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A HOST-PARASITE CATALOGUE OF THE HAEMATOZOA OF THE SUB-SAHARAN BIRDS

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ABSTRACT

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The prevalence of avian haematozoa in 826 species of birds representing 73 families of sub-Saharan birds as recorded in the literature or in the files of the International Reference Centre for Avian Haematozoa and the Veterinary Research Institute is presented. The most commonly occurring blood parasites were members of the genus *Haemoproteus* which were represented by 63 species which occurred in 19,1 % of the sample. Twenty-five species of *Leucocytozoon* were recorded in 8,3 % of the birds and represented the second most frequently encountered group of haematozoa. Species of *Plasmodium, Trypanosoma,* and filarioids (as microfilariae) occurred in 3,5 %, 2,5 % and 2,8 % respectively of the birds sampled; species of *Aegyptianella, Atoxoplasma, Babesia* and *Hepatozoon* were infrequently seen.

An annotated list of the birds examined for haematozoa is presented and brief descriptions of the species of *Haemoproteus* and *Leucocytozoon* in birds of the sub-Saharan zone are included.

INTRODUCTION

Avian haematozoa have consistently intrigued parasitologists since Danilewsky (1885) first described *Trypanosoma avium* from owls and other birds in Russia. Interest in such parasites was further heightened following Ross's (1898) discovery of the life cycle of a *Plasmodium* sp. in chickens which was transmitted by the 'grey mosquito', a discovery which set the stage for the use of avian haematozoa as models for arthropod-borne diseases. Since Danilewsky's time, some 5500 articles (exclusive of books and theses) concerning avian blood parasites have appeared in print. Many of these articles are surveys listing the blood parasites of the avifauna of specific but restricted portions of the world. Relatively few authors have undertaken the task of summarizing the data recorded on the prevalence of blood parasites in birds of a specific Wallacean life zone. Greiner, Bennett, White & Coombs (1975) compiled the results of the examinations of some 58 000 birds of the Nearctic region and White, Greiner, Bennett & Herman (1979) compiled similar records for the birds of the Neotropical region; Peirce (1981a) compiled the records for the birds of the western Palearctic in Western Europe. However, no one has endeavoured to compile the results of the examinations for blood parasites that occur in the rich and diversified avifauna of the Wallacean Ethiopian life zone of the African continent south of the Sahara. Such examinations were first recorded by Hirst in 1905 and have continued, at various levels of intensity, until the present. The objective of this present study is to compile all the records of examinations for avian haematozoa of the avifauna of the Ethiopian life zone to present a consolidated overview of what has been done in the past. It is hoped that this compilation will clearly indicate the shortcomings of our present knowledge and present a challenge to African ornithologists and parasitologists to strive to fill in the blanks of our understanding of this fascinating field.

Many parasitologists feel that the identification of avian haematozoa is beyond them because it refers to a highly specific aspect of the discipline. It is our intention to present, through the medium of the annotated tables, the appropriate criteria to allow most ornithologists and parasitologists to identify the blood parasites encountered to the genus and to a reasonable estimate of the species involved. It is also hoped that such an annotated table will dispel the notion that the realm of avian haematozoa is restricted to a chosen few specialists.

Organization of the catalogue

This catalogue is designed primarily for the parasitologist and non-ornithologist unfamiliar with the phylogenetic organization of the avian orders, families, genera and species usually employed in ornithological texts. Indeed, the current fluidity in ornithological thinking concerning the correct placing of an avian taxon is so great that, while the ornithological specialist has problems in comprehending recent taxonomic and nomenclatural re-arrangements, the non-specialist is completely lost. Therefore, this host-parasite listing is arranged alphabetically, first by avian family, then by genus and finally by species, utilizing the scientific names. Ordinal designations are disregarded totally as are the use of local and dialectic names which vary too widely throughout the continent to be of value. Blood parasites for each avian host are listed also alphabetically, as are the author citations, which are listed in full in the References section.

The prevalence of avian haematozoa in sub-Saharan birds is presented in Table 1 by family and species of the avian host and the genus of blood parasite. Generically, the parasites are listed as *Leucocytozoon, Haemoproteus, Plasmodium,* Microfilariae

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(= Filaroidea), *Trypanosoma* and Others. The "Others" refers to seldom encountered haematozoan groups such as *Atoxoplasma, Aegyptianella, Babesia, Haemogregarina, Hepatozoon, Lankesterella* and non-defined parasites. This table shows the relative effort made to survey the birds of various families and clearly indicates those avian groups which require considerable additional input to provide a statistically adequate sample. It is surprising, for example, that the family Coliidae, considered to be among the more common garden birds (Newman, 1972) in the Republic of South Africa, is represented by only 27 examinations and that only three corvids have been examined. Many other similar anomalies occur. The prevalence of parasitism by host family is summarized at the end of Table 1.

Table 2 represents an annotated listing of the blood parasites in each species of bird examined. The results are presented as the genus and species of parasite found in each avian host examined and includes those species that were examined but in which no blood parasites were found. The source of the information is presented by a literature citation or reference to an unpublished source. Such unpublished sources are referred to as the records held by—

IRCAH = International Reference Centre for Avian Haematozoa; and

VRI = Veterinary Research Institute, Onderstepoort.

All citations refer to natural infections not experimental infections.

Also included are annotated lists of the 73 species of the genus *Haemoproteus* and 27 species of the genus *Leucocytozoon* which have been recorded in or are expected to occur in the avifauna of the sub-Saharan region. The annotated lists cite the type host and family, the author of the parasite and the date of its most recent re-description or revision. The annotated lists also include a brief description of the salient points of the morphology of the parasite that can be used to assist in its identification together with a generalized illustration of the macrogametocyte. The illustration of the macrogametocyte is chosen as this is the least variable of the erythrocytic stages likely to be encountered. The microgametocytes of both *Haemoproteus* and *Leucocytozoon* are generally similar (in the broad sense) to the macrogametocyte and only differ in the usual sexual characteristics of having a large, diffuse nucleus and pale staining cytoplasm, as first defined by Mathis & Leger (1911). In a few species, other differences occur and these are noted for the appropriate species involved. In our opinion, it is far better to attempt to give a specific identification that refers to morphological characteristics, that can assist a specialist in correctly placing the taxon involved, than to beg the issue and provide only a generic identification that assists no one.

The 14 species of the genus *Plasmodium* which have been recorded or are expected to be found in Ethiopian birds are listed also and the host range and occurrence of these parasites is defined in general terms. However, no annotated list is presented as this group have been described ably and reviewed by Garnham (1966) and little additional information has been accumulated concerning these species since that time. Although avian *Plasmodium* have long been studied intensively and more is known about these parasites than any other avian group, their prevalence is low and the various parasites are only infrequently encountered in wild avian populations except in highly specific circumstances. The lower frequency with which infections with *Plasmodium* are seen in wild birds could be due in part, to the short duration of most infections. In addition the higher pathogenicity of these parasites elicits a more severe immune response, which either rapidly eliminates the parasites from the blood (FWH unpublished results) or the host from the population. Many infections of *Plasmodium* are at a chronic or sub-patent level and seldom detected by blood film diagnosis. Such infections are best detected by sub-inoculation techniques which are seldom employed in blood parasite surveys. All these factors undoubtedly contribute to the low prevalence encountered.

The families and species of birds

Avian taxonomy and nomenclature are in a highly fluid state, especially as the result of recent advances in both biochemical and molecular biological techniques for assessing evolutionary relationships. A number of phylogenetic arrangements of the birds of the world have been proposed, using these new techniques, over the past decade; all have certain similarities but all differ in one or more major aspects. For the non-specialist in ornithological systematics preparing a checklist of parasites of birds, a specific standard must be employed to present a framework about which the checklist is formulated. In this present study, Edward's (1982, 1986) "A coded workbook of the birds of the world" has been adopted as the basic framework, but when generic and/or specific names disagree, Robert's Birds of Southern Africa (Maclean, 1985) has been used as the final arbitrator on the principle that this work has engendered considerable trust and acceptance by workers with sub-Saharan birds.

The families and species of blood parasites

In the preparation of this host-parasite checklist, certain guidelines were followed. In particular, this publication follows the protocols established by Bennett, Whiteway & Woodworth-Lynas (1982) in the production of their host-parasite catalogue of the avian Haematozoa. Entries are based on primary sources wherever possible and secondary sources such as Coatney (1936) and Berson (1964) were used only when the primary sources could not be consulted.

Negative records for blood parasite examinations are only cited when no parasite record was available for that host species. The negative records for such species are given in Table 1 and it is clear, when such negative records are based on inadequate sample size. It is hoped that ornithologists and others will respond to these inadequacies by increasing the data base.

Blood parasites are, for the most part, Protozoa and the majority belong to the Apicomplexan families of Haemoproteidae, Leucocytozoidae and Plasmodiidae. The other blood parasites such as *Atoxoplasma, Babesia, Lankesterella* and *Toxoplasma,* are encountered infrequently. In fact, it is moot whether *Toxoplasma (sensu stricto)* occurs in birds. The status of *Lankesterella* is in question, with some authorities considering this to be a mite-vectored avian blood parasite (Baker, Lainson & Killick-Kerndrick, 1959; Lainson, 1960) while others (Box, 1971) consider it to be an intestinal coccidian parasite in an abnormal location in the blood stream. *Aegyptianella* are rickettsiae of the family Anaplasmataceae and therefore not protozoa; early authors believed *Aegyptianella* to be babesioids as well. This error was due to the relatively poor quality of microscopes used at the time. Avian piroplasms (babesioids) were all referred to the genus *Nuttallia.* However, Peirce (1975) showed that the name *Nuttallia* was preoccupied and thus not available, relegating all species formerly in the genus *Nuttallia* to the Apicomplexan genus *Babesia,* a group transmitted by ticks. *Haemogregarina* are common blood parasites of poikilothermic vertebrates but their presence has never been confirmed in birds. Reports of *Haemogregarina* in birds therefore should be investigated closely.

In birds the gametocytes of *Hepatozoon* are found only in circulating monocytes. Only four species have been described from birds and the life cycles are unknown. Circumstantial evidence suggests that ticks are the transmitting agents (Bennett & Peirce, 1989b). The present study does not pretend to make a ruling on these divergent opinions, and the various groups are cited as they appear in the literature.

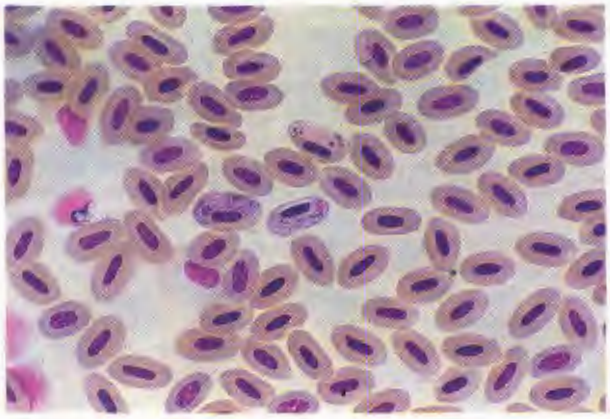
Another frequently occurring group of blood parasites are the microfilariae of the Filaroidea. The microfilariae that appear in the peripheral circulation of birds present a serious problem in taxonomy. During the first half of this century (and to a certain extent to the present time), it was assumed that microfilariae represent nematodes that were highly host specific and many species of filariids (under the erroneous generic designation of *Microfilaria* or *Microfilarium*, which do not exist nomenclaturally) were described. Compounding the problem is the fact that microfilariae can only be specifically identified when associated with the adult worm. Therefore, no attempt has been made to summarize the species of microfilariae recorded from birds. Excellent summaries on this aspect have been presented by Sonin (1966, 1968) and Anderson & Freeman (1969).

For a considerable period of time, the prevailing philosophy among blood and other parasitologists has been the "one host-one parasite" approach to the systematics of the group. This philosophy, particularly prevalent in the first quarter of the century, has been modified, through experimental approaches, to the current belief that the parasite is host family specific. This philosophy is well-represented by the haemoproteids where Atkinson (1986) has shown that haemoproteids are, experimentally, specific at the sub-familial level. Fallis, Desser & Khan (1974) have shown that leucocytozoids are host family specific. However, for most species described there has been little attempt to determine the life cycle, mode of transmission, cross-infectivity or even comparison of the morphology with other species. Consequently, it is probable, that under experimental protocols it will be shown that at least some of these accepted species will fall as synonyms. It is indeed unfortunate that species of *Haemoproteus* and *Leucocytozoon* can only be transmitted to their vertebrate hosts through the agency of the sporozoite from the appropriate vectors. Therefore, the confirmation of the host specificity and biology of each species is still in the future until the vector(s) of each species has(ve) been experimentally ascertained.

The avian malaria parasites of the genus *Plasmodium*, have for the most part, a more catholic host range and the erection of a new species in this genus is now dependent on a careful analysis of morphology in both vertebrate and invertebrate hosts, life cycles and cross-infectivity. Few new species have been described in the past 30 years and none from sub-Saharan birds; Garnham's (1966) epic work still provides the best review of this genus.

The members of the Trypanosomatidae pose a difficult problem in that most of the species are highly pleomorphic and few studies have been carried out to determine life cycles, vectors and host specificity. Current approaches to trypanosome identification and taxonomy involve extensive use of cultural and serological techniques (e.g. Kirkpatrick & Suthers, 1988), techniques that cannot be used on stained specimens on a dried blood film. Nearly 90 species of avian trypanosomes have been named, primarily on the one host-one parasite philosophy (Bennett *et al.*, 1982, pp. 229–230) but it is probable that experimental studies will show that the majority are synonyms of a few widely distributed species. Baker (1976) has provided an excellent review of the subject.

