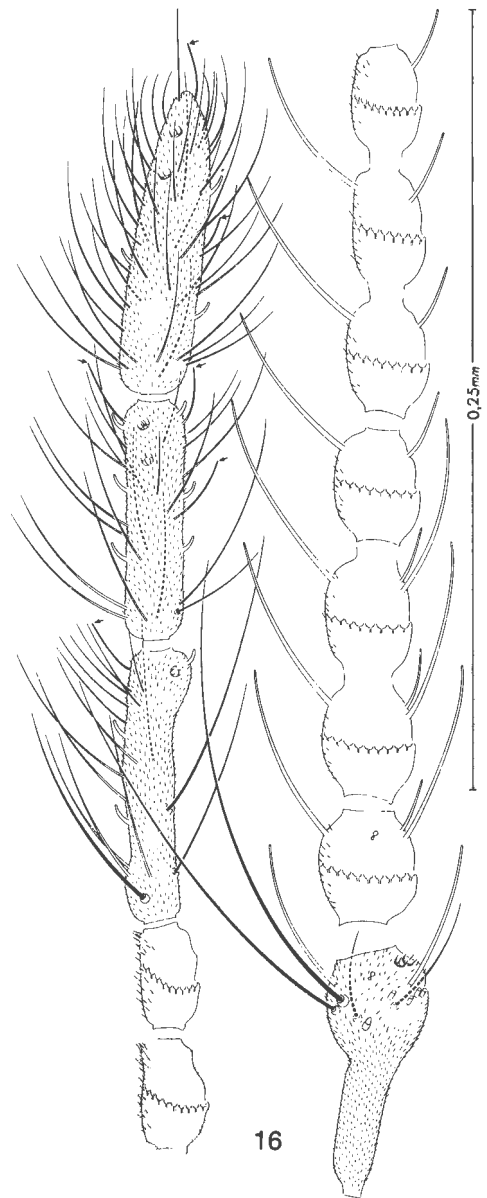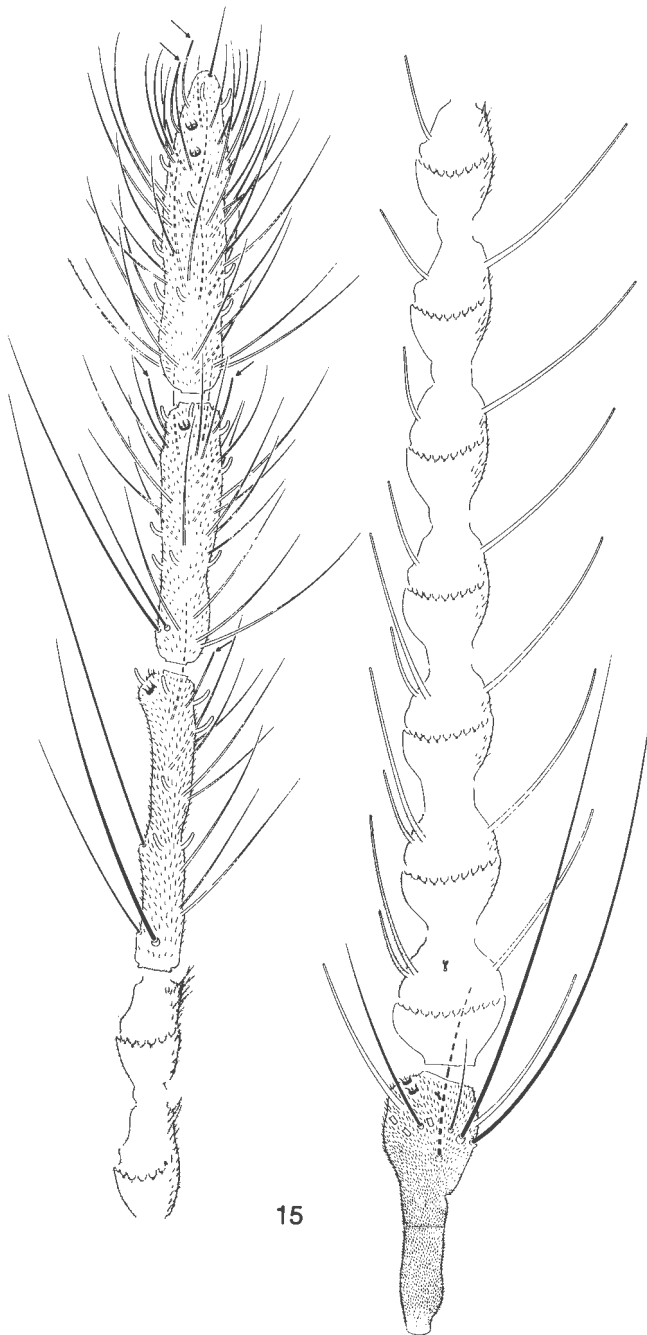
Culicoides (Avaritia) bolitinos sp. nov.

(Fig. 4, 6, 8, 10, 12, 14, 16, 18, 20; Table 1–7)

Culicoides pallidipennis sensu Nevill 1968: 61. South Africa.

Culicoides 1348 sensu Braverman 1978: 167. Zimbabwe.

FIG. 13 *C. (Avaritia) imicola*. Genitalia, female: spermathecae and sclerotization surrounding gonopore
FIG. 14 *C. (Avaritia) bolitinos* sp. nov. Genitalia, female: spermathecae and sclerotization surrounding gonopore
FIG. 15 *C. (Avaritia) imicola*. Antenna, male: segments XI–XV on left, segments III–X on right
FIG. 16 *C. (Avaritia) bolitinos* sp. nov. Antenna, male: segments XI–XV on left, segments III–X on right

Culicoides sp. 49 sensu Nevill, Venter, Edwardes, Pajor, Meiswinkel & Van Gas 1988: 103. South Africa.

