A TAXONOMIC AND ZOOGEOGRAPHICAL STUDY OF THE HAEMOPROTEIDAE AND LEUCOCYTOZOIDAE OF THE AVIAN FAMILY PYCNONOTIDAE

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by

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ABSTRACT

An extensive collection of blood films from the avian family Pycnonotidae, collected across the range of their distribution from Africa to the Philippines, provided an opportunity to survey the blood parasites of this host family and to study the taxonomy and zoogeography of the Haemoproteidae and Leucocytozoidae.

Of the 9834 bulbuls of 69 species examined for blood parasites, 23.0% harboured haematozoa. Haemoproteus was the most commonly occurring blood parasite, recorded from 15.7% of the total pycnonotids examined, followed in prevalence by Leucocytozoon (4.6%), microfilaria (3.1%), Plasmodium (1.1%) and Trypanosoma (0.7%).

Five species of Plasmodium (P. circumflexum, P. polare, P. relictum, P. rouxi and P. vaughani) and three species of Trypanosoma (T. avium, T. calmettei and T. paddae) were identified. Microfilaria were recorded but not identified. Three haemoproteid species were found in the bulbuls. Haemoproteus sanguinis Chakravarty and Kar 1945 was resurrected from synonymy with Haemoproteus otocompsae de Mello 1935 and both species were redescribed. A new species, Haemoproteus philippini sp. n., was described for the first time. Leucocytozoon brimonti Mathis and Leger 1910, Leucocytozoon dubreuili and Leucocytozoon majoris were also identified. It was recommended that Leucocytozoon brimonti be considered a

valid species and that Leucocytozoon molpastis de Mello 1936 be synonymized with it.

When the haemoproteid species were examined by host genera, H. otocompsae and H. sanguinis were found to occur more often in Pycnonotus while H. philippini sp. n. occurred more frequently in Hypsipetes and Criniger.

The zoogeographic distribution of Haemoproteus and Leucocytozoon were examined. As evidenced by prevalence rate, H. otocompsae was more common in bulbuls towards the western end of their range, particularly in India; H. philippini sp. n. was a more easterly parasite, reaching its peak prevalence in pycnonotids in the Philippines; and H. sanguinis was fairly evenly distributed across the range of the host family. Leucocytozoon prevalence showed an upward trend from the eastern end of the pycnonotid range to the western end.

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INTRODUCTION

Avian haematozoa, because of their similarity to human *Plasmodium*, have received worldwide study since Danilewsky first reported them in 1884. Garnham (1966), reviewed in depth the early history of these studies, particularly of *Plasmodium*, and Huff (1965) has shown that sporogony of the avian forms of *Plasmodium* occurs primarily in non-anopheline species of Culicidae.

The genus *Haemoproteus*, which was erected by Kruse (1890), was later subdivided by Bennett *et al*. (1965) into the genera *Parahaemoproteus* for haemoproteids with sporogony in Ceratopogonidae, and *Haemoproteus* for haemoproteids with sporogony in Hippoboscidae. Levine and Campbell (1971) however, considered *Parahaemoproteus* to be a subgenus of *Haemoproteus*, since too little was known of the vectors and life cycles of most species to assign them to either group. This move was adopted by Bennett (1972 *et seq*.). Bennett and Peirce (1985) reviewed the vectors of *Haemoproteus*.

The genus *Leucocytozoon* has been variously ascribed to Danilewsky, Berestneff and Ziemann but Bennett *et al*. (1975) determined that the generic authority should be accorded to Sambon (1908). Fallis *et al*. (1974) have shown that sporogony of this genus occurs only in Simuliidae.

Numerous reviews of these parasites have appeared in

the literature over the last several decades, the most recent and comprehensive of which is that of Bennett et al. (1982) who summarized knowledge of these blood parasites, their hosts and geographic distribution. Bennett listed 196 species and varieties of Haemoproteus, 96 of Leucocytozoon and 75 of Plasmodium, with the majority of these species requiring review.

Two species of Haemoproteus, H. otocompsae de Mello 1935 and H. sanguinis Chakravarty and Kar 1945, and two species of Leucocytozoon, L. brimonti Mathis and Leger 1910 and L. molpastis de Mello 1937, have been described from the Pycnonotidae.

The bulbuls themselves are a widespread paleotropic family found throughout Africa, southern Asia, the Malay archipelago, the Philippines and the Moluccas, with one species reaching the temperate zone in eastern Asia. They are common, noisy inhabitants of forests, sparsely wooded or brushland habitats, open brushy grassland, and cultivated land and gardens. They fill all niches from man-disturbed areas, including cities, to undisturbed forests (McClure et al. 1978). They are gregarious, living in groups, with some species in large flocks, and they often mix with other birds in wandering feeding parties (McClure et al. 1978). Most eat fruit, berries and some insects, while a few are mainly insectivorous. Only the temperate zone species (Hypsipetes amaurotis) is migratory, while many of the tropical species are

wanderers, the movements of which are not well understood, and some are sedentary (McClure et al. 1978).

An extensive collection of blood films from bulbuls in the files of the International Reference Centre for Avian Haematozoa provided an opportunity to study the haematozoa of the pycnonotids, especially the haemoproteids and leucocytozoids, from both a taxonomic and zoogeographical standpoint. This thesis will concentrate on both the taxonomy and distribution of the Haemoproteidae and Leucocytozoidae of this family across its distributional range.

MATERIALS AND METHODS

Blood smears were taken from netted live birds by clipping a toenail or by following the protocols of Bennett (1970). The slides were air-dried, fixed in 100% methanol or ethanol and stained with a variety of stains (Wright's, Field's or Giemsa's). It was noted that the "quick" stains faded badly after a few years, making the slides difficult to read. Initial screening of the blood films and parasite identification to the generic level was done either by the contributor at the point of collection, or by the staff at the International Reference Centre for Avian Haematozoa.

Taxonomic Analysis

For the purpose of this study, positive slides were rescreened and parasites were identified to the species level where possible. Haemoproteid parasites, parasitized and unparasitized erythrocytes were drawn with the aid of a camera lucida and measured using a Zeiss MOP-3 Digital Analyzer. Morphometric parameters measured (Bennett and Campbell 1972; Forrester et al. 1977) included: parasite length, width and area; parasite nuclear length, width and area; erythrocyte length, width and area; and erythrocyte nuclear length, width and area. Ratios derived from these measurements included: the nuclear displacement ratio (NDR), percent hypertrophy/atrophy of infected

erythrocytes and their nuclei, and various area percentages. Pigment granules were counted and the sex ratios determined for each haemoproteid species. Photomicrographs were obtained using a Zeiss Photomicroscope III.

Statistical Analyses

Statistical analyses of the morphometric parameters of the haemoproteid species were done using procedures from the Statistical Package for the Social Sciences (SPSS), Release 8.1, run on the Newfoundland and Labrador Computer Services IBM-370-158.

Means and standard deviations for all measurements were obtained using SPSS procedure FREQUENCIES, which prints frequency distribution tables and summary statistics for discrete variables.

Analysis of variance was used to determine whether significant statistical differences existed between the haemoproteid species with regard to mean values of the parameters measured. SPSS procedure ONEWAY, which performs a univariate analysis of variance, was run on each of the following gametocyte variables : length, width and area, nuclear displacement ratio, and number of pigment granules for both macro- and microgametocytes; and nuclear length, width and area for macrogametocytes only. Microgametocyte nuclear parameters were not analysed because of the small number of measurable nuclei.

Differences in prevalence of the haemoproteid species among the bulbul genera were tested for statistical significance using T-tests on arcsine transformations of the data (Sokal and Rohlf 1969).

Zoogeographical Analysis

To facilitate the zoogeographical examination of the bulbul haematozoa, two PL/1 programs were developed to edit, store and summarize the distributional data.

Further breakdown of the zoogeographical data was accomplished using SPSS procedure CROSSTABS which provides joint frequency distributions of cases in the form of contingency tables. This presentation of the data allowed examination of the distributional relationships of the haematozoa with regard to both host species and geographic area.

Throughout this thesis, the term "rate of infection" is to be regarded as the equivalent of "prevalence of infection" where prevalence is defined as the proportion of infected birds in a sample.

RESULTS AND DISCUSSION

The bulbuls were sampled across the range of their distribution from western Africa to southeastern Asia and north to Japan, with these records supplemented by records from the literature . A total of 9834 birds of 69 species were examined for blood parasites (Table 1). A total of 2263 (23.0%) birds of 51 species were found to harbour haematozoa. The most commonly occurring blood parasite genus was *Haemoproteus* which was found in 1545 (15.7%) birds of 37 species, followed by *Leucocytozoon* which occurred in 452 (4.6%) birds of 36 species. *Plasmodium* was found in 105 (1.1%) birds of 21 species, *Trypanosoma* in 67 (0.7%) birds of 22 species and microfilaria in 302 (3.1%) birds of 27 species.

Plasmodium, *Trypanosoma* and Microfilaria

Of the 105 *Plasmodium* infections found in the bulbuls, 5 were identified as *P. circumflexum*, 3 as *P. polare*, 4 as *P. relictum*, 25 as *P. rouxi* and 21 as *P. vaughani*, with the remaining 48 infections unidentified to species. The identification of these *Plasmodium* species in the bulbuls is not surprising since the avian plasmodia are known to occur in a wide range of host species. According to Bennett *et al.* (1982), *P. circumflexum* is found in 115 species of birds, *P. polare* in 31, *P. relictum* in 270, *P. rouxi* in 59 and *P. vaughani* in 174.

Table 1.

Prevalence of haematozoa in the Pycnonotidae. (Based on records from the literature and from the files of the International Reference Centre for Avian Haematozoa.)

Host	Total birds	Infct. birds	Total birds infected with				
			Haem.	Leuc.	Plasm.	Tryp.	Micro.
Chlorocichla flavicollis	12	2	-	1	-	1	-
Chlorocichla flaviventris	3	1	-	-	-	1	-
Criniger bres	177	39	27	4	-	-	3
Criniger calurus	1	0	-	-	-	-	-
Criniger finschi	4	0	-	-	-	-	-
Criniger flaveolus	19	3	3	-	-	-	-
Criniger ochraceus / pallidus *	279	86	67	22	-	-	3
Criniger phaeocephalus	197	3	-	1	-	1	1
Hypsipetes amaurotis	28	8	4	-	1	-	-
Hypsipetes borbonica	4	0	-	-	-	-	-
Hypsipetes charlottae	19	10	6	3	1	-	5
Hypsipetes crassirostris	3	1	1	-	-	1	-
Hypsipetes criniger	102	4	4	1	-	-	-
Hypsipetes everetti	2	1	-	-	-	-	1
Hypsipetes flavala	43	11	6	6	-	1	-
Hypsipetes indicus	25	0	-	-	-	-	-
Hypsipetes madagascariensis	112	21	14	4	4	1	-
Hypsipetes malaccensis	5	1	-	1	-	1	-
Hypsipetes mcclellandii	309	111	64	52	-	1	4
Hypsipetes palawanensis	6	0	-	-	-	-	-
Hypsipetes philippinus	414	212	190	8	1	4	16

Table 1 (Continued).

Host	Total birds	Infct. birds	Total birds infected with				
			Haem.	Leuc.	Plasm.	Tryp.	Micro.
Hypsipetes propinquus	38	27	26	4	-	5	-
Hypsipetes rufigularis	3	1	-	-	-	-	1
Hypsipetes siquijorensis	72	55	55	-	-	-	-
Hypsipetes thompsoni	18	1	-	1	-	-	-
Hypsipetes viridescens	12	1	-	1	-	-	-
Ixonotus guttatus	1	0	-	-	-	-	-
Nicator gularis	4	0	-	-	-	-	-
Phyllastrephus albigularis	38	0	-	-	-	-	-
Phyllastrephus cerviniventris	5	0	-	-	-	-	-
Phyllastrephus fischeri	6	2	1	-	-	1	-
Phyllastrephus strepitans	15	3	3	-	-	-	-
Phyllastrephus terrestris	3	0	-	-	-	-	-
Pycnonotus atriceps	189	22	6	8	-	-	3
Pycnonotus aurigaster	51	11	7	4	-	-	-
Pycnonotus barbatus	221	97	49	52	17	10	18
Pycnonotus bimaculatus	1	0	-	-	-	-	-
Pycnonotus blanfordi	1091	557	526	2	25	1	-
Pycnonotus brunneus	81	18	7	7	1	1	3
Pycnonotus cabanisi	1	0	-	-	-	-	-
Pycnonotus cafer	298	74	23	29	6	13	22
Pycnonotus curvirostris	19	1	-	-	-	-	1
Pycnonotus cyaniventris	8	0	-	-	-	-	-
Pycnonotus erythropthalmos	46	14	3	9	1	-	1
Pycnonotus eutilotus	55	2	1	1	-	-	-

Table 1 (Continued).

Host	Total birds	Infct. birds	Total birds infected with				
			Haem.	Leuc.	Plasm.	Tryp.	Micro.
Pycnonotus finlaysoni	200	38	9	18	5	1	3
Pycnonotus flavescens	186	7	5	4	1	-	1
Pycnonotus goiavier	2714	350	172	63	11	3	125
Pycnonotus gracilirostris	1	0	-	-	-	-	-
Pycnonotus importunus	9	3	-	2	-	-	-
Pycnonotus jocosus	258	62	32	19	2	-	3
Pycnonotus latirostris	11	0	-	-	-	-	-
Pycnonotus leucogenys	81	15	6	4	3	1	4
Pycnonotus luteolus	66	40	40	-	-	-	-
Pycnonotus melanicterus	217	167	144	78	12	4	2
Pycnonotus melanoleucos	6	1	-	1	1	-	-
Pycnonotus plumosus	1339	87	12	5	4	4	57
Pycnonotus simplex	100	12	9	1	1	-	3
Pycnonotus sinensis	121	12	5	2	1	-	1
Pycnonotus striatus	10	1	1	-	-	-	-
Pycnonotus taivanus	3	0	-	-	-	-	-
Pycnonotus urostictus	45	2	-	-	-	-	2
Pycnonotus virens	224	12	7	3	2	2	2
Pycnonotus xanthopygos	32	31	3	29	2	2	11
Pycnonotus xanthorrhous	40	0	-	-	-	-	-
Pycnonotus zeylanicus	25	5	-	1	-	-	4
Setornis criniger	2	1	-	-	-	-	-
Spizixos canifrons	64	0	-	-	-	-	-
Spizixos semitorques	6	0	-	-	-	-	-

Table 1 (Concluded).

Host	Total birds	Infct. birds	Total birds infected with				
			Haem.	Leuc.	Plasm.	Tryp.	Micro.
Unidentified bulbuls	24	17	7	1	3	7	2
TOTAL :	9834	2263	1545	452	105	67	302
% of total examined :		23.0	15.7	4.6	1.1	0.7	3.1

Haem. = Haemoproteus, Leuc. = Leucocytozoon, Plas. = Plasmodium, Tryp. = Trypanosoma, Micr. = microfilaria. As a result of multiple infections in a single bird, the total of infections listed may exceed the total number of infected birds.

* Note : Field separation of Criniger ochraceus and Criniger pallidus was unreliable so both species are considered together (McClure et al. 1978).

Knowledge on the genus Plasmodium has been well summarized by Garnham (1966), while Greiner et al. (1975) provided a detailed key to the avian species. The pycnonotid hosts of Plasmodium are summarized in Appendix A.

Of the 67 trypanosome infections recorded from the bulbuls in this study, 17 were referrable to the T. avium complex, 7 to the T. calmettei complex and 1 to the T. paddae complex. Included in this total were records from the literature of 2 T. everetti and 2 T. pycnonoti infections from the pycnonotidae. A total of 38 trypanosome infections were not identified to species. Current knowledge on Trypanosoma taxonomy and nomenclature was summarized by Baker (1976) and life cycles were dealt with by Bennett (1961). These authors have shown that the extreme pleomorphism of the trypanosomes makes morphological criteria unreliable indicators of species, and also that host specificity is unsupportable as a basis for species differentiation. The pycnonotid hosts of Trypanosoma are summarized in Appendix B.

The rarity of Plasmodium and Trypanosoma in the bulbuls is not surprising since McClure et al. (1978), who sampled 55,289 birds across southern Asia, reported a prevalence of only 0.8% for Plasmodium and 0.2% for Trypanosoma. Numerous studies (e.g. Herman 1968, Woo and Bartlett 1982) have shown the inadequacy of the single blood film technique for diagnosing these parasites and have demonstrated that the use of more sensitive detection

techniques, such as isodiagnosis and the hematocrit centrifuge technique, yield much higher rates of infection for Plasmodium and Trypanosoma than is found by examination of peripheral blood smears. Thus the paucity of both Plasmodium and Trypanosoma infections is most probably a reflection of the unsuitability of the diagnostic technique, rather than the actual occurrence of these two parasites in pycnonotid populations.

No attempt was made in this study to identify the species of microfilaria found in the bulbuls since specific identification can only be accomplished by associating the microfilariae with the adult worms (Bennett et al. 1982). The microfilaria have been reviewed in depth by Anderson and Freeman (1969), and by Sonin (1966, 1968). The pycnonotid hosts of microfilaria are summarized in Appendix C.

Because of the relatively small numbers of Plasmodium, Trypanosoma and microfilaria found in this study, as well as the taxonomic problems encountered in dealing with the latter two, these parasites will not be considered further. Haemoproteus and Leucocytozoon were the dominant blood parasites found in the bulbuls and will be examined in detail with regard to their taxonomy, distribution and zoogeography.

Taxonomy

Haemoproteus

Historical

Haemoproteus was first reported from the Pycnonotidae by Zupitza (1909) who recorded 'Halteridium' from several unidentified bulbuls. Since then, numerous references to bulbul haemoproteids have been made in the literature, but with few exceptions, identification of the parasites does not proceed beyond the generic level, and only two species have been described. Because of the difficulty of obtaining the journals in which they appeared, these descriptions are presented in total.