The most commonly encountered of the avian blood parasites were species of the genus *Haemoproteus* (Table 1), which occurred in 19,4 % of the birds examined and represented 59,7 % of all the blood parasite infections. All haemoproteids can be classified, morphologically, into one of five morphological forms (Plate 2, Fig. 1–6) and more than one species of haemoproteid can occur in a single avian family (Bennett & Peirce, 1988). The rhabdosomal parasites (Fig. 5) which enucleate the host erythrocyte have been recorded only from sub-Saharan birds. The discoid forms (Fig. 6) have been seen only in birds from the New World, particularly Central and South America. Classically, all haemoproteids were believed to be transmitted by hippoboscid flies. However, recent work (summarized by Bennett & Peirce, 1990a) has shown that only *Haemoproteus columbae* is unequivocally transmitted by a hippoboscid. All other species of *Haemoproteus* for which the vector is known, are transmitted by ornithophilic biting midges of the genus *Culicoides* (Diptera: Ceratopogonidae). It is anticipated that it will be found that most African haemoproteids are transmitted by species of *Culicoides.*



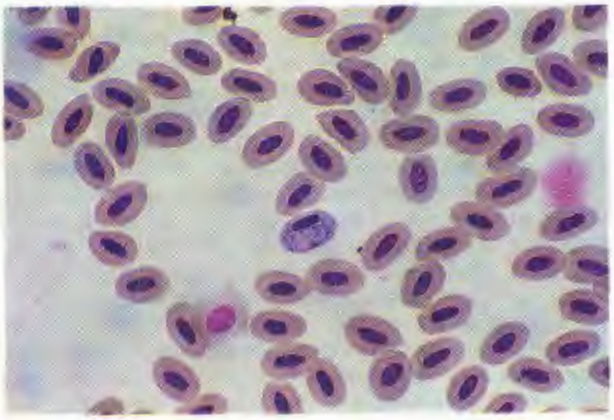
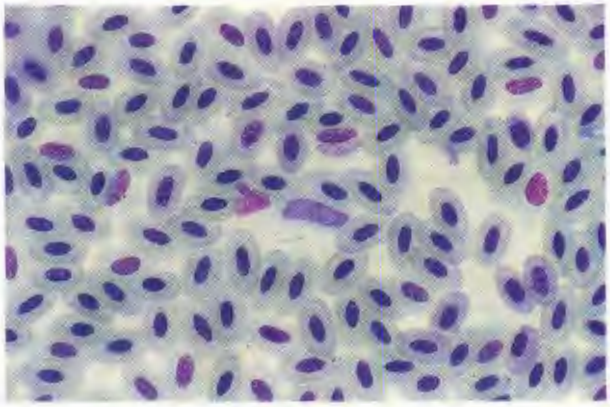


PLATE 1.

FIG. A. *Haemoproteus halcyonis* demonstrating sexual dimorphism in the Apicomplexa; macrogametocyte dark blue with compact red nucleus and microgametocyte light blue with large, diffuse nucleus.

FIG. B. *Haemoproteus columbae*. Note how parasite displaces erythrocyte nucleus laterally to periphery of cell.



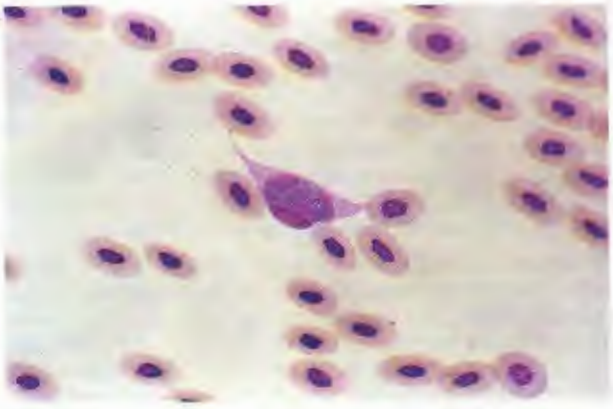
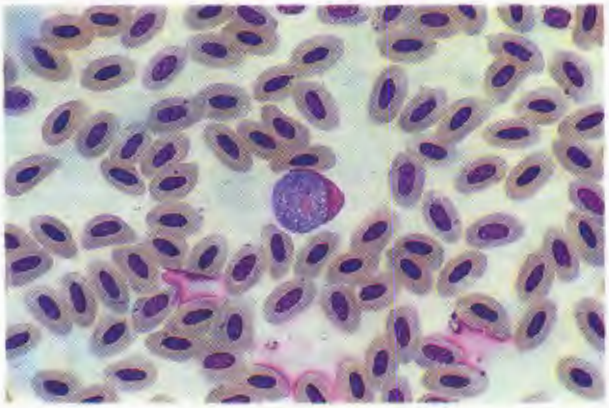


FIG. C. *Haemoproteus enucleator*. Note rod-shaped parasite lying in cell from which nucleus has been eliminated.

FIG. D. *Leucocytozoon neavei*, demonstrating fusiform shape.



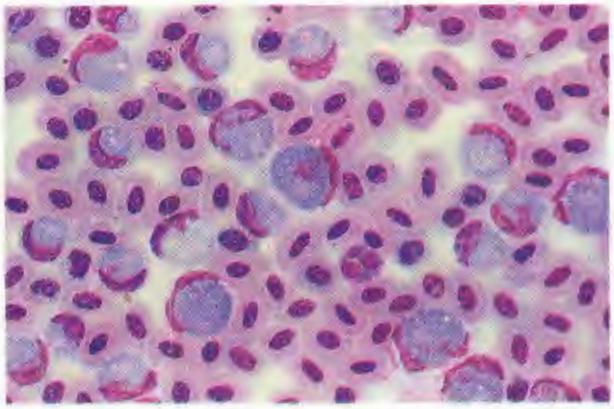


FIG. E. *Leucocytozoon brimonti*, demonstrating round shape.

FIG. F. Massive infection of *Leucocytozoon marchouxi*.

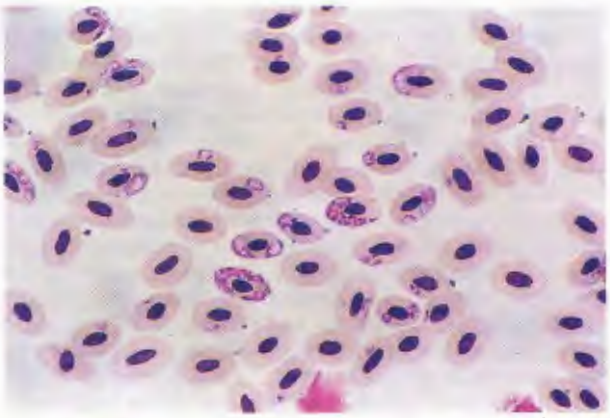


FIG. G. Infection of *Plasmodium circumflexum*, demonstrating all the stages of the parasite normally seen in the peripheral blood.

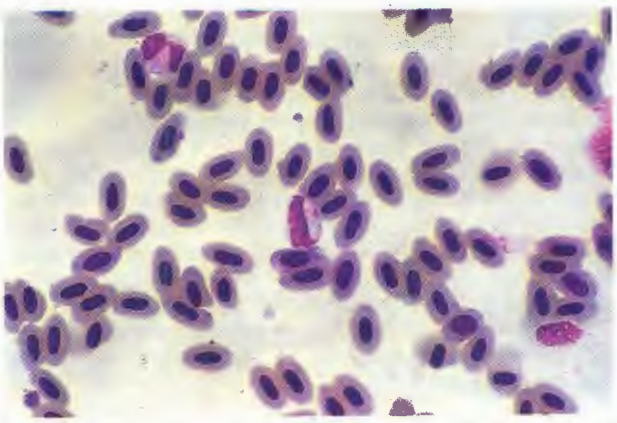


FIG. H. *Hepatozoon atticorae;* parasite lies in a deformed monocyte.

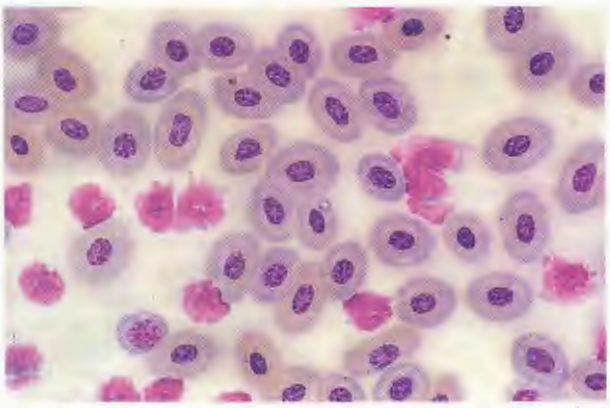


FIG. I. *Babesia* sp.

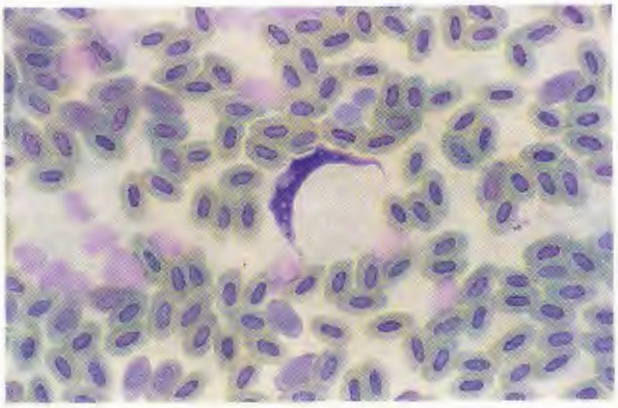


FIG. J. *Trypanosoma avium*-like.

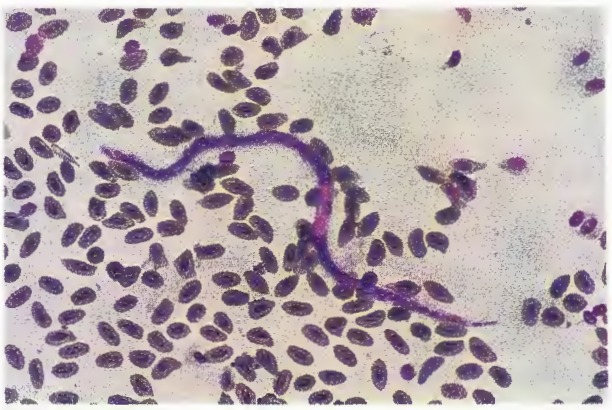


FIG. K. Microfilaria.

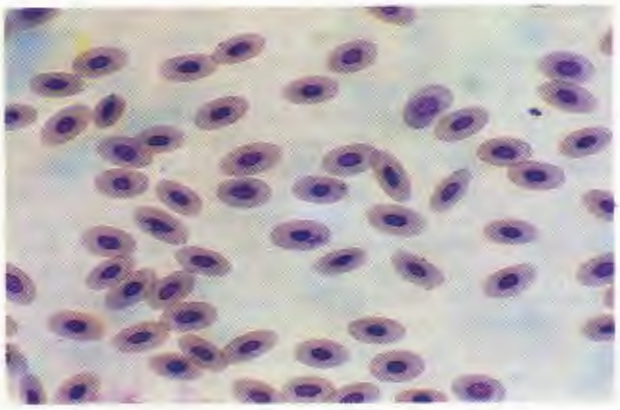


FIG. L. *Aegyptianella* sp.

Haemoproteids (normally) produce a long-lasting infection with a prepatent period of 14–21 days. The comparative lack of clinical or pathological effects associated with a haemoproteid infection shows this to be a rather benign group of parasites. The lack of effect might be interpreted as a long-term evolutionary association of this family of parasites with their avian hosts to establish such a complementary equilibrium status. Studies for the reason(s) for such a lack of pathogenicity in this group might provide significant insight into why other haemosporidan parasites are so pathogenic. A summary of the haemoproteids of sub-Saharan birds by morphological form is appended to the annotated list of the haemoproteids.

The second most frequently encountered group of blood parasites were species of the genus *Leucocytozoon,* which occurred in 8,1 % of the birds examined and 24,7 % of the infected birds. Fallis & Desser, (1977) have shown that species of *Leucocytozoon* are host family specific, and this assumption has been applied throughout the range of leucocytozoids seen and described from birds. All leucocytozoids can be classified morphologically to fit 8 morphological forms (Plate 3, Fig. 7–14). However, the leucocytozoids are unique in that all species that occur in birds of the avian order Passeriformes have only a single morphological form—round or ovoid—while most leucocytozoids that occur in the lower avian orders have two morphological forms—round and fusiform (elongate). The round form is believed to be produced by hepatic schizogony while the fusiform gametocytes are believed to be the result of schizogony in the kidneys, spleen and reticuloendothelial system (Fallis & Desser, 1977). Therefore, many leucocytozoid species have two forms. All species of *Leucocytozoon* for which the life cycle is known, are transmitted by ornithopilic blackflies (Diptera: Simuliidae). The related genus and species *Akiba caulleryi,* considered as a sub-genus of *Leucocytozoon* by Levine (1988), is transmitted by species of ornithophilic *Culicoides,* primarily in southeastern Asia and the record in guineafowl in Tanzania (Fallis, Jacobson & Raybould, 1973b) is probably in error, the round free form merely representing one of the morphs of *L. neavei.* Leucocytozoids produce a short-term infection of high intensity which rapidly drops to a chonic level in which the intensity of parasitism is low; the prepatent period is 6–10 days. Most species of *Leucocytozoon* produce a relatively benign course of infection. However, three species, *Leucocytozoon simondi* of ducks, *L. smithi* of turkeys and *L. (A.) caulleryi* of chickens can produce high mortalities in domestic flocks. Possibly the process of domestication has removed the resistance that wild populations of the same species seem to enjoy. In addition, the concentration of large domestic flocks may increase vector density, thereby producing more severe infections. A summary of the leucocytozoids of sub-Saharan birds by morphological form is appended to the annotated list of the leucocytozoids.

Species of *Plasmodium* occurred in only 3,5 % of the sample (Table 1) and represented 10,3 % of the infected birds. All avian species of *Plasmodium* are transmitted by species of *Culex, Aedes, Mansonia, Culiseta* and others, but none of the vectors is a member of the genus *Anopheles.* Most species of malaria have a broad host distribution (Bennett *et al.,* 1982, p. 225). Malarial infections usually produce a high intensity parasitaemia at the outset of the infection which rapidly declines to a low level. The prepatent period of the various species is variable and ranges from 12–21 days as a result of sporozoite transmission; patency by blood passage is much faster and can be as short as 24 h depending on route of infection and level of parasitaemia of the donor's blood. The relatively long prepatency periods of *Haemoproteus* and *Plasmodium* in natural infections mean, that nestlings under two weeks of age are unlikely to show a parasitaemia although they might be infected with these parasites. Some species of *Plasmodium* can be highly pathogenic, causing widespread mortality among specific avian populations, particularly among domestic poultry flocks; chief among these are *Plasmodium gallinaceum* and *P. durae* in chickens and turkeys respectively. However, *Plasmodium relictum* can cause severe mortality among colonies of *Passer* species and is a major cause of mortality among zoo birds such as penguins (Garnham, 1966). The distribution of the sub-Saharan species of avian Haemosporidia (Apicomplexa) by host family/sub-family is summarized at the end of this introduction to provide a rapid and ready reference to the species of parasite expected to occur in a given avian species.

