

THE LOUSE FLY *LIPOPTENA PARADOXA* NEWSTEAD, 1907 (DIPTERA: HIPPOBOSCIDAE): DESCRIPTION OF ITS ADULT AND PUPARIUM AND BIOLOGY IN SOUTH AFRICA

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ABSTRACT

VISAGIE, ELIZE J., HORAK, I. G. & BOOMKER, J., 1992. The louse fly *Lipoptena paradoxa* Newstead, 1907 (Diptera: Hippoboscidae): description of its adult and puparium and biology in South Africa. *Onderstepoort Journal of Veterinary Research*, 59, 303–314 (1992)

Lipoptena paradoxa Newstead, 1907 is re-described using scanning electron microscopy and its puparium is described for the first time. The distribution of the fly is restricted to the eastern half of South Africa, generally at altitudes below 600 m. Its preferred hosts are all browsing antelope namely, bushbuck, nyala, kudu and common duikers. The largest numbers of flies were present on kudu in the Kruger National Park from July or August to January and large numbers were recovered from these animals' tails from November to January. Considerably more female than male flies were collected.

INTRODUCTION

Conventional descriptions of the adults of the louse fly, *Lipoptena paradoxa* Newstead, 1907 (Diptera: Hippoboscidae) have been published in Newstead, Dutton & Todd (1907), and by Ferris (1930), Bequaert (1940; 1942), Tendeiro (1951) and Maa (1963; 1965; 1969). No descriptions based on scanning electron microscopic examination of the fly have been published nor has the puparium been described. There are a number of rather incomplete descriptions of the exterior of the puparia of various other hippoboscid flies (Ferris & Cole, 1922; Ferris, 1923; Schuurmans-Stekhoven, 1926; Bequaert, 1953; Maa, 1969; Theodor, 1975), while Baker (1990) has given a detailed description of the external features of the puparium of *Lipoptena mazamae* Rondani, 1878.

The distribution of *L. paradoxa* is confined to sub-Saharan Africa where it has been recorded from Ethiopia, Ghana, Kenya, Burundi, Uganda, Congo, Zaïre, Tanzania, Angola, Malawi, Zambia, Mozambique, Zimbabwe, Botswana and South Africa (Bequaert, 1942; Haeselbarth, Segerman & Zumpt, 1966; Maa, 1968; 1969; Hutson & Oldroyd, 1980). Within the Republic of South Africa it has been recorded in Transvaal, Natal and the Cape Province (Bedford, 1926; Maa, 1969; Boomker, Du Plessis & Boomker, 1983; Horak, Keep, Spickett & Boomker, 1989; Horak, Boomker, Spickett & De Vos, 1992).

The fly has been recovered from roan antelope (*Hippotragus equinus*), oribi (*Ourebia oribi*), grysbok (*Rhaphicerus melanotis*), common duiker (*Sylvicapra grimmia*), impala (*Aepyceros melampus*), bushbuck (*Tragelaphus scriptus*), lesser kudu (*Tragelaphus imberbis*), nyala (*Tragelaphus angasii*), kudu (*Tragelaphus strepsiceros*), eland (*Taurotragus oryx*), common reedbuck (*Redunca arundinum*) and waterbuck (*Kobus ellipsiprymnus*) (Bedford, 1926; Bequaert, 1940, 1942; Haeselbarth *et al.*, 1966; Maa, 1968; 1969; Boomker *et al.*, 1983; Horak *et al.*, 1989; 1992).

L. paradoxa has an interesting life cycle in that the 3 larval instars develop *in utero* and the ensuing prepupa is deposited on the host animal. The prepupa falls to the ground and pupates. The imago that hatches is winged, but the wings break off once a host is found, the fly thus becoming confined to the host.

In this paper important taxonomic features of *L. paradoxa* are illustrated by means of scanning electron photomicrographs and the morphology of the puparium is described for the first time. The fly's geographic distribution and host-preference within the Republic of South Africa, which had hitherto been based on collections from individual animals, are now more clearly defined by surveys conducted in various regions on numerous hosts. The seasonal abundance of *L. paradoxa* on kudu in the Kruger National Park, eastern Transvaal Lowveld is discussed, as well as the ratio of male to female flies on these and other antelopes.

TAXONOMY

MATERIALS AND METHODS

Scanning electron microscopy (SEM)

Adult flies

Both fresh material and material stored in alcohol were used for SEM purposes. Dirt on specimens was removed with KOH or NaHPCl in an ultrasonic cleaner, or carefully brushed off with acetone before drying. Fresh specimens were frozen for 24 h or more, whereafter relevant structures were dissected out under a stereoscopic microscope and freeze-dried for 24 h. Specimens stored in alcohol were dehydrated in graded ethyl alcohol and completely desiccated in an oven at 35 °C. All specimens were stored in a desiccator until mounted on stubs using a chloroform-based adhesive. Small specimens were mounted with colourless nail varnish. Specimens were sputter-coated with gold and examined with an ISI 100 scanning electron microscope.

Puparia

Pupae were obtained from flies collected from immobilised bushbuck and kept in an incubator at 25 °C and 30 % RH until eclosion. The empty puparia were cut in half, mounted and sputter-coated as described for the adult flies.

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***Lipoptena paradoxa* Newstead, 1907**

Lipoptena paradoxa Newstead, 1907: 91;

Echestypus paradoxus Bruce, Hammerton & Bruce, 1911: 228;

Eschetypus paradoxus Curson, 1928: 182, laps cal.;

Echestypus parvipalpis Speiser, 1907: 3, 5; Falcoz, 1929: 52.

The institutions from which dry, or alcohol preserved, or slide-mounted specimens were obtained for study and comparison are listed below:

- BMNH — British Museum (Natural History)
- KGP — Kalahari Gemsbok National Park
- KNP — Kruger National Park
- NMSA — Natal Museum, South Africa
- SAMC — South African Museum, Cape Town
- SANC — South African National Collection of Insects
- VRIO — Veterinary Research Institute, Onderstepoort
- ZMHB — Museum für Naturkunde der Humboldt Universität zu Berlin

There are 2 syntype females. One of these is preserved in 70 % ethyl alcohol and the other is mounted under a coverslip on a glass slide. Information concerning these flies is given verbatim from the labels. Lines on the labels are separated by a slash (/), and different labels, from the top of the pin to the bottom, by a double slash (//).

Cotype: female; *Lipoptena paradoxa* / Newst. Type lot / On antelope / Kasongo / 28-1-05 Dutton & Todd // Kasongo / Congo Free State / 28-1-1905 / Drs Dutton & Todd / Recd. fr. R. Newstead // On antelope // *Lipoptena* / Co / type / *paradoxa* / Newstead // BMNH.

We hereby designate the alcohol preserved specimen as the lectotype and the other fly becomes a paralectotype.

Material examined

The material listed below was collected in South Africa by the authors and is deposited at the National Museum, Bloemfontein, Republic of South Africa.