De Mello (1935) named and briefly described Haemoproteus otocompsae from a Pycnonotus jocosus shot at Malim, India as follows:

" Sexual dimorphism. ♀ pale blue at Leishman, and rose at May Grunwald-Giemsa, seldom vacuolated. Nucleus spherical, sub-central, seldom elongated, situated on the convex border of the parasite. Pigment scattered over the body. ♂ colorless at Leishman, pale rose at May Grunwald-Giemsa. Nucleus very large, granular without definite outline, sub-central. Pigment located on poles. Red cell hypertrophied nucleus displaced."

De Mello (1936) redescribed the same material and provided illustrations of the new parasite. His redescription reads:

" Female gametocyte with the protoplasm staining pale blue at Leishman and pink by May-Grunwald-Giemsa (this tinctorial reaction is characteristic of this Haemoproteus in contrast with others the female gametocytes of which are stained violet blue or deep blue by May-Grunwald-Giemsa and the males pink). The protoplasm is always homogeneous, seldom with vacuoles. Nucleus generally spherical and subcentral; more rarely, elongated, located on the convex border of the parasite.

Pigment scattered throughout the body, the granules being sometimes very few, sometimes very abundant. The form of the parasite is almost always halteridial.

Male gametocyte with the protoplasm unstained and colorless by Leishman, pale pink by May-Grunwald-Giemsa, seldom vacuolated. Nucleus very large, without definite outline and constituted by chromatic masses scattered here and there. Its position is subcentral. Pigment with granules located especially at the poles. Form generally halteridial.

Red cell hypertrophied in the longitudinal sense, nucleus displaced. Aberrant deformations of the globules frequently seen."

Haemoproteus sanguinis was described from another Pycnonotus jocosus from Calcutta, India by Chakravarty and Kar (1945) who included line drawings and rudimentary measurements in their description:

" The early gametocytes are oval in outline with one of the ends pointed. In these forms no pigment could be seen. The cytoplasm is clear, takes up a bluish stain and contains a rod-like elongated chromatin mass representing the nucleus. Afterwards, the parasites assume a spherical form and the pigment granules appear for the first time in the cytoplasm. As the parasites grow they become oval in shape with the ends rounded. In stages measuring 6.6u x 3.3u, sexual dimorphism could not be observed; in a later stage, however, they become differentiated as male and female gametocytes.

Both the male and female gametocytes are found in large numbers in the red-blood corpuscles, and the majority of them are somewhat crescent-shaped in appearance, while some are broadly oval in form occupying only one side of the red-blood corpuscles.

The female gametocytes have a deeply stained cytoplasm containing the nucleus and irregularly scattered pigments. The pigments are either rod-shaped or granular. The shape of the nucleus varies from spherical to oval and takes up a deeper stain than the male gametocytes. The female gametocytes measure 9 - 13.2u x 3.3 - 4.4u.

The male gametocytes have a very faintly stained cytoplasm which appears almost unstained in Giemsa stain. The pigments have the same form as in the female but they are aggregated either at one or both poles of the parasites. The nucleus is spherical in outline, bigger in size than the female and stains lighter. It contains several faintly stained granules. The male gametocytes measure 11u x 3.3u."

Both species were reevaluated by Peirce (1984c) who redescribed H. otocompsae based on infections found in 15 Pycnonotus barbatus naumanni from Zambia, and synonymized H. sanguinis with it on the basis of the published description. Haemoproteus otocompsae and H. sanguinis are herein redescribed, and a new haemoproteid, Haemoproteus philippini sp. n. from Hypsipetes philippinus from the Philippines is also described. In addition, 16 new host records were established for H. otocompsae and 25 for H. sanguinis, while 23 host species were recorded for H. philippini sp. n. (Appendix D).

Results

Haemoproteus otocompsae de Mello 1935

TYPE HOST: Pycnonotus jocosus (Linnaeus)

TYPE LOCALITY: Malim (Bardez), India

IMMATURE GAMETOCYTE: Youngest forms seen develop lateral to the host cell nucleus in mature erythrocytes, often with noticeable nuclear displacement.

MACROGAMETOCYTE (Fig. 1, Table 2): Semi-halteridial with rounded ends, parasite lateral to and markedly displacing host cell nucleus; margin entire, not amoeboid; cytoplasm coarsely granular, vacuolate, staining blue; parasite nucleus median to submedian, round to ovoid, staining pink; pigment granules yellow-brown, discrete, randomly distributed; host cell hypertrophied in length and area with no change

Figure 1,

Haemoproteus otocompsae

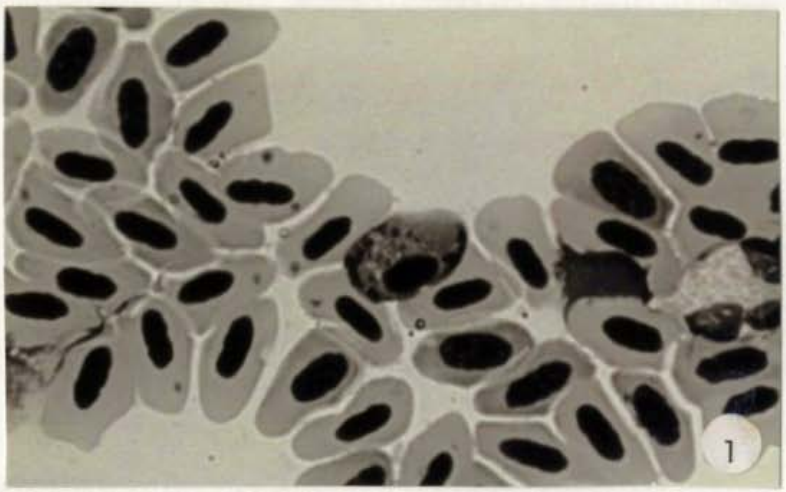
macrogametocyte

Figure 2.

Haemoproteus otocompsae

microgametocyte

Note: Unparasitized erythrocyte
Approximately 12 µm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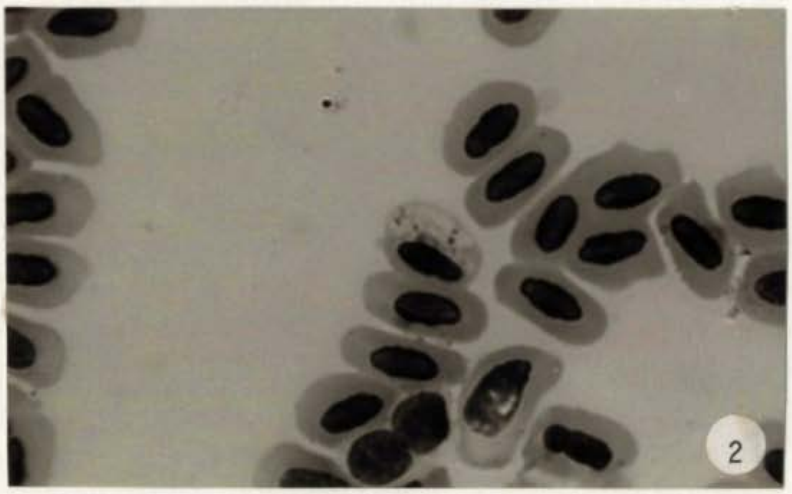
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Table 2.

Morphometric parameters of three species of haemoproteids from the Pycnonotidae.

Parameter	H. otocompsae	H. philippini sp. n.	H. sanguinis
UNPARASITIZED ERYTHROCYTE	N = 55	N = 55	N = 55
Erythrocyte			
Length	11.7 (0.5)	12.0 (0.6)	11.7 (0.6)
Width	6.6 (0.4)	6.6 (0.4)	6.4 (0.4)
Area	61.9 (4.3)	62.9 (6.1)	59.4 (4.3)
Erythrocyte Nucleus			
Length	5.0 (0.6)	5.6 (0.3)	5.6 (0.3)
Width	2.5 (0.3)	2.5 (0.2)	2.5 (0.3)
Area	12.5 (1.9)	11.2 (1.2)	11.5 (1.5)
% area of total cell	20.2	17.8	19.4
NDR*	1.00(0.08)	1.00(0.09)	1.00(0.07)
ERYTHROCYTE PARASITIZED BY MACROGAMETOCYTE	N = 55	N = 55	N = 55
Erythrocyte			
Length	12.5 (0.8)	13.8 (0.9)	12.7 (0.7)
Width	6.6 (0.7)	6.5 (0.5)	6.4 (0.6)
Area	67.7 (5.9)	74.0 (7.7)	66.1 (5.8)
% Hypertrophy - Atrophy of Erythrocyte			
Length	+6.8	+15.0	+8.5
Width	0.0	-1.5	0.0
Area	+9.4	+17.6	+11.3
Erythrocyte Nucleus			
Length	5.7 (0.6)	5.4 (0.4)	5.4 (0.4)
Width	2.3 (0.3)	2.5 (0.3)	2.2 (0.3)
Area	11.1 (1.4)	10.8 (1.0)	10.1 (1.5)
NDR	0.49(0.24)	0.83(0.21)	0.84(0.14)
% area of host cell-parasite complex	16.4	14.6	15.3
% Hypertrophy - Atrophy of Erythrocyte Nucleus			
Length	-5.3	-3.7	-3.7
Width	-8.7	0.0	-13.6
Area	-12.6	-3.7	-13.9

Table 2 (Continued).

Parameter	H. otocompsae	H. philippini sp. n.	H. sanguinis
MACROGAMETOCYTE	N = 55	N = 55	N = 55
Length	16.7 (1.9)	13.6 (1.4)	13.8 (1.3)
Width	3.3 (0.7)	1.4 (0.6)	2.4 (0.3)
Area	49.2 (5.7)	26.6 (7.7)	35.5 (5.2)
% area of host cell - parasite complex	72.7	35.9	53.7
Number of pigment granules	9.6 (5.1) N=44	7.6 (2.4) N=39	15.4 (5.4) N=45
Macrogametocyte Nucleus	N = 42	N = 45	N = 35
Length	3.4 (0.8)	2.8 (0.8)	2.9 (0.6)
Width	2.4 (0.6)	1.6 (0.5)	1.5 (0.5)
Area	6.7 (2.7)	3.5 (1.4)	3.5 (1.3)
% area of parasite	13.6	13.2	9.9
ERYTHROCYTE PARASITIZED BY MICROGAMETOCYTE	N = 55	N = 55	N = 55
Erythrocyte			
Length	12.7 (0.8)	13.9 (0.8)	12.8 (0.6)
Width	6.8 (0.7)	6.4 (0.5)	6.6 (0.5)
Area	70.8 (6.0)	74.0 (6.7)	68.2 (5.3)
% Hypertrophy - Atrophy of Erythrocyte			
Length	+8.5	+15.8	+9.4
Width	+3.0	-3.1	+3.1
Area	+14.4	+17.6	+14.8
Erythrocyte Nucleus			
Length	5.8 (0.6)	5.5 (0.5)	5.5 (0.3)
Width	2.3 (0.2)	2.4 (0.3)	2.2 (0.3)
Area	11.2 (1.6)	10.9 (1.3)	10.2 (1.3)
NDR	0.55(0.18)	0.85(0.15)	0.80(0.14)
% area of host cell-parasite complex	15.8	14.7	15.0
% Hypertrophy - Atrophy of Erythrocyte Nucleus			
Length	-3.4	-1.8	-1.8
Width	-8.7	-4.2	-13.6
Area	-11.6	-2.8	-12.7

Table 2 (Concluded).

Parameter	H. otocompsae	H. philippini sp. n.	H. sanguinis
MICROGAMETOCYTE	N = 55	N = 55	N = 55
Length	17.5 (2.2)	13.9 (1.2)	14.5 (1.3)
Width	3.3 (0.7)	1.5 (0.5)	2.6 (0.4)
Area	51.0 (6.0)	28.1 (4.9)	39.4 (5.0)
% area of host cell - parasite complex	72.0	38.0	57.8
Number of pigment granules	10.7 (4.2) N=42	8.8 (2.3) N=42	14.8 (4.7) N=49
Microgametocyte Nucleus	N = 7	N = 5	N = 1
Length	5.5 (2.3)	3.4 (2.2)	5.9
Width	2.7 (0.6)	1.4 (0.3)	2.2
Area	11.8 (4.3)	4.4 (4.5)	13.5
% area of parasite	23.1	11.6	34.3
SEX RATIO (FEMALES : MALES)	1.0 : 0.1	1.0 : 0.4	1.0 : 0.2

* NDR = Nuclear Displacement Ratio

Note : Linear measurements in micrometres; area measurements in micrometres squared; standard deviations in parentheses; hypertrophy noted as (+), atrophy (-); N = number measured.

in width; host cell nucleus atrophied in length, width and area.

MICROGAMETOCYTE (Fig. 2, pg. 17; Table 2, pg. 18): Cytoplasm staining very pale blue, almost colorless, finely granular; parasite slightly larger than macrogametocyte; parasite nucleus median, staining very pale pink, ovoid, diffuse; host cell hypertrophied in length, width and area; host cell nucleus atrophied in length, width and area; remaining characteristics as for the macrogametocyte.

REDESCRIPTION BASED ON: Neohapantotype - IRCAH blood film 42195 from Pycnonotus luteolus (Lesson) collected by Dr. H. Elliott McClure on 18 January 1971 at Point Calimere, Tamil Nadu, India.

PARANEOHAPANTOTYPE: IRCAH blood film 8612 from Hypsipetes criniger (Blyth), collected by Laird, 5 October 1962, Subang, Selangor, Federation of Malaysia; blood film 42286 from Pycnonotus goiavier (Scopoli), collected by McClure, 11 April 1966, Maloh, Siaton, Negros Oriental, Republic of the Philippines; blood film 2108 from Pycnonotus leucogenys (J.E. Gray), collected by Jahangirhejad, 1968, Bandar Abbas, Iran; blood film 12363 from Pycnonotus melanicterus (Gmelin), collected by McClure, 7 December 1967, Sakaerat, Pakthong Chai, Nakhon Ratchasina (Korat), Thailand.

ADDITIONAL HOST RECORDS: see Appendix D.

DISTRIBUTION: Zambia, Kenya, Iran, India, Thailand, Malaysia and the Philippines.

COMMENTS: Haemoproteus otocompsae belongs to the group of morphologically similar large haemoproteids, exemplified by H. borgesi Tendeiro 1947, which occupy more than 70% of the host cell - parasite complex and almost totally displace the host cell nucleus.

With the exception of Peirce (1984a,c), no new records of H. otocompsae have been reported in the literature since its redescription by de Mello (1936). However, Leger and Leger (1914a) presented several characteristics of an unnamed haemoproteid from Pycnonotus barbatus from northern Senegal, Africa. The parasite was described as one which hypertrophied the host cell, displaced the host cell nucleus, and was oval in shape with large, fairly numerous pigment granules. From this brief description, it appears that this haemoproteid may be referrable to H. otocompsae. De Mello (1935, 1936) noted that H. otocompsae was "perhaps similar to the unnamed H. of Picnonotus (sic) barbatus recorded by A. and M. Leger (sic) in Senegal."

Haemoproteus philippini sp. n.

TYPE HOST: Hypsipetes philippinus (J. R. Forster)

TYPE LOCALITY: Camp Lookout, Valencia, Negros Oriental, Republic of the Philippines.

IMMATURE GAMETOCYTE: Youngest forms seen develop lateral to the host cell nucleus in mature erythrocytes.

MACROGAMETOCYTE (Fig. 3; Table 2, pg. 18): Parasite with marked central constriction lateral to host cell nucleus, closely appressed to it, and causing slight nuclear displacement; margin entire, not amoeboid; cytoplasm coarsely granular, vacuolate, staining blue; parasite nucleus subterminal, ovoid, staining pink; pigment granules yellow-brown, discrete, randomly distributed; host cell hypertrophied in length and area, and atrophied in width; host cell nucleus atrophied in both length and area, with no change in width.

MICROGAMETOCYTE (Fig. 4; Table 2, pg. 18): Cytoplasm staining pale blue, finely granular; parasite slightly larger than macrogametocyte; parasite nucleus usually without specific boundaries, often precluding measurement; host cell hypertrophied in length and area, and atrophied in width; host cell nucleus atrophied in length, width and area; remaining characteristics as for the macrogametocyte.

HAPANTOTYPE MATERIAL: IRCAH blood film 11765 from Hypsipetes philippinus (J. R. Forster) deposited in the collection of the International Reference Centre for Avian Haematozoa; collected by Dr. H. Elliot McClure on 18 August 1964 at Camp Lookout, Valencia, Negros Oriental, Republic of the Philippines.

Figure 3.

Haemoproteus philippini sp. n.

macrogametocyte

Figure 4.

Haemoproteus philippini sp. n.

microgametocyte

Note: Unparasitized erythrocyte
approximately 12 um


3


4

PARAHAPANTOTYPE MATERIAL: All material collected by McClure. IRCAH blood film 42100 from Hypsipetes amaurotis (Temminck), collected 20 October 1966, Tsunoshima, Yamaguchi Prefecture, Japan; blood film 42102 from Hypsipetes amaurotis (Temminck), collected 1 May 1969, Lanyu (Orchid Island), Taiwan; blood film 8794 from Hypsipetes flavala (Blyth), collected 21 March 1962, Mount Brinchang, Pahang, Federation of Malaysia; blood film 42126 from Hypsipetes madagascariensis (P. L. S. Muller), collected 11 April 1971, Maharashtra, India; blood film 9891 from Pycnonotus melanicterus (Gmelin), collected 14 January 1965, Phunamtok, Saraburi, Thailand; all parahapantotype material deposited in the collection of the International Reference Centre for Avian Haematozoa.

ADDITIONAL HOST RECORDS: see Appendix D.

