A TAXONOMIC STUDY OF THE HAEMOPROTEIDAE (APICOMPLEXA: HAEMOSPORINA) OF THE AVIAN FAMILIES FRINGILLIDAE, EMBERIZIDAE, PARULIDAE, THRAUPIDAE AND ICTERIDAE

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by

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ABSTRACT

The haemoproteids (Haemosporina: Haemoproteidae) of the avian families Fringillidae, Emberizidae, Parulidae, Thraupidae and Icteridae *sensu* Edwards (1986) were reviewed, and eight species determined to be valid, all of the basic halteridial or microhalteridial form as defined by Bennett and Peirce (1988). *Haemoproteus fringillae* (Fringillidae), *H. mazzai* (Emberizidae), *H. chloris* (Emberizidae) and *H. quiscalus* (Icteridae) were redescribed from hapantotype or neohapantotype material from a wider range of hosts and/or locations than in the original descriptions. *Haemoproteus loxiae, H. acanthis* and *H. emberiza* were declared *nomina nuda*. *H. globulosus, H. macropigmentatus, H. serini,* and *H. tarkakovskyi* were declared synonyms of *H. chloris*, and *H. hedymelis* was declared a synonym of *H. mazzai*. The new haemoproteid species *Haemoproteus coatneyi* (Emberizidae), *H. paruli* (Parulidae), *H. coereba* (Parulidae), and *H. thraupi* (Thraupidae) were described. All hapantotype, neohapantotype and parahapantotype material was deposited in the collection of the International Reference Centre for Avian Haematozoa, Department of Biology, Memorial University of Newfoundland.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF PLATES

INTRODUCTION

The avian families Fringillidae, Emberizidae, Parulidae, Thraupidae and Icteridae *sensu* Edwards (1986) are assemblages of nine-primaried passerine birds, species of which are found worldwide, occupying a diverse range of niches (Peters 1970, Campbell and Lack 1985). Under various systems of classification they include the true finches, cardueline finches, Hawaiian honeycreepers, conebills, cardinals, canaries, buntings, North American wood warblers, bananaquits, tanagers and grackles and are thought to represent some of the most evolutionarily advanced passerine species (Campbell and Lack 1985). New interpretations of anatomical data and the development of biochemical techniques including electrophoresis and DNA hybridization (Sibley and Ahlquist 1984) have resulted in major changes in avian taxonomy in recent years, particularly in location of genera within family groupings. In 1983, the American Ornithologists' Union (A.O.U.) revised their check-list of the birds of North America; in particular, the check-list changed the order and content of many families and reduced several families to sub-familial status. Clements (1978) also reorganized an earlier (1974) edition of his worldwide check-list, and Edwards (1986) published a new and different edition of the *Birds of the World*, altering the family status of several groups. Edward's check-list was chosen for the current study as the most recent and most comprehensive treatment of passeriform systematics.

The results of these changing classifications have an impact on taxonomic studies of the avian blood parasites of the genus *Haemoproteus*. Bird host-family,

and/or subfamily specificity, successfully demonstrated in cross-transmission studies for eight host bird families, is one of the main taxonomic criteria of this group of apicomplexan protozoans (Bennett and Peirce 1988, Atkinson 1986). In most of the avian families studied to date, this host-family (subfamily) specificity has been used in conjunction with the morphological features of the erythrocyte-inhabiting gametocytes in the description of new parasite species. The gametocytes are products of the asexual developmental stage occurring in the avian host, and are the primary diagnostic stage.

Gametocyte morphology can be variable within a particular species both at the same and different geographical locations, among host species within a family, and indeed within a particular individual over time (Bennett and Campbell 1972, 1973, Bennett *et al.* 1985, Bennett *et al.* 1986, Bennett and Peirce 1988). Therefore, in the absence of cross-transmission studies, species differentiation of haemoproteid parasites which are morphologically similar is still largely based on the family of the bird host (Bennett and Peirce 1988).

A total of 12 species of 'halteridial type' *Haemoproteus* (Bennett and Peirce 1988) have been named or described from members of the Fringillidae, Emberizidae, Parulidae, Thraupidae and Icteridae, some on the basis of the 'one-host - one parasite' concept, others on the basis of morphology. Eight of these species were originally described before guidelines for defining a species were published (Helmy Mohammed 1958, Bennett and Campbell 1972 *et seq.*) Three species, *H. acanthis*, *H. emberiza* and *H. loxiae* have simply been named in publication but there are no

species descriptions. Most haemoproteids in the bird families considered in the current study have been identified as *Haemoproteus* sp., *H. fringillae*, *H. orizivorae* (Bennett et al. 1982, Peirce 1984). In practice, the term '*H. fringillae/orizivorae* complex' (Peirce 1983) has been used to identify the haemoproteids found in many host families in the absence of detailed studies on these parasites. The distribution of *Haemoproteus orizivorae* has recently been restricted to the avian subfamily Poephilinae of the Estrildidae (Bennett and Peirce 1991). *Haemoproteus fringillae* is the only species described from members of the Fringillidae. Within the family Emberizidae, seven species have been described from the Carduelinae; *H. acanthis, H. loxiae, H. chloris, H. globulosus, H. macropigmentatus, H. serini and H. tartakovskyi*; two species from the Cardinalinae; *H. mazzai* and *H. hedymelis*; and one species from the Emberizinae, *H. emberiza*. Only *H. quiscalus* has been described from the Icteridae. No haemoproteid species have been described from the Thraupidae or Parulidae (subfamilies Parulinae and Coerebinae).