115 specimens, Pafuri (23° 27' S, 31° 19' E), KNP, Transvaal (Tvl), ex kudu, 1981; 5 ♂, 5 ♀, Pafuri, KNP, ex bushbuck, 6 Oct. 1981; 5 ♂, 5 ♀, Pafuri, KNP, ex nyala, 6 Oct. 1981; 198 specimens, Satara (24° 23' S, 31° 47' E), KNP, ex kudu 8 Oct. 1982; 5 ♂, 5 ♀, Riekerks Laager (24° 30' S, 28° 29' E), Tvl, ex common duiker, 5 Nov. 1980; 1 ♂, 1 ♀, Skukuza (24° 58' S, 31° 36' E), KNP, ex kudu, 8 Jan. 1990; 1 ♂, 1 ♀, Skukuza (24° 58' S, 31° 36' E), KNP, ex kudu, 8 Jan. 1990; 1 ♂, 1 ♀, Skukuza, KNP, ex impala, 23 Apr. 1980; 1 ♀, Skukuza, KNP, ex lion, 14 Oct. 1986; 69 ♂, 94 ♀, Skukuza, KNP, ex bushbuck, 10 Jan. 1990; 13 ♂, 40 ♀, Skukuza, KNP, ex bushbuck, 6 Mar. 1990; 147 ♂, 282 ♀, Skukuza, KNP, ex bushbuck, 8 Mar. 1990; 166 ♂, 401 ♀, Skukuza, KNP, ex bushbuck, 4 Apr. 1990; 2 ♀, Kruger Gate (24° 59' S, 31° 29' E), KNP, ex cheetah, 3 July 1988; 2225 specimens, southern

KNP (between 25° 06'–25° 21' S and 31° 27'–31° 36' E), ex kudu, 1981–1983; 1 ♂, 2 ♀, Mbyamiti (25° 15' S, 31° 36' E), KNP, ex impala, 21 Jan. 1981; 5 ♂, 5 ♀, Malelane (25° 28' S, 31° 31' E), KNP, ex kudu, 7 Dec. 1981; 5 ♂, 5 ♀, Umfolozi (between 28° 12'–28° 21' S and 31° 42'–31° 59' E), Natal, ex nyala, 18 Mar. 1983; 1 ♂, Charters Creek (28° 14' S, 32° 25' E), Natal, ex red duiker, 21 Mar. 1983; 5 ♂, 5 ♀, Charters Creek, Natal, ex bushbuck, 22 Mar. 1983; 5 ♂, 5 ♀, Weza State Forest (30° 35' S, 29° 45' E), Natal, ex bushbuck, April 1984; 5 ♂, 5 ♀, Andries Vosloo Kudu Reserve (33° 07' S, 26° 40' E), Cape Province, ex kudu, 21 Oct. 1985; 3 ♂, Southwell (33° 32' S, 26° 41' E), Cape Province, ex caracal, January 1986.

Material borrowed from other institutions:

1 ♀, Monze (16° 16' S, 27° 29' E), Northern Rhodesia (Zambia), ex bushbuck, 1959 (SAMC); 1 ♀, Chipangali (locality uncertain), Zambia, ex common duiker, 13 May 1963 (NMSA); 1 ♂, 4 ♀, Beira (19° 50' S, 34° 52' E), Mozambique, ex oribi, 15 Nov. 1941 (SAMC); 1 ♀, Pafuri, KNP, Tvl, ex nyala, date not given (VRIO); 1 ♂, 5 ♀, Nylsvley (24° 29' S, 28° 42' E), Tvl, ex kudu, 11 Sept. 1980 (VRIO); 11 ♂, 17 ♀, Skukuza, KNP, ex bushbuck, 15 Nov. 1982 (KNP); 10 ♂, 5 ♀, Skukuza, KNP, ex bushbuck, 18 Nov. 1982 (KNP); 1 ♂, Skukuza, KNP, ex impala, 2 June 1984 (KNP); 3 ♂, 5 ♀, Mbyamiti, KNP, ex kudu, 13 Aug. 1984 (KNP); 1 ♂, 4 ♀, Berg en Dal (25° 26' S, 31° 26' E), KNP, ex kudu, 31 Oct. 1986 (KNP); 2 ♂, 2 ♀, Barberton (25° 48' S, 31° 03' E), Tvl, host not given, 20 Aug. 1924 (SANC); 2 ♂, 1 ♀, Barberton, Tvl, ex bushbuck, 9 Oct. 1919 (SANC); 2 ♂, Ndumu (between 26° 50'–26° 56' S and 32° 09'–32° 21' E), Natal, host not given, 8 Oct. 1970 (VRIO); 7 specimens, Zululand (locality not supplied), host not given, 1922 (SANC); 1 ♂, Umfolozi, Natal, ex common duiker, 26 Oct. 1965 (NMSA); 1 ♀, Umfolozi, Natal, ex nyala, 26 Oct. 1965 (NMSA); 4 ♀, Bucklands* (locality uncertain), Cape Province, ex kudu, 21 Aug. 1976 (SAMC); 1 ♀, Bucklands (locality uncertain), Cape Province, ex kudu, 10 Oct. 1976 (SAMC); 2 ♀, Bucklands (locality uncertain), Cape Province, ex kudu, 29 Mar. 1977 (SAMC); 1 ♂, Bucklands (locality uncertain), Cape Province, ex kudu, 16 June 1977 (SAM); 6 ♀, Harvest Vale (locality uncertain), Cape Province, host not given, 3 May 1910 (SANC).

DESCRIPTION OF IMAGO

Female

Length (head and thorax): 1.87–2.1 mm.

Head: width 1.0–1.1 mm, extended behind eyes; mediovertex 0.18–0.30 mm × 0.15–0.22 mm, nearly as long as or slightly longer than wide, about as long as frontoclypeus and slightly longer than postvertex (0.12–0.20 mm). Clypeus fused with frons, median longitudinal furrow rather short, ending in a circular pit; pretilinal area distinct but short; inner orbit

* This farm probably adjoins the Andries Vosloo Kudu Reserve from which some of our own material was collected

