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Trypanosomes of some sub-Saharan birds

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ABSTRACT

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Linear measurements and derived indices from striated trypanosomes in nine species of sub-Saharan birds representing seven families of the Passeriformes, were compared. The dimensions of the striated trypomastigotes from the Carduelinae, Estrildidae, Nectarinidae, Passeridae, Pycnonotidae, Turdinae and Zosteropidae were similar to each other as well as to those of the striated trypanosomes from the boreal owl (Strigidae). All these trypanosomes were considered to be *Trypanosoma avium* Danilewsky, 1885. A further 20 avian species were considered to harbour *T. avium*, thus greatly extending the reported host range of this trypanosome. Non-striated trypanosomes from the estrildid *Uraeginthus angolensis* closely resembled *Trypanosoma bouffardi* Leger & Blanchard, 1911 in appearance and dimensions, and were considered to be of this species. Additional host records for *T. bouffardi* from an additional nine avian species have been reported. The uniquely small and stumpy *Trypanosoma everetti* Molyneux, 1973 was reported from an additional 18 avian species. A large non-striated trypanosome from the laughing dove, *Streptopelia senegalensis*, was identified as *Trypanosoma hannae* Pittaluga, 1905 and this species was re-described. An infection of this parasite was also found in a single *Streptopelia capicola* and a single *Streptopelia semitorquata.* Two trypanosomes seen in the francolin, *Francolinus natalensis*, were identified as *Trypanosoma calmettei* Mathis & Léger, 1909.

INTRODUCTION

Danilewsky (1885) first noted trypanosomes in the blood of the owl *Strix aluco;* the trypomastigote had a striated appearance. In 1889 he described *Trypanosoma avium major* and *T. avium minus* from an unspecified owl (usually considered to be *Athene noctua*) and the European roller *Coracias garrulus*, stressing that there was a continuum in size between large and small forms, and concluding that they all belonged to the same taxon. Since that time, 96 nominal species and two varieties (Bishop & Bennett 1992) have been described from birds, the majority on the one-host-one-parasite philosophy prevalent during the first half of this century. Numerous species were thus described, but the rate of description of new species on this basis, as stated by Baker (1976), "... has (mercifully) declined". Initially, absolute mensural values were employed as diagnostic criteria in conjunction with their occurrence in a specific avian host. Later, it became evident that trypanosomes are highly pleomorphic protozoa (Wenyon 1926: "... are very polymorphic") and indices (Hoare 1972) were developed to help compare the mensural values obtained for these parasites.

Recent work with avian trypanosomes has utilized a number of techniques in addition to using mensural and morphological characteristics. Woo & Bartlett

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(1982) used the development of the parasites in various culture media to help define the species, while Kirkpatrick, Terway-Thompson & Iyengar (1986) used both lectin-binding and electrophoresis patterns in addition to isoenzyme analysis, and Molyneux & Gordon (1975) used cross-immunity studies. Other criteria include host and/or vector specificity (Baker 1976). These and other criteria currently in use are well summarized by Appanius (1991). However, all these techniques are dependent on the availability of a well-equipped laboratory, and since these are usually far removed from the sites where the host birds were sampled, they can, for practical purposes, only infrequently be used.

Specimens in stained blood films, frequently identified only as *Trypanosoma* sp., are regarded as a new species because of the occurrence in a new host, or given the name of a trypanosome previously described or recorded from that host species. These diagnostic approaches are not satisfactory as they do little to truly define the parasite seen. This is especially true when the morphology of the parasites in blood films from birds of different avian families and/or orders appear to be the same morphologically. To further confuse matters, although it is assumed that each trypanosome found in each species of avian host is distinct, experimental transmissions of one avian trypanosome to a number of species of birds of widely differing phylogenetic relationships has been carried out on a number of occasions (Bennett 1961; 1970; Chatterjee & Ray 1971; Woo & Bartlett 1982). These experiments shatter the hypothesis that avian trypanosomes are host-species specific. Therefore, it is probable that morphologically identical trypanosomes from widely differing avian hosts are indeed of the same species. If critical morphological studies show that trypomastigotes from different bird species/families/orders are similar, then it is highly probable that they represent the same taxon.