Female (Fig. 4, 6, 8, 10, 14; Table 1–7)

Head. Eyes (Fig. 4); bare; contiguous for a distance of a little more than 1 facet. Antenna (Fig. 6, Table 1, 2, 3, 4, 5 and 7); slender, basal segments IV–X barrel-shaped with V and VI only slightly longer than wide, segments XI–XIV faintly vasiform narrowing perceptibly subapically, XV nearly parallel-sided only narrowing apically; lengths of antennal segments III–XV (n=25): 35,4–22,4 – 22,5 – 24,0–25,3–25,1–25,8–28,1–39,2–39,7–39,8–39,7–66,8 μm; total length of antenna 392,4–480,0 μm mean 433,8 μm (n=25); widths of antennal segments III–XV (n=25): 26,6–20,1–17,5–16,8–15,8–16,5–15,9–15,5–14,9–15,2–15,6–15,4–16,5 μm AR 0,96–1,12 mean 1,04 (n=54); sensilla coeloconica present on segments III, XII–XV with 3 coeloconica on III and 1 on each of segments XII–XV; 1 of 56 antennae examined had a coeloconica on XI (Table 2); sensilla chaetica distribution on segments III–XV: 5–3–2–3–2–3–2–3–0–0–0–0–0, with 1 of 59 antennae examined having 1 chaetica on XI (Table 3); sensilla trichodea distribution of the LLc type, i.e. each of segments IV–X with 2 long and 1 short blunt-tipped trichodea, segment III with only 2 long blunt-tipped trichodea; AtR 1,59–2,17 mean 1,85 (n=56); segments XI–XV each with 13–33 sharp-tipped sensilla trichodea of varying lengths and thicknesses as also 2–7 short blunt-tipped sensilla basiconica per segment (Fig. 6). The distributions of the sensilla coeloconica, chaetica and trichodea appear in Table 1. Palp (Fig. 8; Table 6): rather short, slender, pale brown throughout; lengths of palpal segments I–V: 18,3–44,5–38,7–23,4–24,5 μm (n=25); total length 132,0–165,6 μm, mean 148,5 μ (n=25); III rather short and slender almost barrel-shaped but not inflated, carrying 3–4 rather short chaetica, with a small round and shallow subapical pit of diameter about half the width of segment, margin of pit smooth in sideview; PR 1,86–2,72, mean 2,33 (n=52); P/H ratio 0,71–0,94, mean 0,81 (n=20); mandible with 12–14 fine teeth (n=10); Legs: brown with all femora narrowly pale basally; fore-femora rather broadly pale subapically, middle femora narrowly pale subapically and hind femora entirely brown apically; all femoral-tibial knees dark; all tibiae brown with a distinct narrow subbasal pale band and with apices of fore-tibiae brown; apices of middle tibiae paling imperceptibly, those of hind tibiae broadly pale; tarsi pale brown; TR 1,54–1,75, mean 1,63 (n=40); comb on hind tibia with 5 spines, the 1st being slightly longer and thicker than the remainder. Wing (Fig. 10): length 0,87–1,04 mm, mean 0,93 mm (n=20); breadth 0,46–0,52 mm, mean 0,53 mm (n=20); CR 0,53–0,60, mean 0,56 (n=20); macrotrichia rather scanty confined to apical third of wing. Wing pattern very similar to that of *C. imicola*, main differences as follows: 3rd dark costal spot in the centre of cell R_5 with its distal margin not indented medianally by a pointed extension of the 4th pale coastal spot in cell R_5 but is more or less straight and runs transversely, anteriad to posteriad, across cell R_5 and is often ragged rather than smooth; as a result the 4th pale costal spot adjoining the wing margin in R_5 has its proximal margin also straight, transverse and ragged rather than pointed as seen in *C. imicola*. It must be noted that this is subject to variation which includes those specimens which will have this proximal margin faintly convex thus the tendency for this 4th pale spot to have a muted form of the pointed extension always seen in *C. imicola*. The median 3rd of the upper and lower margin of vein M_2 is broadly dark but gradually tapers and fades to leave the apex of vein

M_2 pale or narrowly darkened. In darker variants the apex of vein M_2 can be fairly broadly darkened. In both pale and dark variants, however, vein M_2 never possesses the preapical pale excision that is always seen subapically on the upper margin in *C. imicola*.

Abdomen (Fig. 14): 2 round to gently ovoid rather darkly pigmented spermathecae, without hyaline punctations, each with rather short and narrow, smooth necks, subequal in size measuring 45 × 34 μm and 39 × 29 μm; rudimentary 3rd spermatheca short and slender, slightly rugose with a small bulbous head this expanded in occasional specimens, measuring 12 × 7 μm; sclerotized ring on common spermathecal duct, cylindrical, smooth, and parallel-sided, a little longer than broad less than half the length of the rudimentary spermatheca; genital sclerotization surrounding oviduct as shown in Fig. 14.

Thorax: light brown throughout when in alcohol; scutellum with 1 long median bristle and 1 shorter, thinner bristle on each corner (n=20).