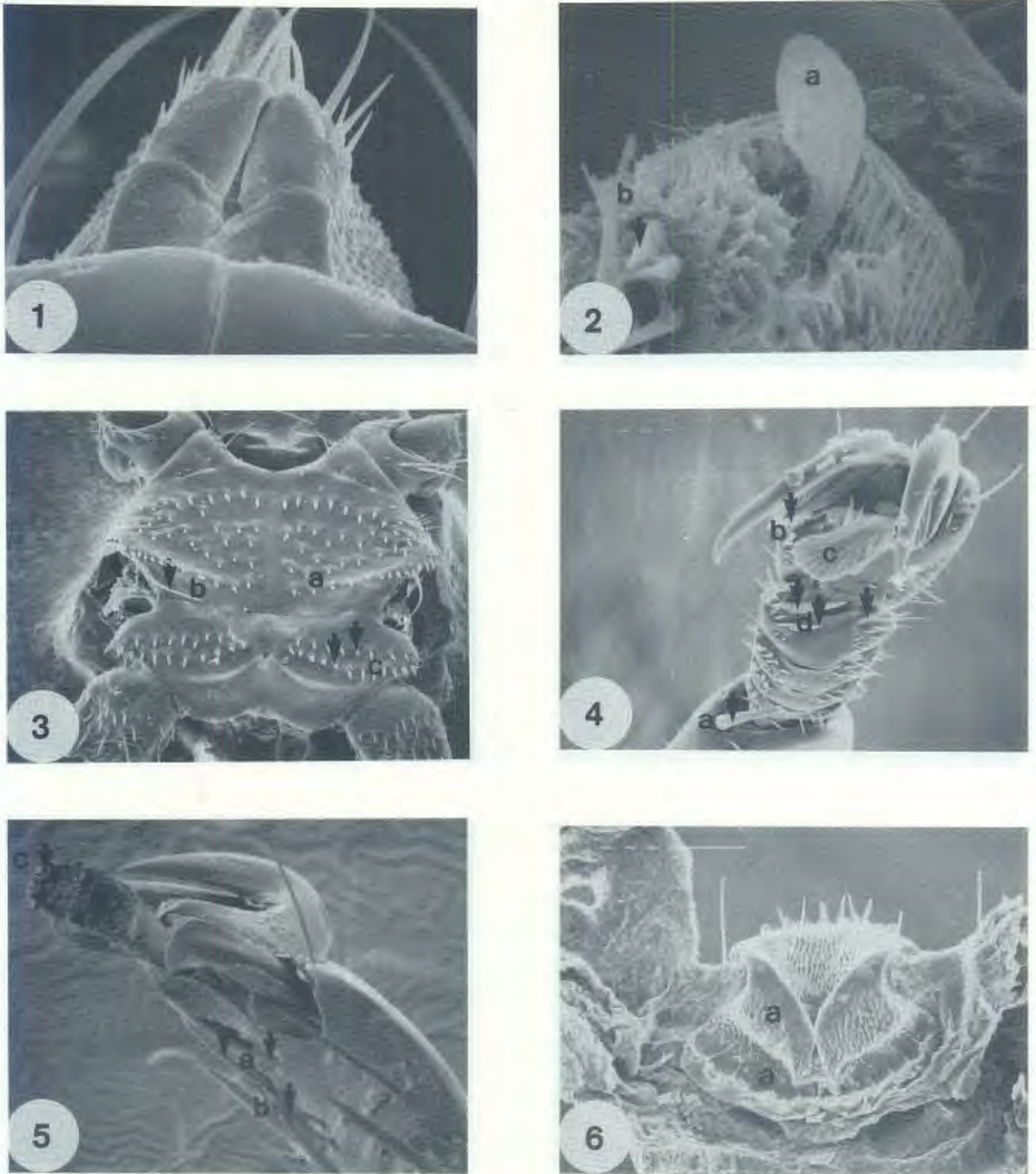


FIG. 1-6 *Lipoptena paradoxa* (female fly)

- (1) Extended palpi with setae at the apex
- (2) Tip of antenna with arista (a) and setae (b)
- (3) Ventral view of the thorax showing the mesosternum with 4 or 5 rows of short spines (a) and 1 pair of posterolateral bristles (b). The metabasisternum has spines in 2 regular rows (c)
- (4) First tibia with an apical spur (a), vestigial anterior pulvillus (b), well-developed posterior pulvillus (c), and the 4th and 5th tarsal segments with 1 large and 2 small spines (d)
- (5) Third tarsus with 2 large plantar spines (a), a small ventral spine (b), and the long and well developed posterior pulvillus (c)
- (6) Postgenital plate (a) after removal of the pregenital plate

(Scale: — — — — — 100 μ m; — — — — — 10 μ m; — — — — — 0,1 μ m)

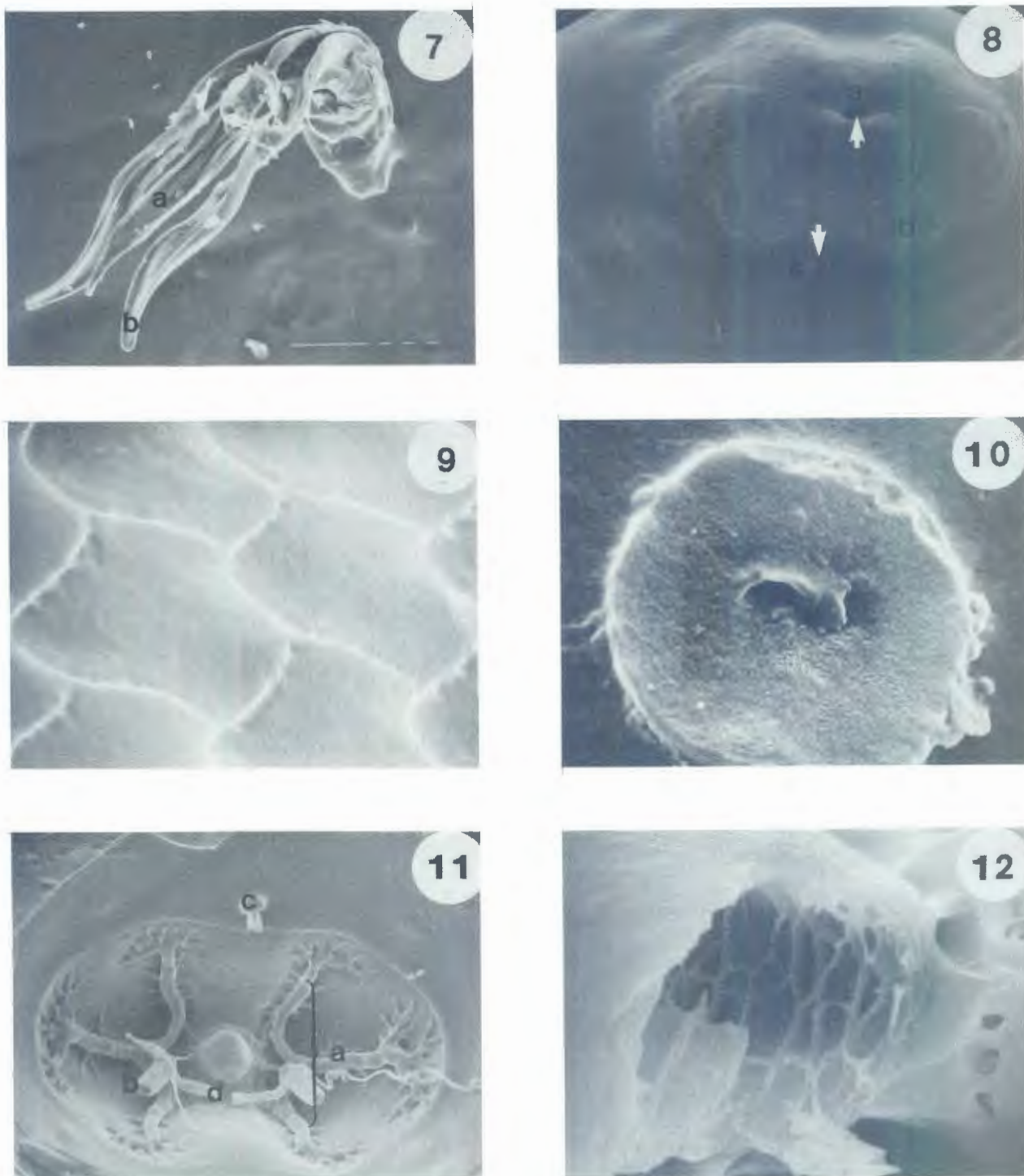


FIG. 7–12 *Lipoptena paradoxa*

- (7) Male genitalia showing the aedeagus (a) and the parameres (b)
- (8) Posterior end of the puparium with central depression and tracheal openings (a), spiracles (b) and the anal opening (c)
- (9) Cuticular pattern between the spiracles on the puparium
- (10) Spiracular pore on puparium with small central opening surrounded by a circular plate
- (11) Interior of the posterior part of the puparium with 3 large tracheal branches on either side (a), each with smaller radiating branches. A large branch (b) with a smaller side branch (d) extends into the body. The apical pit is visible at (c)
- (12) Supporting cuticular meshwork in a tracheal branch of the puparium

(Scale: — — — — — 100 μm ; — — — — — 10 μm ; — — — — — 0,1 μm)

0,15–0,20 mm, narrower than eye (0,28–0,32 mm), with 1 long vertical bristle; 2 short orbital bristles and 5 fine, very short orbital setae in an inner curved row. Anterior margin of frontoclypeus, between longitudinal furrow and apex of antennal pit, bearing 6 small setae; 5 short setae and 1 long bristle ventrally, next to palpi; 2 long bristles and 4 short setae below eye. Outer margin of eye bears a series of fine spines and a few scattered short fine setae are present on the postgena. A few setae on the gula at the concave margin of prosternal lobes. Postvertex short and very wide, flattened semi-elliptically. Rudimentary or vestigial palpi, only barely or not at all visible beyond anterior margin of frontoclypeus from above. However, SEM of a newly hatched fly shows extended palpi each with 7 setae on the apex (Fig. 1). Antennae short, sub-globular and recessed in antennal pits, which are surrounded by a continuous rim. Fig. 2 provides a more detailed picture of the antennal setae and arista.