A three-year (1991–1994) study of some 10700 birds from southern Africa provided the material for a detailed study of the trypanosomes found in these birds. Striated trypanosomes were the most frequently encountered group, and the morphological and mensural characteristics of such striated trypomastigotes from seven species of birds representing seven families/subfamilies of the Passeriformes were compared to indicate whether these parasites were indeed closely similar and whether they could represent the same taxon in a widely differing array of hosts. Additionally, the mensural and morphological characteristics of four non-striated trypanosomes were compared to determine whether such species were similar and whether they represented a common taxon.

MATERIALS AND METHODS

Birds were netted by co-operating bird ringers from a number of areas in South Africa, Botswana and Zimbabwe. Blood smears were made from the brachial vein or other small vessels in the wing, and air-dried. The smears and accompanying data sheets were then sent to the Department of Veterinary Tropical Diseases, Faculty of Veterinary Science at Onderstepoort in South Africa, where they were fixed in May-Grünwald-Giemsa and stained with Giemsa's stain at a pH of 7,2. They were then shipped to the International Reference Centre for Avian Haematozoa, where the slides were screened and the trypanosomes studied.

Trypanosomes were drawn with the aid of a camera lucida and the various mensural characteristics were determined with the use of a Zeiss MOP-3 Digital Analyzer. The mensural characteristics taken were as follows: PA = total length without flagellum; PK = posterior end to centre of kinetoplast; PN = posterior end to centre of nucleus; NA = centre of nucleus to anterior end; KN = centre of kinetoplast to centre of nucleus; BW = body width at the centre of the nucleus; FF = length of free flagellum; AT = area of the trypomastigote; AN = area of the nucleus. The indices derived from these measurements were: PK/PA; PN/PA; PN/NA (nuclear index); PN/KN (kinetoplast index); BW/PA (body-width index) and AN/AT (nuclear-area index). These measurements and indices are used throughout the text and in the tables. The free flagellum was frequently poorly stained and could not be measured accurately; this was particularly true for *Trypanosoma avium* and, for this species, the length of the free flagellum is not given (Table 1). Photomicrographs were taken with a Zeiss Photomicroscope III and all material was deposited in the collection of the International Reference Centre for Avian Haematozoa.

RESULTS AND DISCUSSION

The trypanosomes encountered were divided into five groups on the basis of gross morphology. The first and most commonly encountered group was that with striated trypomastigotes and they were considered to be *Trypanosoma avium* Danilewsky, 1885. The second most frequently occurring group was that with small stumpy trypanosomes with a large nucleus and a posterior kinetoplast that was completely consistent with Molyneux's (1973b) description of *Trypanosoma everetti,* and all such trypanosomes were referred to this species. The third most frequently encountered group was that with small, non-striated trypanosomes that were consistent with Léger & Blanchard's (1911) description of *Trypanosoma bouffardi*. The fourth group of trypanosomes was recovered mainly from the columbid, *Streptopelia senegalensis*, and these were considered to be *Trypanosoma hannae* Pittaluga, 1905. The fifth form encountered was a single infection of two trypomastigotes in the francolin, *Francolinus natalensis*, and they were considered

TABLE 1 Length and area measurements (in µm) of *Trypanosoma avium* from South African birds