Male (Fig. 12, 16, 18, 20; Table 1 & 7)

Head. Eyes bare. Antenna (Fig. 16, Table 1): apparently inseparable from that of *C. imicola* having the same sensilla coeloconica, trichodea and chaetica distributions (n=50; see under *C. imicola* and Table 1). Lengths of segments III–XV: 55,2–31,2–31,2–31,2–31,2–31,2–31,2–28,8–28,8–28,8–72,0–62,4–76,8 μm (n=1). Abdomen. Genitalia (Fig. 18, 20) very similar to *C. imicola*. Tergum 9 (Fig. 18) nearly square fractionally waisted medianally, not tapering distad, finely spiculate throughout except for narrow strips of the anterior and posterior margins, bears 11–16 chaetica, mean 13,6 (n=20); apicolateral processes replaced on the lateral corners by broadly rounded relatively hyaline flanges that are devoid of spiculae but each carrying a fine, rather short 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; the posterior margin of tergum is gently concave and lacks a median indentation or infuscation; 2 well developed cerci (Fig. 20) as seen in *C. imicola*. Sternum 9 (Fig. 20) with a moderately wide and deep excavation, membrane within the excavated area with 0–18 spiculae, mean 2,56 (n=50), of these 40 % had no spiculae and only 2 % had more than 10 spiculae; basimere with dorsal and ventral spiculae these a little longer and more sparsely distributed than on tergum; basimere also possesses chaetica as illustrated (Fig. 20), basimere 2,5 × as long as broad with basal infuscate collar and well developed dorsal and ventral roots of the form typical for the subgenus *Avaritia*. Distimere as in *C. imicola*. Aedeagus also practically inseparable from that of *C. imicola*, in some specimens relatively more elongate; height of arch variable from being moderately low to fairly high; pigmented and shaped much as in *C. imicola*, 0,9 × as long as basimere; parameres 0,8 × the length of aedeagus, of the general shape and pigmentation as described for *C. imicola*.

Etymology. The ancient Greek adjective for cow dung is BORITIVOS, the larval habitat of the new species.

Type material

South Africa: Holotype ♀ (slide Timbavati 8), Timbavati near Roodewal camp, west-central Kruger National Park, 17. XII. 1985, R. Meiswinkel, reared from half of 1 buffalo dung pat collected off short grass on the margin of the dry Timbavati river.

50 ♀♀ 41 ♂♂ paratypes all from same dung pat. Slides from this type series have been deposited in the following Museums:
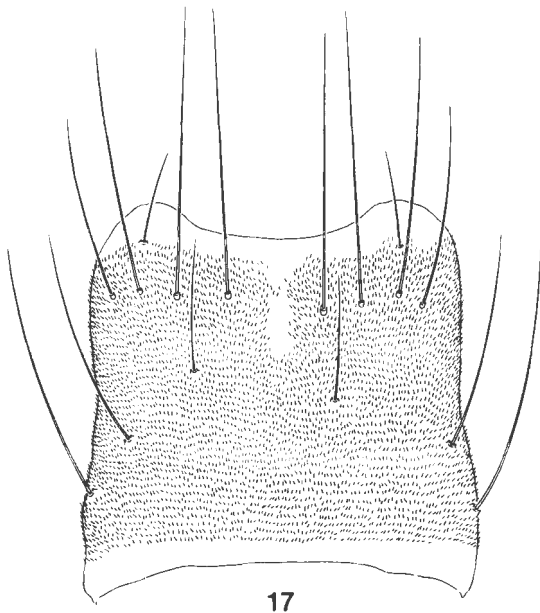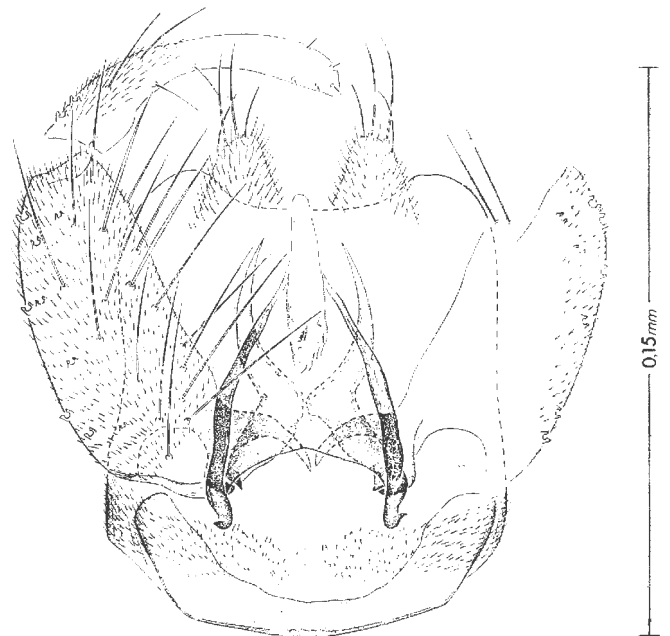
17
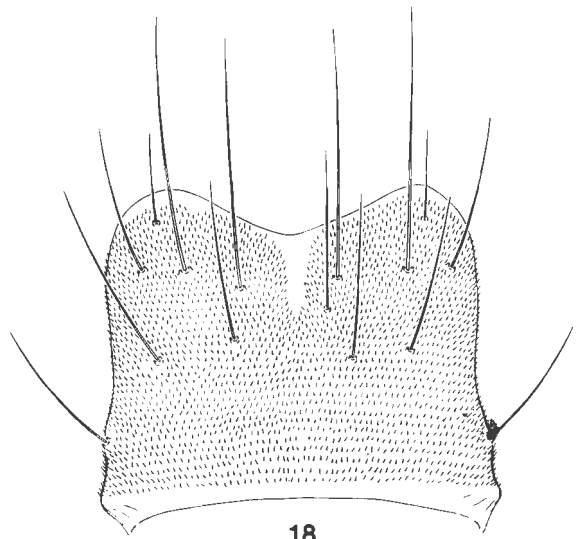
18

20

19

FIG. 17 C. *(Avaritia) imicola*. Genitalia, male: tergum IX
FIG. 18 C. *(Avaritia) bolitinos* sp. nov. Genitalia, male: tergum IX

FIG. 19 C. *(Avaritia) imicola*. Genitalia, male
FIG. 20 C. *(Avaritia) bolitinos* sp. nov. Genitalia, male

1 ♀ 1 ♂ paratype (slides Timbavati 24 and 15); British Museum (Natural History).

1 ♀ 1 ♂ paratype (slides Timbavati 21 and 14); United States National Museum, Washington.