Avian trypanosomes and microfilariae occurred in about 5,3 % of the sample respectively. Little is known about the life cycles, pathogenicity, transmission or cross-infectivity of the African forms of these parasites but they do not appear to cause gross pathological effects. The trypanosomes usually form a low intensity parasitaemia and are difficult to detect in blood smear preparations. A concentration technique such as the hematocrit centrifuge, is required to reliably assess the prevalence of these parasites (Bennett, 1962). Some of the microfilariae tend to be periodic and occur in the peripheral circulation at some times in greater profusion than at other times. This can be a confounding element in assessing the prevalence of microfilariae.

The records of blood parasites for sub-Saharan birds from zoos are omitted from this catalogue as they probably contracted their infections at the zoo. Records from domesticated and exotic birds are excluded.

THE DISTRIBUTION OF THE SUB-SAHARAN SPECIES OF AVIAN HAEMOSPORIDIA BY HOST FAMILY/ SUB-FAMILY

ACCIPITRIDAE: *Haemoproteus elani, H. janovyi, H. nisi, Hepatozoon adiei, Leucocytozoon toddi;* many species of *Plasmodium*

ALAUDIDAE: *Haemoproteus alaudae*

ALCEDINIDAE: *Haemoproteus enucleator, H. fusca, H. halcyonis, Leucocytozoon* sp., various species of *Plasmodium*

ANATIDAE: *Haemoproteus nettionis*

ANHINGIDAE: *Haemoproteus* sp., *Leucocytozoon vandenbrandeni*

APODIDAE: *Hepatozoon* sp.

ARDEIDAE: *Haemoproteus hartmanni, Leucocytozoon ardeae;* various species of *Plasmodium*

BALAENICIPITIDAE: *Haemoproteus* sp., *Leucocytozoon* sp.

BUBALORNITHIDAE: *Haemoproteus bubalornis, Leucocytozoon* sp., various species of *Plasmodium*

BUCEROTIDAE: *Haemoproteus* sp., *Leucocytozoon* sp., various species of *Plasmodium*

BURHINIDAE: *Haemoproteus* sp., various species of *Plasmodium*

CAPITONIDAE: *Haemoproteus cornuata, H. thereicerycis, H. xantholaemae, Leucocytozoon* sp.

CAPRIMULGIDAE: *Haemoproteus* sp., *Leucocytozoon caprimulgi*

CHARADRIIDAE: *Haemoproteus nascimentoi, Leucocytozoon sousadiasi*

CICONIIDAE: *Haemoproteus crumenium, H. peircei,* various species of *Plasmodium*

COLIIDAE: *Leucocytozoon* sp.

COLUMBIDAE: *Haemoproteus columbae, Leucocytozoon marchouxi, Plasmodium circumflexum, P. nucleophilum, P. vaughani*

CORACIIDAE: *Haemoproteus coraciae, Leucocytozoon eurystomi*

CORVIDAE: *Haemoproteus danilewskyi*

CUCULIIDAE: *Haemoproteus centropi, Leucocytozoon centropi*

DICRURIDAE: *Haemoproteus dicruri, Leucocytozoon* sp.

EMBERIZIDAE: *Haemoproteus chloriis, H. macropigmentatus, Leucocytozoon* sp., various species of *Plasmodium*

ESTRILDIDAE: *Haemoproteus africanus, H. uraeginthus, Leucocytozoon fringillinarum, Leucocytozoon* sp., various species of *Plasmodium* including *P. circumflexum, P. relictum, P. rouxi* and *P. vaughani*

FALCONIDAE: *Haemoproteus tinnunculi, Leucocytozoon toddi*

FREGATIDAE: *Haemoproteus* sp.

FRINGILLIDAE: *Haemoproteus fringillae, Leucocytozoon fringillinarum,* various species of *Plasmodium* including *P. circumflexum, P. relictum, P. rouxi* and *P. vaughani*

GRUIDAE: *Babesia balearicae, Haemoproteus balearicae, H. antigonis, Leucocytozoon* sp.

HIRUNDINIDAE: *Babesia rustica, Haemoproteus prognei, H. stellaris, Hepatozoon atticorae, Leucocytozoon* sp., various species of *Plasmodium* including *P. nucleophilum, P. polare, P. relictum* and *P. vaughani*

INDICATORIDAE: *Haemoproteus indicator, Leucocytozoon* sp.

JACANIDAE: *Leucocytozoon* sp.

LANIIDAE: Laniinae: *Haemoproteus lanii, Hepatozoon* sp., *Leucocytozoon* sp., various species of *Plasmodium* including *P. relictum, P. rouxi* and *P. vaughani*

Malaconotinae: *Haemoproteus cublae, Hepatozoon sp., Leucocytozoon balmorali, Leucocytozoon* sp., *Plasmodium relictum, P. rouxi, P. vaughani*

LARIIDAE: *Haemoproteus lari*

MEROPIDAE: *Haemoproteus lairdi, H. manwelli, H. meropis, Leucocytozoon* sp., various species of *Plasmodium* including *P. vaughani*

MOTACILLIDAE: *Haemoproteus anthi, Leucocytozoon* sp., *Plasmodium vaughani*

MUSCICAPIDAE: Muscicapinae. *Haemoproteus balmorali, Leucocytozoon* sp., *Plasmodium circumflexum, P. nucleophilum, P. rouxi* and *P. vaughani*

Sylviinae: *Haemoproteus sylvae, H. wenyoni, Hepatozoon* sp., *Leucocytozoon* sp., various species of *Plasmodium* including *P. polare, P. relictum, P. rouxi* and *P. vaughani*

Timaliinae: *Haemoproteus fallisi, Leucocytozoon dubreuili,* many species of *Plasmodium* including *P. circumflexum, P. elongatum, P. nucleophilum, P. polare, P. relictum* and *P. vaughani*

Turdiinae: *Haemoproteus fallisi; Leucocytozoon dubreuili,* many species of *Plasmodium* including *P. circumflexum, P. elongatum, P. nucleophilum, P. polare, P. relictum* and *P. vaughani*

MUSOPHAGIDAE: *Haemoproteus montezi, Leucocytozoon dinizi, Plasmodium vaughani*

NECTARINIIDAE: *Haemoproteus sequeirae, Leucocytozoon* sp., various species of *Plasmodium* including *P. elongatum, P. relictum, P. rouxi* and *P. vaughani*

ORIOLIDAE: *Haemoproteus orioli, Leucocytozoon* sp., *Plasmodium* sp.

OTIDAE: *Haemoproteus tendeiroi, H. telfordi, Leucocytozoon* sp., *Plasmodium* sp.

PARIDAE: *Leucocytozoon majoris, Plasmodium relictum*

PASSERIDAE: *Haemoproteus passeris, Leucocytozoon* sp., various species of *Plasmodium* including *P. circumflexum, P. nucleophilum, P. polare, P. relictum, P. rouxi* and *P. vaughani*

PHALACROCORACIDAE: *Haemoproteus* sp.

PHASIANIDAE: Meleagrinae: *Leucocytozoon smithi, Plasmodium durae*

Numidinae: *Haemoproteus pratasi, Leucocytozoon neavei, Plasmodium circumflexum, P. fallax, P. juxtanucleare, P. relictum*

Phasianinae: *Haemoproteus rileyi, Leucocytozoon macleani, L. peaolopesi, L. schoutedeni, Plasmodium durae, P. juxtanucleare, P. relictum* and others.

PICIDAE: *Haemoproteus borgesi, Leucocytozoon squamatus*

PLOCEIDAE: *Haemoproteus quelea, Hepatozoon* sp., *Leucocytozoon* sp., various species of *Plasmodium* including *P. cathemerium, P. circumflexum, P. nucleophilum, P. relictum, P. rouxi* and *P. vaughani*

PRIONOPIDAE: *Haemoproteus* sp., *Hepatozoon* sp., *Leucocytozoon* sp.

PROMEROPIDAE (= MELLIPHAGIDAE): *Leucocytozoon anellobiae, Plasmodium cathemerium*

PSITTACIDAE: *Haemoproteus* sp.

PYCNONOTIDAE: *Haemoproteus otocompsae, H. philippinensis, H. sanguinis, Leucocytozoon brimonti,* various species of *Plasmodium* including *P. circumflexum, P. relictum, P. rouxi* and *P. vaughani*

RALLIDAE: *Haemoproteus gallinulae, H. porzanae*

SAGITTARIDAE: *Leucocytozoon beaurepairei*

SCOLOPACIDAE: *Haemoproteus contortus, H. rotator, H. scolopaci*

SPHENISCIDAE: *Babesia* sp., *Plasmodium relictum*

STRIGIDAE: *Haemoproteus noctuae, H. syrnii, Leucocytozoon ziemanni,* various species of *Plasmodium* including *P. fallax, P. gundersi* and *P. relictum*

STRUTHIONIDAE: *Leucocytozoon struthionis*

STURNIDAE: *Haemoproteus pastoris, Leucocytozoon* sp., various species of *Plasmodium* including *P. circumflexum, P. nucleophilum, P. relictum* and *P. vaughani*

THRESKIORNITHIDAE: *Haemoproteus pelouroi, H. plataleae*

TYTONIDAE: *Haemoproteus phodili, H. tytoni, Leucocytozoon ziemanni*

UPUPIDAE: *Leucocytozoon* sp., *Plasmodium garnhami*

ZOSTEROPIDAE: *Haemoproteus killangoi, H. zosteropis, Hepatozoon* sp., *Leucocytozoon zosteropis, Plasmodium relictum, P. vaughani*

AN ANNOTATED LIST OF THE SPECIES OF THE GENUS *HAEMOPROTEUS* IN SUB-SAHARAN BIRDS

Note—all figure numbers refer to figures on Plate 2

Haemoproteus africanus Bennett & Peirce, 1991 (1991b)

TYPE HOST: *Mandingoa nitidula* (ESTRILDIDAE).

MACROGAMETOCYTE (Fig. 2). Parasite halteridial with margins entire; parasite of medium to large size, occupying 75–80 % of the host erythrocyte which is not hypertrophied but in which the host cell nucleus is markedly displaced laterally to the periphery; parasite nucleus round to broadly triangular, medial in location and usually located at the outer margin of the parasite; pigment granules prominent, averaging 12 per parasite; volutin granules uncommon; immature gametocyte with margins entire.

Haemoproteus alaudae Celli & Sanfelice, 1891

TYPE HOST: *Alauda arvense* (ALAUDIDAE)

MACROGAMETOCYTE (Fig. 2, 4). Redescribed by Bennett & Peirce (1990b). Parasite highly halteridial with some forms approaching a circumnuclear condition (as seen in Fig. 4), margins entire; parasite causes little hypertrophy of host erythrocyte and can slightly displace erythrocyte nucleus laterally (as in Fig. 2); parasite nucleus round to ovoid, usually terminal to sub-terminal and rarely central; pigment granules average 10 per parasite; volutin granules frequently present and when they occur, obscure the true pigment granules; immature gametocyte with margins entire.

Haemoproteus anthi de Mello, 1936

TYPE HOST: *Anthus novaeseelandia* (MOTACILLIDAE)

MACROGAMETOCYTE (Fig. 2). Redescribed by Bennett & Peirce (1990b). Parasite halteridial with margins entire; parasite highly pleomorphic, causing considerable hypertrophy in host cell area and a variable lateral displacement of the erythrocyte nucleus; parasite nucleus central to sub-central, round to ovoid and normally appressed to the outer margin of the parasite; pigment granules average 11 per parasite; immature gametocytes with amoeboid margins.

Haemoproteus antigonis de Mello, 1936

TYPE HOST: *Anthropoides virgo* (GRUIDAE)

MACROGAMETOCYTE (Fig. 2, 3). Redescribed by Bennett, Greiner & Campbell (1975). Parasite halteridial with margins entire; parasite pleomorphic, causing considerable hypertrophy in area and variable displacement of erythrocyte nucleus; parasite nucleus central, broadly ovoid; pigment granules pronounced, average 19 per parasite; immature gametocytes with margins entire.

Haemoproteus balearicae Peirce, 1973 (1973b)

TYPE HOST: *Balearica pavonina* (GRUIDAE)

MACROGAMETOCYTE (Fig. 1). Parasite microhalteridial with amoeboid margins; occupying 50% or less of host erythrocyte and rarely displaces erythrocyte nucleus or hypertrophies host cell; parasite nucleus round to ovoid, terminal to sub-terminal; pigment granules average 7 per parasite; immature gametocytes with highly amoeboid margins.

Haemoproteus balmorali Peirce, 1984 (1984a)

TYPE HOST: *Muscicapa flava* (Musicapinae, MUSCICAPIDAE)

MACROGAMETOCYTE (Fig. 2, 3). Redescribed by Bennett, Bishop & Peirce (1991a). Parasite halteridial with margins entire but amoeboid poles rarely displaces erythrocyte nucleus laterally but does not hypertrophy host cell; parasite nucleus round to ovoid, central to sub-central; pigment granules average 15 per parasite; immature gametocyte with margins entire, but poles can be amoeboid.

Haemoproteus belopolskyi Valkiunas, 1989

TYPE HOST: *Hippolais icterina* (Sylviinae, MUSCICAPIDAE)

MACROGAMETOCYTE (Fig. 2, 4). Parasite circumnuclear (Fig. 4) but occasionally highly halteridial (Fig. 2); parasite of large size, occupying 80–85 % of the host erythrocyte, which is hypertrophied but in which the host cell nucleus is not displaced laterally; parasite nucleus round to ovoid, sub-terminal in location; pigment granules average 17 per parasite; volutin granules not seen; immature gametocyte with highly amoeboid margins.