Character [a]	Carduelinae	Estrildidae	Nectarinidae	Passeridae
N [b]	16	26	9	6
PA	45,6 ± 5,1[c]	39,8 ± 3,6	52,6 ± 5,0	45,2 ± 3,3
PK	11,1 ± 1,7	9,9 ± 1,7	11,9 ± 1,7	9,7 ± 0,8
PN	21,7 ± 2,5	18,2 ± 2,1	24,4 ± 2,8	21,8 ± 1,5
NA	23,9 ± 3,5	21,2 ± 2,6	28,3 ± 4,4	23,4 ± 2,4
KN	10,8 ± 1,7	8,9 ± 1,1	12,4 ± 1,8	11,9 ± 0,8
BW	5,3 ± 2,1	6,1 ± 1,2	5,0 ± 0,6	5,2 ± 0,5
AT	130,5 ± 48,8	131,2 ± 23,1	131,7 ± 15,6	115,9 ± 16,9
AN	14,8 ± 5,5	16,3 ± 3,6	16,3 ± 2,5	14,0 ± 2,9
PK/PA	0,24 ± 0,04	0,24	0,22 ± 0,03	0,21 ± 0,08
PN/PA	0,47 ± 0,03	0,47	0,46 ± 0,05	0,48 ± 0,02
PN/NA	0,92 ± 0,01	0,88	0,87 ± 0,02	0,93 ± 0,09
PN/KN	0,2 ± 0,03	0,21	0,17 ± 0,1	0,18 ± 0,01
AN/AT	0,16 ± 0,04	0,13	0,12 ± 0,02	0,12 ± 0,02
BW/PA	0,16 ± 0,04	0,15	0,10 ± 0,01	0,11 ± 0,02

Character	Pycnonotidae	Turdinae	Zosteropidae	Strigidae
N	9	16	22	23
PA	47,0 ± 3,3	48,3 ± 3,5	43,5 ± 4,6	53,2 ± 8,2
PK	11,0 ± 2,7	10,0 ± 1,6	8,6 ± 1,6	15,0 ± 2,7
PN	21,8 ± 3,1	23,0 ± 2,1	19,8 ± 2,7	26,5 ± 3,8
NA	25,2 ± 2,6	25,3 ± 2,1	23,5 ± 2,8	26,6 ± 5,3
KN	10,5 ± 1,0	12,8 ± 1,3	11,4 ± 1,5	11,8 ± 2
BW	4,4 ± 1,2	4,8 ± 0,9	4,8 ± 1,2	5,1 ± 0,9
AT	118,0 ± 20,1	116,6 ± 18,0	111,1 ± 26,8	150,9 ± 39,6
AN	12,8 ± 4,9	12,3 ± 4,2	14,9 ± 4,6	13,1 ± 2,7
PK/PA	0,23 ± 0,04	0,20 ± 0,03	0,19 ± 0,03	0,28
PN/PA	0,46 ± 0,05	0,47 ± 0,03	0,45 ± 0,04	0,51
PN/NA	0,87 ± 0,10	0,91 ± 0,09	0,85 ± 0,10	1,0
PN/KN	0,21 ± 0,03	0,18 ± 0,01	0,17 ± 0,02	0,23
AN/AT	0,10 ± 0,04	0,10 ± 0,03	0,13 ± 0,03	0,10
BW/PA	0,10 ± 0,01	0,10 ± 0,02	0,11 ± 0,03	0,10

[a] Mensural characters as listed in Materials and methods
[b] N = sample size
[c] Data presented as mean ± standard deviation

to be *Trypanosoma calmettei* Mathis & Léger, 1909 as they resembled the illustration of this species.

Avian trypanosomes usually occur in low intensities, and blood smears are a poor method for determining the prevalence of any given avian trypanosome in a population. Concentration techniques such as the haematocrit centrifuge (Bennett 1962; Woo 1969) are far superior means for establishing the true prevalence of parasitism, but they are generally not applicable in a field situation. Therefore, while the prevalence of avian trypanosomes in sub-Saharan birds has been recorded (Bennett, Earlé, Huchzermeyer & Du Toit 1992), this prevalence is minimal. While the additional 10700 birds sampled in this study were not included in the Bennett *et al.* (1992) study, the prevalence of avian trypanosomes found, is similar to that reported earlier and again, this must be regarded as minimal.

Trypanosoma avium Danilewsky, 1885
(Fig. 1–6, Table 1)

Baker (1976) considered that the name *Trypanosoma avium* Danilewsky, 1885 should be restricted to trypanosomes from Old World owls (Strigiformes), but Bennett, Siikamäki, Rätti, Allander, Gustafsson & Squires-Parsons (unpublished data 1994) reviewed this species and, on the basis of Scandinavian material, considered that all striated trypanosomes were *Trypanosoma avium*. The mensural data and derived indices reported by Bennett *et al.* (unpublished data 1994) for trypomastigotes from Tengmalm's (Boreal) owl *Aegolius funereus* were considered to be those of *T. avium,* and are used as the basis of comparison with the striated trypanosomes (Table 1) from sub-Saharan Africa.