DISTRIBUTION: Uganda, India, Bhutan, Thailand, Malaysia, the Philippines, Taiwan, and Japan.

COMMENTS: Haemoproteus philippini sp. n. falls into the group of small dumbbell-shaped haemoproteids which occupy less than 50% of the host cell - parasite complex. This group includes H. fringillae Labbe 1894, H. porzanae (Galli-Valerio 1907), H. killangoi Bennett and Peirce 1981 and H. bilobata Bennett and Nandi 1981. As seen in Table 3, H. philippini sp. n. most closely approximates H. porzanae in size, number

Table 3.

Comparison of selected parameters of small haemoproteids resembling H. philippini sp. n.

Parameter	H. bilobata	H. killangoi	H. philippini sp. n.	H. porzanae
Shape	dumbbell	dumbbell	dumbbell	dumbbell
Ends	entire	amoeboid	entire	amoeboid
Macrogametocyte				
Length	13.1	12.8	13.6	13.7
Width	0.8	1.4	1.4	1.7
Area	37.8	31.0	26.6	25.0
% area of erythrocyte/ parasite complex	39.0	44.0	35.9	48.2
% hypertrophy/ atrophy of erythrocyte				
Length	+ 5.4	+ 7.8	+15.0	+ 1.0
Width	- 6.3	+11.0	- 1.5	- 4.0
Area	+ 4.0	+11.5	+17.6	- 2.9
No. of pigment granules	16.9	8.9	7.6	9.9
% hypertrophy/ atrophy of erythrocyte nucleus				
Length	-27.0	- 4.0	- 3.7	+ 6.7
Width	0.0	- 4.0	0.0	- 4.8
Area	-24.0	- 7.5	- 3.7	+ 4.5
Nuclear displacement ratio (NDR)	0.98	1.00	0.83	0.72
Host family	Capitonidae	Zosteropidae	Pycnonotidae	Rallidae

of pigment granules and degree of nuclear displacement, but it is distinguishable from H. porzanae in that the ends of the parasite are not amoeboid and that it causes considerable erythrocyte length and area hypertrophy but less erythrocyte nuclear distortion. It is distinguishable from H. killangoi which has amoeboid ends and causes no nuclear displacement. It is more distinctly bilobed than H. fringillae and has only half the number of pigment granules. It has less than half the number of pigment granules of H. bilobata, causes more lateral nuclear displacement and no rotation of the erythrocyte nucleus, and causes more erythrocyte hypertrophy, but less distortion of the erythrocyte nucleus. In short, H. philippini sp. n. is a small, extremely bilobed haemoproteid which slightly displaces the erythrocyte nucleus laterally, and for its small size causes extensive erythrocyte hypertrophy. It occurs in an avian family phylogenetically remote from those in which similar haemoproteids occur.

Haemoproteus philippini sp. n. was named after the host and region in which it most frequently appeared, Hypsipetes philippinus from the Philippines.

Haemoproteus sanguinis Chakravarty and Kar 1945

TYPE HOST: Pycnonotus jocosus (Linnaeus)

TYPE LOCALITY: Calcutta, West Bengal, India.

IMMATURE GAMETOCYTE: Youngest stages seen initiate development in a polar position in mature erythrocytes, the young gametocytes extending along the length of the host cell nucleus as they mature.

MACROGAMETOCYTE (Fig. 5; Table 2, pg. 18): Halteridial, parasite lateral to and slightly displacing host cell nucleus; margin entire, not amoeboid; cytoplasm coarsely granular, vacuolate, staining pale blue; parasite nucleus submedian to subterminal, roughly ovoid, staining pink; pigment granules yellow-brown, discrete, randomly distributed; host cell hypertrophied in length and area, with no change in width; host cell nucleus atrophied in length, width and area.

MICROGAMETOCYTE (Fig. 5; Table 2, pg. 18): Cytoplasm colorless; parasite slightly larger than macrogametocyte; nucleus unstaining, precluding measurement; host cell hypertrophied in length, width and area; host cell nucleus atrophied in length, width and area; remaining characteristics as for the macrogametocyte.

REDESCRIPTION BASED ON: Neohapantotype - IRCAH blood film 42183 from Pycnonotus luteolus (Lesson) collected by Dr. H. Elliot McClure on 28 December

Figure 5.

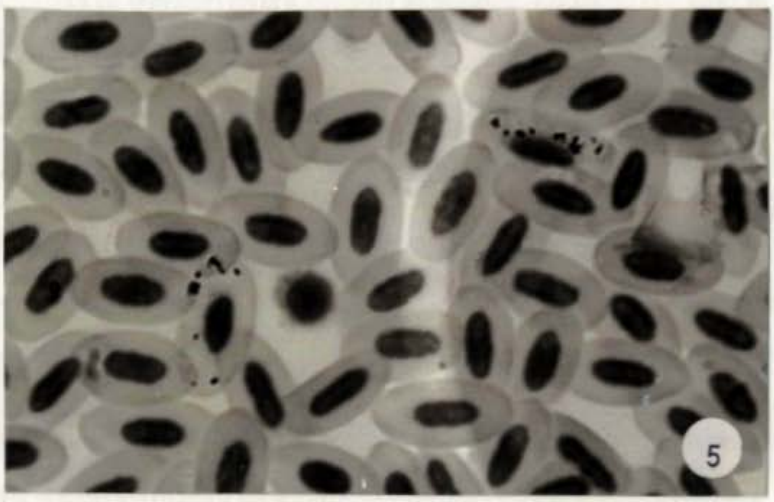
Haemoproteus sanguinis

macrogametocyte
(upper right)

and

microgametocyte
(lower left)

Note: Unparasitized erythrocyte
approximately 12 um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1970 at Point Calimere, Tamil Nadu, India.

PARANEOHAPANTOTYPES: IRCAH blood film 28389 from Pycnonotus barbatus (Desfontaine), collected by Okia, 20 January 1972, Lunyo, Uganda; blood film 9829 from Pycnonotus blanfordi Jerdon, collected by McClure, 6 January 1965, Nonthaburi, Thailand; blood film 42249 from Pycnonotus goiavier (Scopoli) collected by McClure, 28 November 1965, Candugay, Siaton, Negros Oriental, Republic of the Philippines; blood film 10751 from Pycnonotus sinensis (Gmelin), collected by McClure, 8 December 1966, Mong Tseng Peninsula, Hong Kong.

ADDITIONAL HOST RECORDS : see Appendix D.

DISTRIBUTION : Ghana, Zaire, Uganda, Kenya, Tanzania, Comoro Islands, India, Bhutan, Thailand, Malaysia, Indonesia, the Philippines, and Hong Kong.

COMMENTS : Haemoproteus sanguinis is similar to the group of medium-sized haemoproteids, resembling H. columbae Kruse, which occupy approximately 50% of the host cell - parasite complex and only partially displace the host cell nucleus.

Since its description, H. sanguinis has been identified only in Hypsipetes crassirostris from the Comoro Islands (Peirce and Cheke 1977b), in Pycnonotus barbatus from Kenya (Peirce et al. 1977a) and Ghana (Wink and Bennett 1976), and in Pycnonotus virens from Ghana (Wink and Bennett 1976).

Peirce (1984c) synonymized H. sanguinis with H. otocompsae on the basis of the published descriptions. These two haemoproteids however, are clearly distinguishable both qualitatively and quantitatively. Haemoproteus otocompsae is a large, broad haemoproteid, occupying approximately three-quarters of the host cell - parasite complex, and characteristically displacing the host cell nucleus to the periphery of the erythrocyte (NDR = 0.49). This is in contrast to H. sanguinis which is a relatively slender parasite, occupying only one-half the area of the host cell, and causing little nuclear displacement. The differences between these two haemoproteids were shown to be statistically significant on all parameters tested (Table 4).

The descriptions of H. otocompsae and H. sanguinis provided by de Mello (1935) and by Chakravarty and Kar (1945) provided few or no measurements and do not clearly separate these parasites qualitatively, but they are distinguishable on the basis of the illustrations. The H. otocompsae found in this study were readily referrable to the illustrations of this parasite provided by de Mello (1936) and to those of Peirce (1984c). Of the six drawings of H. sanguinis published by Chakravarty and Kar (1945), only one appears to be a mature

Table 4.

Results of analysis of variance on selected morphological parameters of *H. otocompsae*, *H. philippini* sp. n. and *H. sanguinis*.

Parameter	F Ratio	Probability
MACROGAMETOCYTE		
Length	$F_{2,162} = 66.50$	0.0000
Width	$F_{2,162} = 138.26$	0.0000
Area	$F_{2,162} = 179.24$	0.0000
Macrogametocyte Nucleus		
Length	$F_{2,119} = 8.39$	0.0004
Width	$F_{2,119} = 38.30$	0.0000
Area	$F_{2,119} = 37.90$	0.0000
NDR	$F_{2,162} = 53.02$	0.0000
No. pigment granules	$F_{2,125} = 32.90$	0.0000
MICROGAMETOCYTE		
Length	$F_{2,162} = 77.21$	0.0000
Width	$F_{2,162} = 149.48$	0.0000
Area	$F_{2,162} = 255.37$	0.0000
NDR	$F_{2,162} = 55.06$	0.0000
No. pigment granules	$F_{2,130} = 28.61$	0.0000

NDR = Nuclear Displacement Ratio

gametocyte but this was sufficient to identify H. sanguinis in this study.

Peirce (1984c) based his conclusions on a small sample of material from Africa, while the identifications and descriptions in this study are based on a large sample taken from across the range of the pycnonotids, with the haemoproteids under discussion described from their original type locality (India). While more is not necessarily better, in this case the larger sample provided haemoproteids identifiable as H. sanguinis. It is understandable, based on only H. otocompsae material and Chakravarty and Kar's (1945) description of H. sanguinis, why Peirce (1984c) synonymized H. sanguinis with H. otocompsae. However, these haemoproteids were shown to be clearly separable in this study and it is recommended that H. sanguinis stand as a valid species until such time as experimental studies on the life cycles and cross transmission of these parasites proves otherwise.

To summarize, H. otocompsae, H. sanguinis and H. philippini sp. n, are quite distinct species morphologically : H. otocompsae forms large halteridial gametocytes that markedly displace the host cell nucleus, H. sanguinis is a medium-sized halteridial parasite causing little nuclear displacement, while H. philippini

sp. n. is distinguishable due to its small size and extreme central constriction. Oneway analysis of variance showed both the macro- and microgametocytes of the three species to be clearly statistically separate on all parameters measured (Table 4, pg.32).

Key to the haemoproteids

1. Mature gametocytes small (occupying only about 36% of the host cell - parasite complex), with a pronounced central constriction; NDR = 0.8; pigment granules = 8 ..... H. philippini sp. n.

   Mature gametocytes larger, without central constriction 2

2. Mature gametocytes large (occupying 72% of the host cell - parasite complex), noticeably displacing host cell nucleus, NDR = 0.5; pigment granules = 10 ..... H. otocompsae

   Mature gametocytes medium-sized, (occupying 54% of the host cell - parasite complex); only slightly displacing host cell nucleus, NDR = 0.8; pigment granules = 15 ..... H. sanguinis

Discussion

Bennett et al. (1972, 1975a,b) summarized the available experimental data concerning host specificity in the avian haemoproteids. Cited were : Fallis and Wood (1957) (H. nettionis in Anatidae), Fallis and Bennett (1960) (H. mansoni in Tetraonidae), Khan and Fallis (1971) (H. velans in Picidae), Baker (1966a,b) (H. palumbis in Columbidae), and less specifically, work on H. columbae in Columbidae by many authors; additional data was presented by Forrester et al. 1974 (H. meleagridis in Meleagridae). The authors cited presented experimental evidence which led Bennett and his coworkers to conclude, that

haemoproteids are host specific usually at the avian family level. This conclusion served as the basis for utilizing the avian host family as the major taxonomic characteristic for diagnosing the avian haemoproteids. Differences in gametocyte morphology, supported by quantitative measurements, then became the primary diagnostic characteristic for identifying haemoproteid species from the same host family (Greiner et al. 1977). Bennett and Peirce (1985) summarized the known vectors of the haemoproteids.

It has been shown that H. otocompsae, H. sanguinis and H. philippini sp. n. are easily distinguishable from each other both morphologically and morphometrically. Assuming familial specificity, they are also separate from similar haemoproteid species occurring in other avian families, although it is recognized that future experimentation may result in their eventual synonymy.

Leucocytozoon

Historical

Leucocytozoon was first reported from the bulbuls by Mathis and Leger (1910), who described Leucocytozoon brimonti from a Pycnonotus sinensis from Hanoi, North Vietnam and in 1911 provided illustrations of the new parasite. A second species of Leucocytozoon was recorded from the Pycnonotidae by de Mello (1936) who illustrated and briefly described Leucocytozoon molpastis from a

Pycnonotus cafer 'shot at Ponda, India. De Mello's description of L. molpastis constitutes the only record of this parasite in the literature. Leucocytozoon brimonti, however, has been recorded from Pycnonotus barbatus (Bennett and Herman 1976, Zaire; Peirce et al. 1977a, Kenya; Wink and Bennett 1976, Ghana), Pycnonotus importunus (Bennett and Herman 1976, Tanzania; Peirce et al. 1977a, Kenya), Pycnonotus xanthopygos (Bennett and Herman 1976, Africa) and Pycnonotus virens (Bennett et al. 1977, Uganda).

In addition to L. brimonti and L. molpastis, three other Leucocytozoon species have been recorded from the pycnonotids. Leucocytozoon fringillinarum was reported by Peirce et al. (1977c) in Pycnonotus jocosus from Mauritius, and L. dubreuili and L. majoris were recorded by Nandi and Mandal (1978) in Pycnonotus leucogenys from India. Remaining references in the literature to Leucocytozoon in the Pycnonotidae are numerous but identify the parasite only to the generic level (Appendix E).

Results

Comparison of the original descriptions and illustrations of L. brimonti and L. molpastis show these parasites to be indistinguishable on a morphological basis, and since both species are reported from the same host family, it is proposed that L. molpastis be

synonymized with L. brimonti which predates it.

The present study identified L. brimonti (Fig. 6), L. dubreuili (Fig. 7) and L. majoris (Fig. 8) from the bulbul species examined, establishing 21 new host records for L. brimonti, 9 new host records for L. dubreuili, and 17 new host records for L. majoris (Appendix E). In addition, Leucocytozoon was found for the first time in Pycnonotus melanoleucos but was not identifiable to species. Double infections of L. brimonti and L. majoris were found in Criniger pallidus and Pycnonotus melanicterus from Thailand, and in Pycnonotus xanthopygos from Tanzania. A double infection of L. brimonti and L. majoris was found in a Criniger pallidus from Thailand. Double infections of L. majoris and L. dubreuili were found in Hypsipetes mcclellandii and Pycnonotus melanicterus from Thailand.

The distributional range of L. brimonti, known previously only from North Vietnam and Africa, with the addition of new records from India, Thailand, Malaysia, the Philippines and Hong Kong, has now been extended to include the entire distributional range of the host family.

Discussion

Leucocytozoon species have generally been distinguished on the morphology of their gametocytes in the peripheral circulation of the host, and to some

Figure 6.

Leucocytozoon brimonti

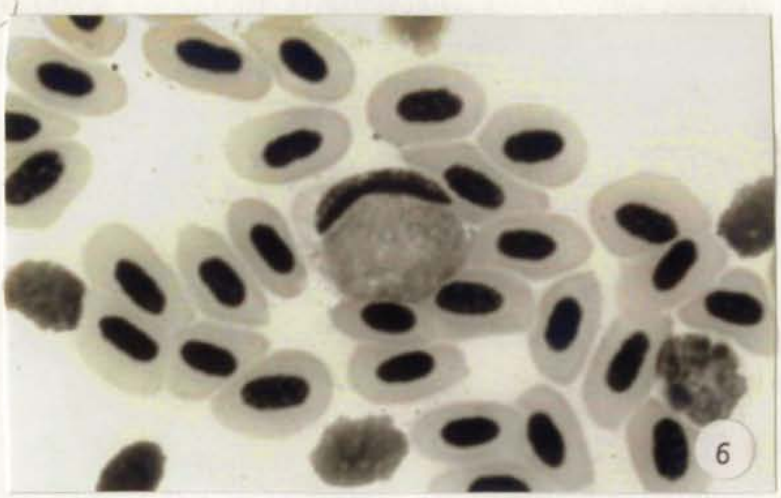
Figure 7.

Leucocytozoon dubreuili

Figure 8.