Haemoproteus borgesi Tendeiro, 1947

TYPE HOST: *Campethera punctuligera* (PICIDAE)

MACROGAMETOCYTE (Fig. 2, 3). Redescribed by Greiner, Mandal & Nandi (1977). Parasite halteri-

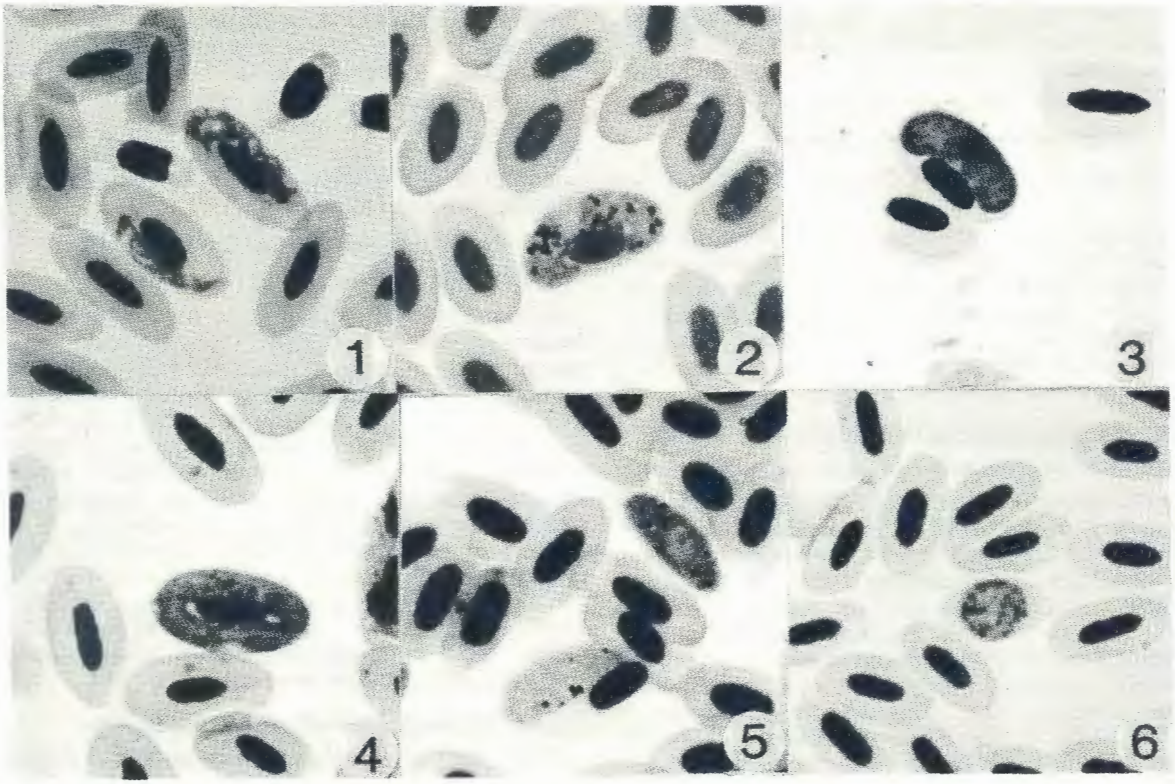


PLATE 2. Morphological forms of *Haemoproteus*. Fig. 1. Microhalteridial *(H. balearicae)*. Fig. 2. Halteridial *(H. indicator)*. Fig. 3. Halteridial *(H. halcyonis)*. Fig. 4. Circumnuclear *(H. janovyi)*. Fig. 5. Rhabdosomal (rod-like) *(H. enucleator)*. Fig. 6. Discoid (in New World birds only) *(H. parus)*.

dial with margins entire; parasite normally displaces erythrocyte nucleus laterally and causes hypertrophy of the host erythrocyte; parasite nucleus round to triangular, terminal to sub-terminal; pigment granules average 12 per parasite; immature gametocytes with margins entire.

***Haemoproteus bubalornis* Bennett & Peirce, 1991 (1991b)**

TYPE HOST: *Bubalornis albirostris* (BUBALORNITHIDAE)

MACROGAMETOCYTE (Fig. 2, 3). Parasite halteridial with margins entire; parasite displaces erythrocyte nucleus laterally and can cause some degree of hypertrophy of the host cell; parasite nucleus round to ovoid, medial to sub-medial in location; pigment granules average 8 per parasite; immature gametocytes with margins entire.

Haemoproteus celli: Synonym of *Haemoproteus noctuae* and/or *Haemoproteus syrnii.*

***Haemoproteus centropi* de Mello, 1936**

TYPE HOST: *Centropus sinensis* (CUCULIDAE)

MACROGAMETOCYTE (Fig. 2, 3). Redescribed by Peirce (1977). Parasite halteridial with margins entire; parasite can cause lateral displacement of erythrocyte nucleus and can cause some hypertrophy of the host cell; parasite nucleus central to subcentral, round to ovoid; pigment granules average 14 per parasite; volutin granules rarely present; immature gametocyte with margins entire. SYNONYM: *Haemoproteus froilanoi* Tendeiro, 1947.

***Haemoproteus chloris* Covaleda Ortega & Gallego Berenguer, 1950**

TYPE HOST: *Carduelis chloriis* (Carduelinae, EMBERIZIDAE)

MACROGAMETOCYTE (Fig. 2). Parasite halteridial with margins entire, causing some lateral displacement of erythrocyte nucleus and hypertrophy of the host cell; parasite nucleus central to subcentral, round to ovoid; pigment granules average 20 per parasite; margins of immature gametocyte entire.

***Haemoproteus columbae* Kruse, 1890**

TYPE HOST: *Columba livia* (COLUMBIDAE)

MACROGAMETOCYTE (Fig. 2, 3). Redescribed by Bennett & Peirce (1990a). Parasite halteridial occupying 50–65 % of the host erythrocyte; parasite can vary from slightly halteridial to almost circumnuclear and causes little host cell hypertrophy but does cause lateral displacement of erythrocyte nucleus; parasite nucleus median, compact, round to avoid; pigment granules average 27 per parasite (note: average only 13 per microgametocyte, one of the few haemoproteids in which the granule numbers differ between the sexes); volutin granules frequently present, obscuring the true pigment granules; parasites frequently highly vacuolate; immature gametocytes

with entire margins but poles of the parasites frequently amoeboid and extended into slender filaments. SYNONYMS: *Haemoproteus maccallumi* Novy & MacNeal, 1904; *H. palumbis* Baker, 1966.

Haemoproteus contortus Bennett, 1979

TYPE HOST: *Numenius phaeopus* (SCOLOPACIDAE)

MACROGAMETOCYTE (Fig. 4). Parasite circumnuclear with highly amoeboid outline; parasite causes only slight hypertrophy of the host erythrocyte and little lateral displacement of the host cell nucleus; parasite nucleus round to ovoid, central; pigment granules small, averaging 24 per parasite; immature gametocytes with amoeboid margins.

Haemoproteus coraciae de Mello & Afonso, 1935

TYPE HOST: *Coracias benghalensis* (CORACIIDAE)

MACROGAMETOCYTE (Fig. 2, 3). Redescribed by Bishop & Bennett (1986). Parasite halteridial with margin entire; displacing host erythrocyte nucleus somewhat laterally but causing slight hypertrophy of the host cell; parasite nucleus round to ovoid, central to sub-central; pigment granules large, averaging 8 per parasite; immature gametocytes with markedly amoeboid margins. SYNONYMS: *Haemoproteus coraciae* var. *benghalensis* de Mello & Afonso, 1935; *H. cruzferreirae* Tendeiro, 1947a; *H. fontesi* Tendeiro, 1947a; *H. fontesi* var. *cyanogaster* Tendeiro, 1947a; *H. velascoi* Tendeiro, 1947a.

Haemoproteus cornuata Bennett & Nandi, 1981

TYPE HOST: *Megalaima asiatica* (CAPITONIDAE)

MACROGAMETOCYTE (Fig. 3). Parasite of large size, broadly sausage shaped and halteridial, with ends of the parasite reflexing to form a deep invagination at the inner lateral margins of the parasite adjacent to the erythrocyte nucleus, thus forming a pair of "horns"; parasite occupying 68 % of the host-cell which is slightly hypertrophic with the host cell nucleus displaced laterally; parasite nucleus small, compact, ovoid, usually median or submedian in position; parasite cytoplasm coarsely granular with average of 28 small granules; immature gametocytes with margins entire.

Haemoproteus crumenium Hirst, 1905

TYPE HOST: *Leptoptilos crumeniferus* (CICONIIDAE)

MACROGAMETOCYTE (Fig. 3). Redescribed by Peirce & Cooper (1977a). Parasite broadly halteridial with margins entire; parasite slightly displaces host erythrocyte nucleus laterally and causes slight hypertrophy of the host cell; parasite nucleus ovoid, sub-central to terminal; pigment granules large, averaging 11 per parasite; immature gametocytes with amoeboid margins. SYNONYM: *Haemoproteus brodkorbi* Forrester, Greiner, Bennett & Kigaye, 1977; Peirce, 1987.

Haemoproteus cublae Peirce, 1984

TYPE HOST: *Dryoscopus cubla* (Malaconotinae, LANIIDAE)

MACROGAMETOCYTE (Fig. 2). Parasite halteridial, filling 50–65 % of host erythrocyte which is only slightly hypertrophied; erythrocyte nucleus rarely displaced laterally but occasionally slightly rotated on its axis; parasite nucleus round to triangular, medially located and usually appressed to the outer margin; pigment granules small, averaging 16 per parasite; volutin granules, when present, tend to concentrate at the poles; immature gametocytes with slightly amoeboid margins.

Haemoproteus danilewskyi Kruse, 1890

TYPE HOST: *Corvus corone* (CORVIDAE)

MACROGAMETOCYTE (Fig. 2, 4). Redescribed by Bishop & Bennett (1990). Parasite large, either nearly circumnuclear or markedly halteridial; occupying 75 % or more of host erythrocyte but causing little host cell hypertrophy and only slight lateral displacement of erythrocyte nucleus; cytoplasm coarsely granular with small vacuoles; parasite nucleus compact, round, ovoid or irregular and medially located; pigment granules averaging 23, but on occasion in clumps thus appearing as only a few large granules; immature with margins entire. SYNONYMS: *Plasmodium danilewskyi* (Grassi & Feletti, 1890); *Halteridium danilewskyi* (Kruse, 1890), Labbé, 1894; *H. corvi* Bhatia, 1938; *H. danilewskyi* var. *cairogensis* Helmy Mohammed, 1958.

Haemoproteus dicruri de Mello, 1936

TYPE HOST: *Dicrurus macrocercus* (DICRURIDAE)

MACROGAMETOCYTE (Fig. 2). Redescribed by Peirce (1984c). Parasite halteridial, filling 50–65 % of host erythrocyte and causing little hypertrophy of the host erythrocyte or lateral displacement of its nucleus; parasite nucleus round, medially located; pigment granules average 15 per parasite; volutin granules sometimes present; immature gametocyte with margins entire.

Haemoproteus elani de Mello, 1936

TYPE HOST: *Elanus caeruleus* (ACCIPITRIDAE)

MACROGAMETOCYTE (Fig. 2). Redescribed by Peirce, Bennett & Bishop (1990). Parasite normally halteridial but highly pleomorphic, with some individuals almost circumnuclear; parasite of moderate size, filling 60–70 % of the host erythrocyte where it causes little hypertrophy but does displace the host cell nucleus laterally; parasite nucleus compact, round and centraly located; pigment granules prominent, averaging 15 per parasite; volutin granules rarely seen but if present, concentrated at the poles; immature gametocytes with margins entire. SYNONYMS: *Haemoproteus buteonis* Wingstrand, 1947; *H. circus* Yakunin & Zhazyltaev, 1977; *H. figueiredoi* Travassos Santos Dias, 1953.

Haemoproteus enucleator Bennett, Okia, Ashford & Campbell, 1972

TYPE HOST: *Ispidina picta* (ALCEDINIDAE)

MACROGAMETOCYTE (Fig. 5). Parasite rhabdosomal (rod-like) in erythrocyte in which the host cell nucleus has been eliminated, (hence the trivial name of "enucleator"); parasite causes extensive hypertrophy (in length) of the host erythrocyte but not in width; parasite nucleus round, compact and centrally located; pigment granules average 15 per para-

site; volutin granules not seen; immature gametocyte with margins entire in erythrocytes with the host cell nucleus located towards one pole just prior to enucleation of the host erythrocyte; parasite known only from the type host throughout eastern Africa from Ethiopia to Tanzania and Uganda.

***Haemoproteus eurystomae* Bishop & Bennett, 1986**

TYPE HOST: *Eurystomus orientalis* (CORACIIDAE)

MACROGAMETOCYTE (Fig. 2, 3). Parasite halteridial with slightly amoeboid poles; parasite of medium to large size, occupying 65–75 % of the host erythrocyte, in which the host cell is little hypertrophied but whose nucleus is displaced laterally towards the periphery; parasite nucleus dense, round to ovoid, centrally located; pigment granules average 23 per parasite; immature gametocyte with margins entire.

***Haemoproteus fallisi* Bennett & Campbell, 1972**

TYPE HOST: *Turdus migratorius* (Turdininae, MUSCICAPIDAE)

MACROGAMETOCYTE (Fig. 1). Redescribed by Bennett, Bishop & Peirce (1991a). Parasite microhalteridial, occupying 50 % or less of host erythrocyte which is not hypertrophied and the host cell nucleus is not displaced laterally; margins of parasite entire but poles can be amoeboid; parasite nucleus round to triangular, terminal to sub-terminal in location; pigment granules average 15 per parasite; immature gametocyte with margins amoeboid. SYNONYM: *Haemoproteus attenuatus* Valkiunas, 1989.

Haemoproteus figueiredoi: Synonym of *Haemoproteus elani.*

***Haemoproteus fringillae* (Labbé, 1894)**

TYPE HOST: *Fringilla coelebs* (FRINGILLIDAE)

MACROGAMETOCYTE: (Fig. 2, 3). Redescribed by Peirce (1984a). Parasite halteridial with margins entire; parasite of medium size occupying 65–75 % of the host erythrocyte which is only slightly hypertrophied; host cell nucleus usually displaced slightly but single parasites displace nucleus to the periphery; parasite nucleus round or oval located centrally or subcentrally; pigment granules elongated and prominent averaging 13 per parasite; parasite often constricted centally; immature gametocyte with entire margins.

***Haemoproteus fusca* Bennett & Campbell, 1973**

TYPE HOST: *Halcyon chloris* (ALCEDINIDAE)

MACROGAMETOCYTE (Fig. 4). Parasite circumnuclear, filling 85–95 % of the available space in the host erythrocyte which is somewhat hypertrophied in all dimensions; host cell nucleus not displaced laterally; parasite nucleus round to ovoid, centrally located; pigment granules dust-like, averaging 34 per parasite; volutin granules rare; immature gametocyte with margins entire.