In this study, the striated trypomastigotes (Table 1) were from the Carduelinae (*Serinus flaviventris*—two individuals from the Cape Province and the Transvaal; *S. mozambicus*—one individual from Zimbabwe), Estrildidae (*Amadina erythrocephala*—six individuals from the Transvaal), Nectarinidae (*Nectarinia amethystina*—one individual from Natal), Passeridae (*Passer domesticus*—one individual from the Transvaal), Pycnonotidae (*Pycnonotus barbatus*—two individuals from the Transvaal), Turdinae (*Cossypha caffra*—one individual from the Transvaal) and Zosteropidae (*Zosterops pallidus*—three individuals from the Cape Province and Transvaal). The means and standard deviations of the mensural characteristics, together with the derived indices of the striated trypomastigotes from the seven avian sources (Table 1), are essentially the same, and broadly overlap. In addition, they are similar to the measurements from Tengmalm's owl, and the eight sets of measurements form a broadly overlapping continuum of trypomastigotes. Additionally, they broadly overlap with the measurements of *T. avium* from the pied flycatcher, *Ficedula hypoleuca*, from Scandinavia (Bennett *et al.* unpublished data 1994). Therefore we conclude that these striated trypanosomes from sub-Saharan and Scandinavian birds represent a single taxon—*Trypanosoma avium* Danilewsky, 1885. An additional 21 hosts of *Trypanosoma avium*, identified in the blood smears of 10 700 birds sampled during the period 1991–1994, are listed in Table 3. They represent 13 families or subfamilies of the Passeriformes and indicate the wide range of avian hosts parasitized by this trypanosome.

Trypanosoma everetti Molyneux, 1973
(Fig. 7, Table 2)

Molyneux (1973b) described *Trypanosoma everetti* from *Estrilda troglodytes*. This trypanosome with its short, stumpy body, large nucleus and kinetoplast situated at the posterior end, makes it, according to Baker (1976), one of the most distinctive and easily recognized of the avian trypanosomes. The morphological and mensural characters of this species were detailed by Bennett *et al.* (unpublished data 1994) and the mensural values are presented (Table 2) for comparison with the other trypanosomes.

TABLE 2 Length and area measurements (in µm) of *Trypanosoma bouffardi*, *T. everetti* and *T. hannae* from sub-Saharan birds

Characters[a]	*T. bouffardi*	*T. everetti* [b]	*T. hannae*
N	30	43	33
PA	36,0 ± 3,8	23,0 ± 1,9	59,9 ± 5,7
PK	13,1 ± 2,4	2,7 ± 0,7	25,2 ± 4,9
PN	19,4 ± 2,8	12,3 ± 1,1	30,6 ± 3,9
NA	16,7 ± 2,5	10,8 ± 1,3	29,0 ± 4,0
KN	6,5 ± 1,0	9,8 ± 1,2	6,6 ± 1,1
BW	5,7 ± 1,0	6,3 ± 1,4	5,8 ± 1,0
AT	80,2 ± 12,3	83,3 ± 20,7	148,1 ± 24,9
AN	10,0 ± 2,5	21,8 ± 8,0	19,1 ± 3,6
PK/PA	0,36 ± 0,05	0,12	0,42 ± 0,07
PN/PA	0,53 ± 0,06	0,54	0,51 ± 0,05
PN/NA	1,12 ± 0,02	1,16	1,10 ± 0,02
PN/KN	0,30 ± 0,04	0,13	0,47 ± 0,10
BW/PA	0,16 ± 0,03	0,25	0,10 ± 0,02
AN/AT	0,12 ± 0,03	0,28	0,13 ± 0,02

[a] Characters as for Table 1 and in Materials and methods
[b] From Bennett *et al.* (unpublished data 1994)