Leucocytozoon majoris

Note: Unparasitized erythrocyte approximately 12 µm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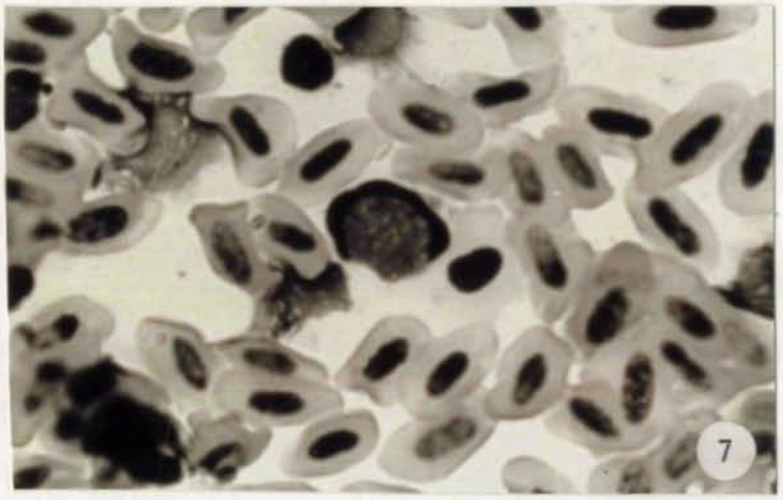
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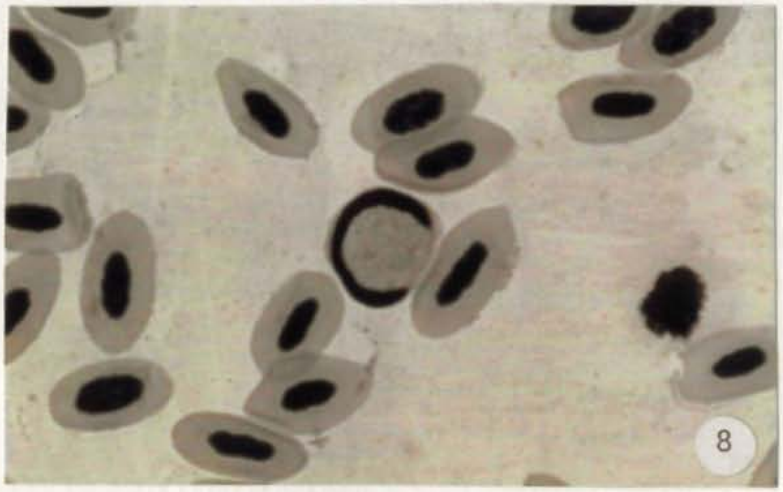
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extent, especially by earlier authors, on the species of host (Bennett et al. 1965). Fallis et al. (1974) identified the major morphological criteria for species identification in the Leucocytozoidae. These included the size, shape and staining characteristics of the parasite, the nature and extent of host cell distortion, and the size, shape and position of the altered host cell nucleus. Bennett and Campbell (1975) examined the variability of these morphological parameters within the Leucocytozoidae and found that species could not be separated on the basis of measurements alone. They concluded that the most reliable morphological character for species definition is a qualitative one - the appearance of the deformed host cell nucleus.

With regard to host specificity, Bennett et al. (1975c) stated that the taxonomy of the genus is largely predicated on the concept of specificity at the familial level. The limited experimental evidence available on Leucocytozoon specificity supports this premise, with the exception of L. fringillinarum which has been experimentally transmitted to several families within the Passeriformes (Fallis and Bennett 1962; Khan 1969, 1970). Examination of mixed infections involving L. fringillinarum, L. dubreuili and L. majoris led Bennett and Cameron (1975) to invalidate the assumption that Leucocytozoon species are host family specific.

From the foregoing, it appears that, at present, the

major criteria for distinguishing species within the genus Leucocytozoon, i.e. parasite morphology and assumed host family specificity, are not always reliable indicators of species. This leaves host order specificity, since no Leucocytozoon species has yet been experimentally transmitted between host orders, and the configuration of the host cell nuclear distortion (Bennett and Campbell 1975), as the prime characteristics for species differentiation within the Leucocytozoidae. On these bases, as well as on the evidence presented by Bennett and Cameron (1975), L. dubreuili and L. majoris were identified in this study. These same criteria also justified the synonymy of L. molpastis with L. brimonti.

The status of L. brimonti itself however is doubtful. Berson (1964) questioned the validity of L. brimonti but did not mention L. molpastis of which he was apparently unaware. Hsu et al. (1973) listed both L. brimonti and L. molpastis as valid species on the basis of their different hosts. Fallis et al. (1974) expressed doubt about the status of both species but included L. brimonti in their checklist as a valid species and L. molpastis as a species inquirenda. Peirce et al. (1977c) considered L. brimonti a synonym of L. fringillinarum and Peirce (1984a) reiterated this position in his Zambian survey.

Although similar, L. brimonti can be distinguished from L. fringillinarum on the basis of the configuration of the host nuclear distortion. While both species are

characterized by a nuclear cap that extends around approximately one-third of the circumference of the parasite, that of L. fringillinarum is usually thinner at the extremities than in the middle, while that of L. brimonti is uniformly thick for its entire length and often appears almost rectangular. However, it should be noted that the shape of the nuclear cap is a variable character which may be somewhat distorted by the blood film preparation technique itself and can be affected by the density of cells on the smear. The difference in host nuclear deformity between the two species is not as marked as that, for example, between L. dubreuili and L. majoris, and it is recognized that future research may result in the eventual synonymy of L. brimonti with L. fringillinarum. However, based on the specimens examined in this study, it is recommended that L. brimonti be considered a valid species until such time as experimental evidence proves otherwise.

Distribution of haemoproteids by host genera

According to Delacour (1943), the bulbul family can be subdivided, on the basis of their anatomy, habits and behaviour, into four principal groups of genera as follows: 1) Pycnonotus, Calyptocichla, Spizixos, Baeopogon and Ixonotus, which are arboreal, with most frequenting bush or parklike country; 2) Criniger, Hypsipetes and Setornis, all of which are forest canopy birds; 3)

Phyllastrephus, Bleda and Nicator, which are forest birds, with some living near the ground in thickets and lower vegetation; and 4) Chlorocichla and Thescelocichla, which live mainly in forest thickets.

Nine bulbul genera, representing all four groups, were examined for blood parasites in this study (Table 5). Most were sampled in small numbers and were negative for Haemoproteus, viz. Chlorocichla, Ixonotus, Nicator, Setornis and Spizixos, while only one H. sanguinis infection was identified in Phyllastrephus. The remaining three genera, Criniger, Hypsipetes and Pycnonotus, were sampled in sufficient quantities to warrant further discussion and will be examined with regard to the distribution of the haemoproteid species.

Criniger, Hypsipetes and Pycnonotus were examined for differences among them in infection rates for H. otocompsae, H. philippini sp. n. and H. sanguinis, and for total haemoproteid infections. Pycnonotus and Criniger demonstrated similar rates of infection with Haemoproteus (Table 6), while Hypsipetes showed a significantly lower overall prevalence for Haemoproteus. There was no statistical difference between Criniger and Hypsipetes in the prevalence of H. otocompsae. Both genera had significantly lower prevalences of H. otocompsae than did Pycnonotus. All three genera demonstrated significant differences in prevalences between them for both H. philippini sp. n. (Hypsipetes > Criniger > Pycnonotus) and

Table 5.

Distribution of bulbul haemoproteid infections by host genera.

Host Genus	Total birds	Total Haem.	Total birds infected with			
			Haem. sp.	Haem. oto.	Haem. phil. sp. n.	Haem. sang.
Chlorocichla	15	0	-	-	-	-
Criniger	677	97	21	2	57	20
% of Total birds				0.3	8.4	3.0
% of Total Haem.				2.1	58.8	20.6
Hypsipetes	1215	370	65	6	280	28
% of Total birds				0.5	23.0	2.3
% of Total Haem.				1.6	75.7	7.6
Ixonotus	1	0	-	-	-	-
Nicator	4	0	-	-	-	-
Phyllastrephus	67	4	3	-	-	1
Pycnonotus	7759	1067	393	93	148	461
% of Total birds				1.2	1.9	5.9
% of Total Haem.				8.7	13.9	43.2
Setornis	2	0	-	-	-	-
Spizixos	70	0	-	-	-	-
Unidentified bulbuls	24	7	7	-	-	-
TOTAL :	9834	1545	489	101	485	510
% of total birds :		15.7	5.0	1.0	4.9	5.2
% of total Haem. :				6.5	31.4	33.0

Haem. = Haemoproteus, Haem. sp. = Haemoproteus sp., Haem. oto. = Haemoproteus otocompsae, Haem. phil. sp. n. = Haemoproteus philippini sp. n., Haem. sang. = Haemoproteus sanguinis.

Note : Because of double infections, the haemoproteid species do not always add up to the total Haemoproteus found in a bulbul genus.

Table 6.

Results of T-tests on arcsine transformations of the proportions of haemoproteids within host genera. ($T_{\alpha=0.05} = 1.96$).

Test	Total Haemoproteus Calc. T	Haemoproteus otocompsae Calc. T	Haemoproteus philippini sp.n. Calc. T	Haemoproteus sanguinis Calc. T
Pycnonotus vs. Criniger	0.38	7.69 *	24.55 *	12.26 *
Pycnonotus vs. Hypsipetes	13.29 *	11.19 *	44.40 *	28.36 *
Criniger vs. Hypsipetes	8.23 *	0.78	8.06 *	8.00 *

Calc. T : calculated T value

* : significant at $\alpha = 0.05$

H. sanguinis (Pycnonotus > Criniger > Hypsipetes).

When the genera are examined individually (Table 5, pg. 43), in the genus Criniger, H. philippini sp. n. was the dominant haemoproteid accounting for 58.8% of the total Haemoproteus infections, followed by H. sanguinis with 20.6%, and H. otocompsae with 2.1%, leaving 18.5% of the haemoproteid infections in Criniger unidentified to species. In the genus Hypsipetes, H. philippini sp. n. was again the dominant Haemoproteus species, accounting for 75.7% of the total haemoproteid infections, with H. sanguinis comprising only 7.6% and H. otocompsae only 1.6%, with 15.1% unidentified to species. In the genus Pycnonotus, H. sanguinis was the dominant haemoproteid comprising 43.2% of the total Haemoproteus infections, followed by H. philippini sp. n. with 13.9% and H. otocompsae with 8.7%, leaving 34.2% of the haemoproteid infections unidentified to species.

Examination of the 35 individual species infected with species of Haemoproteus within these genera (Table 7), showed that the same patterns of haemoproteid infection that exist at the host genus level exist also at the host species level, with only three exceptions. Hypsipetes propinquus showed a higher rate of infection with H. sanguinis than with H. philippini sp. n., and Pycnonotus barbatus and Pycnonotus luteolus both demonstrated a higher prevalence for H. otocompsae than for H. sanguinis.

Table 7.

Distribution of bulbul haemoproteid infections by host species.

Host species	Total birds	Total Haem. %Tb	Haem. oto. %Tb %TH	Haem. phil. sp. n. %Tb %TH	Haem. sang. %Tb %TH
Criniger bres	177	27 15.3	1 0.6 3.7	16 9.0 59.3	9 5.1 33.3
Criniger flaveolus	19	3 15.8	-	-	2 10.5 66.7
Criniger ochraceus / pallidus *	279	67 24.0	1 0.4 1.5	41 14.7 61.2	9 3.2 13.4
Hypsipetes amaurotis	28	4 14.3	-	2 7.1 50.0	-
Hypsipetes charlottae	19	6 31.6	-	4 21.1 66.7	-
Hypsipetes crassirostris	3	1 33.3		-	1 33.3 100.0
Hypsipetes criniger	102	4 3.9	2 2.0 50.0	1 1.0 25.0	-
Hypsipetes flavala	43	6 14.0	-	2 4.7 33.3	1 2.3 16.7
Hypsipetes madagascariensis	112	14 12.5	1 0.9 7.1	11 9.8 78.6	1 0.9 7.1
Hypsipetes mcclellandii	309	64 20.7	-	33 10.7 51.6	1 0.3 1.6
Hypsipetes philippinus	414	190 45.9	-	170 41.1 89.5	1 0.2 0.5

Table 7 (Continued).

Distribution of bulbul haemoproteid infections by host species.

Host species	Total birds	Total Haem. %Tb	Haem. oto. %Tb %TH	Haem. phil. sp. n. %Tb %TH	Haem. sang. %Tb %TH
Hypsipetes propinquus	38	26 68.4	3 7.9 11.6	3 7.9 11.6	8 21.1 30.8
Hypsipetes siquijorensis	72	55 76.4	-	54 75.0 98.2	-
Phyllastrephus fischeri	6	1 16.7	-	-	1 16.7 100.0
Phyllastrephus strepitans	15	3 ** 20.0	-	-	-
Pycnonotus atriceps	189	6 3.2	1 0.5 16.7	1 0.5 16.7	2 1.1 33.3
Pycnonotus auriqaster	61	7 11.5	-	-	1 1.6 14.3
Pycnonotus barbatus	221	49 22.2	15 6.8 30.6	1 0.5 2.0	13 5.9 26.5
Pycnonotus blanfordi	1091	526 48.2	43 3.9 8.2	91 8.3 17.3	178 16.3 33.8
Pycnonotus brunneus	81	7 8.6	1 1.2 14.3	1 1.2 14.3	3 3.7 42.9
Pycnonotus cafer	298	23 7.7	1 0.3 4.3	1 0.3 4.3	9 3.0 39.1
Pycnonotus erythropthalmos	46	3 6.5	-	1 2.2 33.3	1 2.2 33.3

Table 7 (Continued).

Distribution of bulbul haemoproteid infections by host species.

Host species	Total birds	Total Haem. %Tb %TH	Haem. oto. %Tb %TH	Haem. sp. %Tb %TH	phil. n. %Tb %TH	Haem. sang. %Tb %TH
Pycnonotus eutilotus	55	1 1.8	-	-		1 1.8 100.0
Pycnonotus finlaysoni	200	9 4.5	-		2 1.0 22.2	2 1.0 22.2
Pycnonotus flavescens	186	5 2.7	1 0.5 20.0		1 0.5 20.0	1 0.5 20.0
Pycnonotus goiavier	2714	172 6.3	1 0.03 0.6		-	141 5.2 82.0
Pycnonotus jocosus	258	32 12.4	-		2 0.8 6.3	20 7.8 62.5
Pycnonotus leucogenys	81	6 7.4	2 2.5 33.3		-	3 3.7 50.0
Pycnonotus luteolus	66	40 60.6	20 30.3 50.0		-	12 18.2 30.0
Pycnonotus melanicterus	217	44 66.4	6 2.8 4.2		45 20.7 31.3	65 30.0 45.1
Pycnonotus plumosus	1339	12 0.9	1 0.1 8.3		-	-
Pycnonotus simplex	100	9 9.0	1 1.0 11.1		2 2.0 22.2	3 3.0 33.3
Pycnonotus sinensis	121	5 4.1	-		-	4 3.3 80.0

Table 7 (Concluded).

Distribution of bulbul haemoproteid infections by host species.

Host species	Total birds	Total Haem. %Tb	Haem. oto. %Tb %TH	Haem. phil. sp. n. %Tb %TH	Haem. sang. %Tb %TH
Pycnonotus striatus	10	1 ** 10.0	-	-	-
Pycnonotus virens	224	7 3.1	-	-	1 0.4 14.3
Pycnonotus xanthopygos	32	3 9.4	-	-	1 3.1 33.3
Unidentified bulbuls	24	7 **	-	-	-
Remaining species	584	0	-	-	-
TOTAL	9834	1545	101	485	510
%Tb :		15.7	1.0	4.9	5.2
%TH :			6.5	31.4	33.0

Haem. = Haemoproteus
Haem. oto. = Haemoproteus otocompsae
Haem. phil. sp. n. = Haemoproteus philippinus sp. n.
Haem. sang. = Haemoproteus sanguinis
%Tb = % of Total birds
%TH = % of Total Haem.

* Field separation of Criniger ochraceus and Criniger pallidus was unreliable so both species are considered together (McClure et al. 1978).

** Haemoproteids not identified to species level

Note : The haemoproteid species do not always add up to the total Haemoproteus found in a bulbul species because of double infections and because not all are identified to the species level.

Haemoproteus otocompsae

When the prevalence of H. otocompsae is examined at the host species level (Table 7, pg. 46), four bulbul species emerge as the most common hosts of this parasite. This haemoproteid was most prevalent in Pycnonotus luteolus, in which 30.3% of the total individuals examined were found to harbour H. otocompsae, followed by 7.9% of Hypsipetes propinquus, 6.8% of Pycnonotus barbatus and 3.9% of Pycnonotus blanfordi, with the remaining bulbul species infected with this parasite showing prevalences of less than 3.0%. Pycnonotus luteolus and Pycnonotus blanfordi are both birds of forest undergrowth, scrub and cultivated areas, with the former found in India and the latter in southeast Asia. Pycnonotus barbatus is a bulbul of cultivated and open country and is largely confined to Africa. Hypsipetes propinquus is a common forest bulbul in southeast Asia.

Haemoproteus philippini sp. n.

The highest prevalence of H. philippini sp. n. was seen in Hypsipetes siquijorensis in which 75.0% of the total birds examined harboured this parasite, followed by Hypsipetes philippinus with 41.1%, Pycnonotus melanicterus with 20.7%, Criniger ochraceus/pallidus with 14.7%, and Hypsipetes mcclellandii with 10.7% (Table 7, pg. 46). Remaining bulbul species demonstrated infection rates of

less than 10.0%, with the exception of Hypsipetes charlottae (21.1%) which had an inadequate sample size (19). Each of these species is found in the forest canopy. Hypsipetes siquijorensis is confined to several small islands in the Philippines, Hypsipetes philippinus is endemic to the Philippines where it is very common, and Pycnonotus melanicterus, Criniger ochraceus/pallidus, and Hypsipetes mcclellandii are all found in southeast Asia, with Pycnonotus melanicterus found as far west as India.

Haemoproteus sanguinis

The highest prevalence of H. sanguinis in an individual host species was seen in Pycnonotus melanicterus with an infection rate of 30.0%, followed by Hypsipetes propinquus with 21.1%, Pycnonotus luteolus with 18.2% and Pycnonotus blanfordi with 16.3% (Table 7, pg. 46). All are forest bulbuls with Pycnonotus luteolus confined mainly to India, Pycnonotus melanicterus found in India and southeast Asia, and Pycnonotus blanfordi and Hypsipetes propinquus found in southeast Asia. Remaining bulbul species demonstrated prevalences of less than 10.0% for H. sanguinis or were sampled in inadequate numbers.

Haemoproteus sanguinis, the most widely distributed haemoproteid with regard to number of host species infected, was found in 30 bulbul species of the 69 examined, H. philippini sp. n. occurred in 23 species and

H. otocompsae was found in only 18 species (Table 7, pg. 46). This could be interpreted to indicate that H. sanguinis is the oldest species of the three and H. otocompsae the youngest based on the premise that the older the species the more time it has had in which to disperse (Noble & Noble 1971).