***Haemoproteus gallinulae* de Mello, 1936**

TYPE HOST: *Gallinula chloropus* (RALLIDAE)

MACROGAMETOCYTE (Fig. 2). Parasite halteridial, of medium size, occupying 60–70 % of the host erythrocyte; parasite with margins entire; parasite hypertrophies the host erythrocyte and displaces the host nucleus laterally; parasite nucleus round, compact, centrally located; pigment granules small and dust-like, averaging 32 per parasite; immature gametocytes with margins entire.

***Haemoproteus halcyonis* de Mello, 1936**

TYPE HOST: *Halcyon smyrnensis* (ALCEDINIDAE)

MACROGAMETOCYTE (Fig. 2, 3). Parasite large, occupying 75–85 % of the host erythrocyte; parasite halteridial, displacing host cell nucleus laterally to the periphery and causing considerable hypertrophy in all dimensions; parasite nucleus round, median; pigment granules average 24 per parasite; volutin granules frequently encountered, randomly distributed throughout parasite; immature gametocyte with margins entire.

***Haemoproteus hartmanni* Babudieri, 1931**

TYPE HOST: *Egretta intermedia* (ARDEIDAE)

MACROGAMETOCYTE (Fig. 1). Parasite microhalteridial with margins entire, occupying 50 % or less of the host erythrocyte which is not hypertrophied and in which the host cell nucleus is not laterally displaced; parasite nucleus round, sub-terminal; pigment granules large, averaging 11 per parasite; immature gametocytes with margins entire. NOTE: this parasite needs redescription.

***Haemoproteus indicator* Bennett, Caines & Whiteway, 1986**

TYPE HOST: *Indicator indicator* (INDICATORIDAE)

MACROGAMETOCYTE (Fig. 2, 3). Parasite halteridial with margins entire, occupying 70–85% of the host erythrocyte which suffers severe hypertrophy in all dimensions and also a certain degree of lateral displacement of the host cell nucleus; parasite nucleus round, centrally located; pigment granules dust-like, averaging 42 per parasite (NOTE: 24 per microgametocyte; this is another haemoproteid species in which the pigment granule numbers differs between the sexes); volutin granules not seen; immature parasites with margins entire.

***Haemoproteus janovyi* Greiner & Mundy, 1979**

TYPE HOST: *Gyps africanus* (ACCIPITRIDAE)

MACROGAMETOCYTE (Fig. 4). Redescribed by Peirce *et al.*, (1990). Parasite broadly halteridial to, more normally, circumnuclear; parasite large, occupying 80–90 % of the host erythrocyte but causing minimal host cell hypertrophy and little lateral displacement of the host cell nucleus; margins normally entire in most individuals but poles amoeboid in some individuals; pigment granules prominent, averaging 15 per parasite; parasite nucleus compact, central; volutin granules rare but when present, concentrated at the poles; immature gametocyte with margins entire.

***Haemoproteus killangoi* Bennett & Peirce, 1981**

TYPE HOST: *Zosterops senegalensis* (ZOSTEROPIDAE)

MACROGAMETOCYTE (Fig. 1). Parasite microhalteridial, occupying 50 % or less of the host erythro-

cyte which is neither hypertrophied nor has its nucleus displaced laterally; parasite margins entire but poles amoeboid; parasite nucleus round to ovoid, sub-terminal; pigment granules large and prominent, averaging 9 per parasite; volutin granules rare; immature gametocyte with amoeboid margins.

***Haemoproteus lairdi* Bennett, 1978**

TYPE HOST: *Merops variegatus* (MEROPIDAE)

MACROGAMETOCYTE (Fig. 5). Parasite rhabdosomal, filling most of the host erythrocyte from which the host cell nucleus has been ejected; in addition to the enucleation of the host erythrocyte, the parasite causes considerable hypertrophy in the length and area of the host cell; parasite with margins entire; parasite nucleus round, compact and medially located; pigment granules average 17 per parasite; immature gametocytes with entire margins located in erythrocytes in which the host nucleus is displaced markedly towards one pole.

***Haemoproteus lanii* de Mello, 1936**

TYPE HOST: *Lanius schach* (Laniinae, LANIIDAE)

MACROGAMETOCYTE (Fig. 2). Redescribed by Bennett, Peirce & Earlé (1990). Parasites halteridial with entire margins; parasites of medium size, occupying 60–75 % of host erythrocyte which is rarely hypertrophied or otherwise distorted; parasite nucleus round, dense and median to sub-median in position; pigment granules large and prominent, averaging 12 per parasite; volutin granules rarely seen; immature gametocyte with margins entire.

***Haemoproteus lari* (Yakunin, 1972) emend. Levine, 1985**

TYPE HOST: *Larus* sp.—possibly *L. ridibundus* (LARIIDAE)

MACROGAMETOCYTE (Fig. 2). Redescribed by Peirce (1981b). Parasite halteridial with margins entire; parasite of medium size, occupying up to 65 % of the host erythrocyte which is not markedly hypertrophied nor whose nucleus is displaced laterally; parasite nucleus round, central to sub-centrally located; pigment granules average 15 per parasite; volutin granules not seen; immature gametocyte with margins entire.

***Haemoproteus macropigmentatus* (Covaleda Ortega & Gallego Berenguer, 1950**

TYPE HOST: *Carduelis carduelis* (Carduelinae, EMBERIZIDAE)

MACROGAMETOCYTE (Fig. 2). Parasite halteridial with margins entire; parasite of medium size, occupying 60–70 % of the host erythrocyte which is slightly hypertrophied and has its nucleus displaced slightly laterally; parasite nucleus round, centrally located; pigment granules large and prominent (hence the trivial name "macropigmentatus"), averaging 9 granules per parasite; volutin granules rare; immature gametocyte with margins entire.

***Haemoproteus manwelli* Bennett, 1978**

TYPE HOST: *Merops orientalis* (MEROPIDAE)

MACROGAMETOCYTE (Fig. 2, 3). Parasite halteridial with margins entire; parasite of medium size which displaces erythrocyte nucleus to the lateral margin and causes hypertrophy in all dimensions; parasite nucleus round, centrally located; pigment granules large, averaging 10 per parasite; immature parasite with margins entire.

***Haemoproteus meropis* Zargar, 1945 emend. Bennett, 1978**

TYPE HOST: *Merops orientalis* (MEROPIDAE)

MACROGAMETOCYTE (Fig. 2, 3). Redescribed by Bennett (1978). Parasite large, halteridial with margins entire; parasite rarely displaces host erythrocyte nucleus laterally or causes major hypertrophy of the host cell; parasite nucleus round and central to subcentral in location; pigment granules prominent, averaging 14 per parasite; immature gametocyte with amoeboid outlines.

***Haemoproteus montezi* Travassos Santos Dias, 1953**

TYPE HOST: *Tauraco porphyriolophus* (MUSOPHAGIDAE)

MACROGAMETOCYTE (Fig. 2). Redescribed by Bennett & Peirce (1991a). Parasite halteridial with margins entire; parasite of medium size, occupying 50–60 % of the host erythrocyte which is not markedly hypertrophied and whose nucleus is only slightly displaced laterally; parasite nucleus round to ovoid, terminal to sub-terminal in position; pigment granules average 18 per parasite; immature gametocyte with margins entire.

***Haemoproteus motacillae* Bennett & Peirce, 1990, (1990b)**

TYPE HOST: *Motacilla flava* (MOTACILLIDAE)

MACROGAMETOCYTE (Fig. 2.). Parasite halteridial but with pronounced central constriction giving the parasite a bilobed or dumbbell appearance; parasite of small to medium size, occupying 55–60 % of the host erythrocyte in which it causes little hypertrophy or lateral displacement of the host cell nucleus; parasite nucleus compact, round to ovoid and terminal to sub-terminal in location; pigment granules average 14 per parasite; immature gametocyte with highly amoeboid margins.

***Haemoproteus nascimentoi* Tendeiro, 1947 (1947a)**

TYPE HOST: *Vanellus (=Sarciophorus) vanellus* (CHARADRIIDAE)

MACROGAMETOCYTE (Fig. 2, 3). Parasite halteridial with margins entire; parasite of medium size, occupying about 65 % of the host erythrocyte which is only slightly hypertrophied and whose nucleus is only slightly displaced laterally; parasite nucleus round, terminal to sub-terminal; pigment granules average 15 per parasite; immature gametocyte with margins entire.

***Haemoproteus nettionis* (Johnston & Cleland, 1909) Coatney, 1936**

TYPE HOST: *Anas (=Nettion) castaneum* (ANATIDAE)

MACROGAMETOCYTE (Fig. 2, 3). Parasite redescribed by Williams & Bennett (1980). Parasite halteridial with margins entire; parasite of medium to large size, occupying 65–85 % of the host erythro-

cyte which is hypertrophied in all dimensions and whose nucleus is displaced laterally to the periphery of the host cell; parasite nucleus round to ovoid; centrally located; pigment granules average 23 per parasite; volutin granules rarely encountered; immature gametocyte with margins entire.

***Haemoproteus nisi* Peirce & Marquiss, 1983**

TYPE HOST: *Accipiter nisi* (ACCIPITRIDAE)

MACROGAMETOCYTE (Fig. 2, 4). Redescribed by Peirce *et al.* (1990). Parasite usually halteridial but occasionally circumnuclear, with margins of parasite highly amoeboid; parasite of moderate size, filling 60–75 % of the host erythrocyte, causing some hypertrophy of the host erythrocyte but little lateral displacement of the host cell nucleus; parasite nucleus compact, round to ovoid, located centrally; pigment granules large, averaging 14 per parasite; volutin granules frequently encountered, randomly distributed throughout the parasite, concealing the true pigment granules; immature gametocyte with highly amoeboid margins.

***Haemoproteus noctuae* Celli & Sanfelice, 1891**

TYPE HOST: *Athene noctua* (STRIGIDAE)

MACROGAMETOCYTE (Fig. 4). Redescribed by Bishop & Bennett (1989). Parasite circumnuclear with highly amoeboid margins; parasites moderate to large in size, occupying 60–75 % of the host erythrocyte where it causes some hypertrophy of the host cell but no displacement of the host cell nucleus; parasite nucleus round, medially located; pigment granules average 20 per parasite; volutin granules occasionally encountered; immature gametocyte with highly amoeboid margins. SYNONYMS: *Haemoproteus bramae* de Mello, 1936; *H. glaucidi* de Mello, 1936; *H. nebraskensis* (Coatney & Roudabush, 1937) Levine & Campbell, 1971; *H. celli* (Coatney & Roudabush, 1937) Helmy Mohammed, 1958.

***Haemoproteus orioli* de Mello, 1936**

TYPE HOST: *Oriolus oriolus* (ORIOLIDAE)

MACROGAMETOCYTE (Fig. 2). Redescribed by Peirce (1984c). Parasite halteridial with margins entire; parasite of moderate size, occupying 60–70 % of the host erythrocyte which is only slightly hypertrophied but in which the host cell nucleus is somewhat displaced laterally; parasite nucleus round, central to sub-centrally located; pigment granules average 21 per parasite (NOTE: average 14 per microgametocyte); volutin granules not normally encountered; immature gametocyte with margins entire.

***Haemoproteus orizivorae* Anschutz, 1909**

TYPE HOST: *Padda (=Lonchura) orizivora* (PASSERIDAE)

MACROGAMETOCYTE (Fig. 3). Redescribed by Bennett & Peirce (1991b). Parasite halteridial with entire margins and of medium to large size occupying 75–80 % of the area of the host erythrocyte and causing hypertrophy of host cell; parasite nucleus large and round to ovoid or broadly triangular located on the outer margin of the parasite; pigment granules small, averaging 25 per parasite; volutin granules uncommon; immature gametocyte with margins entire. SYNONYMS: *Haemoproteus paddae* Brumpt, 1935; *H. garnhami* Grewal, 1964; *H. lonchuri* Bandyopadhyay & Haldar, 1988.

***Haemoproteus otocompsae* de Mello, 1936**

TYPE HOST: *Pycnonotus jocosus* (PYCNONOTIDAE)

MACROGAMETOCYTE (Fig. 2). Redescribed by Rahal, Bishop & Bennett (1987). Parasite halteridial with margins entire; parasite of moderate size, filling 60–70 % of the host erythrocyte which is slightly hypertrophied and whose nucleus is slightly displaced laterally; parasite nucleus round to ovoid, central to sub-centrally located; pigment granules large and prominent, averaging 10 per parasite; volutin granules, if present, located at the poles; immature gametocyte with margins entire.

***Haemoproteus passeris* Kruse, 1890**

TYPE HOST: *Passer hispaniolensis* (PASSERIDAE)

MACROGAMETOCYTE (Fig. 2, 3). Redescribed by Bennett & Peirce (1991b). Parasite halteridial with margins entire; parasite of medium to large size occupying 75 % of the host erythrocyte which is hypertrophied in all dimensions and the host cell nucleus is displaced laterally towards the margin; parasite nucleus compact, round to ovoid, terminal to sub-terminally located; pigment granules large and prominent, averaging 13 per parasite; volutin granules commonly encountered and when present, clumped at the poles; immature gametocyte with margins entire. HOMONYM: *Haemoproteus wenyoni*, Sergent & Sergent, 1948. SYNONYMS: *Haemoproteus danilewskyi* var. *urbanensis* Sachs, 1953; *H. garnhami* Grewal, 1964; *H. granulosum* Rey Vila, 1945; *H. gymnorhidis* de Mello, 1936; *H. zasukhini* Burtkashvili, 1973.

***Haemoproteus pastoris* de Mello, 1936**

TYPE HOST: *Sturnus (=Pastor) roseus* (STURNIDAE)

MACROGAMETOCYTE (Fig. 2, 3). Redescribed by Bishop & Bennett (1990). Parasite halteridial with margins entire; parasite of medium size, occupying 60–70 % of the host erythrocyte which is slightly hypertrophied and whose nucleus is slightly displaced laterally; parasite nucleus round, centrally located; pigment granules large and prominent, averaging 10 per parasite; volutin granules, when present, randomly distributed; immature gametocyte with margins entire. SYNONYMS: *Haemoproteus morneti* Tendeiro, 1947; *H. sturni* de Mello, 1936.