1 ♀ 1 ♂ paratype (slides Timbavati 12 and 11); Australian National Insect Collection, Canberra.

1 ♀ 1 ♂ paratype (slides Timbavati 19 and 13); Museum National d'Histoire Naturelle, Paris.

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

Other slide material examined

Transvaal: 28 ♀♀ 5 ♂♂ (collection No. 73.354), farm Ludwigs Lust, Hectorspruit, eastern Transvaal, 30. XI. 1973, A. L. Dyce from a series of '55 larvae and pupae from cow pats floated out in sugar; pats 12–20

days old on bare ground near edge of gully with waterhole (obvious camp). Dung beetles had worked and were still active—those species that mine out underneath the pat but leave the outer crust intact; bottom of pat was firmly in contact with the soil'.

2 ♂♂, Pafuri, northern K.N.P., 15. IV. 1986, L. E. O. Braack and R. Meiswinkel, black light 14 m up *Acacia albida* in gallery forest lining Pafuri river.

2 ♀♀, Skukuza, K.N.P., 11. III. 1984, L. E. O. Braack and R. Meiswinkel, black light on bank of Sabie river.

1 ♀ 3 ♂♂, Skukuza, K.N.P., 17. I. 1985, R. Meiswinkel, black light along Sabie river.

5 ♀♀, Murangoni location, ± 15 km west of Thohoyandou, Vendaland, northern Transvaal, 30. I. 1988, R. & P. Meiswinkel, truck-trap 18h42–19h01.

1 ♀ 2 ♂♂, Haenertzburg, northern Transvaal, 21. IV. 1983, R. Meiswinkel, black light at dairy.

33

7 ♀♀, Ebenezer dam, northern Transvaal, 14. VI. 1980, R. Meiswinkel, black light at dairy.

6 ♀♀ 18 ♂♂, Kransberg, Thabazimbi district, north-western Transvaal, IV. 1985, I. T. P. Pajor, ex 3 cattle dung pats.

39 ♀♀ 12 ♂♂, Honeydew, near Johannesburg, M. Wasserthal, black light on smallholding, dates as follows: 1 ♂ 15. XII. 1983; 1 ♂ 7. I. 1984; 3 ♀♀ 1 ♂ 8. II. 1984; 2 ♀♀ 3 ♂♂ 14. II. 1984; 1 ♀ 8. IV. 1984; 7 ♀♀ 14. IV. 1984; 1 ♂ 25. X. 1984; 10 ♀♀ 3 ♂♂ 28. X. 1984; 16 ♀♀ 24. XII. 1984; 1 ♂ 15. II. 1985.

1 ♀, Onderstepoort, 22. VII. 1986, G. J. Venter and I. T. P. Pajor, trucktrap near horses, 16h48–17h05.

9 ♀♀ 2 ♂♂, Onderstepoort, VI. 1985, I. T. P. Pajor, ex cow pats.

9 ♀♀ 4 ♂♂, farm Krugerspan, Sentrum, north-western Transvaal, 18. XI. 1987, G. J. Venter, ex blue wilde-beest dung.

4 ♀♀, farm Krugerspan, Sentrum, north-western Transvaal, 15. IX. 1987, G. J. Venter, ex blue wilde-beest dung.

5 ♀♀ 7 ♂♂, farm Krugerspan, Sentrum, north-western Transvaal, 14. IV. 1987, G. J. Venter, ex blue wilde-beest dung.

Natal: 3 ♀♀ 4 ♂♂, Ngome tea estate, northern Natal, I. 1981, R. Meiswinkel, black light.

2 ♀♀, Umlalazi Coastal Nature Reserve, 128 km north of Durban, 20–23. VII. 1988, E. M. & H. Nevill, black light at back of cabin.

Orange Free State: 1 ♀ 1 ♂, Golden Gate National Park, III. 1985, L. E. O. Braack, black light.

Cape: 11 ♀♀ 1 ♂ farm Welgevallen, Stellenbosch, 20. VI. 1984, A. Kriel, black light.

1 ♀ 3 ♂♂, Jonkershoek near Stellenbosch, 26. XI. 1986, M. Edwardes, black light.

Lesotho: 3 ♀♀, St. Mary's High School, Roma, western Lesotho, 10. II. 1987, G. K. Sweatman, black light.

Zimbabwe: 2 ♀♀ 6 ♂♂, Rekomitjie Research Station, north-western Zimbabwe, 6. II. 1988, R. J. Phelps, light-trap on stream bank.

Malawi: 1 ♀, Limphasa dambo near Nkhata Bay, northern Malawi, 26. X. 1987, R. Meiswinkel, truck-trap 17h45.

18 ♀♀ 5 ♂♂, Vizara Rubber Estate near Nkhata Bay, northern Malawi, 14–15. XI. 1987, R. Meiswinkel, black light near cattle kraal.

Kenya: 1 ♀, Naibor Keju (0° 59′ N, 36° 48′ E), 22. XII. 1971, A. R. Walker, light-trap.

Nigeria: 1 ♀, Kankiya, II. 1957, B. McMillan, at light.

Unmounted light-trap material examined

South Africa: 422 ♀♀ 4 ♂♂ Allerton Regional Veterinary laboratory, Pietermaritzburg, Natal, 15. V. 1986, R. Parker, black light.

89 ♀♀ (61 parous, 28 nulliparous) 6 ♂♂, Skukuza buffalo boma, K.N.P., 14. IV. 1988, R. Meiswinkel & L. E. O. Braack, black light.

6 ♀♀, Skukuza, K.N.P., 12. IV. 1988, P. J. Meiswinkel, black light on bank of Sabie river.

60 ♀♀, 5 ♂♂, Masanje waterhole northern K.N.P., 6. XI. 1985, R. Meiswinkel, black light 18h45–22h30.