Thorax: Prothorax: Pronotum transverse, anterior margin concave and posterior margin angularly convex. Promesonotal suture clearly visible.

Mesothorax: median notal suture very faint, no intrascutal grooves; transverse mesonotal suture broadly interrupted medially; posthumeral suture well-demarcated. Large mesothoracic spiracle at posterolateral edge of humeral callosity. According to Bequaert (1942) mesonotal chaetotaxy of type specimen consists of 6 acrostichals in a curved row, some distance from the middle line. However, they are asymmetrically placed and may vary from 4 to 7 on either side. Three humerals and 2 laterocentrals close to notopleuron, and 2 rows each of 4 or 5 notopleurals, those of posterior row very long; usually 4 (rarely 3 or 5) scutellars in 2 pairs, inner pair very long; 3 or 4 postalar bristles, inner pair very long; 1 pair of very long posterior dorsocentral bristles; prosternal lobes with 2–3 ventral spines and 1 bristle on anterior inner margin. Mesosternum with a pair of long posterolateral bristles, and numerous relatively short spines, arranged more or less in 4–5 regular transverse rows, of which those of the 1st row are the largest.

Metathorax: Metabasisternum with 2 regular rows of spines, length and robustness similar to those of the last 3 rows on the mesosternum (Fig. 3).

Legs: Anterior coxa enlarged bearing oblique marginal row of setae dorsally, 1 of these very long; ventroposteriorly a row of 4 long setae; femora 1–3 with 3, 3 and 5 major dorsal bristles respectively; 1 anterior bristle on femora 1 and 3; tibiae 1–3 with 1, 2 and 3 apical spurs respectively (Fig. 4); tibia 3 with 3 major ventral bristles (plus a few minor ones), which are slightly longer but less robust than longest apical spur; tarsi 1–2 without ventral spines on segments 1–3, but with 1 major and 2 very small ventral spines on each of segments 4 and 5; tarsus 3 with 2, 1 and 1 small anterior spines on under-sides of segments 1–3 respectively, 2 major plantar spines and 1 minor ventral spine on each under-side of segments 4 and 5 (Fig. 5); anterior pulvilli of all legs vestigial, posterior pulvilli well-developed (Fig. 4); claws slightly asymmetrical.

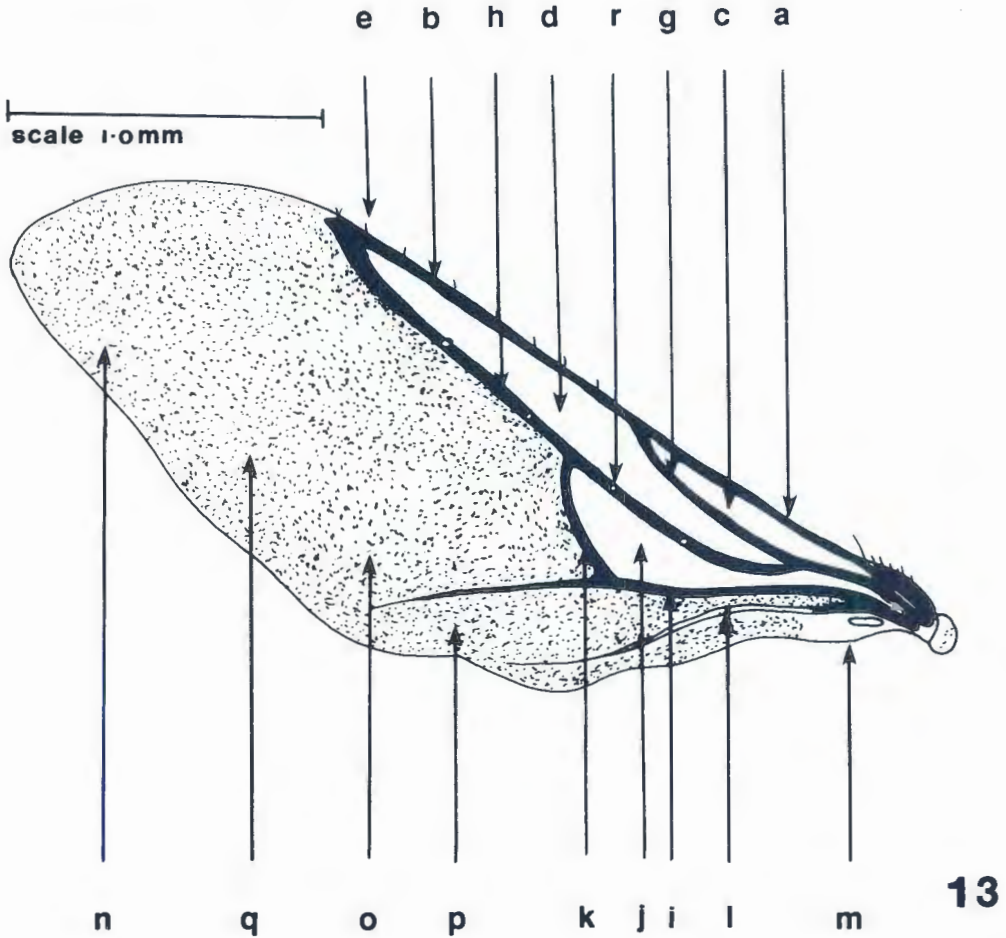
Wings: Length: 2,96 mm. Wing venation (Fig. 13) similar to that of *Lipoptena cervi* Linnaeus 1758 (Bequaert, 1940). Only 3 well-developed longitudinal veins are present, apparently the 1st (R₁), 3rd (R₄ & 5) and 5th (M₃ & C₂); the 6th (2nd An) is incomplete; other veins indicated by concave lines; only 1 cross-vein, between assumed 3rd and 5th longitudinals, and therefore, according to Bequaert (1940), probably a fusion of the anterior basal cross-vein (M₃), anterior cross-vein (r–m) and portion of 4th longitudinal vein (M₁ & M₂); the 3rd longitudinal ends in the tip of the costa at an acute angle without a knob-like swelling; costa thickened only at extreme base and between tips of 1st and 3rd longitudinals. Four sensoria on 3rd (R₄+5) longitudinal vein. The thickened basal costa (CO₁) has 1 long and a few short setae. Apical costa (CO₂) has 8 setulae. Dorsal surface of basal cell and 2nd marginal cell free of microtrichia (Fig. 13). Microtrichia ventrally on basal cell and apical angle of 2nd marginal cell (between CO₂ and R₄+5) (Fig. 14); dorsal and ventral cells 3r, 1m and 2m as well as the axillary cell bear microtrichia. Alula rudimentary; no closed anal cell; haltere well-developed.