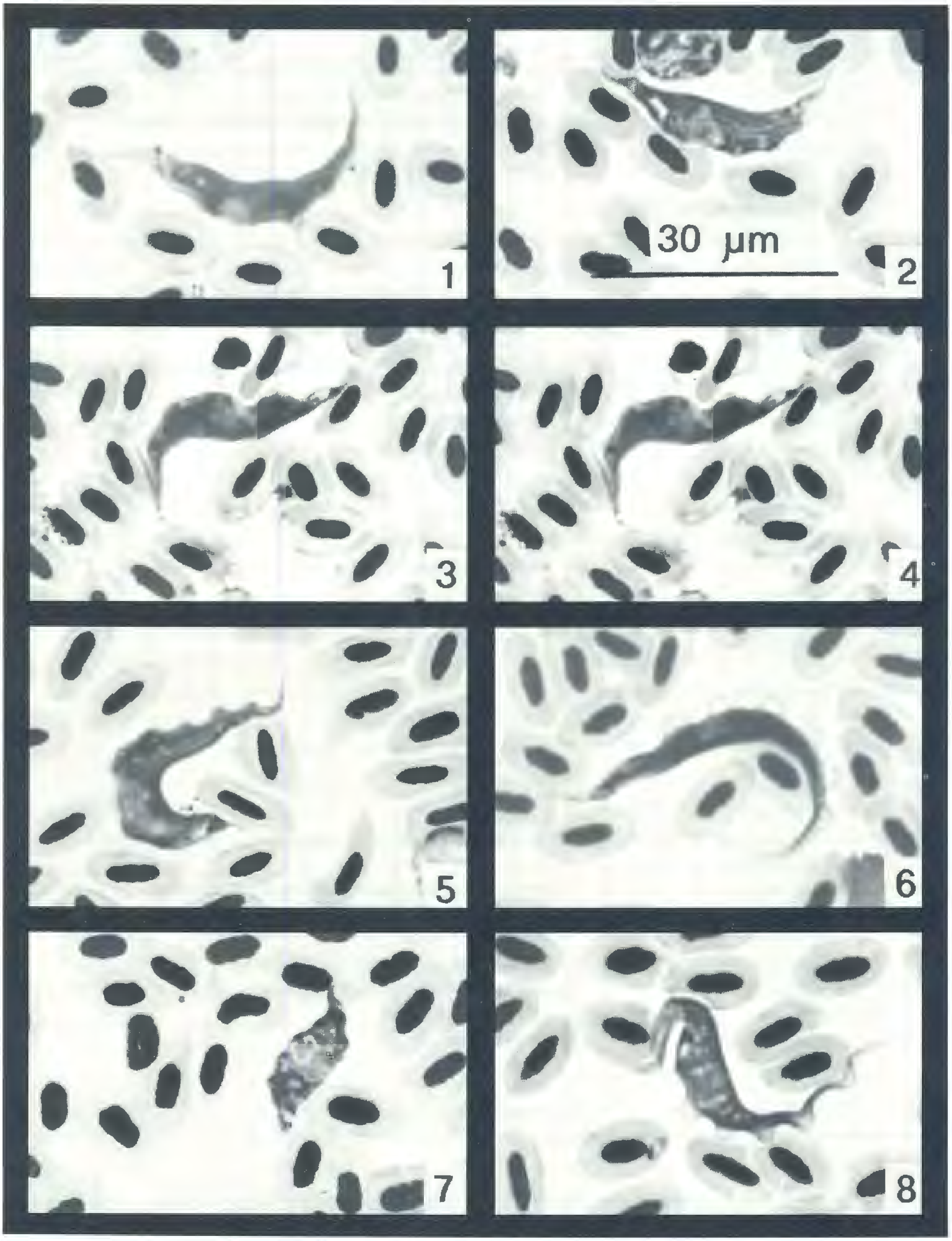

FIG. 1–6 *Trypanosoma avium*

FIG. 1 From *Serinus flaviventris*
FIG. 2 From *Amadina erythrocephala*
FIG. 3 From *Nectarinia amethystina*
FIG. 4 From *Passer domesticus*
FIG. 5 From *Pycnonotus barbatus*
FIG. 6 From *Zosterops pallidus*