Malawi: 70 ♀♀ (49 nulliparous, 39 parous) 1 ♂, Vizara Rubber Estate near Nkhata Bay, northern Malawi, 14–15. XI. 1987, R. Meiswinkel, black light near cattle kraal.

Unmounted reared material examined

South Africa: 4 ♂♂, Nwaswitshaka, southern K.N.P., 5. II. 1986, R. Meiswinkel, ex buffalo dung in middle of sand road.

62 ♀♀, 5 ♂♂, Masanje, northern K.N.P., 6. XI. 1985. R. Meiswinkel & L. E. O. Braack, black light near waterhole (18h45–22h30).

20 ♀♀, 32 ♂♂, Masanje waterhole, northern K.N.P., 6. XI. 1985, R. Meiswinkel, ex buffalo dung on bare soil.

16 ♀♀, 25 ♂♂, Tshalungwa springs, northern K.N.P., 8. XI. 1985, R. Meiswinkel, ex buffalo dung on bare soil.

161 ♀♀, 250 ♂♂, Timbavati riverbed near Roodewal, central K.N.P., 17. XII. 1985, R. Meiswinkel, ex ½ buffalo dung pat on short grass.

395 ♀♀, 261 ♂♂, Northern farm, Johannesburg, 16. II. 1982–10. III. 1982. J. E. Randall & E. M. Nevill, ex 20 cow pats on irrigated pasture of rye grass.

19 ♀♀, 17 ♂♂, Northern farm, Johannesburg, 1. III. 1985, G. J. Venter, ex 8 cow pats on irrigated pasture of rye grass.

48 ♀♀, 41 ♂♂, Irene near Pretoria, 14. III. 1985, G. J. Venter, ex 8 cow pats on short grass.

85 ♀♀, 89 ♂♂, Irene near Pretoria, 16. IV. 1985, G. J. Venter, ex 8 cow pats on short grass.

18 ♀♀, 8 ♂♂, Kaalplaas, Onderstepoort, 22. XI. 1985, G. J. Venter, ex 5 cow pats on bare soil under *Acacia* trees.

19 ♀♀, 13 ♂♂, Kaalplaas, Onderstepoort, 9. I. 1986, G. J. Venter, ex 8 cow pats on bare soil under *Acacia* trees.

7 ♀♀, 17 ♂♂, Kondowe farm near Eiland, north-eastern Transvaal lowveld, 8. IX. 1985, G. J. Venter, ex 8 cow pats on dry ground in mopane veld.

637 ♀♀, 336 ♂♂, Kaalplaas, Onderstepoort, 13. V. 1986, G. J. Venter, ex 8 cow pats on short grass.

343 ♀♀, 634 ♂♂, Blinkwater near Sentrum, north-western Transvaal, 13. IV. 1987, E. M. Nevill, G. J. Venter & J. van Gas, ex 8 cow pats on bare soil in mixed bushveld.

104 ♀♀, 77 ♂♂, Blinkwater near Sentrum, north-western Transvaal, 30. VI. 1987, E. M. Nevill & G. J. Venter, ex 8 cow pats on bare soil in mixed bushveld.

121 ♀♀, 177 ♂♂, Witklip near Sentrum, north-western Transvaal, 12. VIII. 1987, E. M. Nevill & G. J. Venter, ex 8 cow pats on bare soil in mixed bushveld.

89 ♀♀ 19 ♂♂, Hluhluwe Game Reserve, northern Natal, 2. VIII. 1985, E. J. Wright, ex buffalo pats.

6 ♀♀ 7 ♂♂, Hluhluwe Game Reserve, northern Natal, 2. I. 1986, E. J. Wright, ex buffalo pats.

5 ♀♀ 15 ♂♂, farm Krugerspan near Sentrum, north-western Transvaal, 14. IV. 1987, G. J. Venter and E. M. Nevill, ex blue wildebeest pats on bare soil surrounding waterhole in mixed bushveld.

32 ♀♀, 101 ♂♂ farm Krugerspan near Sentrum, north-western Transvaal, 18. XI. 1987, G. J. Venter & E. M. Nevill, ex 15–20 blue wildebeest pats on bare soil surrounding waterhole in mixed bushveld.

Unmounted host material examined

8 ♀♀ Skukuza, K.N.P. 13. VII. 1985, L. E. O. Braack, aspirated off darted buffalo in boma.

DISCUSSION

Taxonomy

Since Kieffer's description of *C. imicola* 75 years ago an extensive literature has grown around this species, much of it under the old name of *C. pallidipennis* Carter, Ingram & Macfie. However, 7 of these many references can be positively said to refer to either the new species *C. bolitinos* or to as yet undescribed closely allied ones. The 1st reference to *C. bolitinos* is that by Nevill (1968) in his description of a significant new breeding site for *C. pallidipennis*. That this was not *C. imicola* was pointed out by Braverman (1978) in his study on the larval habitats of Zimbabwean *Culicoides*. Therein he states: 'M. Cornet (personal communication) has recently shown the species which Nevill obtained from cow dung was not *C. imicola* but another member of this group (C. 1348)'. This communication was noted and repeated by Howarth (1985). Two further sources which point to species other than *C. imicola*, are those of Dipeolu & Ogunrinade (1977) and Lubega & Khamala (1976). These have to do with larval habitats and will be re-evaluated under the biology of *C. bolitinos*. In Khamala & Kettle's review of the East African *Culicoides* (1971), *C. pallidipennis* was treated indifferently and these authors are in error when they state that the sensilla coeloconica distribution is 3,11–15 which is really that of *C. pseudo-pallidipennis*. *C. imicola* has a 3,12–15 distribution. In addition their synonymizing of *C. glabripennis* under *C. pallidipennis* further indicates that they misunderstood *C. imicola* sensu stricto. Finally, the wing picture given by Kitaoka, Kaneko & Shinonaga (1984) to be that of *C. imicola* is clearly that of an undescribed Nigerian species.