Abdomen: basal dorsal sclerotized pleurite I large, transverse, with a marginal row of long bristles and angular row of shorter setae on disc; pleurites II to V well demarcated and lightly sclerotized with a few uniformly spaced setae; 5 median tergal plates, all short and transverse, gradually increasing in size from 1st to 3rd, 4th smaller; 1st and 2nd bear a medially interrupted transverse row of 4 to 6 setae; 3rd and 4th with 1 or 2 setae in each corner; 5th divided into 2 sclerites, each bearing 2 setae; remainder of dorsum usually extensively sclerotized, with traces of segmentation, and a few setae towards edges. Basal ventral sclerite broadly emarginate at apex, somewhat more shallowly than in other species, with broader lobes to the crescent; many sturdy setae along hind margin and a few on disc, 2 of the very long setae are placed near tip of each lobe; ventral portion of pleurites well-demarcated; abdominal spiracles small, more or less sclerotized, with fairly uniformly spaced setae arising from thickened bases, spiracles VI and VII almost enclosed in 4th and 5th tergal plates.

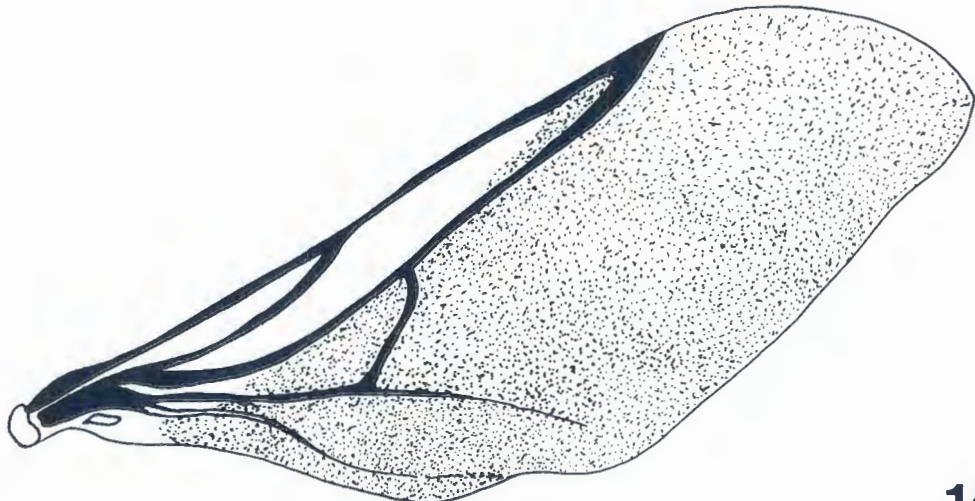
Genitalia: Median pregenital plate elongate, weakly sclerotized, with 3–5 setae in a transverse series on posterior margin, outer pair usually longer and more robust; lateral pre-genital plate entirely wanting; supra-anal plate with very fine and rather robust small setae. Fig. 6 illustrates post-genital plate after removal of pre-genital plate. Infra-anal plate with rather dense posterior setae, about as long as those on supra-anal plate and as stout as those on disc of abdominal venter.

Male

Length (head and thorax): 1,65–1,80 mm. Similar to ♀ in structure and chaetotaxy. Only 4 median tergal plates, corresponding to T₁–4 of female, somewhat larger than in that sex, particularly the 1st and 2nd. Post-genital plate narrow with slightly broader anterior end (Maa, 1965). Parameres (Fig. 7) long, slender, straight, sharply pointed and punc-



13



14

FIG. 13 and 14 *Lipoptena paradoxa*

(13) Wing (dorsal) venation and distribution of microtrichia
 (a) basicosta CO1; (b) apical costa CO2; (c) 1st marginal cell; (d) 2nd marginal cell; (e) setulae; (g) R1;
 (h) R4+5; (i) M3+C1; (j) 1 + 2nd basal cell; (k) M3 + r-m cross-vein; (l) 2nd An; (m) alula—rudimentary;
 (n) 3r cell; (o) 1m cell; (p) 2m cell; (q) microtrichia; (r) sensoria

(14) Distribution of microtrichia on ventral aspect of wing

tate; aedeagus narrow, sharply pointed cone of which the dorsolateral surfaces are covered with small setae.

DESCRIPTION OF PUPARIUM

The small, black, oval puparium of *L. paradoxa* is ca 2,2 mm long and ca 1,6 mm wide. Small anterior buccal opening with a slit-like extension. Circular seam of anterior cap, through which adult escapes, runs across and around surface of puparium, while the semicircular seam passes over the top to the sides and ends in circular seam.

The surface of the puparium is smooth and shiny with an indistinct polygonal pattern. The protruding posterior end of the puparium bears the tracheo-spiracular system. The spiracular pores radiate laterally from a central depression at the posterior end of the puparium, which contains 2 tracheal openings, and form 3 areas with a distinct pentagonal pattern on either side (Fig. 8 and 9). Each spiracular pore consists of a circular plate with a granular appearance and a small central opening (Fig. 10). Ventrally, just anterior to the posterior plate, there is a circular opening (the anus) with a raised cuticular rim described by Maa (1963, 1969) and Baker (1990) as the ventro-apical pit (Fig. 8). Three internal tracheal branches are attached to tracheal openings in the pupal wall on either side of the central depression (Fig. 11). These have shorter secondary branches extending to spiracular openings (Fig. 11). A larger tracheal branch with a smaller side branch extends into body of the pupa on either side (Fig. 11). Internal surface of trachea honeycombed with cuticular thickenings (Fig. 12).

DISCUSSION

Imago

Newstead in his original description of the fly, published in Newstead *et al.* (1907), noted the almost entire absence of external mouthparts, with the only indication of these organs being a minute truncated cone. Ferris (1930), however, stated that the palpi, while extremely small and in some individuals retracted into the head, are clearly recognisable and apparently constitute the cone mentioned above. In our studies, SEM of a newly hatched fly shows extended palpi attached to the head by a membranous structure giving the impression that the palpi are 2-segmented (Fig. 1).

No mention is made of the spines and bristles on the ventral aspect of the thorax by Newstead (Newstead *et al.*, 1907), but Ferris (1930) remarks that the thorax is ventrally beset with rows of tubercle-like setae. Maa (1965) describes the chaetotaxy of the ventral abdomen in greater detail and our findings add to his description.

Although Newstead did not describe the tarsus and claw of *L. paradoxa*, he has illustrated these structures, indicating a single pulvillus (Newstead *et al.*, 1907). Ferris (1930) has, however, illustrated the last tarsal segment as bearing 2 equal-sized pulvilli without commenting upon this in the text. Maa (1956) states that the anterior pulvilli are all vestigial, a finding with which we concur (Fig. 4).

No previous description of the wings of this fly has been published. We obtained newly hatched, winged specimens for this purpose from pupae incubated in the laboratory and based our nomenclature of the wing venation on that supplied by Bequaert (1940; 1942) and Maa (1963).

Puparium

The size and shape of the puparium of *L. paradoxa* is similar to that of *L. mazamae*. Baker (1990) gives a detailed description of the hexagonal pattern, with spherical cuticular extensions, which encircles the posterior end of the puparium of *L. mazamae*, but this is not mentioned in the case of the closely related *Lipoptena depressa* Say, 1823. This pattern does not occur in *L. paradoxa* (Fig. 9).