Although it was expected that all three haemoproteid species would occur equally in each of the three major bulbul genera, from the foregoing, it is seen that definite trends are evident in the distribution of the bulbul haemoproteids with regard to host (Fig. 9). While each of the three haemoproteid species identified occurred in each of the three major pycnonotid genera examined, H. otocompsae and H. sanguinis were most common in Pycnonotus species, while H. philippini sp. n. occurred more frequently in Hypsipetes and Criniger species. This split in prevalence for host genera coincides with the division in relationships of the bulbul genera as described by Delacour (1943) who placed Pycnonotus in a group separate from that of Hypsipetes and Criniger, a grouping which reflects the ecological preferences of these bulbuls.

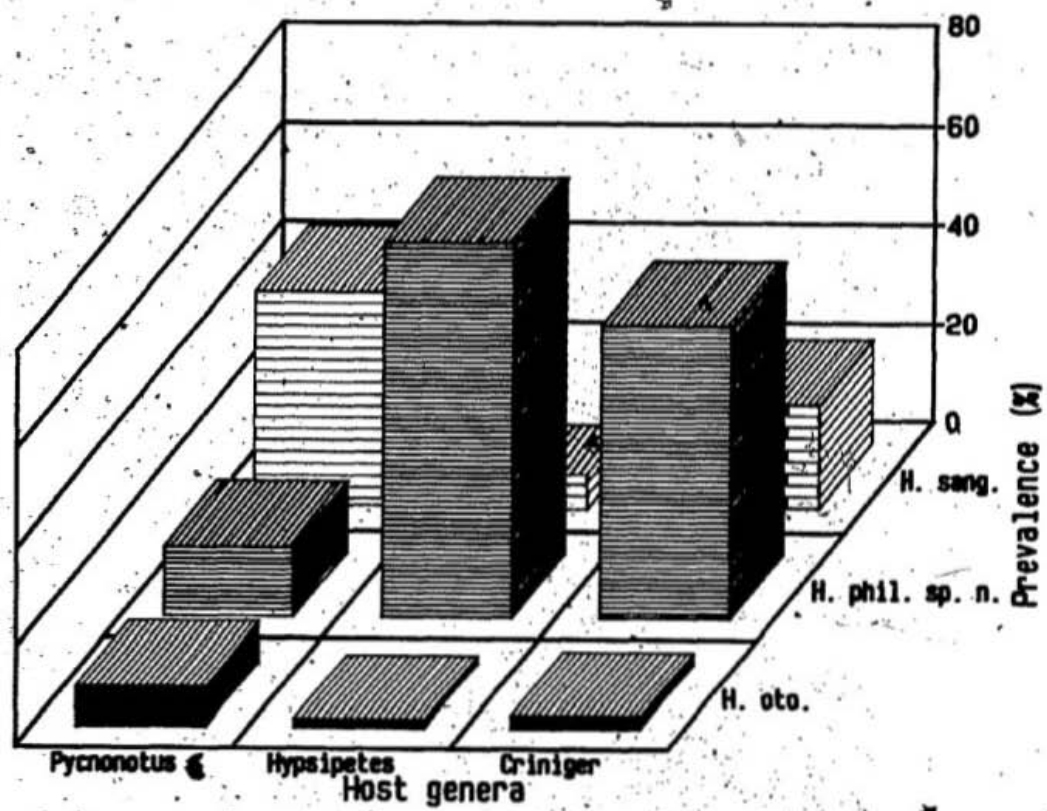
Cameron (1964) stated that the phylogeny and classification of a parasite can only be interpreted in terms of the phylogeny and classification of the host. It is obvious that, in general, related hosts tend to have related parasites. In light of this, the fact that Hypsipetes and Criniger, which are more closely related to

Figure 9.

Comparison of prevalences of bulbul haemoproteids by host genera.

Abbreviations :

H. oto. = Haemoproteus otocompsae
H. phil. sp. n. = Haemoproteus philippini sp. n.
H. sang. = Haemoproteus sanguinis


80
60
40
20
0
Prevalence (%)
H. sang.
H. phil. sp. n.
H. oto.
Pycnonotus
Hypsipetes
Criniger
Host genera

each other than to Pycnonotus, demonstrated a pattern of haemoproteid infection different from that of Pycnonotus is not surprising.

In comparing Pycnonotus, Hypsipetes and Criniger, McClure et al. (1978) described Pycnonotus as a lowland, lower canopy or shrub level, town, farm or forest bird; Criniger as a lower canopy forest bird which seeks slightly higher altitudes than Pycnonotus; and Hypsipetes as a canopy level mountain forest genus which overlaps with the other two. All three genera are similar in habit, with Criniger and Hypsipetes often travelling in mixed flocks, with Pycnonotus frequently joining them while feeding. Given the fact that the vectors involved are unknown and that each of the bulbul genera is infected by all three bulbul haemoproteids (thereby precluding a physiological barrier), in spite of the similarity of habit, it must be assumed that some variable facet of bulbul behaviour either enhances or reduces the potential for host/vector interaction and transmission of the different haemoproteid species, resulting in the patterns of infection described.

Zoogeography

Pycnonotids were sampled from two major continental areas, Africa and Asia (Table 8). The African sample was small, only 710 bulbuls from 17 areas, in contrast to the large Asian collection numbering 9124 birds from 16 areas.

Table 8.

Prevalence of *Haemoproteus* and *Leucocytozoon* in the Pycnonotidae by geographic area.

Area	Total birds	Total Haem.	Total birds infected with				Total Leuc.
			Haem. sp.	Haem. oto.	Haem. phil. sp. n.	Haem. sang.	
AFRICA							
Aldabra Atoll - Comoro Islands	29	1	-	-	-	1	0
Cameroon	18	6	6	-	-	-	0
Congo	3	0	-	-	-	-	1
Ethiopia	104	21	20	-	-	-	21
Ghana	9	2	1	-	-	1	1
Kenya	21	5	1	-	-	4	8
Mauritius / Reunion	55	0	-	-	-	-	10
Morocco	2	0	-	-	-	-	0
Rhodesia	1	0	-	-	-	-	0
Senegal	3	0	-	-	-	-	0
South Africa	2	0	-	-	-	-	1
Tanzania	39	2	1	-	-	1	30
Tchad	5	0	-	-	-	-	-
Uganda	374	17	7	-	1	9	4
United Arab Republic	2	0	-	-	-	-	-
Zaire	8	1	-	-	-	1	6
Zambia	35	16	1	15	-	-	16
Total	710	71	38	15	1	17	98
% infected		10.0	5.4	2.1	0.1	2.4	13.8

Table 8 (Concluded).

Area	Total birds	Total Haem.	Total birds infected with				Total Leuc.
			Haem. sp.	Haem. oto.	Haem. phil. sp. n.	Haem. sang.	
ASIA							
Bhutan	8	2	-	-	1	1	1
Borneo	152	5	4	1	-	-	4
East Pakistan	4	0	-	-	-	-	0
Fiji	4	0	-	-	-	-	0
Hong Kong	68	8	4	-	-	4	2
India	348	78	18	22	11	28	29
Indonesia	98	4	-	-	-	4	4
Iran	29	3	1	2	-	-	2
Iraq	1	0	-	-	-	-	0
Japan	18	1	-	-	1	-	0
Malaysia	3427	38	12	5	11	10	75
Philippines	1436	440	53	1	244	151	31
South Korea	6	0	-	-	-	-	0
Taiwan	115	3	2	-	1	-	0
Thailand	3356	892	357	55	215	295	206
Turkey	6	0	-	-	-	-	0
unknown	48	0	-	-	-	-	0
Total :	9124	1474	451	86	484	493	354
% infected :		16.2	4.9	0.9	5.3	5.4	3.9
Grand total :	9834	1545	489	101	485	510	452
% infected :		15.7	5.0	1.0	4.9	5.2	4.4

Haem.=Haemoproteus, Haem. sp.=Haemoproteus sp., Haem. oto.=Haemoproteus otocompsae, Haem. phil. sp. n.=Haemoproteus philippini sp. n., Haem. sang.=Haemoproteus sanguinis

The rate of infection by Haemoproteus was low in Africa at only 10.0% with a higher rate of infection of 16.2% in Asia, while Leucocytozoon showed a prevalence of 13.8% in Africa and only 3.9% in Asia.

Of the 33 areas in which bulbuls were examined, in only three, Thailand, Malaysia and the Philippines, were they sampled in sufficient numbers to allow examination of the distributional patterns of the blood parasites under discussion, and these will be further discussed.

Thailand

Thailand was divided into three major areas for discussion by McClure et al. (1978) : northern Thailand which is a forested, mountainous inland area forming part of the Himalayan ranges; central Thailand, the central plain which is mainly a rice producing area; and southern Thailand on the Malayan peninsula, which is mostly jungle.

As seen in Fig. 10, Haemoproteus was most prevalent in central Thailand (30.7%), less common in northern Thailand (22.9%) and least common in the south (12.3%), with H. sanguinis, H. philippini sp. n., and H. otocompsae each following this same pattern of prevalence. Leucocytozoon was most common in the north (10.4%), lower in the south (5.5%), and lowest in the central area (4.1%) where Haemoproteus was most common.

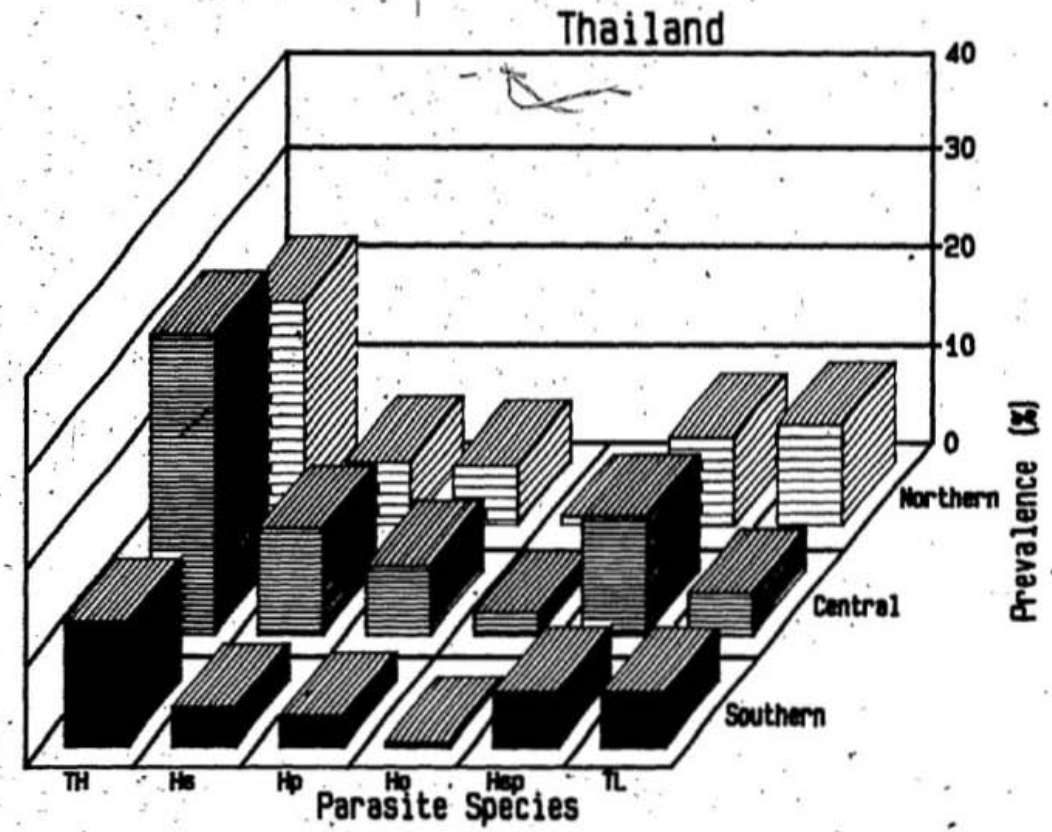
These patterns of prevalence for Haemoproteus and Leucocytozoon in Thailand are not unexpected given that

Figure 10.

Prevalence of *Haemoproteus* and *Leucocytozoon* in Thailand.

Abbreviations :

TH = Total *Haemoproteus*
Hs = *H. sanguinis*
Hp = *H. philippini* sp. n.
Ho = *H. otocompsae*
Hsp = *H.* sp.
TL = Total *Leucocytozoon*


Thailand
40
30
20
10
0
Prevalence (%)
Northern
Central
Southern
TH
Hs
Hp
Ho
Hsp
TL
Parasite Species

the simuliid vectors of Leucocytozoon require rapid running water, a condition more likely to be encountered in the mountainous north, while the higher prevalence of Haemoproteus in the central area is possibly explained by a more favorable environment for its assumed ceratopogonid vectors.

Patterns of infection with regard to host genus were similar in all three regions of Thailand and are consistent with those discussed previously. Approximately the same number of host species were sampled in each area : 18 species in northern Thailand, 19 in southern Thailand and 16 species in central Thailand. Haemoproteus philippini sp. n. infections were concentrated in Criniger and Hypsipetes species while H. otocompsae and H. sanguinis were found in greater numbers in Pycnonotus species. Haemoproteus philippini sp. n. was found in fewer host species (11) than H. sanguinis (18) while H. otocompsae was harbored by only six bulbul species. In relation to each other, in each of these three areas, H. sanguinis was the dominant haemoproteid followed in prevalence by H. philippini sp. n. and H. otocompsae.

Only three host species were common to all three areas : Criniger ochraceus and C. pallidus, which are lower canopy forest birds, and Hypsipetes propinquus which are common forest birds usually found in association with Criniger pallidus (McClure et al. 1978). In each area, the former was most frequently infected with H. philippini sp.

n., but was also infected by H. sanguinis, while the latter, which was represented by a smaller sample size, was infected by all three Haemoproteus species but showed a greater tendency towards infection by H. sanguinis.

Malaysia

Malaysia was split into two main areas for comparison : highland Malaya, more specifically, Mount Brinchang (Pahang), at 2000 meters, one of the highest peaks in the midrange of Malaya, where collections were made in disturbed ericaceous cloud forest; and lowland Malaya, where there were two principal collection sites : Rantau Panjang, a coconut grove - nipah palm - mangrove habitat at sea level on the west coast of Selangor; and Subang, a secondary dipterocarp forest at an altitude of 50 meters near Kuala Lumpur, Selangor (Laird and McClure 1966).

As seen in Fig. 11, Haemoproteus was rare in both highland (3.0%) and lowland (1.0%) Malaya, while Leucocytozoon showed a relatively high prevalence (10.4%) in highland Malaya and was rare in lowland Malaya (1.8%).

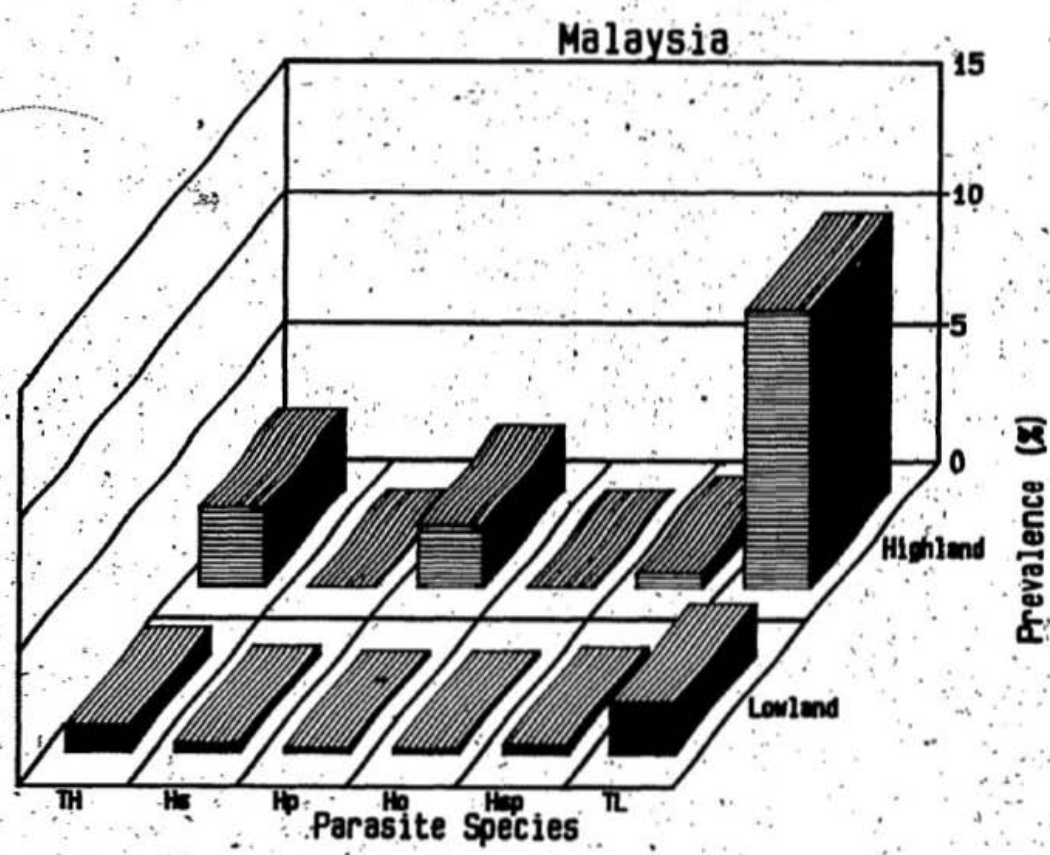
The higher prevalence of Leucocytozoon on Mount Brinchang was presumably due to a greater abundance of lotic breeding habitats for the simuliid vectors in this montane environment than in the lowland areas, while the rarity of Haemoproteus, particularly in the lowlands is more difficult to explain. McClure et al. 1978 recorded

Figure 11.