Differential diagnosis

Ten character states separate the 2 species *C. imicola* and *C. bolitinos*. These are summarized in Table 7 of which 5 are discussed in detail below. The 1st 2, when used in combination, are the most reliable for separating the females of the 2 species under the dissecting microscope. Of the remaining 8 character states 7 require slide mounted material.

1. **Female.** The shape of the proximal margin of the distal pale spot in cell R_5: In *C. imicola* it is distinctly pointed medianally (Fig. 2,9) whereas in *C. bolitinos* this margin is usually straight and runs transversely, anteriad to posteriad, across cell R_5 (Fig. 10). Furthermore in *C. bolitinos* this margin is often ragged, not always smooth. However, it must be noted that this character shows variation in both species: in *C. imicola* the pointed proximal margin can be blunted whereas in *C. bolitinos* there can be a hint of a point appearing medianally, especially in the male wing. This can lead to error in identification but can be avoided when this character is considered in combination with the next (2).

2. **Female. Vein M_2:** In *C. imicola* the distal 3rd of the posterior margin of this vein is dark. However, the distal 3rd of the anterior margin differs in that it is more or less equally divided into a pale preapical section followed by an equally broad dark distal section. This always leaves the apex of vein M_2 broadly dark. This juxtaposition of a pale and a dark area on the anterior distal 3rd of vein M_2 is the single most diagnostic character when the identification of *C. imicola* is based on wing pattern alone. This feature was named by Howarth (1985) as a 'pale preapical excision' and is adopted here. Importantly it appears in both Carter, Ingram & Macfie's original wing illustration of *C. pallidipennis* and in Krêmer's redescription of the holotype of *C. imicola*. In *C. bolitinos*, however, the median 3rd of both the posterior and anterior margins of vein M_2 are broadly and entirely dark but taper and fade simultaneously leaving the apex of vein M_2 pale. Only in specimens showing a darkened wing pattern, which can be quite common, will the apex of vein M_2 be narrowly to farily broadly darkened on 1 or both margins. In either pale or dark variants, however, *C. bolitinos* will never possess the pale preapical excission so diagnostic for *C. imicola*.

3. **Female. Palps:** A t-test (2 tailed) was performed on the palpal measurements data to establish if there were any significant differences in segmental lengths between *C. imicola* and *C. bolitinos*. It was found that segments II–V in *C. imicola* were significantly longer than those of *C. bolitinos* (Table 6). The result is that *C. imicola* has a longer palp than *C. bolitinos*. In consequence the shorter palp and proboscis of *C. bolitinos* means that this species has a lower proboscis/head ratio (P/H) than *C. imicola* (Table 7).

4. **Female. Antennae:** Two t-tests were performed: (1) comparison of the lengths of female antennal segments III–XV between *C. imicola* and *C. bolitinos*, and (2) a comparison between the 2 species of the ratios of these segments where the length of each segment is divided by the width. In the 1st test each antennal segment of *C. imicola* was found to be significantly longer than its counterpart in *C. boliti-*

TABLE 4 Comparison of lengths (µm) of female antennal segments III–XV in *C. imicola* (n=25) and *C. bolitinos* sp. nov. (n=25), and calculated t-values of significance.

Antennal segment	C. imicola		C. bolitinos		t-value
	Range	Mean	Range	Mean	
III	36,0–40,2	37,4	32,4–38,4	35,4	4,6888
IV	24,0–26,4	24,4	20,4–24,6	22,4	6,2352
V	21,6–25,8	24,2	20,4–26,4	22,5	4,7140
VI	24,0–27,6	25,9	21,0–27,0	24,0	4,3643
VII	24,0–28,8	27,1	21,6–27,6	25,3	4,0819
VIII	24,0–28,8	26,9	21,6–25,8	25,1	3,9692
IX	24,0–28,8	27,3	24,0–28,8	25,8	3,4904
X	26,4–33,6	29,8	25,2–30,0	28,1	3,8624
XI	36,0–45,6	41,3	36,0–45,6	39,2	3,1263
XII	39,6–48,0	43,4	36,0–44,4	39,7	5,4674
XIII	39,6–49,2	44,1	36,0–44,4	39,8	5,9936
XIV	39,6–49,2	44,3	34,8–44,4	39,7	6,0013
XV	63,6–78,0	70,8	57,6–81,6	66,8	2,6019
Total length	435,0–494,4	466,0	391,8–480,0	433,8	5,2481

TABLE 5 Comparison of ratios of female antennal segments III–XV in *C. imicola* (n=25) and *C. bolitinos* sp. nov. (n=25), and calculated t-values of significance (n.s. = not significant)

Antennal segment	*C. imicola*		*C. bolitinos*		t-value
	Range	Mean	Range	Mean	
III	1,20–1,51	1,37	1,25–1,50	1,36	0,4954 (n.s.)
IV	1,00–1,29	1,18	1,03–1,25	1,12	3,3549
V	1,24–1,45	1,34	1,17–1,48	1,28	2,9962
VI	1,33–1,61	1,50	1,29–1,56	1,43	2,8473
VII	1,46–1,85	1,66	1,38–1,77	1,60	2,2460
VIII	1,46–1,85	1,64	1,33–1,70	1,52	3,6955
IX	1,43–1,92	1,72	1,48–1,83	1,67	3,0541
X	1,63–2,16	1,88	1,62–1,92	1,81	1,9752 (n.s.)
XI	2,31–3,08	2,71	2,31–2,92	2,63	1,6532 (n.s.)
XII	2,44–3,08	2,78	2,44–2,79	2,60	4,4999
XIII	2,54–3,15	2,82	2,22–2,85	2,54	4,2294
XIV	2,36–3,08	2,76	2,07–2,88	2,50	4,4039
XV	3,53–4,69	4,11	3,69–4,62	4,04	0,8226 (n.s.)