FIG. 7 *Trypanosoma everetti* from *Pytilia melba*

FIG. 8 *Trypanosoma hannae* from *Streptopelia senegalensis*

TABLE 3 Additional hosts of *Trypanosoma* spp. in sub-Saharan Africa

Trypanosoma	Host family	Host species
T. avium	Columbidae	*Streptopelia senegalensis*
	Estrildidae	*Amadina fasciata, Pytilia melba, Uraeginthus angolensis*
	Fringillidae	
	Carduelinae	*Serinus gularis, S. mennelli, S. sulphuratus*
	Malacotininae	*Dryoscopus cubla*
	Muscicapidae	
	Monarchinae	*Terpsiphone viridis*
	Muscicapinae	*Sigelus silens*
	Sylviinae	*Parisoma subcaeruleum, Phylloscopus trochilus*
	Turdinae	*Turdus gurneyi*
	Nectarinidae	*Nectarinia manoensis*
	Passeridae	*Passer melanurus, Philetairus socius, Plocepasser mahali*
	Ploceidae	*Ploceus velatus*
	Pycnonotidae	*Pycnonotus nigricans*
	Zosteropidae	*Zosterops senegalensis*
T. bouffardi	Estrilidae	*Pytilia melba, Uraeginthus granatinus*
	Viduinae	*Vidua chalybeata*
	Muscicapidae	
	Sylviinae	*Acrocephalus gracilirostris, Parisoma subcaeruleum*
	Passeridae	*Passer domesticus*
	Ploceidae	*Ploceus capensis, P. velatus*
	Zosteropidae	*Zosterops pallidus*
T. calmettei	Phasianidae	
	Phasianinae	*Francolinus natalensis*
T. everetti	Alcedinidae	*Ispidina picta*
	Estrildidae	*Pytilia melba*
	Fringillidae	
	Carduelinae	*Serinus flaviventris, S. gularis, S. mozambicus, S. sulphuratus*
	Muscicapidae	
	Sylviinae	*Acrocephalus baeticatus, Parisoma subcaeruleum*
	Turdinae	*Turdus olivaceus*
	Nectarinidae	*Nectarinia famosa*
	Ploceidae	*Euplectes ardens, Ploceus velatus*
	Pycnonotidae	*Andropadus importunus, Pycnonotus capensis, Phyllastrephus terrestris*
	Sturnidae	*Cinnyrinclus leucogaster*
	Upupidae	*Upupa epops*
	Zosteropidae	*Zosterops pallidus*
T. hannae	Columbidae	*Streptopelia capicola, S. semitorquata*

This species was commonly encountered, in low intensities, in 18 additional species of birds (Table 3) representing nine families/subfamilies of Passeriformes and two species (Alcedinidae, Upupidae) of the Coraciformes.

Trypanosoma bouffardi **Léger & Blanchard, 1911** (Fig. 9–12, Table 2)

Trypanosoma bouffardi was described in 1911 by Leger & Blanchard from a West African ploceid, *Ploceus melanocephalus* and it was subsequently redescribed and studied by Molyneux (1973a). In the present study, this trypanosome occurred with the greatest frequency in the estrildid finch, *Uraeginthus angolensis*, in the environs of Gaborone, Botswana. This trypanosome was distinctive because of the intensity of the infection in the host which was far in excess of that normally encountered among avian trypanosomes. In several individuals, intensities of 6–8 trypanosomes/field at a magnification of 400 X were encountered; an intensity approaching that at