Prevalence of Haemoproteus and Leucocytozoon in Malaysia.

Abbreviations :

TH = Total Haemoproteus
Hs = H. sanguinis
Hp = H. philippini sp. n.
Ho = H. otocompsae
Hsp = H. sp.
TL = Total Leucocytozoon


Malaysia
15
10
5
0
Highland
Lowland
Prevalence (%)
TH
Hs
Hp
Ho
Hsp
TL
Parasite Species

more than 90 species of potential arthropod vectors for haemosporozoans in the Rantau Panjang area, which considering the low rate of infection for Haemoproteus, points to the need for closer examination of vector species in order to determine which vectors might be involved in transmission. If suitable vectors are found to be available, some behavioural or physiological characteristic must either segregate the bulbuls in this area from close vector contact or make them less susceptible to infection.

Haemoproteus philippini sp. n. was the only haemoproteid encountered in highland Malaya, in contrast to the lowland areas where all three bulbul haemoproteids were found, all demonstrating very low prevalence rates of less than 1.0% each.

Even though the number of haemoproteid infections in Malaysia was very low, a trend was observed in the distribution of the haemoproteid species with regard to host species. Haemoproteus philippini sp. n. was most often found in Hypsipetes and Criniger species, while H. sanguinis preferred Pycnonotus species. Too few H. otocompsae were identified to make a statement on host patterns.

Only two pycnonotid species were common to both highland and lowland Malaya, viz. Hypsipetes charlottae and Hypsipetes flavala, but were taken in such small numbers in both areas that a comparison could not be made.

The Philippines

Bulbuls were collected on six islands in the Philippines, from largest to smallest, Luzon, Mindanao, Negros, Palawan, Mindoro and Siquijor. The Philippines lie entirely within the tropical zone, with the monsoons bringing heavy rainfalls, and the larger islands traversed by mountain ranges.

As seen in Fig. 12, not counting Mindoro which had an inadequate sample size, Haemoproteus was highest in prevalence in the Philippines on Siquijor, followed by Negros, Mindanao, Palawan, and Luzon. Leucocytozoon had its highest rate of infection on Negros with lower rates on Mindanao and Palawan and was absent from Luzon, Mindoro and Siquijor.

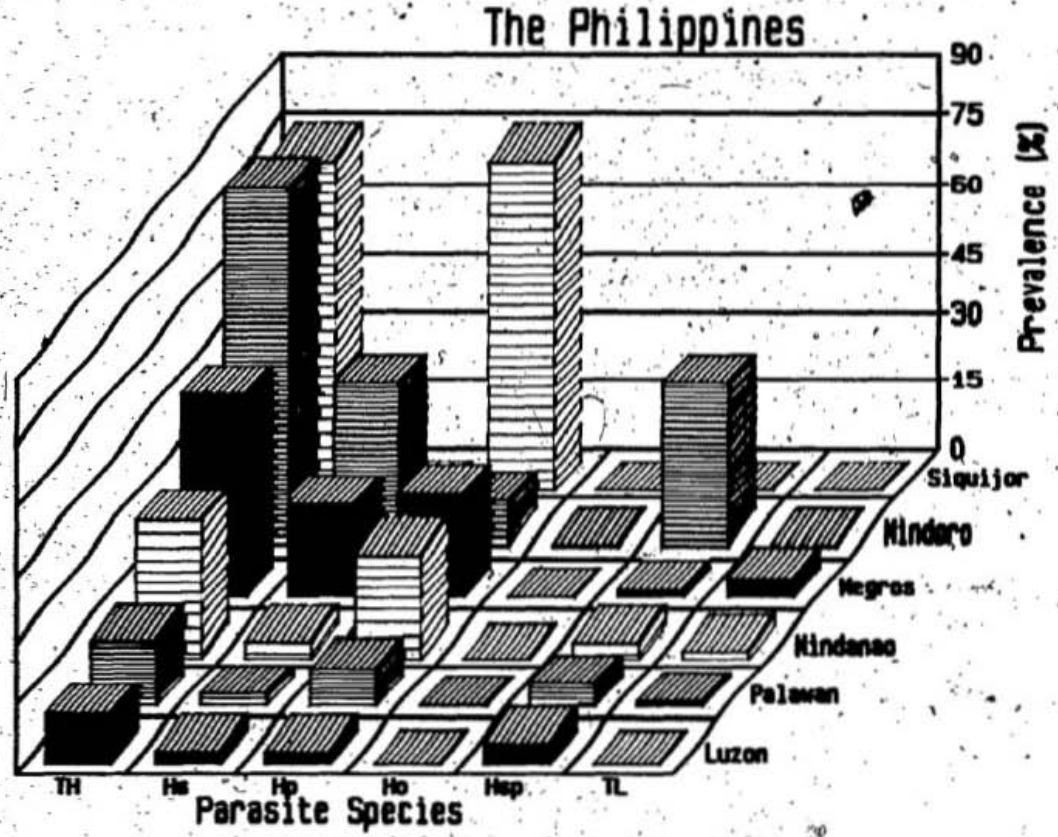
Haemoproteus philippini sp. n. was the most commonly occurring haemoproteid followed by H. sanguinis and H. otocompsae. The only occurrence of H. otocompsae in the Philippines was one infection found on Negros. Haemoproteus philippini sp. n. was most prevalent on Siquijor (76.4%) where it was the only haemoproteid species found, then dropped sharply in prevalence on Negros (23.5%) and Mindanao (23.3%), experienced another marked decline on Mindoro (9.1%) and Palawan (9.0%), and recorded its lowest prevalence on Luzon (2.8%). Haemoproteus philippini sp. n. showed a clear difference in prevalence between the more southerly islands,

Figure 12.

Prevalence of *Haemoproteus* and *Leucocytozoon* in the Philippines.

Abbreviations :

TH = Total *Haemoproteus*
Hs = *H. sanguinis*
Hp = *H. philippini* sp. n.
Ho = *H. otocompsae*
Hsp = *H.* sp.
TL = Total *Leucocytozoon*


The Philippines
90
75
60
45
30
15
0
Prevalence (%)
Siquijor
Mindoro
Negros
Mindanao
Palawan
Luzon
TH
Hs
Hp
Ho
Hsp
TL
Parasite Species

Mindanao, Negros and Siquijor, and the northern islands, Luzon, Palawan and Mindoro. Haemoproteus sanguinis appeared most often on Mindoro (36.4%), and recorded a fairly high prevalence rate on Negros (20.9%), with low but fairly equal rates of infection on Mindanao (3.3%), Palawan (3.2%) and Luzon (2.6%), and was absent from Siquijor. Haemoproteus philippini sp. n. showed a slightly higher rate of infection than H. sanguinis on Luzon and Negros, and a significantly higher rate on Mindanao and Palawan. Mindoro, which had a small sample size, had a much higher rate of infection with H. sanguinis than with H. philippini sp. n.

It was generally observed that, with the exception of Palawan, as the size of the island decreased, the rate of infection with Haemoproteus increased. Also with the exception of Palawan, H. philippini sp. n., the most common haemoproteid in the Philippines, was generally harboured by Hypsipetes philippinus (69.3%), a forest edge bulbul endemic to the Philippines, while H. sanguinis was usually associated with Pycnonotus goiavier (95.4%), a common garden and farmyard bulbul. On Siquijor, a tiny island off Negros, Hypsipetes siquijorensis replaced Hypsipetes philippinus as the major host for H. philippini sp. n. On Palawan, most of the H. philippini sp. n. infections were found in Criniger bres, a forest bulbul. Pycnonotus goiavier and Hypsipetes philippinus were the only species common to the islands examined in this study,

with the exception of Siquijor on which only Hypsipetes siquijorensis was sampled.

Comparison of similar areas

It was expected, in highland Malaya and northern Thailand where the bulbuls were sampled in mountainous areas, that the prevalence of blood parasites would be similar. The same was expected of India and central Thailand where the sampling sites were situated mainly in low lying areas with many paddy fields.

Comparison of highland Malaya and northern Thailand

Highland Malaya and northern Thailand, as expected since they are both mountainous areas, demonstrated identical prevalence rates for Leucocytozoon of 10.4% each. However, these two areas differed significantly in the prevalence of Haemoproteus, which was found in only 3.0% of the bulbuls examined in highland Malaya, in contrast to an infection rate of 22.9% in northern Thailand (Fig. 13). This marked difference in prevalence of Haemoproteus between these two areas could perhaps be related to a difference in vector potential between the two areas.

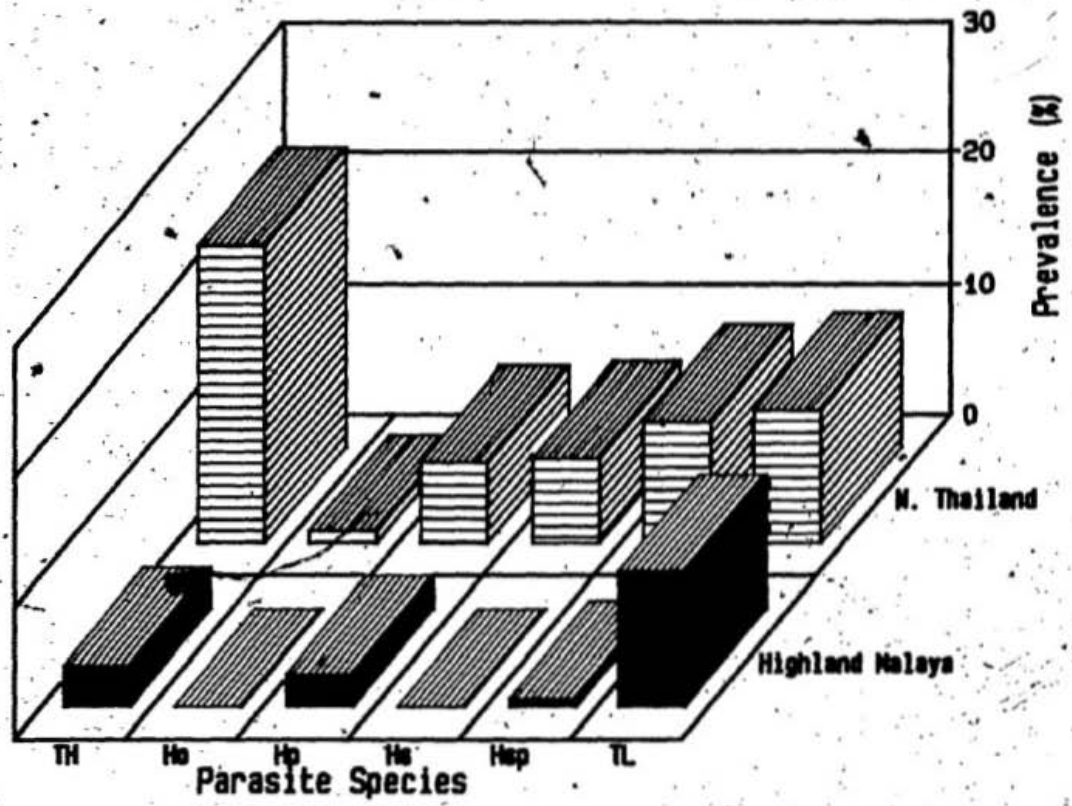
With regard to the haemoproteid species, H. otocompsae was rare in northern Thailand (0.9%), and was not encountered in highland Malaya; H. philippini sp. n. was found in 6.3% of the bulbuls examined in northern

Figure 13.

Comparison of prevalences of *Haemoproteus* and *Leucocytozoon* in highland Malaya and northern Thailand.

Abbreviations :

TH = Total *Haemoproteus*
Hs = *H. sanguinis*
Hp = *H. philippini* sp. n.
Ho = *H. otocompsae*
Hsp = *H.* sp.
TL = Total *Leucocytozoon*


30
20
10
0
Prevalence (%)
N. Thailand
Highland Malaya
TH
Hb
Hp
Hs
Hsp
TL
Parasite Species

Thailand but in only 2.4% in highland Malaya; and H. sanguinis showed a prevalence of 6.7% in northern Thailand and was not found in highland Malaya.

The difference in infection rates for H. philippini sp. n. and H. sanguinis between these two regions could be explained by a difference in the host species composition of bulbul populations in the two areas, since it has been shown that haemoproteid distribution is influenced by the phylogenetic relationships between the bulbuls, as reflected in their ecological relationships. However, it was found that a strong affinity existed between the bulbul populations of highland Malaya and northern Thailand, as evidenced by the fact that five of the six pycnonotid species examined in highland Malaya were common to northern Thailand. Of these species, only one, Hypsipetes mcclellandii, was sampled in sufficient numbers to be compared between the two areas. Of 156 Hypsipetes mcclellandii examined in northern Thailand, 60 (38.5%) were found to harbour H. philippini sp. n. and one was infected with H. sanguinis, in contrast to only 2 (1.4%) H. philippini sp. n. infections found in 147 birds of this species collected in highland Malaya. This data suggests that there may be a more efficient vector system attacking Hypsipetes mcclellandii in northern Thailand than in highland Malaya.

Comparison of central Thailand and India

Haemoproteids were more prevalent in central Thailand with 30.7% of the total bulbuls examined harbouring these parasites compared to 22.2% in India. The rate of infection by Leucocytozoon in India (8.3%) was double that of central Thailand (4.1%) (Fig. 14).

Haemoproteus otocompsae was more common in India (6.3%) than central Thailand (2.2%), while H. philippini sp. n. demonstrated a higher prevalence in central Thailand (7.0%) than India (3.3%), and H. sanguinis showed a similar rate of infection in both India (8.1%) and central Thailand (10.7%) (Fig. 14).

Distribution of haemoproteid species by country

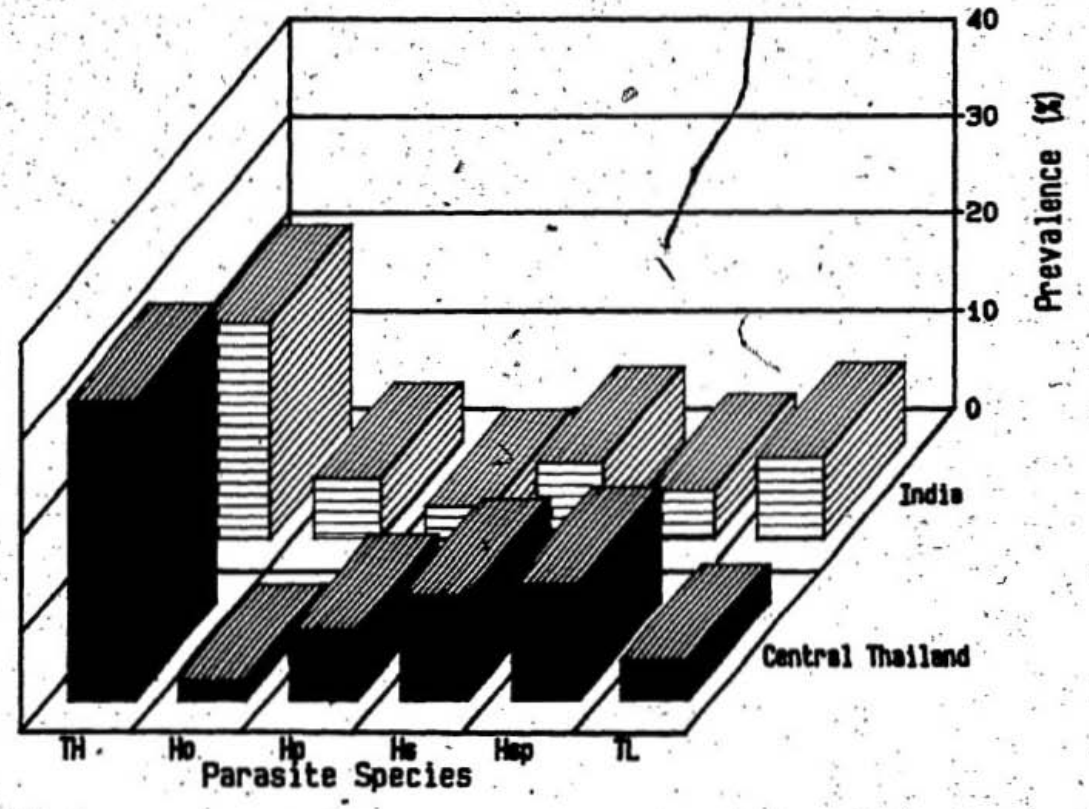
Of the three species of Haemoproteus found, H. otocompsae was the rarest, identified in 101 birds (6.5%) of 3 genera and 16 species; H. philippini sp. n. was much more common, found in 485 birds (31.4%) of 3 genera and 22 species; and H. sanguinis was most common, recorded from 510 birds (33.0%) of 4 genera and 29 species. Double infections of H. otocompsae and H. philippini sp. n. were found in 7 birds of 2 genera and 4 species; of H. philippini sp. n. and H. sanguinis in 30 birds of 3 genera and 5 species; and of H. otocompsae and H. sanguinis in 3 birds of 1 genus and 2 species. Unidentified haemoproteid species were found in 489 birds (31.7%). (Percentages were calculated based on the total number of Haemoproteus infections.)

Figure 14.

Comparison of prevalences of *Haemoproteus* and *Leucocytozoon* in central Thailand and India.

Abbreviations:

TH = Total *Haemoproteus*
Hs = *H. sanguinis*
Hp = *H. philippini* sp. n.
Ho = *H. otocompsae*
Hsp = *H.* sp.
TL = Total *Leucocytozoon*


40
30
20
10
0
Prevalence (%)
India
Central Thailand
TH
Ho
Hp
Hs
Hsp
TL
Parasite Species

Haemoproteus otocompsae

Haemoproteus otocompsae was identified from bulbuls in only six countries of the 32 examined (Table 8, pg. 55). It was rare in the Philippines (0.1%) and Malaysia (0.2%), showed only a slightly higher prevalence in Thailand (1.6%), and reached its highest prevalence in India (6.3%) and Iran (6.9%). Its occurrence in Africa was limited to Zambia (42.9%) and Kenya (100.0%) where its unusually high infection rates are probably attributable to small sample sizes, a truer picture represented by an infection rate of 2.1% for H. otocompsae for Africa as a whole.