TABLE 6 Comparison of lengths (μm) of female palpal segments I–V in *C. imicola* (n=25) and *C. bolitinos* sp. nov. (n=25), and calculated t-values of significance (n.s. = not significant)

Palpal segment	*C. imicola*		*C. bolitinos*		t-value
	Range	Mean	Range	Mean	
I	15,6–24,0	19,0	13,2–21,6	18,3	1,0961 (n.s.)
II	50,4–57,6	54,2	39,6–49,2	44,5	14,0000
III	40,8–51,6	46,8	33,6–43,2	38,7	10,2607
IV	25,2–32,4	30,6	20,4–24,0	23,4	10,4543
V	24,0–30,0	27,0	18,0–28,8	24,5	3,4126
Total length	165,6–182,4	176,1	132,0–165,6	148,5	14,0530

nos (Table 4). However, most showed a moderate discriminatory ability with the highest t-values seen only from segments IV, XII–XIV (Table 4). The 2nd test showed the ratios to be even less discriminatory with 4 segments showing no significance but as in the 1st test segments IV, XII–XIV were again the most discriminatory (Table 5). These antennal ratio findings are of interest as they give a result that highlights 1 of the key characters used by Howarth (1985) to separate the 2 species *C. imicola* and *C. brevitarsis* collected in Laos. He stated that the ratio for antennal segments VI–IX in *C. brevitarsis* was 1,4 as opposed to 1,7 seen in *C. imicola*. The ratios found on segments VI–IX in South African material of *C. imicola* (n=25) agreed quite well with those of Howarth but were of no real value in separating this species from *C. bolitinos* (n=25) whose ratios overlapped considerably with those of *C. imicola* (Table 5). However, a higher discriminatory value is to be found between segments XII–XIV (Table 5) and though there is still a fair amount of overlap between the 2 species it is more useful than the ratios of segments VI–IX. As the Afrotropical *C. bolitinos* appears to be both the taxonomical and ecological equivalent of the Asian, Australian, eastern Palaearctic *C. brevitarsis*, it is important that these 2 species can be separated from their congener, *C. imicola*, by the use of ratios derived from different groups of female antennal segments. This is good evidence that *C. bolitinos* and *C. brevitarsis* are not conspecific and, furthermore, illustrates that these measured differences are species-specific and not induced by the shared environmental factor of having cow and buffalo dung as a larval habitat.

5. Male. The males of *C. imicola* and *C. bolitinos* differ most significantly in that the membrane of sternum 8 in *C. imicola* (Fig. 19) is sparsely to rather heavily spiculate (8–145 spiculae, mean 47; n=50) whereas in *C. bolitinos* (Fig. 20) this mem-

brane has 0–18 spiculae, mean 2,56 (n=50). More subtle differences involve the shape of the aedeagus and the precise shape of the parameres and the hyaline, apicolateral flanges of tergum 9 (Fig. 17, 18). The appreciation of these differences requires near perfectly mounted series and even so remain difficult to quantify.

Larval habitat of *C.* bolitinos

Extensive rearing from a variety of substrates over the past 4 years in South Africa has shown that *C. bolitinos* has the dung of the African buffalo and that of various races of domesticated *Bos* as its primary larval habitat. *C. bolitinos*, on a few occasions, has also been reared in low numbers from the dung of the blue wildebeest. During the wetter, rainy season the dung pats of this animal resemble small cow or buffalo pats and will then yield low numbers of *C. bolitinos*. In the dry season, however, wildebeest dung is more pellet-like and thus lacks the necessary moisture to sustain *Culicoides* immatures (personal observations; G. J. Venter, Veterinary Research Institute, Onderstepoort, unpublished data). At best the *C. bolitinos*-wildebeest association is a short one confined to the rainy season and will be considered no further.

As described by Nevill (1968) the larval habitat of *C. bolitinos* (= *C. pallidipennis* in that study) is 'dry pats with a very hard crust, a dry sponge-like centre, and a moist lower layer about an inch thick in direct contact with damp soil underneath'. In South Africa *C. bolitinos* has never been reared from dung dropped in streams or waterlogged areas where it disintegrates to enrich the surrounding medium of mud and water organically. This, in part, satisfies the requirements of *C. imicola* though this species occurs in highest numbers where there is also a grass cover, preferably short (Mellor & Pitzolis, 1979; Pajor, unpublished data, 1987).

Fresh cattle and buffalo dung will produce its 1st adult *C. bolitinos* after 8–10 days and can continue to yield for

TABLE 7 Ten characters used to separate *C. imicola* from *C. bolitinos* sp. nov.

C. imicola	*C. bolitinos*
Taxonomic	
♀— proximal margin of distal pale spot in cell R5 pointed	— this margin almost straight, transverse and ragged
— apex of vein M_2 broadly dark this preceded by a broad, pale preapical excision	— apex of vein M_2 pale or occasionally darkened on upper and lower margin; no pale preapical excision
— palp longer: 165,6–182,4 μm mean 176,1 μm (n=25)	— palp shorter: 132,0–165,6 μm mean 148,5 μm (n=25)
— 2nd palpal segment longer, 50,4–57,6 μm, mean 54,2 (n=25)	— 2nd palpal segment shorter, 39,6–49,2 μm, mean 44,5 μm (n=25)
— 3rd palpal segment longer, 40,8–51,6 μm, mean 46,8 μm (n=25)	— 3rd palpal segment shorter, 33,6–43,2 μm, mean 38,7 μm (n=25)
— PR 2,40–3,38 mean 2,86 (n=172)	— PR 1,86–2,72 mean 2,33 (n=52)
— P/H ratio >1: 1,01–1,22 mean 1,07 (n=20)	— P/H ratio <1: 0,71–0,94 mean 0,81 (n=20)
— antennal segments IV, XII–XIV longer (see Table 4)	— antennal segments IV, XII–XIV shorter (see Table 4)
♂— membrane of sternum 9 with 8–145 spiculae, mean 47 (n=50)	— membrane with 0–18 spiculae, mean 2,56 (n=50), 40 % have the membrane bare
Biological	
Larval habitat is the permanently moist grassed margins of streams, furrows and vleis especially where grass is kept short by grazing animals	Larval habitat exclusively the dung of large herbivores such as the African buffalo, blue wildebeest and cattle