Baker (1990) also observed that the remainder of the puparial surface of *L. mazamae* has a polygonal pattern with distinct pits. The surface of the puparium of *L. paradoxa* is covered with a mesh of microscopic lines without pits. More research is needed to determine whether the differences in surface pattern and sculpturing are taxonomically important.

Anteriorly the ventral slit-like extension of the buccal opening of *L. paradoxa* is much larger and folded more deeply than that of *L. mazamae*. Posteriorly the number and arrangement of the spiracles also differ. We consider the large opening below the posterior end of the puparium (Fig. 11), which is referred to as the ventro-apical pit (Maa, 1963, 1969; Baker, 1990), to be the anal opening and it seems to be similar to that of *L. mazamae*. Details of the anal opening, and internal and external structure of the puparium of *L. paradoxa* are given in Fig. 8 and 11.

Previous descriptions of the tracheal branches of *Lipoptena* do not mention the 2 larger tracheal branches with 2 smaller side branches which extend forward into the body of the pupa (Fig. 11). The internal and external structure of the spiracular pores on the posterior end of the puparium also requires further investigation.

BIOLOGY

METHODS, RESULTS AND DISCUSSION

Geographic distribution

This was ascertained from the collection localities of specimens lent to us for taxonomic study and those we collected ourselves during surveys of ectoparasites of various hosts (Boomker *et al.*, 1983; Horak *et al.*, 1989; 1992).

The geographic distribution of *L. paradoxa* within the Republic of South Africa is depicted in Fig. 15.

The fly is present in the eastern half of the country and then particularly in those regions where there are woodland, thickets or scrub of sufficient height to provide shelter for the hosts. It occurs at altitudes from a few metres to 2 000 m above sea level. Most collections, however, were made at altitudes below 600 m. The eastern regions of South Africa lie within the summer rainfall region of this country. With the possible exception of the south-western Cape

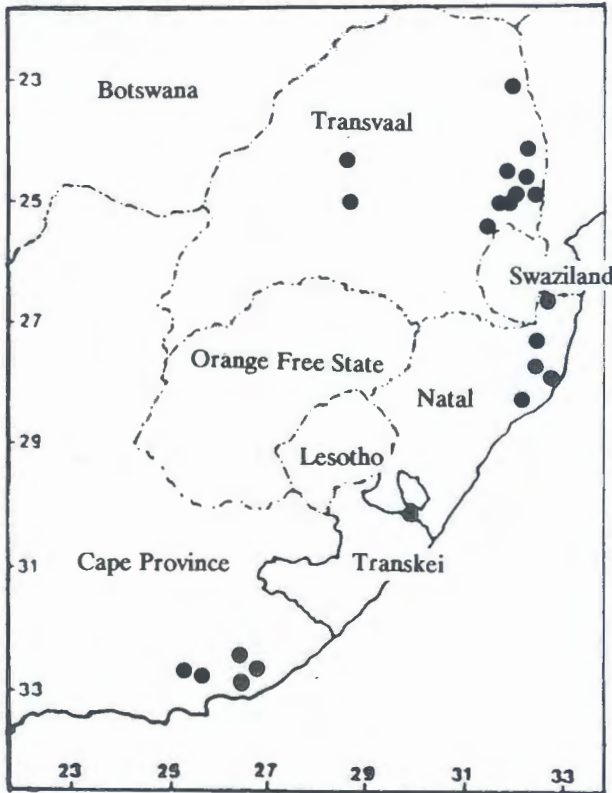


FIG. 15 The geographic distribution of *Lipoptena paradoxa* within the Republic of South Africa

Province, which has a mediterranean climate, the eastern half of the country is moister than the west.

The preferred hosts of the fly all prefer savanna woodland or thickets and generally avoid open country (Smithers, 1983). Thus within its distribution range *L. paradoxa* is restricted to localities in which its preferred hosts occur and hence in which woodland or thickets predominate.

Hosts

Host preference was determined from animals we have examined within the distribution range of the fly during various surveys of ectoparasites, some of which have been published (Boomker *et al.*, 1983; Horak, Keep, Flamand & Boomker, 1988; Horak *et al.*, 1989; 1992). The species and numbers of animals examined are listed in Table 1.

Of all the species examined only those from which *L. paradoxa* was recovered are listed in Table 2. The regions in which these hosts were examined and the total numbers of flies collected are also given in this table.

Bushbuck, nyala, kudus and possibly common duikers are the preferred hosts. Twelve of the 16 common duikers examined in the central Transvaal were infested, but not 1 of the 13 seen in south-eastern Natal.

The preferred hosts are all browsers and consequently are found in or near woodland or thickets where browse is plentiful (Smithers, 1983). Although common duikers may be considered preferred

TABLE 1 Birds and mammals examined for ectoparasites, including *Lipoptena paradoxa*, at various localities in South Africa within the distribution range of the fly. The preferred hosts of *L. paradoxa* are indicated in bold type

Species	Common name	Total No. examined
Birds		
<i>Numida meleagris</i>	Helmeted guineafowl	194
Mammals		
<i>Lepus saxatilis</i>	Scrub hare	312
<i>Crocuta crocuta</i>	Spotted hyaena	2
<i>Acinonyx jubatus</i>	Cheetah	2
<i>Panthera pardus</i>	Leopard	3
<i>Panthera leo</i>	Lion	5
<i>Felis caracal</i>	Caracal	22
<i>Lycaon pictus</i>	Wild dog	1
<i>Canis adustus</i>	Side-striped jackal	1
<i>Equus burchelli</i>	Burchell's zebra	33
<i>Potamochoerus porcus</i>	Bushpig	8
<i>Phacochoerus aethiopicus</i>	Warthog	68
<i>Giraffa camelopardalis</i>	Giraffe	2
<i>Connochaetes taurinus</i>	Blue wildebeest	47
<i>Cephalophus natalensis</i>	Red duiker	23
<i>Sylvicapra grimmia</i>	Common duiker	29
<i>Aepyceros melampus</i>	Impala	140
<i>Capra hircus</i>	Domestic goat (Angora)	48
<i>Ovis aries</i>	Domestic sheep (Dorper)	48
<i>Bos sp.</i>	Domestic cattle	46
<i>Syncerus caffer</i>	Buffalo	4
<i>Tragelaphus strepsiceros</i>	Kudu	133
<i>Tragelaphus angasii</i>	Nyala	9
<i>Tragelaphus scriptus</i>	Bushbuck	26
<i>Taurotragus oryx</i>	Eland	3
<i>Redunca arundinum</i>	Reedbuck	27

hosts, where they and bushbuck were shot in the same habitat in the Weza State Forest, south-eastern Natal, not 1 of the 13 duikers was infested, while 6 of the 13 bushbuck were (Horak *et al.*, 1989; Table 2). All the bushbuck examined at other localities were infested and harboured considerably larger individual burdens than any of the animals shot in the Weza Forest.

All other animal species we found to be infested harboured very low individual burdens. Where fairly large numbers had been examined, as in the case of impala, red duikers and caracals only a small percentage of hosts was infested. We cannot comment on the host status of roan antelope, grysbok, oribi and waterbuck listed as hosts by Haeselbarth *et al.* (1966) and Maa (1969). We have either not examined these animals or have not examined them within the distribution range of the fly. Although Haeselbarth *et al.* (1966) list common reedbuck as a host not 1 of the 27 animals we examined was infested.