Haemoproteus philippini sp. n.

Haemoproteus philippini sp. n. showed its highest rate of occurrence in the Philippines (17.0%), with much lower infection rates in Japan (5.6%), Taiwan (0.9%), Malaysia (0.3%), Thailand (6.4%), India (3.2%) and Bhutan (12.5%). Of these, Japan and Bhutan represented small collections of less than twenty bulbuls each. Haemoproteus philippini sp. n. was rare in Africa where it was found only in Uganda (0.3%). (Table 8, pg. 55).

Haemoproteus sanguinis

Haemoproteus sanguinis was the most uniformly distributed of the bulbul haemoproteids in Asia. It was found in Hong Kong (5.9%), the Philippines (10.5%),

Indonesia (4.1%), Malaysia (0.3%), Thailand (8.8%), Bhutan (12.5%) and India (8.0%). It was the common haemoproteid of bulbuls in Africa with infections found in Ghana (11.1%), Zaire (12.5%), Uganda (2.4%), Kenya (19.0%), Tanzania (2.6%), and Aldabra and the Comoro Islands (3.4%). (It should be noted that sample sizes were small in Ghana, Zaire and Kenya resulting in probable inflation of the prevalence rates.) (Table 8, pg. 55).

Trends in geographic distribution of the haemoproteids

Examination of prevalences showed definite trends in the geographic distribution of the bulbul haemoproteids (Fig. 15), (Only the major sampling areas in which all three haemoproteids were identified are shown.) Haemoproteus otocompsae increased in prevalence from east to west with a focus of infection in India and a decrease further west in Africa. Within Asia, it was the more "westerly" parasite. Haemoproteus philippini sp. n. was centred in the Philippines and generally presented lower infection rates the greater the distance from the Philippines. It was the more "easterly" parasite. Haemoproteus sanguinis was the most uniformly distributed haemoproteid occurring more or less across the distribution of the bulbuls and showing relatively stable prevalences through India and mid-southeast Asia.

The east-west trend in the distribution of the bulbul

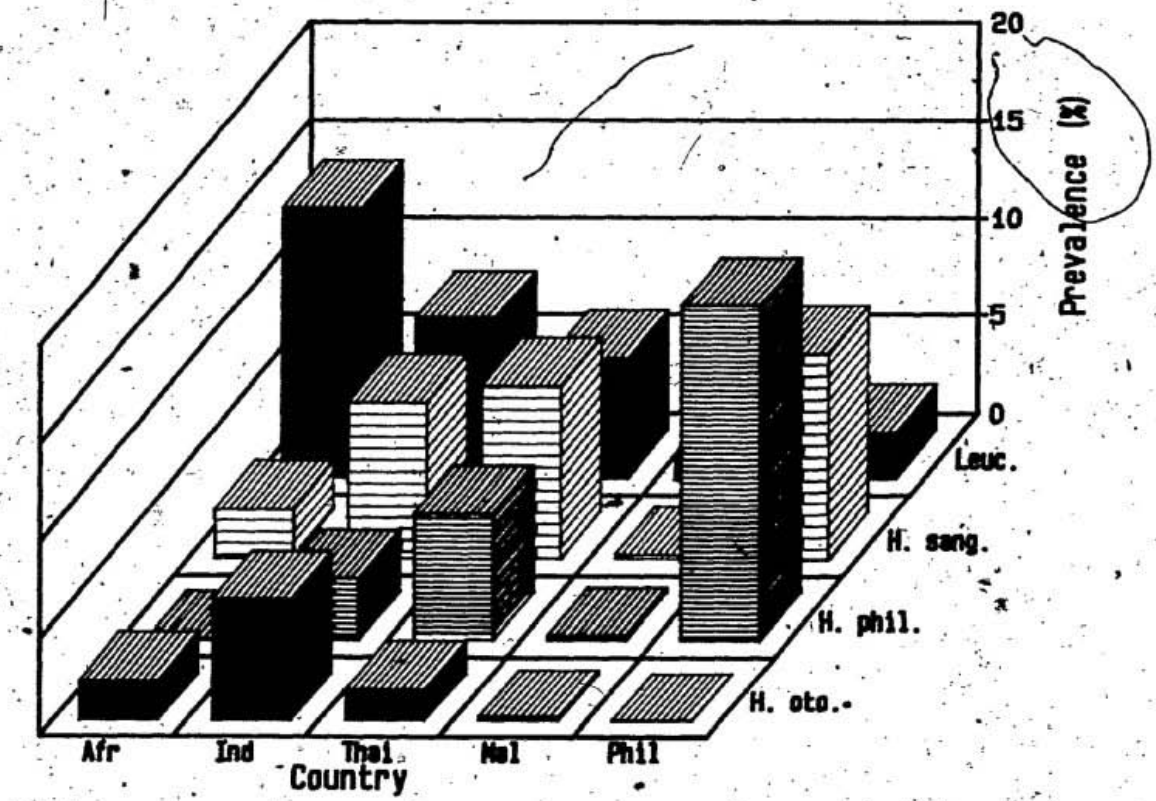
Figure 15.

Trends in the geographic distribution of Haemoproteus and Leucocytozoon in the Pycnonotidae

Abbreviations :

H. oto. = H. otocompsae
H. phil. = H. philippini sp. n.
H. sang. = H. sanguinis
Leuc. = Leucocytozoon

Afr = Africa
Ind = India
Thai = Thailand
Mal = Malaysia
Phil = The Philippines


20
15
10
5
0
Prevalence (%)
Leuc.
H. sang.
H. phil.
H. oto.-
Afr
Ind
Thai
Mal
Phil
Country

haemoproteids is made more obvious if the countries in which only a single haemoproteid species was found are traced across Asia - a definite cline appears with H. philippini sp. n. identified as the only haemoproteid in Japan and Taiwan, while H. sanguinis appears further west in Hong Kong and Indonesia, with H. otocompsae appearing even further west, in Iran.

In the east, H. otocompsae and H. sanguinis were found only as far east as the Philippines, while H. philippini sp. n. reached Japan. In the west, H. philippini sp. n. was distributed as far as Uganda, while H. otocompsae reached Zambia and H. sanguinis was found furthest west, in Ghana.

No haemoproteid infections were recorded from South Korea, Fiji, East Pakistan, Iraq and Turkey, most probably due to the very small number of bulbuls collected in each of these countries (N = 6 or less) rather than to an actual lack of haemoproteids.

Of the three haemoproteid species, H. sanguinis was the dominant parasite in Africa, India, Thailand and Indonesia. Haemoproteus philippini sp. n. replaced H. sanguinis as the dominant haemoproteid in Malaysia and the Philippines and as the only haemoproteid species in Taiwan and Japan. With the exception of Africa, India and Iran, if H. sanguinis was dominant, H. philippini sp. n. was second in prevalence and vice versa. Haemoproteus otocompsae, where it appeared, was always third in

prevalence, except in Africa and India where it replaced H. philippini sp. n. as second in prevalence to H. sanguinis and in Iran where it was the only haemoproteid species recorded. In short, H. philippini sp. n. was the dominant haemoproteid in bulbuls in southeast Asia, H. sanguinis was dominant in southwest Asia and Africa, and H. otocompsae was second in prevalence in Africa and India.

Leucocytozoon

Of the three species of Leucocytozoon found : L. brimonti occurred in 156 birds (34.5%) of 3 genera and 25 species, L. dubreuili in 29 birds (6.4%) of 3 genera and 9 species, and L. majoris in 80 birds (17.7%) of 3 genera and 19 species. Double infections of L. brimonti and L. dubreuili were found in 2 birds of 2 species; of L. brimonti and L. majoris in 6 birds of 1 genus and 3 species; and of L. dubreuili and L. majoris in 2 birds of 2 species. Unidentified Leucocytozoon species were found in 181 birds (40.0%). (Percentages were calculated based on the total number of Leucocytozoon infections.)

The prevalence of Leucocytozoon was highest in Africa at 13.8% and significantly lower in Asia at 3.9%. In Africa it was found in Uganda (1.1%), Mauritius (18.2%), Zaire (75.0%), Tanzania (76.9%), Ghana (11.1%), Kenya (38.1%), South Africa (50.0%), Ethiopia (20.2%), Zambia

(45.7%), and the Congo (33.1%). In Asia, Leucocytozoon was found in the Philippines (2.2%), Hong Kong (2.9%), Indonesia (4.1%), Malaysia (2.2%), Thailand (6.1%), India (8.2%), Bhutan (12.5%), and Iran (6.7%). It was not encountered in Fiji, Japan, South Korea, Taiwan, Iraq and Turkey (Table 8, pg. 55).

The overall pattern of distribution for the leucocytozoids of the bulbuls was an upward trend in prevalence from east to west (Fig. 15, following pg. 73).

SUMMARY AND CONCLUSIONS

1. Of the total bulbuls (9834) examined for blood parasites, 23.0% were infected with haematozoa.

2. Haemoproteus was the most commonly occurring blood parasite genus, found in 15.7% of the total bulbuls examined, followed in occurrence by Leucocytozoon in 4.6%, microfilaria in 3.1%, Plasmodium in 1.1%, and Trypanosoma in 0.7%.

3. Five species of Plasmodium (P. circumflexum, P. polare, P. relictum, P. rouxi and P. vaughani), and three species of Trypanosoma (T. avium, T. calmettei and T. paddae), were identified from the bulbuls. The microfilaria were not identified to species.

4. Haemoproteus otocompsae, H. sanguinis, and H. philippini sp. n. were recorded from the pycnonotids. H. sanguinis was resurrected from synonymy with H. otocompsae, and both species were redescribed; H. philippini sp. n. was described for the first time.

5. Leucocytozoon brimonti, L. dubreuili and L. majoris were identified in this study. It was recommended that L. brimonti be considered a valid species until proven otherwise experimentally, and it was proposed that L. molpastis be synonymized with L. brimonti.

6. Haemoproteus otocompsae, H. philippini sp. n. and H. sanguinis were all found in each of the three major bulbul genera examined, Criniger, Hypsipetes and Pycnonotus.

7. Haemoproteus otocompsae and H. sanguinis were found more often in Pycnonotus species, while H. philippini sp. n. was more frequently encountered in Hypsipetes and Criniger species. These differences in occurrence were found to be statistically significant.

8. This split on host genus by the haemoproteid species coincides with Delacour's (1943) phylogenetic division of the bulbul genera, a division which reflects the ecological preferences of the bulbuls.

9. Haemoproteus sanguinis, the most widely distributed haemoproteid with regard to number of host species, was found in 30 bulbul species, H. philippini sp. n. in 23 and H. otocompsae in 18.

10. Pycnonotids were sampled across the range of their distribution from western Africa to southeastern Asia and north to Japan.

11. The major sampling areas, Thailand, Malaysia and the Philippines, were examined in detail with regard to the distribution of the haemoproteids and Leucocytozoon, and areas of similar topography, (highland Malaysia and northern Thailand; central Thailand and India), were compared. In addition, the prevalence of the haemoproteids was examined for each country sampled.

12. Haemoproteus otocompsae, which was the least common of the bulbul haemoproteids, increased in prevalence from east to west with a focus of infection in India.

13. Haemoproteus philippini sp. n. was most prevalent in the Philippines, and generally presented lower infection rates the greater the distance from the Philippines.

14. Haemoproteus sanguinis, the most common of the bulbul haemoproteids, was also the most uniformly distributed, occurring more or less across the distribution of the bulbuls and showing relatively stable rates of infection through India and mid-southeast Asia.

15. Comparison of the prevalences of the bulbul haemoproteids by country showed H. philippini sp. n. to be the dominant haemoproteid in bulbuls in Southeast Asia, and H. sanguinis to be dominant in southwest Asia and Africa. Haemoproteus otocompsae, while never dominant, did become the second most prevalent haemoproteid in India.

16. The prevalence of Leucocytozoon was examined by country and it was found that this parasite showed an upward trend in prevalence from east to west.

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Appendix A.

Summary of pycnonotid hosts of *Plasmodium* species.

Host	*Plasmodium* sp.	Author
Hypsipetes amaurotis (Temminck)	*P. rouxi*	Kano 1950
	P. vaughani	Kano 1950
	P. sp.	Kano & Kimura 1950; this study
Hypsipetes charlottae (Finsch)	*P.* sp.	this study
Hypsipetes madagascariensis (Muller)	*P. rouxi*	Manwell *et al.* 1976; McClure *et al.* 1978; this study
	P. sp.	McClure *et al.* 1978
Hypsipetes philippinus (J.R. Forster)	*P.* sp.	Hegner & Chu 1930
Pycnonotus aurigaster (Viellot)	*P.* sp.	Hamerton 1943
Pycnonotus barbatus (Desfontaine)	*P. circumflexum*	this study
	P. relictum	Ashford *et al.* 1976
	P. rouxi	Ashford *et al.* 1976; Bennett & Herman 1976; Peirce 1984a; this study
	P. sp.	Ashford *et al.* 1976; Bennett *et al.* 1974; Hamerton 1942; Peirce & Backhurst 1970
Pycnonotus blanfordi Jerdon	*P. circumflexum*	this study
	P. polare	this study
	P. relictum	McClure *et al.* 1978; this study
	P. vaughani	McClure *et al.* 1978;
	P. sp.	this study

Appendix A (Continued).

Host	Plasmodium sp.	Author
Pycnonotus brunneus Blyth	P. vaughani	this study
	P. sp.	McClure et al. 1978
Pycnonotus cafer (Linnaeus)	P. relictum	Grewal 1964; this study
	P. rouxi	McClure et al. 1978; this study
	P. vaughani	McClure et al. 1978; this study
	P. sp.	McClure et al. 1978
Pycnonotus erythropthalmos (Hume)	P. vaughani	this study
	P. sp.	McClure et al. 1978
Pycnonotus finlaysoni Strickland	P. vaughani	this study
	P. sp.	Kongtong 1967 (unpub.); McClure et al. 1978
Pycnonotus flavescens Blyth	P. rouxi	this study
Pycnonotus goiavier (Scopoli)	P. circumflexum	this study
	P. dissanaikei	McClure et al. 1978
	P. rouxi	Laird 1962; McClure et al. 1978; this study
	P. vaughani	this study
	P. sp.	McClure et al. 1978; this study
Pycnonotus jocosus (Linnaeus)	P. relictum	Plimmer 1912
	P. sp.	McClure et al. 1978; this study
Pycnonotus leucogenys (J.E. Gray)	P. vaughani	this study
	P. sp.	McClure et al. 1978; this study

Appendix A (Concluded).

Host	Plasmodium sp.	Author
Pycnonotus melanicterus (Gmelin)	P. circumflexum	this study
	P. polare	this study
	P. rouxi	McClure et al. 1978; this study
	P. vaughani	Laird 1962; this study
	P. sp.	McClure et al. 19[illegible]
Pycnonotus melanoleucos (Eyton)	P. vaughani	this study
Pycnonotus plumosus Blyth	P. rouxi	this study
	P. vaughani	this study
	P. sp.	McClure et al. 1978; this study
Pycnonotus simplex Lesson	P. circumflexum	this study
Pycnonotus sinensis (Gmelin)	P. vaughani	this study
Pycnonotus virens (Cassin)	P. sp.	this study
Pycnonotus xanthopygos (Ehrenburg)	P. rouxi	Bennett & Herman 1976
	P. vaughani	this study
	P. sp.	this study
Spizixos semitorques (Swinhoe)	P. rouxi	Manwell et al. 1976
	P. sp.	Manwell et al. 1976

Appendix B.

Summary of pycnonotid hosts of *Trypanosoma* species.

Host	*Trypanosoma* sp.	Author
Chlorocichla flavicollis (Swainson)	*T.* sp.	Ashford *et al.* 1976; Bennett *et al.* 1977
Chlorocichla flaviventris Smith	*T. avium*	this study
Criniger phaeocephalus (Hartlaub)	*T.* sp.	McClure *et al.* 1978; this study
Hypsipetes crassirostris Newton	*T. everetti*	Peirce & Cheke 1977
Hypsipetes flavala (Blyth)	*T.* sp.	McClure *et al.* 1978; this study
Hypsipetes madagascariensis (P.L.S. Muller)	*T. avium*	this study
	T. sp.	McClure *et al.* 1978
Hypsipetes malaccensis Blyth	*T. calmettei*	this study
	T. sp.	McClure *et al.* 1978
Hypsipetes mcclellandii (Horsfield)	*T.* sp.	this study
Hypsipetes philippinus (J.R. Forster)	*T. avium*	this study
	T. calmettei	this study
	T. paddae	this study
	T. sp.	McClure *et al.* 1978; this study
Hypsipetes propinquus (Oustalet)	*T. avium*	this study
	T. calmettei	this study
	T. sp.	McClure *et al.* 1978
Phyllastrephus fischeri (Reichenow)	*T. everetti*	Peirce *et al.* 1976

Appendix B (Continued).