***Haemoproteus peircei* Forrester, Greiner, Bennett & Kigaye, 1977**

TYPE HOST: *Ephippiorhynchus senegalensis* (CICONIIDAE)

MACROGAMETOCYTE (Fig. 4). Parasite broadly halteridial (as in Fig. 3, microgametocyte only) to circumnuclear (macrogametocyte), with margins entire; parasite pleomorphic, the halteridial form causing considerable hypertrophy and lateral dis-

placement of erythrocyte nucleus; parasite nucleus central; pigment granules numerous.

***Haemoproteus pelouroi* Tendeiro, 1947**

TYPE HOST: *Bostrychia (=Hagadashia) hagedash* (THRESKIORNITHIDAE)

MACROGAMETOCYTE (Fig. 1.). Redescribed by Bennett, Greiner & Campbell (1975). Parasite microhalteridial with margins amoeboid; parasite of small size, occupying 50 % or less of the host erythrocyte, which is not hypertrophied and whose nucleus is not displaced laterally; parasite nucleus round to triangular, terminal to sub-terminal in location; pigment granules large and prominent, averaging 10 per parasite; immature gametocyte with amoeboid margins.

***Haemoproteus philippinensis* Rahal, Bishop & Bennett, 1987**

TYPE HOST: *Hypsipetes flavala* (PYCNONOTIDAE)

MACROGAMETOCYTE (Fig. 1). Parasite microhalteridial, with marked central constriction closely appressed to length of erythrocyte nucleus and poles inflated as bulbs; margins entire; parasite nucleus ovoid, sub-terminal; pigment granules large, averaging 8 per parasite; immature gametocytes with margins entire.

***Haemoproteus phodili* Bishop & Bennett, 1989**

TYPE HOST: *Phodilus badius* (TYTONIDAE)

MACROGAMETOCYTE (Fig. 2). Parasite halteridial with margins entire and frequently with a slender central portion presenting a bilobed or dumbbell appearance; parasite of medium size, filling 55–65 % of host erythrocyte which is only slightly hypertrophied and in which the host cell nucleus is only slightly displaced laterally; parasite nucleus round, terminal to sub-terminal in location; pigment granules average 14 per parasite; volutin granules rarely encountered; immature gametocyte with margins entire.

***Haemoproteus plataleae* de Mello, 1936**

TYPE HOST: *Platalea leucoridia* (THRESKIORNITHIDAE)

MACROGAMETOCYTE (Fig. 2, 3). Redescribed by Bennett *et al.* (1975). Parasite broadly halteridial, varying from thick sausage-shape to slender and highly halteridial; parasite of large size, filling most of the host erythrocyte which is grossly hypertrophied in all dimensions and whose nucleus is displaced to the margin of the host cell; parasite nucleus round, centrally located; pigment granules small and dust-like and difficult to see, averaging 45 granules per parasite; volutin granules, when present, concentrated at the poles and conceal true pigment granules; immature gametocyte with margin entire. SYNONYM: *Haemoproteus galathea* Laird & Laird, 1959.

***Haemoproteus porzanae* Galli-Valerio, 1907**

TYPE HOST: *Porzana pusilla* (RALLIDAE)

MACROGAMETOCYTE (Fig. 1). Redescribed by Bennett (1980). Parasite microhalteridial with margins entire but poles amoeboid, centre portion thin causing the parasite to present a bilobed appearance; parasite of small size, occupying 50 % or less of the host erythrocyte which is not hypertrophied and whose nucleus is not displaced laterally; parasite nucleus round to ovoid, terminal to sub-terminal in location; pigment granules large and prominent, averaging 10 per parasite; immature gametocytes with margins entire.

***Haemoproteus pratasi* Tendeiro, 1947**

TYPE HOST: *Numida meleagris* (Numidinae, PHASIANIDAE)

MACROGAMETOCYTE (Fig. 2, 3). Redescribed by Bennett & Peirce (1989a). Parasite broadly halteridial with margins entire; parasite of large size, occupying 70–80 % of the host erythrocyte, causing little host cell hypertrophy but displacing the host cell nucleus laterally; parasite nucleus large, dense and ovoid, centrally placed; pigment granules average 19 per parasite; volutin granules frequently present, and when present, usually clumped at the poles of the parasite; immature gametocyte with amoeboid margins.

***Haemoproteus prognei* Coatney & Roudabush, 1937**

TYPE HOST: *Progne subis* (HIRUNDINIDAE)

MACROGAMETOCYTE (Fig. 2, 3). Redescribed by White & Bennett (1978). Parasite halteridial with margins entire; parasite of small to moderate size, occupying 55–65 % of the host erythrocyte which is not hypertrophied or whose nucleus is not displaced laterally; parasite nucleus round to ovoid, central to sub-central in position; pigment granules large, averaging 13 per parasite; immature gametocyte with margins entire.

***Haemoproteus quelea* (Marullaz, 1912) Coatney, 1936**

TYPE HOST: *Quelea erythrops* (PLOCEIDAE)

MACROGAMETOCYTE (Fig. 2, 3). Redescribed by Bennett & Peirce (1991b). Parasite halteridial with margins entire; parasite of medium size, occupying 70–75 % of host erythrocyte, causing some hypertrophy and markedly displacing the host nucleus laterally to the margin; parasite nucleus round to ovoid, medial to sub-medial in location; pigment granules average 18 per parasite; volutin granules rarely encountered; immature gametocyte with margins entire.

***Haemoproteus rileyi* Malkani, 1936**

TYPE HOST: *Pavo cristatus* (Phasianinae, PHASIANIDAE)

MACROGAMETOCYTE (Fig. 2). Redescribed by Bennett & Peirce (1989a). Parasite halteridial with margins entire; parasite of large size, occupying 75–80 % of the host erythrocyte which is not grossly hypertrophied and in which the host cell nucleus is markedly displaced laterally; nucleus of parasite round and medially located; pigment granules large, prominent and average 11 per parasite; volutin granules not usually encountered, but if present, numerous; immature gametocytes with margins amoeboid. SYNONYMS *Haemoproteus ammoperdis* Subkhonov, 1980; *H. bambusicolae* Manwell, Allen

& Kuntz, 1976; *H. chapini* van den Berghe, Chardome & Peel, 1963; *H. santosdiasi* Son, 1960.

Haemoproteus rotator Bennett, 1979

TYPE HOST: *Capella stenura* (SCOLOPACIDAE)

MACROGAMETOCYTE: Parasite pleomorphic, broadly U-shaped about the erythrocyte nucleus which is rotated through 45–90° about its axis in 65 % of all mature gametocytes; parasite occupying 85 % of host erythrocyte which is slightly hypertrophied; erythrocyte nucleus markedly atrophied; parasite cytoplasm coarsely granular with small pigment granules averaging 22,6 per parasite; immature gametocyte with entire margins.

Haemoproteus sanguinis Chakravarty & Kar, 1945

TYPE HOST: *Pycnonotus jocosus* (PYCNONOTIDAE)

MACROGAMETOCYTE (Fig. 1). Redescribed by Rahal *et al.*, (1987). Parasite microhalteridial with margins entire; parasite of small size occupying 55 % or less of the host erythrocyte and causing little hypertrophy or displacement of the host cell nucleus; parasite nucleus round, centrally located; pigment granules average 15 per parasite; volutin granules not usually encountered; immature gametocyte with margins entire.

Haemoproteus scolopaci Galli-Valerio, 1929

TYPE HOST: *Scolopax rusticola* (SCOLOPACIDAE)

MACROGAMETOCYTE (Fig. 2, 3). Redescribed by Bennett (1979). Parasite halteridial with margins entire; parasite of moderate size, occupying 60–70 % of the host erythrocyte which is only slightly hypertrophied and whose nucleus is only slightly displaced laterally; parasite nucleus round to ovoid; centrally located; pigment granules average 16 per parasite; volutin granules not normally encountered; immature gametocyte with margins entire.

Haemoproteus sequeirae Tendeiro, 1947

TYPE HOST: *Nectarinia coccinogaster* (NECTARINIIDAE)

MACROGAMETOCYTE (Fig. 2). Redescribed by Bennett, Peirce & Caines (1985). Parasite halteridial with margins entire; parasite of small to medium size, occupying 55–65 % of the host erythrocyte which is only slightly hypertrophied and whose nucleus is rarely displaced laterally; parasite nucleus round to ovoid, central to sub-centrally located; pigment granules large and prominent, averaging 7 per parasite; immature gametocyte with margins entire. SYNONYM: *Haemoproteus raymundi* de Mello, 1936.

Haemoproteus stellaris White & Bennett, 1978

TYPE HOST: *Pseudhirundo (=Hirundo) griseopyga* (HIRUNDINIDAE)

MACROGAMETOCYTE (Fig. 2). Parasite halteridial with margin entire; parasite of medium size, occupying 60–70 % of the host erythrocyte which is only slightly hypertrophied and whose nucleus is only slightly displaced laterally; parasite nucleus round, compact and located sub-terminally; pigment granules very large and prominent, averaging 2–3 per parasite and always arranged as a clump in star-shape at one pole (hence the trivial name "stellaris"); volutin granules not seen; immature gametocyte with margins entire.

Haemoproteus sturni: Synonym of *Haemoproteus pastoris.*

Haemoproteus sylvae Bennett, Bishop & Peirce, 1991 (1991a)

TYPE HOST: *Parisoma subcaeruleum* (Sylviinae, MUSCICAPIDAE)

MACROGAMETOCYTE (Fig. 2). Parasite halteridial, frequently dumbbell or bipolar in shape with margins entire; parasite of small to medium size, occupying 65 % of the host erythrocyte which is slightly hypertrophied in all dimensions, but the host cell nucleus is only displaced slightly laterally; parasite nucleus round to ovoid, terminal to sub-terminal in location; pigment granules prominent, averaging 10 per parasite; volutin granules not seen; immature gametocyte with margins amoeboid.

Haemoproteus syrnii (Keysselitz & Mayer, 1909) Bishop & Bennett, 1989

TYPE HOST: *Strix aluco* (STRIGIDAE)

MACROGAMETOCYTE (Fig. 2, 3). Parasite halteridial with margins entire; parasite of medium size occupying 60–65 % of the host erythrocyte which is slightly hypertrophied and the host cell nucleus is slightly displaced laterally; parasite nucleus oval to elongate, medially located; pigment granules average 21 per parasite; volutin granule frequently encountered, granules usually clumped at the poles; immature with margins entire. SYNONOMS: *Haemoproteus glaucidii* de Mello, 1936; *H. celli* (Coatney & Roudabush, 1937) Helmy Mohammed, 1958; *H. multiparasitans* Covaleda Ortega & Gallego Berenguer, 1950; *H. aegyptius* (Helmy Mohammed, 1958) Levine & Campbell, 1971.

Haemoproteus telfordi Bennett, Forrester, Greiner & Campbell, 1975

TYPE HOST: *Eupodotis melanogaster* (OTIDIDAE)

MACROGAMETOCYTE (Fig. 4). Parasite circumnuclear with margins entire; parasite of medium to large size, occupying 75–85 % of the host erythrocyte which is hypertrophied in area but in which the host cell nucleus is not displaced laterally; parasite nucleus round to triangular, centrally located; pigment granules average 17 per parasite; volutin granules uncommon; immature gametocyte with margins entire.

Haemoproteus tendeiroi Travassos Santos Dias, 1953

TYPE HOST: *Eupodotis melanogaster* (OTIDIDAE)

MACROGAMETOCYTE: (Fig. 3). Parasite broadly halteridial with margins entire occupying 70 % or more of the host erythrocyte; host cell nucleus displaced laterally usually to the periphery but erythrocyte only slightly hypertrophied; parasite cytoplasm coarse with prominent pigment granules averaging 17,5 per parasite; parasite nucleus broadly ovoid; immature gametocyte with margins entire.

Haemoproteus thereicerycis de Mello, 1935

TYPE HOST: *Thereiceryx zeylanica inornata* (CAPITONIDAE)

MACROGAMETOCYTE: (Fig. 3). Redescribed by Bennett & Nandi (1981). Parasite of large size, broadly sausage shaped to halteridial with margins entire. Occupying 75 % of host cell with host cell nucleus markedly displaced laterally in the hypertrophic cell. Sometimes the parasite enucleates the host erythrocyte. Parasite cytoplasm granular with small scattered pigment granules averaging 31 in number; nucleus medium sized, compact, dense, ovoid usually median or submedian in position; immature gametocytes with margins entire.

Haemoproteus timalus Bennett, Bishop & Peirce, 1991 (1991a)

TYPE HOST: *Turdoides rubiginosus* (TIMALIIDAE)

MACROGAMETOCYTE (Fig. 1). Parasite microhalteridial with margins entire but of small size, occupying 50–60 % or less of the host erythrocyte, which is only slightly hypertrophied and the host cell nucleus is not displaced laterally; parasite nucleus round to ovoid, terminal to sub-terminal in location; pigment granules average 11 per parasite clumped at poles; volutin granules when present at poles. Immature gametocyte with margins highly amoeboid.

Haemoproteus tinnunculi (Wasielewski & Wülker, 1918) Wingstrand, 1947

TYPE HOST: *Falco tinnunculus* (FALCONIDAE)

MACROGAMETOCYTE: (Fig. 3). Redescribed by Peirce *et al.*, (1990). Parasite broadly halteridial with margins entire; filling about 75 % of host erythrocyte but causing little host cell hypertrophy; host cell nucleus displaced somewhat laterally; parasite nucleus round to ovoid central to sub-centrally located; pigment granules averaging 23 per parasite, scattered but occasionally polar; immature gametocyte with margins entire. SYMONYM: *Haemoproteus cerchneisi* Bhatia, 1938.

Haemoproteus turtur: Synonym of *Haemoproteus columbae.*

Haemoproteus tytoni Bishop & Bennett, 1989

TYPE HOST: *Tyto alba* (TYTONIDAE)

MACROGAMETOCYTE (Fig. 4). Parasite circumnuclear with amoeboid margins; parasite of medium to large size, occupying 75–85 % of the host erythrocyte which is slightly hypertrophied, but the host cell nucleus is not displaced laterally; parasite nucleus round to ovoid, centrally located; pigment granules averae 22 per parasite; volutin granules can be present, scattered randomly throughout the parasite; immature gametocyte with margins amoeboid.