a further 20 days (personal observations; G. J. Venter, unpublished data). This is, however, strongly dependent on the drying out of the dung which hastens or triggers pupation. Larval life is prolonged in dung which is brought in from the field and stored in containers in the laboratory, these pats being protected from such important extrinsic factors as the heating and drying rays of the sun and the working of dung beetles. An important intrinsic factor that almost totally inhibits either oviposition by adults or larval development is the souring and subsequent fermentation of dung from high-energy supplement-fed cattle that are rarely or never put out to pasture (personal observations; A. L. Dyce, 48 Queens rd, Asquith, N.S.W. 2077, Australia, personal communication, 1987). The factors that govern oviposition as well as increased or depressed emergence merit further investigation.

On irrigated rye-grass pastures an average of 200 adult *C. bolitinos* will emerge from a single cow pat (J. E. Randall, E. M. Nevill, unpublished data). In the wild or natural state the highest number of *C. bolitinos* yet reared was 512 adults from ½ of a very large *Syncerus caffer* pat collected on short, dry grass in the dry bed of the Timbavati river, Kruger National Park.

In light of the above, 4 studies on the larval habitats of Afrotropical *Culicoides* merit reappraisal. These are the papers on Kenyan *Culicoides* by Lubega & Khamala (1976) and Walker (1977), that on Nigerian *Culicoides* by Dipeolu & Ogunrinade (1977) and finally, the study on various Zimbabwean species (Braverman, 1978). Lubega & Khamala (1976) found the immatures of *C. imicola* 'in mud from edges of puddles, pools, lakes, rivers and streams, exposed or covered by growing vegetation, usually frequented by livestock for drinking water'. They also reared it from 'drying cowdung pats in open grassland'. Similarly, Walker (1977), in his study on the seasonal fluctuations of Kenyan *Culicoides*, reared 3 specimens of *C. pallidipennis* from 61 cow pats collected from 4 sampling sites. In Nigeria, Dipeolu & Ogunrinade (1977), conducting their studies at the research farm of the University of Ibadan, said that *C. imicola*, comprising 95,4 % of the total *Culicoides* reared, was dominant 'in an open dairy paddock containing mostly white Fulani cattle. The paddock was littered with cattle dung pats over which emergenc traps were placed'. In these 3 studies the rearing of *Culicoides imicola* from cow pats matches the larval habitat of *C. bolitinos* in South Africa. Though this niche may in those countries be filled by a species other than *C. bolitinos* it will quite likely not be *C. imicola*. In this regard it is relevant to note that the wing photograph published by Kitaoka, Kaneko & Shinonaga (1983) of a Nigerian specimen of *C. imicola* is in fact that of an undescribed species which has 2 prominent yellow, admedian vittae on the scutum (personal observations; S. Kitaoka, Mitaka, Tokyo 181, Japan, personal communication, 1986) these being absent in both *C. imicola* and *C. bolitinos*. Such taxonomic uncertainty renders the results from the above larval habitat studies imprecise.

The 4th study, that by Braverman on the larval habitats of Zimbabwean *Culicoides* has produced results only in partial agreement with South African studies. From '221 cow pats incubated in the laboratory which yielded 698 *Culicoides*, only 44 *C. imicola* were reared and they were confirmed by Dr M. Cornet to be true *C. imicola*'. Furthermore '*C. zuluensis, C. schultzei* grp and *C. onderstepoortensis* were present together with *C. gulbenkiani*' which 'was abundant (comprising 92 % of those reared) mainly in cow dung situated over damp soil' (Braverman, 1978). In South Africa the only species to be reared along with *C. bolitinos* from cow dung pats is *C. gulbenkiani*. However, *C. gulbenkiani* is often the only species reared from cow pats as it has larval habitat requirements subtlely different from that of *C. bolitinos* (Nevill *et al.*, 1988). *C. zuluensis, C. schultzei* grp. *C. onderstepoortensis* and most importantly, *C. imicola*, have never in South Africa been reared from dung pats as was reportedly found in Zimbabwe by Braverman (1978). He did, however, qualify these findings by adding that this was 'most probably because in several instances the cow dung was collected with the soil underneath which contained odd individuals of these species'. In larval habitat studies it is essential to record in detail whether the dung was collected from a stream margin along with mud and vegetation or whether it was taken in well irrigated, long-grassed pasture with some of the soil underneath. These 2 situations will, in the main, produce *Culicoides* species different to those found in discrete pats dropped on hard, bare or shortly grassed ground. A combination of these sites would explain the heterogenicity of the species reared by Braverman (1978).

CONCLUSION

The present study has shown that *C. bolitinos*, like *C. imicola*, is widespread in the Afrotropical region, and that it occurs throughout the Republic of South Africa. However, the larval habitat preference of *C. bolitinos* can lead to it being either rare or common but localized in its distribution. Of importance is that *C. bolitinos* is now recognized as a species being clearly separate from *C. imicola* with which it has been confused in the past.

Secondly, the intimate association with game animals such as the African buffalo and the blue wildebeest and with cattle, strongly implicates *C. bolitinos* as a vector of cattle viruses. For this reason, and also because it appears to be both the morphological and ecological equivalent of the Oriental-Australasian-eastern Palaearctic *C. brevitarsis*, *C. bolitinos* is deserving of detailed investigations into its biology about which too little is known.

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