Host	Trypanosoma sp.	Author
Pycnonotus barbatus (Desfontaine)	T. avium	Wink & Bennett 1976; this study
	T. pycnonoti	Kerandel 1913; Peirce 1984a; Peirce et al. 1977
	T. sp.	Ashford et al. 1976; Kerandel 1909; Peirce & Backhurst 1970
Pycnonotus blanfordi Jerdon	T. sp.	McClure et al. 1978; this study
Pycnonotus brunneus Blyth	T. sp.	McClure et al. 1978
Pycnonotus cafer (Linnaeus)	T. sp.	David & Nair 1965; Grewal 1964, 1965; McClure et al. 1978
Pycnonotus finlaysoni Strickland	T. calmettei	this study
	T. sp.	McClure et al. 1978
Pycnonotus goiavier (Scopoli)	T. sp.	McClure et al. 1978; this study
Pycnonotus jocosus (Linnaeus)	T. avium bakeri	Chatterjee & Ray 1971
Pycnonotus leucogenys (J.E. Gray)	T. sp.	David & Nair 1955; McClure et al. 1978
Pycnonotus melanicterus (Gmelin)	T. sp.	Laird 1962; McClure et al. 1978; this study
Pycnonotus plumosus Blyth	T. avium	this study
	T. calmettei	this study
	T. sp.	McClure et al. 1978; this study
Pycnonotus sinensis (Gmelin)	T. brimonti	Mathis & Leger 1910, 1911
Pycnonotus virens (Cassin)	T. avium	Bennett et al. 1974, 1977; this study

Appendix B (Concluded).

Host	*Trypanosoma* sp.	Author
Pycnonotus xanthopygos (Ehrenburg)	*T. avium*	Bennett & Herman 1976
	T. calmettei	this study
	T. sp.	this study
Pycnonotus sp.	*T.* sp.	Maya & David 1912
unidentified bulbul	*T. avium*	Zupitza 1909

Appendix C.

Summary of pycnonotid hosts of microfilaria species.

Host	Microfilaria sp.	Author
Chlorocichla falkensteini (Reichenow)	M. sp.	Schwetz 1938
Criniger bres (Lesson)	M. sp.	McClure et al. 1978;
Criniger ochraceus / pallidus	M. sp.	McClure et al. 1978; this study
Criniger pallidus Swinhoe	M. sp.	Coatney et al. 1960
Criniger phaeocephalus (Hartlaub)	M. sp.	McClure et al. 1978; this study
Hypsipetes charlottae (Finsch)	M. sp.	this study
Hypsipetes everetti (Tweeddale)	M. sp.	this study
Hypsipetes flavala (Blyth)	M. sp.	Plimmer 1912
Hypsipetes mccleilandii Horsfield	M. sp.	McClure et al. 1978; this study
Hypsipetes philippinus (J.R. Forster)	M. sp.	McClure et al. 1978; this study
Hypsipetes rufigularis Sharpe	M. sp.	McClure et al. 1978
Pycnonotus atriceps (Temminck)	M. sp.	McClure et al. 1978; this study
Pycnonotus aurigaster (Vieillot)	M. sp.	Hamerton 1943
Pycnonotus barbatus (Desfontaine)	M. sp.	Ashford et al. 1976; Bennett et al. 1974; Cowper 1969; Hamerton 1930; Oosthuizen & Markus 1967; Peirce 1984a; Peirce & Backhurst 1970; this study
Pycnonotus brunneus Blyth	M. sp.	McClure et al. 1978; this study

Appendix C (Continued).

Host	Microfilaria sp.	Author
Pycnonotus cafer (Linnaeus)	M. buckleyi	Grewal 1965
	M. jeeti	Grewal 1965
	M. turdoidis	Nooruddin & Ahmed 1967
	M. sp.	Farooqui & Ahmed 1967; Peirce 1969
Pycnonotus curvirostris (Cassin)	M. sp.	Bennett et al. 1977; this study
Pycnonotus erythropthalmos (Hume)	M. sp.	McClure et al. 1978; this study
Pycnonotus finlaysoni Strickland	M. sp.	McClure et al. 1978; this study
Pycnonotus flavescens Blyth	M. sp.	McClure et al. 1978; this study
Pycnonotus goiavier (Scopoli)	M. sp.	McClure et al. 1978; this study
Pycnonotus jocosus (Linnaeus)	M. sp.	McClure et al. 1978; this study
Pycnonotus leucogenys (J.E. Gray)	M. sp.	this study
Pycnonotus luteolus (Lesson)	M. pycnonoti	de Mello 1937a, 1937b
	M. sp.	de Mello 1936
Pycnonotus melanicterus (Gmelin)	M. sp.	McClure et al. 1978; this study
Pycnonotus plumosus Blyth	M. sp.	McClure et al. 1978; this study
Pycnonotus simplex Lesson	M. sp.	McClure et al. 1978; this study
Pycnonotus sinensis (Gmelin)	M. brimonti	Mathis & Leger 1910
	M. sp.	McClure et al. 1978; this study

Appendix C (Concluded).

Host	Microfilaria sp.	Author
Pycnonotus urostictus (Salvadori)	M. sp.	McClure et al. 1978; this study
Pycnonotus virens (Cassin)	M. sp.	Bennett et al. 1977; this study
Pycnonotus xanthopygos (Ehrenburg)	M. sp.	Bennett & Herman 1976; this study
Pycnonotus zeylanicus (Gmelin)	M. sp.	McClure et al. 1978; this study

Appendix D.

Summary of pycnonotid hosts of *Haemoproteus* species.

Host	*Haemoproteus* sp.	Author
Bleda canicapilla (Hartlaub)	*H.* sp.	Hamerton & Rewell 1948
Criniger bres (Lesson)	*H. otocompsae*	this study
	H. philippini	this study
	H. sanguinis	this study
	H. sp.	Kongtong 1967 (unpub.); McClure *et al.* 1978; this study
Criniger flaveolus (Gould)	*H.* sp.	McClure *et al.* 1978; this study
	H. sanguinis	this study
Criniger ochraceus / *pallidus*	*H. otocompsae*	this study
	H. philippini	this study
	H. sanguinis	this study
	H. sp.	McClure *et al.* 1978; this study
Criniger pallidus Swinhoe	*H.* sp.	Coatney *et al.* 1960; Kongtong 1967 (unpub.)
Hypsipetes amaurotis (Temminck)	*H. philippini*	this study
	H. sp.	McClure *et al.* 1978; Ogawa 1911; this study
Hypsipetes charlottae (Finsch)	*H. philippini*	this study
	H. sp.	McClure *et al.* 1978; this study
Hypsipetes crassirostris Newton	*H. sanguinis*	Peirce & Cheke 1977
Hypsipetes criniger (Blyth)	*H. otocompsae*	this study
	H. sanguinis	this study
	H. sp.	McClure *et al.* 1978; this study

Appendix D (Continued).

Host	Haemoproteus sp.	Author
Hypsipetes flavala (Blyth)	H. philippini	this study
	H. sanguinis	this study
	H. sp.	McClure et al. 1978; this study
Hypsipetes madagascariensis (P.L.S. Muller)	H. otocompsae	this study
	H. philippini	this study
	H. sanguinis	this study
	H. sp.	Hamerton 1936; Manwell et al. 1976; McClure et al. 1978
Hypsipeter mcclellandii Horsfield	H. philippini	this study
	H. sanguinis	this study
	H. sp.	Kongtong 1967 (unpub.); McClure et al. 1978; this study
Hypsipetes philippinus (J.R. Forster)	H. philippini	this study
	H. sanguinis	this study
	H. sp.	Hegner & Chu 1930; McClure et al. 1978; this study
Hypsipetes propinquus (Oustalet)	H. otocompsae	this study
	H. philippini	this study
	H. sanguinis	this study
	H. sp.	Kongtong 1967; McClure et al. 1978; this study
Hypsipetes siquijorensis (Steere)	H. philippini	this study
	H. sp.	McClure et al. 1978; this study
Phyllastrephus fischeri (Reichenow)	H. sp.	Bennett & Herman 1976; this study

Appendix D (Continued).

Host	Haemoproteus sp.	Author
Phyllastrephus strepitans (Reichenow)	H. sp.	Ashford et al. 1976; Garnham 1950
Pycnonotus striceps (Temminck)	H. otocompsae	this study
	H. philippini	this study
	H. sanguinis	this study
	H. sp.	McClure et al. 1978; this study
Pycnonotus auriqaster (Viellot)	H. sanguinis	this study
	H. sp.	McClure et al. 1978
Pycnonotus barbatus (Desfontaine)	H. otocompsae	Peirce 1984a
	H. philippini	this study
	H. sanguinis	Peirce et al. 1977; Wink & Bennett 1976; this study
	H. sp.	Ashford et al. 1976; Bennett et al. 1974; Bennett & Herman 1976; Bray 1964 ; Cowper 1969; Garnham 1950; Hamerton 1932; Leger & Leger 1914; this study
Pycnonotus blanfordi Jerdon	H. otocompsae	this study
	H. philippini	this study
	H. sanguinis	this study
	H. sp.	Kongtong 1967 (unpub.); McClure et al. 1978; this study
Pycnonotus brunneus Blyth	H. otocompsae	this study
	H. philippini	this study
	H. sanguinis	this study
	H. sp.	McClure et al. 1978

Appendix D (Continued).

Host	Haemoproteus sp.	Author
Pycnonotus cafer (Linnaeus)	H. otocompsae	this study
	H. philippini	this study
	H. sanguinis	this study
	H. sp.	Gautom et al. 1983; Grewal 1965; McClure et al. 1978; Peirce 1969; this study
Pycnonotus erythropthalmos (Hume)	H. philippini	this study
	H. sanguinis	this study
	H. sp.	McClure et al. 1978
Pycnonotus eutilotus (Jardine & Selby)	H. sanguinis	this study
	H. sp.	McClure et al. 1978
Pycnonotus finlaysoni Strickland	H. philippini	this study
	H. sanguinis	this study
	H. sp.	McClure et al. 1978
Pycnonotus flavescens Blyth	H. otocompsae	this study
	H. philippini	this study
	H. sanguinis	this study
	H. sp.	McClure et al. 1978
Pycnonotus goiavier (Scopoli)	H. otocompsae	this study
	H. sanguinis	this study
	H. sp.	McClure et al. 1978
Pycnonotus gracilirostris (Cabanis)	H. sp.	Schwetz 1938
Pycnonotus jocosus (Linnaeus)	H. otocompsae	de Mello 1935, 1936, 1937
	H. philippini	this study
	H. sanguinis	Chakravarty & Kar 1945; this study

Appendix D (Continued).

Host	Haemoproteus sp.	Author
	H. sp.	Kongtong 1967 (unpub.); McClure et al. 1978; Peirce 1969; this study
Pycnonotus leucogenys (J.E. Gray)	H. otocompsae	this study
	H. sanguinis	this study
	H. sp.	McClure et al. 1978; this study
Pycnonotus luteolus (Lesson)	H. otocompsae	this study
	H. sanguinis	this study
	H. sp.	McClure et al. 1978; this study
Pycnonotus melanicterus (Gmelin)	H. otocompsae	this study
	H. philippini	this study
	H. sanguinis	this study
	H. sp.	Coatney et al. 1960; Kongtong 1967 (unpub.); McClure et al. 1978; this study
Pycnonotus nigricans (Viellot)	H. sp.	Enigk 1942
Pycnonotus plumosus Blyth	H. otocompsae	this study
	H. sp.	McClure et al. 1978; this study
Pycnonotus simplex Lesson	H. otocompsae	this study
	H. philippini	this study
	H. sanguinis	this study
	H. sp.	McClure et al. 1978; this study
Pycnonotus sinensis (Gmelin)	H. sanguinis	this study
	H. sp.	McClure et al. 1978; this study

Appendix D (Concluded).

Host	Haemoproteus sp.	Author
Pycnonotus striatus (Blyth)	H. sp.	McClure et al. 1978;
Pycnonotus virens (Cassin)	H. sanguinis	this study
	H. sp.	Bennett et al. 1977; this study
Pycnonotus xanthopygos	H. otocompsae	Peirce 1984b
	H. sanguinis	this study
	H. sp.	Bennett & Herman 1976; this study
unidentified bulbul	H. sp.	Zupitza 1909; this study

Appendix E.

Summary of pycnonotid hosts of *Leucocytozoon* species.

Host	*Leucocytozoon* sp.	Author
Chlorocichla falkensteini (Reichenow)	*L.* sp.	Schwetz 1938
Chlorocichla flaviventris (Swainson)	*L.* sp.	Ashford *et al.* 1976
Criniger bres (Lesson)	*L. brimonti*	this study
	L. sp.	McClure *et al.* 1978; this study
Criniger ochraceus / pallidus	*L. brimonti*	this study
	L. dubreuili	this study
	L. majoris	this study
	L. sp.	McClure *et al.* 1978; this study
Criniger pallidus Swinhoe	*L.* sp.	Coatney *et al.* 1960; Kongtong 1967 (unpub.)
Criniger phaeocephalus (Hartlaub)	*L. dubreuili*	this study
	L. sp.	McClure *et al.* 1978;
Hypsipetes amaurotis (Temminck)	*L.* sp.	Ogawa 1911
Hypsipetes charlottae (Finsch)	*L. majoris*	this study
	L. sp.	McClure *et al.* 1978; this study
Hypsipetes criniger (Blyth)	*L. brimonti*	this study.
Hypsipetes flavala (Blyth)	*L. brimonti*	this study
	L. majoris	this study
	L. sp.	McClure *et al.* 1978; this study
Hypsipetes madagascariensis (P.L.S. Muller)	*L. dubreuili*	this study
	L. sp.	Coatney *et al.* 1960; McClure *et al.* 1978; this study

Appendix E (Continued).

Host	Leucocytozoon sp.	Author
Hypsipetes malaccensis Blyth	L. brimonti	this study
	L. sp.	McClure et al. 1978
Hypsipetes mcclellandii Horsfield	L. brimonti	this study
	L. dubreuili	this study
	L. majoris	McClure et al. 1978; this study
Hypsipetes philippinus (J.R. Forster)	L. brimonti	this study
	L. majoris	this study
	L. sp.	McClure et al. 1978; this study
Hypsipetes propinquus (Oustalet)	L. brimonti	this study
	L. sp.	McClure et al. 1978; this study
Hypsipetes thompsoni (Bingham)	L. brimonti	this study
	L. sp.	McClure et al. 1978;
Hypsipetes virescens (Temminck)	L. majoris	this study
Hypsipetes viridescens (Steere)	L. sp.	McClure et al. 1978
Pycnonotus striceps (Temminck) (Reichenow)	L. brimonti	this study
	L. dubreuili	this study
	L. majoris	this study
	L. sp.	McClure et al. 1978; this study
Pycnonotus aurigaster (Vieillot)	L. majoris	this study
	L. sp.	Coatney et al. 1960; Hamerton 1943; McClure et al. 1978
Pycnonotus barbatus (Desfontaine)	L. brimonti	Bennett & Herman 1976; Peirce et al. 1977; Wink & Bennett 1976; this study

Appendix E (Continued).

Host	Leucocytozoon sp.	Author
	L. fringillinarum	Peirce 1984a
	L. majoris	this study
	L. sp.	Ashford et al. 1976; Bennett et al. 1974; Hamerton 1942; Leger & Leger 1914; Peirce 1976; Peirce & Backhurst 1970; Schwetz 1931; this study
Pycnonotus blanfordi Jerdon	L. brimonti	this study
	L. sp.	McClure et al. 1978
Pycnonotus brunneus Blyth	L. brimonti	this study
	L. sp.	McClure et al. 1978; this study
Pycnonotus cafer (Linnaeus)	L. brimonti	this study
	L. dubreuili	this study
	L. majoris	this study
	L. molpastis	de Mello 1936
	L. sp.	Grewal 1965; McClure et al. 1978; this study
Pycnonotus erythropthalmos (Hume)	L. brimonti	this study
	L. sp.	McClure et al. 1978 this study
Pycnonotus eutilotus (Jardine & Selby)	L. sp.	McClure et al. 1978; this study
Pycnonotus finlaysoni Strickland	L. brimonti	this study
	L. majoris	this study
	L. sp.	Kongtong 1967 (unpub.); McClure et al. 1978; this study

Appendix E (Continued).

Host	Leucocytozoon sp.	Author
Pycnonotus flavescens Blyth	L. brimonti	this study
	L. majoris	this study
	L. sp.	McClure et al. 1978; this study
Pycnonotus goiavier (Scopoli)	L. brimonti	this study
	L. majoris	this study
	L. sp.	McClure et al. 1978; this study
Pycnonotus importunus (Vieillot)	L. brimonti	Bennett & Herman 1976; Peirce et al. 1977; this study
	L. sp.	this study
Pycnonotus jocosus (Linnaeus)	L. brimonti	this study
	L. fringillinarum	Peirce et al. 1977
	L. majoris	this study
	L. sp.	McClure et al. 1978; this study
Pycnonotus leucogenys (J.E. Gray)	L. dubreuili	Nandi & Mandal 1978
	L. majoris	Nandi & Mandal 1978
Pycnonotus melanicterus (Gmelin)	L. brimonti	this study
	L. dubreuili	this study
	L. majoris	this study
	L. sp.	Coatney et al. 1960; Kongtong 1967 (unpub.); Laird 1962; McClure et al. 1978; this study
Pycnonotus melanoleucos (Eyton)	L. sp.	this study
Pycnonotus plumosus Blyth	L. brimonti	this study
	L. sp.	McClure et al. 1978; this study

Appendix E (Concluded).

Host	Leucocytozoon sp.	Author
Pycnonotus simplex Lesson	L. majoris	this study
	L. sp.	McClure et al. 1978
Pycnonotus sinensis (Gmelin)	L. brimonti	Mathis & Leger 1910, 1911; this study
	L. sp.	McClure et al. 1978;
Pycnonotus tephrolaemus (Bannerman)	L. sp.	Cheke 1972
Pycnonotus virens (Cassin)	L. brimonti	Bennett et al. 1977
Pycnonotus xanthopygos (Ehrenburg)	L. brimonti	Bennett & Herman 1976; this study
	L. dubreuili	this study
	L. majoris	this study
	L. sp.	this study
Pycnonotus zeylanicus (Gmelin)	L. brimonti	this study
Pycnonotus sp.	L. sp.	Maya & David 1912