Study area for biology on kudus

This has been described by Boomker, Horak & De Vos (1989). In summary the site is situated in the southern part of the Kruger National Park between latitudes 25° 06'–25° 21' S and longitudes 31° 27'–31° 36' E and an altitudinal range from 200–350 m. The vegetation is classified as Lowveld (Acocks, 1988). The days are warm to very hot in summer and mild in winter and frost occurs occasionally. Rainfall varies from 600–700 mm per annum and usually falls in summer.

TABLE 2 Hosts in various regions of South Africa from which the authors have collected *Lipoptena paradoxa*

Host species	No. examined	No. infested	Total number of flies recovered
North-eastern Transvaal Lowveld			
Impala	4	0	0
Kudu	2	2	501
Nyala	2	2	314
Bushbuck	3	3	559
Eastern Transvaal Lowveld			
Cheetah	2	1	2
Lion	5	1	1
Impala	134	3	6
Kudu	97	96	5 082
Bushbuck	8	8	2 768
Eland	2	1	8
Central Transvaal			
Common duiker	16	12	277
North-eastern Natal			
Red duiker	23	1	2
Impala	2	0	0
Nyala	9	9	635
Bushbuck	2	2	564
South-eastern Natal			
Common duiker	13	0	0
Bushbuck	13	6	156
South-eastern Cape Province			
Caracal	22	1	3
Kudu	34	29	514
Eland	1	0	0

Survey animals

Each month from April 1981 to March 1983, 4 kudus were shot in the study area. At each occasion an attempt was made to obtain 1 adult male, 1 adult female, 1 young adult male and 1 juvenile or calf of either sex. The animals were aged according to the criteria described by Simpson (1971). Collections were made not less than 3 weeks or more than 5 weeks apart. A total of 96 kudus were shot but only 95 were examined as the material collected from 1 had been inadequately preserved. For statistical reasons, the animals were grouped, according to age, into calves, 0–12 months old (age group 1), juveniles, 13–24 months old (age group 2), young adults, 25–48 months old (age group 3) and prime or old adults, 49 months and older (age group 4) (Boomker *et al.*, 1989).

Four bushbuck were chemically immobilised in the Skukuza region of the KNP and live flies for pupal studies were collected from them.

Parasite recovery

The carcasses of the kudus were transported to the laboratory at Skukuza where they were processed for parasite recovery. The carcass of each animal was skinned and half the skin of the head and half the skin of the neck, body and upper legs, the whole skin of the tail, and 1 lower front leg and lower back leg with skin attached were placed

separately in plastic bags. A tick-detaching agent [Triatix; Coopers SA (Pty) Ltd] was added to the skins in the bags and these were stored overnight. The following morning the skins were thoroughly scrubbed with brushes with 40 mm long steel bristles and washed. The tick-detaching agent remaining in the plastic bags and the material obtained from scrubbing and washing the skins were sieved over sieves with 0.15 mm apertures. The residues in the sieves were collected and preserved separately in 10% formalin.

Representative samples of the material collected were examined under a stereoscopic microscope for the presence of lice, ticks and louse flies. The remainder of the material was examined macroscopically for adult ticks and louse flies. Only the data pertaining to the louse flies are reported here, those obtained for the lice and ticks have been published by Horak *et al.* (1992). The kudus were also examined for internal parasites and the findings published (Boomker *et al.*, 1989).

Observations on flies

The seasonal abundance of the flies on the kudus during the 2 years of the survey is illustrated in Fig. 16. The largest numbers of flies were present on the kudus from August 1981 to January 1982 and from July 1982 to January 1983. Large numbers of flies were recovered from the tails of the kudus from November to January during both years of the survey.

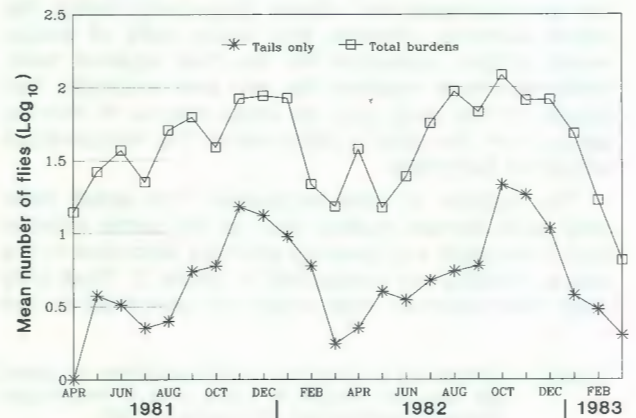


FIG. 16 The seasonal abundance of *Lipoptena paradoxa* on kudus in the southern region of the Kruger National Park

The pattern of abundance on the kudus could be due to the seasonal preference of the flies or the behaviour of the kudus. If it is due to the former, it would indicate that large numbers of flies hatched in mid-winter and early spring after prolonged pupal periods and infested the kudus. Since hippoboscids produce only a single mature 3rd instar larva at a time, with perhaps several days between successive larvae, it implies that each female fly would have to survive for several weeks or months to produce sufficient larvae to ensure the survival of the species. These flies and their offspring, which emerged after shorter pupal periods during summer,

would then be responsible for the 5 to 6 month period of peak abundance on the kudu.

If the pattern of abundance was caused by the behaviour of the kudu this would presuppose that kudu frequent habitat that is favourable for the survival of pupae from July or August to January. Such habitat would be dense riverine scrub and bush, the preferred habitat of bushbuck, or wooded slopes of hills and in valleys, where kudu tend to shelter during midday. The bushbuck immobilised during March and April 1990 and a bushbuck killed in a car accident in the Park during June 1982 (months of low *L. paradoxa* abundance on kudu), harboured considerably more flies than kudu, even during the periods of peak abundance on the latter animals. In addition 2 kudu shot during July 1980 in the Skukuza area, where the vegetation is much denser than in the study area, also harboured large numbers of louse flies (184 and 282). This seems to indicate that the pattern of abundance on kudu in the study area could be due to the antelopes' seasonal habitat choice within that region rather than the seasonal preference of the flies.

The large numbers of flies found on the tails of the kudu from November to January could be an attempt to escape grooming activities of the host during a period of peak abundance. Evans (1950) has described seasonal differences in the distribution of keds (*Melophagus ovinus*) in the fleece of various body regions of sheep. Amongst the preferred hosts of the louse flies, kudu have the shortest and sparsest hair cover. Especially during the warm summer months the bushy tails of kudu would afford protection for the flies against heat, firstly as cover against the sun and secondly, because of the long hair, an ideal means of moving away from the host's skin where the temperature would be fairly high.

The number of flies recovered from adult male and adult female kudu shot in the same months and from adult and juvenile animals also shot in the same months are compared in Table 3. Thus only data from animals that could be paired as to the

TABLE 3 Differences in *Lipoptena paradoxa* burdens on paired age and sex groups of kudu shot in the Kruger National Park from April 1981 to March 1983

Kudu age	Kudu sex	Number of animals*	Mean number of flies	Significance	Wilcoxon value	
					Calculated	Table
Juveniles	Both sexes	14	78			
Adults	Males	14	62	P=0,10	19	22
Juveniles	Both sexes	13	86			
Adults	Females	13	31	P=0,04	17	18
Juveniles	Both sexes	15	78			
Adults	Both sexes	15	45	P=0,10	28	31
Adults	Males	15	63			
Adults	Females	15	26	P=0,01	11	16

* These animals could be paired with animals of different ages or sexes as both animals of each pair were shot during the same month

months in which they were shot were used for comparison employing the paired Wilcoxon T-test.