Haemoproteus uraeginthus Bennett & Peirce, 1991 (1991b)

TYPE HOST: *Uraeginthus bengalus* (ESTRILDIDAE)

MACROGAMETOCYTE (Fig. 5). Parasite rhabdosomal, with margins entire; parasite of small size in a host erythrocyte which is grossly hypertrophied in all dimensions and from which the host cell has been eliminated; parasite nucleus round, compact and centrally located; pigment granules average 17 per parasite; volutin granules not seen; immature gametocyte with margin entire; parasite known only from the type host in the type locality of N'Djemena, Tchad.

Haemoproteus wenyoni de Mello, Braz da Sa, de Sousa, Dias & Noronha, 1916

TYPE HOST: *Orthotomus sutorius* (Sylviinae; MUSCICAPIDAE)

MACROGAMETOCYTE (Fig. 2, 3). Redescribed by Bennett, Bishop & Peirce (1991a). Parasite halteridial with margins entire; parasite medium to large in size, occupying 70–75 % of the host erythrocyte which is hypertrophied and the host cell nucleus is only slightly displaced laterally; parasite nucleus round to ovoid, sub-terminally located; pigment granules average 24 per parasite (NOTE: average 18 per microgametocyte); volutin granules rarely occur; immature gametocytes with margins highly amoeboid.

Haemoproteus xantholaemae (Zargar, 1945) amend. Levine & Campbell, 1971

TYPE HOST: *Xantholaema (=Megalaima) haemacephala* (CAPITONIDAE)

MACROGAMETOCYTE (Fig. 3). Parasite of medium size, narrow, slightly halteridial with entire margins; occupying 54 % of host cell; host cell only slightly hypertrophied with its nucleus displaced laterally; parasite cytoplasm finely granular with randomly scattered small granules averaging 19 in number; nucleus medium sized, compact, dense, ovoid usually median or submedian in position; immature gametocytes with entire margins.

Haemoproteus zosteropis Chakravarty & Kar, 1945

TYPE HOST: *Zosterops palpebrosus* (ZOSTEROPIDAE)

MACROGAMETOCYTE (Fig. 2, 3). Redescribed by Bennett and Peirce (1981). Parasite halteridial with margins entire; parasite of medium size, occupying 60–70 % of the host erythrocyte which is only slightly hypertrophied and the host cell nucleus is only slightly displaced laterally; parasite nucleus round to triangular, terminal to sub-terminal in position; pigment granules average 15 per parasite; volutin granules can occur; immature gametocyte with margins entire.

MORPHOLOGICAL FORM OF THE HAEMOPROTEIDS OF SUB-SAHARAN BIRDS (refer to Plate 2, Fig. 1–6).

Note: most frequently encountered form listed first; less frequently encountered forms are in parentheses

Fig. No.	*Haemoproteus* species	Host family
1	*balearicae*	GRUIDAE
1	*fallisi*	TURDIDAE
1	*hartmanni*	ARDEIDAE
1	*killangoi*	ZOSTEROPIDAE
1	*pelouroi*	THRESKIORNITHIDAE
1	*philippinensis*	PYCNONOTIDAE

1	*porzanae*	RALLIDAE
1	*sanguinis*	PYCNONOTIDAE
2 (4)	*alaudae*	ALAUDIDAE
2 (3)	*africanus*	ESTRILDIDAE
2	*anthi*	MOTACILLIDAE
2 (3)	*antigonis*	GRUIDAE
2 (3)	*balmorali*	Muscicapinae, MUSCICAPIDAE
2 (4)	*belopolskyi*	Sylviinae, MUSCICAPIDAE
2 (3)	*borgesi*	PICIDAE
2 (3)	*bubalornis*	BUBALORNITHIDAE
2 (3)	*centropi*	CUCULIDAE
2	*chloriis*	Carduelinae, FRINGILLIDAE
2 (3)	*columbae*	COLUMBIDAE
2 (3)	*coraciae*	CORACIIDAE
2 (3)	*crumenium*	CICONIIDAE
2	*cublae*	Malaconotinae, LANIIDAE
2	*dicruri*	DICRURIDAE
2	*elani*	ACCIPITRIDAE
2 (3)	*eurystomae*	CORACIIDAE
2	*gallinulae*	RALLIDAE
2 (3)	*halcyonis*	ALCEDINIDAE
2 (3)	*indicator*	INDICATORIDAE
2	*lanii*	Laniinae, LANIIDAE
2 (3)	*lari*	LARIDAE
2	*macropigmentatus*	Carduelinae, FRINGILLIDAE
2 (3)	*manwelli*	MEROPIDAE
2 (3)	*meropis*	MEROPIDAE
2	*montezi*	MUSOPHAGIDAE
2	*motacillae*	MOTACILLIDAE
2 (3)	*nascimentoi*	CHARDRIIDAE
2 (3)	*nettionis*	ANATIDAE
2 (4)	*nisi*	ACCIPITRIDAE
2	*orioli*	ORIOLIDAE
2	*otocompsae*	PYCNONOTIDAE
2 (3)	*passeris*	PASSERIDAE
2 (3)	*pastoris*	STURNIDAE
2	*phodili*	TYTONIDAE
2 (3)	*plataleae*	THRESKIORNITHIDAE
2 (3)	*pratasi*	Numidinae, PHASIANIDAE
2 (3)	*prognei*	HIRUNDINIDAE
2 (3)	*quelea*	PLOCEIDAE
2	*rileyi*	Phasianinae, PHASIANIDAE
2 (3)	*scolopaci*	SCOLOPACIDAE
2	*sequeirae*	NECTARINIIDAE
2	*stellaris*	HIRUNDINIDAE
2	*sylvae*	Sylviinae, MUSCICAPIDAE
2 (3)	*syrnii*	STRIGIDAE
2 (3)	*wenyoni*	Sylviinae, MUSCICAPIDAE
2 (3)	*zosteropis*	ZOSTEROPIDAE
4	*contortus*	SCOLOPACIDAE
4	*fusca*	ALCEDINIDAE
4	*janovyi*	ACCIPITRIDAE
4	*noctuae*	STRIGIDAE
4	*peircei*	CICONIIDAE
4	*tytoni*	TYTONIDAE
5	*enucleator*	ALCEDINIDAE
5	*lairdi*	MEROPIDAE
5	*uraeginthus*	EMBERIZIDAE
6	Discoid forms have not yet been recorded in sub-Saharan birds.	

AN ANNOTATED LIST OF THE SPECIES OF THE GENUS *LEUCOCYTOZOON* IN SUB-SAHARAN BIRDS

Note—all figure numbers refer to figures on Plate 3

Leucocytozoon anellobiae Cleland & Johnston, 1911 emend. Johnston, 1912

TYPE HOST: *Anthochaera (=Anellobia) chrysoptera* (MELIPHAGIDAE)

MACROGAMETOCYTE. Redescribed by Mackerras & Mackerras (1960). Parasite with a single morph, round to ovoid, as in Fig. 7 & 8; host cell nucleus covering approximately 75 % of the circumference of the parasite. Known only from Gurney's sugarbirds *(Promerops gurneyi)* in South Africa (Bennett & De Swardt, 1989)

Leucocytozoon ardeae Rodhain, Pons, Vandenbranden & Bequaert, 1913 (1913a)

TYPE HOST: *Ardea goliath* (ARDEIDAE)

MACROGAMETOCYTE. Parasite with a single morph, round to ovoid, as in Fig. 8 & 9; host cell nucleus covering 80–90 % of the circumference of the parasite. SYNONYMS: *Leucocytozoon ardeolae* de Mello, 1936; *L. iowense* Coatney, 1938; *L. sanarelli* Babudieri, 1931.

Leucocytozoon audieri: Synonym of *Leucocytozoon toddi*

Leucocytozoon bacelari: Synonym of *Leucocytozoon toddi*

Leucocytozoon balmorali Peirce, 1984

TYPE HOST: *Dryoscopus cubla* (Malaconotinae, LANIIDAE)

MACROGAMETOCYTE. Parasite with a single, round morph similar to that seen in Fig. 7 & 8; host cell nucleus covers approximately 30–40 % of the circumference of the parasite.

Leucocytozoon beaurepairei Travassos Santos Dias, 1954

TYPE HOST: *Sagittarius serpentarius* (SAGITTARIDAE)

MACROGAMETOCYTE. Parasite with two morphs; a round morph as in Fig. 8 in which the host cell nucleus covers approximately 50 % of the circumference of the parasite; a fusiform morph as in Fig. 12 which can be large, up to 67 µm in length. This species has only been recorded from the type host and the type locality on a single occasion.

Leucocytozoon brimonti Mathis & Leger, 1911

TYPE HOST: *Pycnonotus sinensis* (PYCNONOTIDAE)

MACROGAMETOCYTE. Parasite with a single morph, round, similar to Fig. 8 & 9; host cell nucleus covers approximately 50–60 % of the circumference of the parasite; parasite widespread throughout the distributional range of the Pycnonotidae. SYNONYM: *Leucocytozoon molpastis* de Mello, 1936.

Leucocytozoon caprimulgi Kerandel, 1913

TYPE HOST: *Caprimulgus fossii* (CAPRIMULGIDAE)

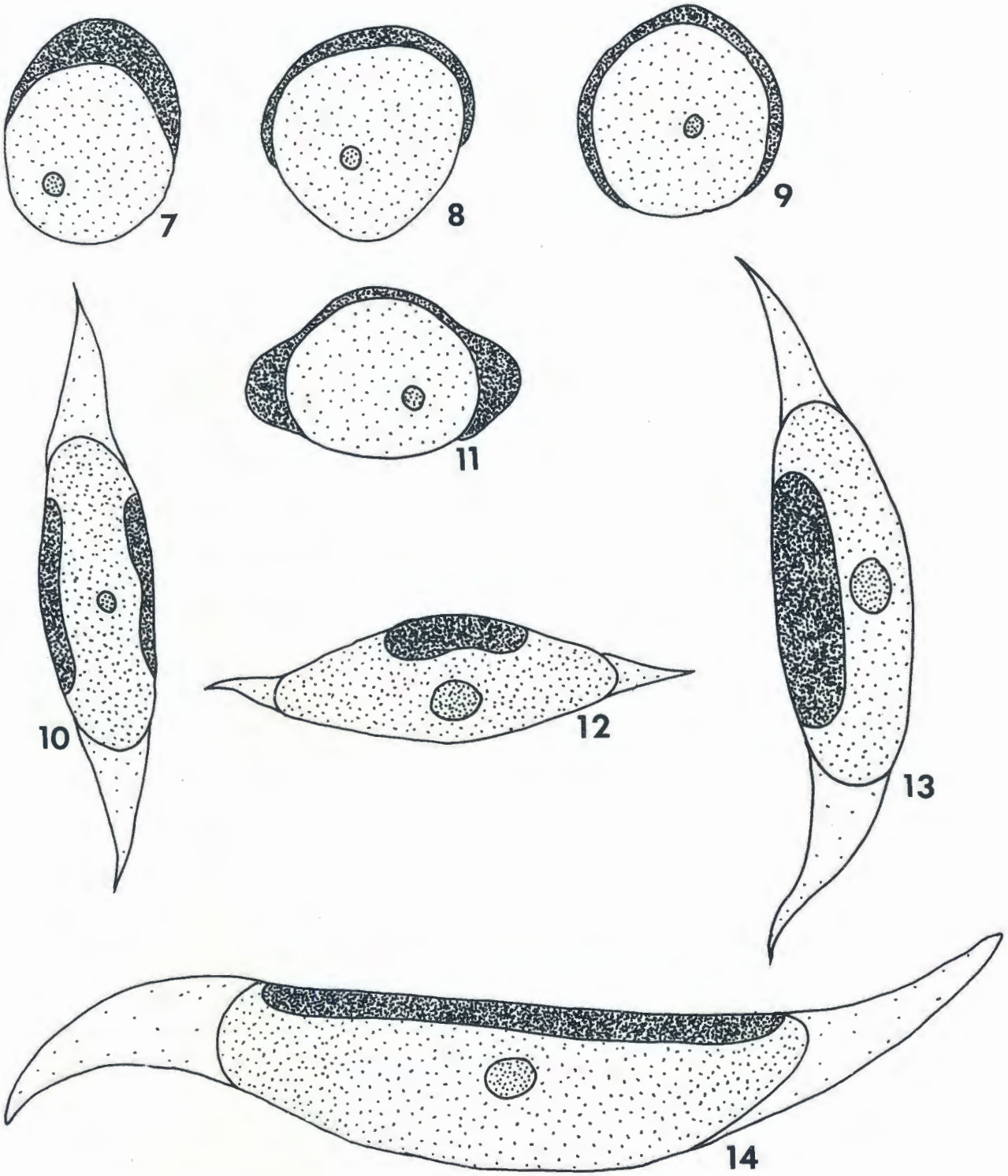


PLATE 3. Morphological forms of *Leucocytozoon*. Fig. 7. Round form with host cell nucleus as a pronounced cap. Fig. 8. Round form with host cell nucleus as a thin band covering approximately 50 % of the circumference of the parasite. Fig. 9. Round form with host cell nucleus as a thin band covering 80 % or more of the circumference of the parasite. Fig. 10. Fusiform parasite with host cell nucleus split into two portions. Fig. 11. Round form with host cell nucleus forming a pronounced double cap. Fig. 12. Fusiform parasite with host cell nucleus covering only small part of one side of the parasite. Fig. 13. Fusiform parasite with host cell nucleus covering most of one side of the parasite. Fig. 14. Large fusiform parasite with host cell nucleus covering entire side of parasite.

MACROGAMETOCYTE. Parasite with two morphs; a round morph as in Fig. 7–9 in which the host cell nucleus covers approximately 50 % of the circumference of the parasite; fusiform morph similar to Fig. 12 & 14; fusiform cell up to 40 µm in length.

***Leucocytozoon centropi* Fantham, 1926**

TYPE HOST: *Centropus superciliosus* (CUCULIDAE)

MACROGAMETOCYTE. Parasite with one morph which is round as in Fig. 7–9 and the host cell nucleus covers approximately 80 % of the circumference of the parasite. This parasite is closely similar to *L. coccyzus* Coatney & West, 1938 in appearance and size, differing primarily in the shape of the host cell nucleus and the extent to which it covers the circumference of the parasite; *L. coccyzus* is considered to be a synonym of *L. centropi*.