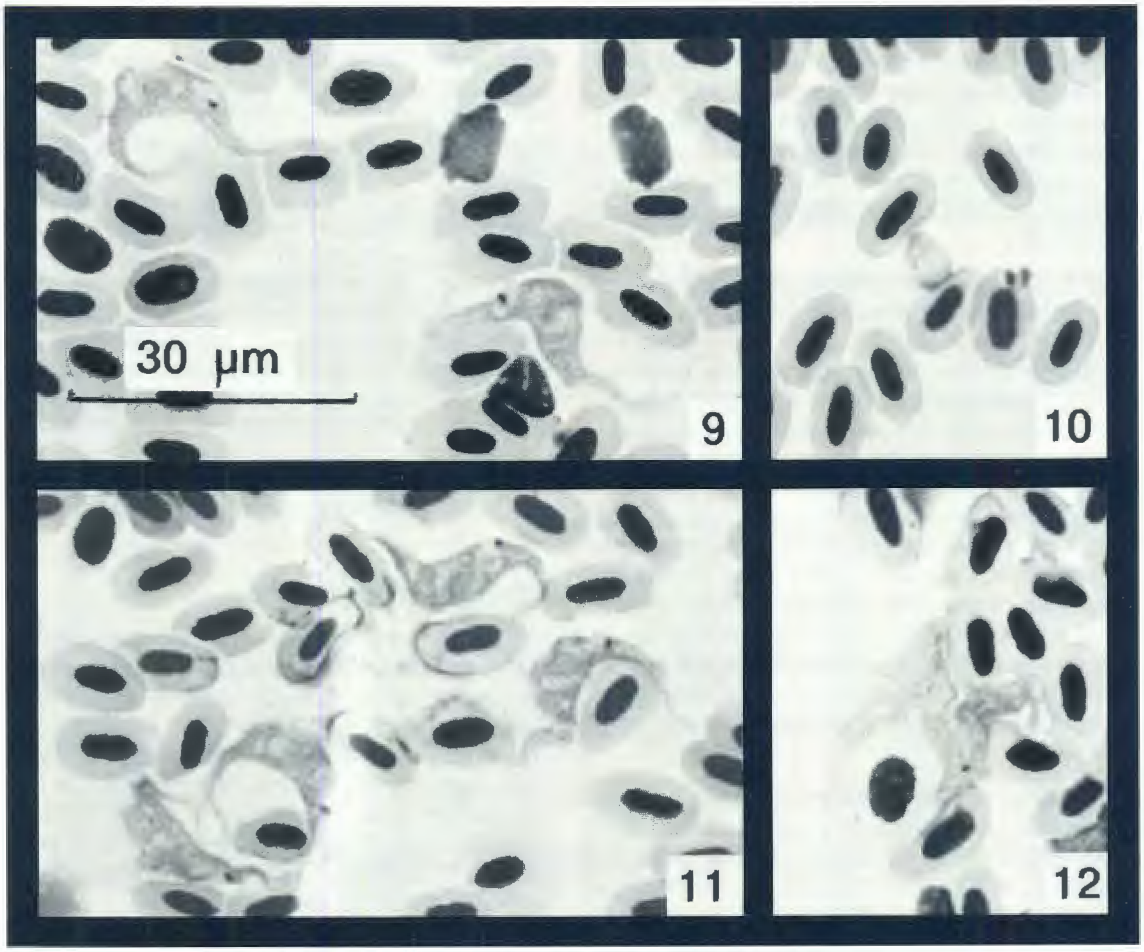

FIG. 9–12 *Trypanosoma bouffardi,* all from *Uraeginthus angolensis*

FIG. 9 and 11 Several trypomastigotes in one field to show intensity of infection
FIG. 10 Amastigote in peripheral circulation
FIG. 12 Dividing trypomastigotes in peripheral circulation

times seen among the mammalian trypanosomes. In addition, there were several examples of trypomastigotes dividing in the circulating blood (Fig. 12), a situation rarely encountered or reported on in the avian species of these parasites. In addition, an amastigote (Fig. 10) was seen in the circulating peripheral blood.

The mensural characters of this trypanosome (Table 2) were distinct from the other species measured. Its appearance (Fig. 9, 11) was also distinctive and permitted ready identification. It was seen in nine species of passeriforms of six families/subfamilies (Table 3). It was particularly common in birds from Botswana (five host records) and the drier parts of the Transvaal (five host records), with fewer records from the Cape Province and Natal.