Adult male and juvenile kudu harboured significantly more flies than adult female kudu.

The smaller number of flies recovered from the adult female animals when compared with the adult males and the juveniles could be due to more efficient grooming by the females or to hormonal differences between the females and the other 2 groups of kudu. It could also be due to transference of flies from female animals to their calves, or as a result of differences in the resistance status of the various groups. If it was due to size one could expect males to harbour most flies, followed by females and then juveniles. There can, however, be many other reasons for these differences. In the case of ixodid tick infestation on domestic cattle, cows carry significantly fewer maturing females of *Boophilus microplus* than do male animals (Seifert, 1971). The 15 adult female kudu used for comparative purposes in the present study also carried significantly fewer nymphs and adults of the ixodid tick *Amblyomma hebraeum* and adults of *Boophilus decoloratus* than did the 15 adult male animals shot at the same time (Horak *et al.*, 1992). Similar differences were, however, not evident for the other tick species on the kudu.

The sex ratios of newly hatched flies, those collected from immobilised bushbuck, those collected from dead kudu, and those collected from common duikers by Boomker *et al.* (1983), are summarized in Table 4.

TABLE 4 The sex ratio of *Lipoptena paradoxa* hatching from pupae and recovered from bushbuck, kudu and common duikers in South Africa

Origin of flies	Number of animals examined	Number of male flies	Number of female flies	Sex ratio
Pupae	—	25	31	1:1,24
Immobilised bushbuck	4	395	817	1:2,07
Kudu	90*	853	1 253	1:1,47
Common duikers	16	103	173	1:1,68

* 96 kudu shot in total, flies for sex ratio determination only available from 90

The sex ratio of newly hatched flies was 1 male:1,24 females, on immobilised bushbuck it was 1:2,07 and on kudu and common duikers 1:1,47 and 1:1,68, respectively.

More females than males emerged from the pupae. A similar phenomenon has also been observed for *Hippobosca equina* (Hafez, Hilali & Fouda, 1977) and *Hippobosca longipennis* (Hafez & Hilali, 1978). In addition, the female flies probably also survive for longer on their hosts than do males if the findings for *H. equina* and *H. longipennis* are applicable (Hafez *et al.*, 1977; Hafez & Hilali, 1978). This would further accentuate the difference in the sex ratio. A single mating is apparently sufficient for the female to produce all her prepupae (Hafez *et al.*, 1977).

TABLE 5 The pupal period of *Lipoptena paradoxa* pupae incubated at various temperatures and relative humidities. The pupae were deposited by flies collected from bushbuck in the Kruger National Park

Pupal deposition date	Number of pupae incubated	Temperature (°C)	Relative humidity (%)	Number of adults emerged	Pupal period (days)
8 March 1990	11	25	30	1	32
8 March 1990	11	30	55	6	24
6 April 1990	47	25	30	23	23–28
6 April 1990	47	30	55	33	23–26

Observations on pupae

Flies captured on immobilised bushbuck were kept alive for as long as possible (1 or 2 days) without a blood-meal to allow them to produce fully developed larvae which became pupae. The pupae were placed in small glass tubes with gauze stoppers. These were suspended in plastic nets in long plastic jars which were half-filled with saturated solutions of $MgCl_2$ or glucose to produce humidities of 30 % and 55 % respectively.

To determine the effect of temperature on pupal duration, pupae were incubated at constant temperatures of 25° (30 % relative humidity) and of 30 °C (55 % relative humidity). The tubes were examined daily for adult emergence.

A total of 22 pupae were obtained within 24 h from 282 female flies collected from an immobilised bushbuck during March 1990. A total of 401 female flies collected from an immobilised bushbuck during April 1990 produced 94 pupae within 24 h. Approximately 1/4 of the latter flies thus produced prepupae within 24 h. This indicates that the period between the deposition of successive prepupa by individual flies may be as short as 4 days. Evans (1950) reports this period to be 7–8 days for *M. ovinus* and Hafez & Hilali (1978) found that for *H. longipennis* it could be 3–5 (mean 3.6) days during the warmer months and 3–8 (mean 6.4) days during the cooler months.

The numbers of flies that hatched from pupae after they had been incubated at various temperatures and relative humidities are summarized in Table 5.

There was considerable overlap in the pupal periods of the flies that hatched from those pupae kept at higher temperatures and humidities and of those kept at lower temperatures and humidities.

The greatest numbers of flies hatched during the daylight hours between 07:00 and 15:00. The newly emerged flies were very active and their wings expanded within a few minutes. However, some of the flies died just after emergence, while the wings of others failed to expand.

The pupal period of approximately 23–26 days recorded at 30 °C and 55 % RH corresponds fairly closely to the 20–26 days at 30 °C and 65 % RH recorded for *H. equina* by Hafez *et al.* (1977) and 19–23 days at 30 °C and 75 % RH for *H. longipennis* (Hafez & Hilali, 1978). The rate of emergence of adult *H. longipennis* from pupae was highest between 07:00 and 09:00, with few emerging at midday and none at night (Hafez & Hilali, 1978).

Most of the *L. paradoxa* adults emerged in the early morning, but emergence continued till 15:00.

An attempt was made to ascertain the life-span and rate of reproduction of *L. paradoxa* by feeding newly emerged flies on a penned Cameroon goat. The flies were contained in a plastic tube with a gauze-covered lid at the 1 end and with the other end fixed tightly by means of glue and Elastoplast to the shaved neck of the goat.

The flies did not feed on the goat and all died.

Both *H. equina* and *H. longipennis* will feed successfully on guinea pigs and reproduce (Hafez *et al.*, 1977; Hafez & Hilali, 1978). As we were unable to get *L. paradoxa* to feed on the goat we consequently had to rely on pupae produced by flies collected from immobilised bushbuck for our studies on the life cycle.

The density of the vegetation frequented by the preferred host is probably essential for the survival of the pupae. The prepupae produced by the flies are not motile and rapidly darken and harden. In the field these prepupae would fall to the ground and the pupae would form on the soil surface, where they would be exposed to the elements. Hence, the dense type of vegetation preferred by the tragelaphine antelope is also the most suitable for the survival of the pupae.

ACKNOWLEDGEMENTS

We wish to thank the Faculty of Veterinary Science, University of Pretoria; Dr Errol Nevill, Veterinary Research Institute, Onderstepoort; Dr L. E. O. Braack, Kruger National Park; Dr Mervyn Mansell, National Collection of Insects, Pretoria; the Natal Museum, Pietermaritzburg; the South African Museum, Cape Town; and the State Museum, Windhoek, Namibia for making study material available. We are grateful to Mr A. M. Spickett and Miss Andrea van Niekerk of the Veterinary Research Institute, Onderstepoort for the statistical analysis and drawing of the graphs respectively. The senior author also expresses her thanks to Drs S. Louw and J. Irish, Mrs Annamé Wels and Miss Liz de Villiers of the National Museum, Bloemfontein. The Bloemfontein Municipal Zoo supplied the goat for the feeding experiments.

We also wish to thank Dr J. G. H. Londt of the Natal Museum for his critical review of the manuscript and many helpful suggestions.

This research was funded by the National Museum, Bloemfontein and the Foundation for Research Development.

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