***Leucocytozoon dinizi* Tendeiro, 1947 (1947a)**

TYPE HOST: *Crinifer piscator* (MUSOPHAGIDAE)

MACROGAMETOCYTE. Parasite with a single, round to ovoid morph as in Fig. 7 & 8 in which the host cell nucleus is a cap-like structure or it can be less cap-like but extended as a thin band for 50–60 % of the circumference of the parasite. The parasite is limited to musophagids in Africa.

***Leucocytozoon dubreuili* Mathis & Leger, 1911**

TYPE HOST: *Turdus musicus* (Turdinae, MUSCICAPIDAE)

MACROGAMETOCYTE. Parasite with a single morph as in Fig. 11; parasite round to ovoid with host cell nucleus drawn out on both sides to form a double-capped structure (bipolar cap); the life cycle and redescription of this species together with the systematics of the leucocytozoids of the Turdinae were reported by Khan & Fallis (1970). Cosmopolitan parasite of thrushes. SYNONYMS: *Leucocytozoon francai* Nikitin, 1927; *L. giovannolai* Travassos Santos Dias, 1954; *L. mirandae* Franca, 1912; *L. shaartusicum* Subkhonov, 1980.

***Leucocytozoon eurystomi* Kerandel, 1913**

TYPE HOST: *Eurystomus glaucurus* (CORACIIDAE)

MACROGAMETOCYTE. Parasite with two morphs; one is a round parasite with the host cell nucleus forming a cap similar to, but not as pronounced, as in Fig. 7; the second is a fusiform cell as in Fig. 14; the fusiform morphs can be fairly large but normally are in the range of 35–40 µm; parasites of rollers in the Old World. SYNONYMS: *Leucocytozoon francae* Tendeiro, 1947; *L. leitaoi* Tendeiro, 1947.

***Leucocytozoon fringillinarum* Woodcock, 1910**

TYPE HOST: *Fringilla coelebs* (FRINGILLIDAE)

MACROGAMETOCYTE. Parasite with a single round morph as in Fig. 7, in which the host cell nucleus forms a cap covering about 50 % of the parasite circumference; a cosmopolitan parasite occurring in a wide variety of hosts. The parasite has been shown to be transmitted by a variety of sylvatic ornithophilic simuliids (Bennett, 1960) to at least four bird families.

***Leucocytozoon liothricis* Laveran & Marullaz, 1914 emend. Coatney, 1937**

TYPE HOST: *Liothrix lutea* (Timalinae, MUSCICAPIDAE)

MACROGAMETOCYTE. Parasite with a single, round morph as in Fig. 8 & 9; host cell nucleus extending 80–90 % (sometimes almost 100 %) as a thin band around the circumference of the parasite; parasites of babblers in the Old World.

***Leucocytozoon macleani* Sambon, 1908 (1908b)**

TYPE HOST: *Phasianus colchicus* (Phasianinae, PHASIANIDAE)

MACROGAMETOCYTE. Redescribed by Sacchi & Prigioni (1985). Parasite with both round and fusiform morphs as in Fig. 8 & 12; round form with host cell nucleus flattened covering about 20–25 % of the circumference of the parasite; fusiform morph fairly small (mean of 17,9 µm in length).

***Leucocytozoon majoris* Laveran, 1902**

TYPE HOST: *Parus major* (PARIDAE)

MACROGAMETOCYTE. Parasite with a single round morph as in Fig. 8; host cell nucleus extends as a thin band about 50–60 % of the circumference of the parasite; cosmoplitan parasite of titmice.

***Leucocytozoon marchouxi* Mathis & Leger, 1911**

TYPE HOST: *Streptopelia tranquebarica* (COLUMBIDAE)

MACROGAMETOCYTE. Parasite with a single round morph as in Fig. 7 & 9; the host cell nucleus extends 50–60 % of the circumference of the parasite as a thin band that is not markedly extended into a cap; the parasite is a cosmopolitan parasite of pigeons and doves and can occur in extremely intense infections as in Fig. 8.

Leucocytozoon martyi: Synonym of *Leucocytozoon toddi.*

***Leucocytozoon neavei* Balfour, 1906 emend. Sambon, 1909**

TYPE HOST: *Numida meleagris* (Numidinae, PHASIANIDAE)

MACROGAMETOCYTE. Parasite with two morphs; the first is round as in Fig. 7 & 8 in a cell with the host cell nucleus forming a small cap or extending as a thin band 50–60 % about the circumference of the parasite; fusiform morph as in Fig. 13; parasite is a small leucocytozoid measuring up to 30 µm in length; parasite endemic to African guineafowls. SYNONYM: *Leucocytozoon costae* Tendeiro, 1947 emend. Bray, 1964.

***Leucocytozoon peaolopesi* Travassos Santos Dias, 1951**

TYPE HOST: *Francolinus afer* (Phasianinae, PHASIANIDAE)

MACROGAMETOCYTE. Parasite with two morphs; the first morph is round as in Fig. 8 & 9 in which the host cell nucleus covers 50–80 % of the circumference of the parasite as a thin band that does not form a marked cap; the fusiform morph is as in Fig. 10,

with the host cell nucleus split in two portions, frequently forming a Y- or a V-shape and closely similar to but larger than, *L. smithi* of turkeys; this parasite is apparently an endemic parasite of African francolin.

Leucocytozoon sakharoffi Sambon, 1908

TYPE HOST: *Corvus corax* (CORVIDAE)

MACROGAMETOCYTE. Parasite with a single round morph as in Fig. 9; host cell nucleus extended as a thin band for 80–90 % around the circumference of the parasite; cosmopolitan parasite of corvids.

Leucocytozoon schoutedeni Rodhain, Pons, Vandenbranden & Bequaert, 1913 (1913a)

TYPE HOST: *Gallus gallus* (Phasianinae, PHASIANIDAE)

MACROGAMETOCYTE. Parasite with a single round morph as in Fig. 7 & 8; host cell nucleus extends as a thin band, usually without marked cap, for 50–60 % of the circumference of the parasite. The parasite has been shown to be transmitted by at least four species of ornithophilic simuliids in Kenya (Fallis *et al.*, 1973b), viz. *Simulium adersi, S. vorax, S. nyassalandicum* and *S. "impukane";* presumably it is transmitted by other ornithophilic simuliids throughout the sub-Saharan region.

Leucocytozoon smithi Laveran & Lucet, 1905

TYPE HOST: *Meleagris gallopavo* (Meleagrinae, PHASIANIDAE)

MACROGAMETOCYTE. Parasite with two morphs; the first morph is as in Fig. 7 & 8, in which the host cell nucleus extends as a thin band without a marked cap for 50–60 % of the circumference of the parasite; fusiform morph as in Fig. 10 in which the host cell nucleus is bifurcated and extends on each side of the parasite; parasite endemic to New World turkeys but widely introduced cosmopolitan at the turn of the 20th century; specific to turkeys throughout their current distributional range.

Leucocytozoon sousadiasi Tendeiro, 1947 (1947a) emend. Bray, 1964

TYPE HOST: *Vanellus tectus* (CHARADRIIDAE)

MACROGAMETOCYTE. Parasite with a single, fusiform morph, as in Fig. 13; the parasite is small, with the elongated host cell not more than 43 µm in length; the species is known only from the type host and original description and represents one of the two known fusiform leucocytozoids with a single morph and lacking the hepatic cycle round morph.

Leucocytozoon squamatus Nandi, 1986

TYPE HOST: *Picus squamatus* (PICIDAE)

MACROGAMETOCYTE. Parasite with two morphs; a round morph as in Fig. 7 & 8, in which the host cell nucleus forms a thin band with a small cap covering approximately 60 % of the circumference of the parasite; an elongated morph as in Fig. 12; a cosmopolitan parasite of woodpeckers.

Leucocytozoon struthionis Walker, 1912

TYPE HOST: *Struthio camelus* (STRUTHIONIDAE)

MACROGAMETOCYTE. Parasite with a single round morph as in Fig. 7 in which the host cell nucleus forms a marked cap and extends approximately 40–50 % about the circumference of the parasite; parasite restricted to ostriches and endemic to the sub-Saharan region. Preliminary evidence suggests that this parasite occurs most frequently in young birds and will be most easily detected in birds of 6–8 weeks of age.

Leucocytozoon toddi Sambon, 1908

TYPE HOST: *Kaupifalco monogrammicus* (ACCIPITRIDAE)

MACROGAMETOCYTE. Parasite with a single, highly pleomorphic morph which ranges from broadly ovoid (Fig. 12) to highly elongated (Fig. 14); a cosmopolitan parasite of accipitrids. This species was extensively redescribed by Greiner & Kocan (1977) who included all leucocytozoids of the Falconiformes (including all members of the Falconidae and Accipitridae) as this species. SYNONYMS: *Leucocytozoon audieri* Laveran & Nattan-Larrier, 1911; *L. bacelari* Tendeiro, 1947; *L. circaeti* Sergent & Fabiani, 1922; *L. martyi* Commes, 1918; *L. mathisi* Franca, 1912; *L. mathisi* var. *buteonis* Coatney & Roudabush, 1937; *L. muratovi* Subkhonov, 1980; *L. neophrontis* Todd & Wolbach, 1912.

Leucocytozoon vandenbrandeni Rodhain, 1931

TYPE HOST: *Anhinga rufa* (ANHINGIDAE)

MACROGAMETOCYTE. Parasite with a single round morph similar to that seen in Fig. 7 but the host cell nuclear cap does not extend around the circumference of the parasite to the same extent; parasite recorded only from the type host on one occasion in sub-Saharan Africa.

Leucocytozoon ziemanni Laveran, 1903

TYPE HOST: *Athene noctua* (STRIGIDAE)

MACROGAMETOCYTE. Parasite with two morphs; the first is round as in Fig. 8 & 9, in which the host cell nucleus extends as a thin band without a cap about 50–60 % of the circumference of the parasite; fusiform morph as in Fig. 12, the parasite and the host cell extending up to 45 µm in length; cosmopolitan parasites of owls. SYNONYMS: *Leucocytozoon danilewskyi* Ziemann, 1898; *L. lutzi* Carini, 1920; *L. ziemanni* var. *bubonis* Fantham, 1926; *L. ziemanni* var. *nebraskensis* Coatney & Roudabush, 1937.

Leucocytozoon zosteropis Peirce, Cheke & Cheke, 1977

TYPE HOST: *Zosterops borbonnica* (ZOSTEROPIDAE)

MACROGAMETOCYTE. Parasite with a single round morph as in Fig. 7 & 8, in which the host cell nucleus forms a thin band with a small cap that extends about 50–60 % about the circumference of the parasite; parasite currently known only from sub-Saharan birds and may be endemic to the Ethiopian region.

MORPHOLOGICAL FORM OF THE LEUCOCYTOZOIDS OF SUB-SAHARAN BIRDS (refer to Plate 3, Fig. 7–14).

NOTE: most frequently encountered forms listed first; less frequently encountered forms are in parenthesis. R=round morph; F=fusiform morph.

Fig.	*Leucocytozoon* species	Host family
7 (8)	*anellobiae*	MELLIPHAGIDAE/PROMEROPIDAE
7 (8)	*balmorali*	Malaconotinae, LANIIDAE
7 (9)	*caprimulgi* (R)	CAPRIMULGIDAE
7 (8, 9)	*centropi*	CUCULIDAE
7 (8)	*dinizi*	MUSOPHAGIDAE
7 (8)	*eurystomi* (R)	CORACIIDAE
7 (9)	*marchouxi*	COLUMBIDAE
7 (8)	*neavei* (R)	Numidinae, PHASIANIDAE
7 (8)	*schoutedeni*	Phasianinae, PHASIANIDAE
7 (8)	*smithi* (R)	Meleagrinae, PHASIANIDAE
7 (8)	*squamatus*	PICIDAE
7	*struthionis*	STRUTHIONIDAE
7	*vandenbrandeni*	ANHINGIDAE
7 (8)	*zosteropis*	ZOSTEROPIDAE
8 (9)	*ardeae*	ARDEIDAE
8	*beaurepairei* (R)	SAGITTARIDAE
8 (9)	*brimonti*	PYCNONOTIDAE
8 (9)	*liothricis*	Timalinae, MUSCICAPIDAE
8	*majoris*	PARIDAE
8 (9)	*peaolopesi* (R)	Phasianinae, PHASIANIDAE
8 (9)	*ziemanni*	STRIGIDAE
9	*sakharoffi*	CORVIDAE
10	*peaolopesi* (F)	Phasianinae, PHASIANIDAE
10	*smithi* (F)	Meleagrinae, PHASIANIDAE
11	*dubreuili*	Turdinae, MUSCICAPIDAE
12	*beaurepairei*	SAGITTARIDAE
12 (14)	*caprimulgi* (F)	CAPRIMULGIDAE
12	*squamatus* (F)	PICIDAE
12 (14)	*toddi* (F)	ACCIPITRIDAE
12	*ziemanni* (F)	STRIGIDAE
13	*neavei* (F)	Numidinae, PHASIANIDAE
13	*sousadiasi* (F)	CHARADRIIDAE
14	*eurystomi* (F)	CORACIIDAE

THE SPECIES OF *PLASMODIUM* IN SUB-SAHARAN BIRDS

Plasmodium species	Hosts
cathemerium Hartmann, 1927	Broadly in Passeriformes
circumflexum Kikuth, 1931	Broadly throughout the avian orders
durae Herman, 1941	Phasianidae: Meleagrinae, Phasianinae
elongatum Huff, 1930	Wide variety of species
fallax Schwetz, 1930	Originally described from Strigiformes
garnhami Guindy, Hoogstraal & Helmy Mohammed, 1965	*Upupa epops*
gundersi Bray, 1962	*Ciccaba woodfordi*, Strigidae
juxtanucleare Versiani & Gomes, 1941	Phasianidae—Phasianinae & Meleagrinae
nucleophilum Manwell, 1935	Widely in Passeriformes
octamerium Manwell, 1968	Synonym of *P. vaughani*
polare Manwell, 1935	Widely in Passeriformes and other orders
quelea Marullaz, 1912 (1912a)	*Species incertae sedis*
relictum Grassi & Feletti, 1891	Widely throughout all avian orders—most common of avian malarias
rousseloti Bray, 1964	In Emberizidae—*species incertae sedis*
rouxi Sergent, Sergent & Catanei, 1928	Passseriformes; noted for bow-tie shape of schizont
vaughani Novy & McNeal, 1904	Widely in all avian orders, especially in Passeriformes