Trypanosoma hannae **Pittaluga, 1905**
(Fig. 8, Table 2)

Trypanosoma hannae was first seen and described by Hanna in 1903, in a rock dove *(Columba livia)* from India; however, he did not name the parasite. Subsequently, Pittaluga, in a review of the *Trypanosoma tidae,* using Hanna's description, named the parasite, *T. hannae*, after him. The correct latinization of the name, Hanna, would have been "hannai," and some authors have used this term, but as Baker (1976) points out, the original spelling has nomenclatural precedence and should be retained. Subsequently, this species has been recorded from a number of Old World localities in a variety of columbiform species (Bennett, Whiteway & Woodworth-Lynas 1982). It is difficult to tell, however, whether these identifications were based on the morphology of the trypomastigote or whether it was the only parasite the authors knew that came from a columbiform. Pittaluga's (1905) description gave only the total length and width, but he did comment on its large size. There has been no re-description of this species, and the mensural characters (Table 2) are provided for the first time to permit comparison of this large, non-striated avian trypanosome with others; the appearance of the parasite is quite distinctive. In this study, *Trypanosoma hannae* was frequently found in the laughing dove *Streptopelia senegalensis*, in localities ranging from Zimbabwe to Cape Town, but it was most frequently found in birds in the Pretoria region. A single infection of this species (Table 3) was found in a *Streptopelia capicola* and *S. semitorquata*.

Stephens & Christophers (1908), on the basis of Hanna's original (1903) description, named *Trypanosoma columbae*. However, other than giving the length and width, they provided no further information and thus effectively created a *nomen nudum;* Baker (1976) reduced *T. columbae* to a junior synonym of *T. hannae*. Edouard Sergent (1941a) described and illustrated a trypanosome from a then unspecified dove which he named *Trypanosoma oenae* (1941b), when it was determined that the host was *Oena capensis*. The measurements provided indicated a small trypanosome approximately half the size of *T. hannae*, and the illustrations confirm that it was not the latter species. It was reported to have a large elliptical blepharoplast which was terminal. This parasite has not been reported since, but may well be a valid species.

In this study, *Trypanosoma avium* was seen in a single columbid, viz. a *Streptopelia senegalensis* from the Kruger National Park. *T. avium* has also been reported from *Streptopelia senegalensis* in Senegal (Bennett, Blancou, White & Williams 1978) and *Turtur tympanistra* from Uganda (Bennett, Okia & Cameron 1974). *Trypanosoma avium* has also been reported in North America, from *Columba fasciata*, by Stabler, Kitzmiller & Braun (1977), *Zenaida asiatica*, by Stabler & Holt (1963) and *Zenaida macroura*, by a number of authors (see Bennett *et al.* 1982). It appears, therefore, that three distinct *Trypanosoma* species have been reported from the columbiforms.

Trypanosoma calmettei Mathis & Léger, 1909

A single infection with only two trypomastigotes was seen in a francolin, *Francolinus natalensis*, from Zimbabwe. These trypanosomes were closely similar to the illustration of *Trypanosoma calmettei* provided by Mathis & Léger in 1909, and were identified as this species.

This study has shown the occurrence of trypomastigotes with the same mensural and morphological characteristics in a variety of phylogenetically diverse avian hosts. The work of a number of authors has shown that, experimentally, trypanosomes from a single avian host can be transmitted to a variety of other avian species, and these studies have effectively shown that avian trypanosomes are not host specific. Hoare (1972), in his monograph on the mammalian trypanosomes, clearly indicates that many species of mammalian-inhabiting trypanosomes constitute morphologically indistinguishable races. These races differ in such characteristics as antigenic structure (serodemes), host range (xenodemes) and impact upon the host (nosodemes). Presumably, a similar situation occurs among the avian trypanosomes. Thus it is quite possible, as has been shown in the present study, to find one morphological entity in a wide range of avian hosts. Thus trypanosomes with a similar appearance and mensural characters can, at present, all be assigned to the same taxon. Of course, confirmation by cross-transmission experiments, culture techniques, molecular analyses and DNA fingerprinting is essential. For practical purposes, however, there will be a continued reliance on mensural and morphological characters to provide the basis for specific diagnoses of avian trypanosomes, and it is hoped that the data presented in this study will contribute to such diagnoses.

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