The collection of the International Reference Centre for Avian Haematozoa contains samples of blood smears taken from many of these bird species across their distributional range, and in some cases from the same individual over a period of time. This material provides the basis to evaluate the haemoproteids from these families and determine which of the 12 currently described species are valid and whether additional species occur.

MATERIALS AND METHODS

The blood smear material for this taxonomic study was collected by contributors from around the world, including the author, and deposited in the collection of the International Reference Centre for Avian Haematozoa (IRCAH), Department of Biology, Memorial University of Newfoundland. All samples were from wild-caught birds and were of natural infections. Some birds were retrapped and provided samples on two or more occasions. The data set is extensive; over 1,200 blood smears containing haemoproteids were selected from the collection and examined. The host species and geographic locations of selected specimens are given in Appendix A. Table 1 lists the classifications of the host families under consideration according to Edwards (1986), Clements (1978) and the A.O.U. (1983) for comparative purposes. Parahapantotype material was available for two *Haemoproteus* species. All type material was deposited in the collection of the IRCAH.

Preparation of blood smears

Blood smears were taken from live netted birds by pricking the brachial vein to obtain a few drops of peripheral blood and making a thin smear following the protocols of Bennett (1970). Some material from blood of dead birds was examined but was of little taxonomic use. The slides were air-dried, fixed in 100% methanol or ethanol, and stained with a variety of stains (Giemsa's, Wright's, Hasting's). Some

Table 1. Classifications of avian hosts reviewed in the current study.

Edwards 1986	Clements 1978	A.O.U. 1983
FRINGILLIDAE	FRINGILLIDAE	FRINGILLIDAE
Fringillinae	(contains species from Edwards' Emberizidae)	Fringillinae
		Carduelinae
EMBERIZIDAE		EMBERIZIDAE
Carduelinae		
Cardinalinae		Cardinalinae
Emberizinae		Emberizinae
PARULIDAE		Parulinae
Parulinae	PARULIDAE	
Coerebinae		Coerebinae
Conirostrinae	COEREBIDAE	
THRAUPIDAE		Thraupinae
	THRAUPIDAE	
ICTERIDAE		Icterinae
Icterinae	ICTERIDAE	
Doliconychinae		

material was stained in the country of origin, but most were stained at the IRCAH with Giemsa's stain (buffered to pH 7.2) for 45 minutes and washed in slightly acidic (pH 6.5) tap water. Initially, all smears were screened by the contributor or IRCAH staff, and where possible parasites were identified to genus. For this study, slides were examined under 40x and 100x oil immersion objectives on a Zeiss II Photomicroscope, for the length of time necessary to identify the haemoproteids (up to 120 minutes per slide).

Taxonomic study of haemoproteids

Samples of uninfected erythrocytes and parasites within infected erythrocytes of selected bird species within each family (40 individual host birds) were drawn and measured with a Zeiss MOP-3 Digital Analyzer. Photomicrographs were obtained using a Zeiss II Photomicroscope. Line drawings were made from *camera lucida* drawings on a Zeiss RA microscope using a 20x objective. More macrogametocytes than microgametocytes were drawn because of their relative frequency and value in species diagnosis (Bennett and Campbell 1972). Gametocyte length, width and area, gametocyte nucleus length, width and area, erythrocyte length, width and area, and erythrocyte nucleus length, width and area were measured and various ratios derived according to the protocols of Helmy Mohammed (1958), Bennett and Campbell (1972) and Forrester *et al.* (1977). Some of these ratios were used to indicate the relative hypertrophy or atrophy of erythrocytes caused by the parasite and the size of the parasite relative to the infected cell. In addition, the nuclear displacement

ratio (NDR) as defined by Bennett and Campbell (1972), was used to indicate the degree of lateral displacement of the erythrocyte nucleus caused by the gametocyte. The number, arrangement, size and shape of pigment granules, often characteristic of haemoproteid species were also recorded, as was the presence of volutin granules (von Brand 1966, White and Bennett 1978). Where possible, gametocyte sex ratios were determined, and qualitative characters such as parasite outline and nuclear position were recorded. Information on the age and sex of the host bird, as well as the date of capture were noted to assess what effect these might have on the parasite's morphology.

RESULTS AND DISCUSSION

TAXONOMY

Historical

Kruse (1890) first erected the genus *Haemoproteus* and described *H. columbae* in the pigeon *Columba livia*. The parasite occurring in the pigeons (Columbidae) was studied by Sergent and Sergent (1906, 1907), Aragão (1908), and Adie (1915) who confirmed the vector as a louse fly, *Lynchia maura* (Hippoboscidae). For many years following, it was assumed that hippoboscids were the vectors of all haemoproteids.

New species were named or described from several avian families, often based on a 'one host species - one parasite species' concept rather than studies of morphological differences. This resulted in a proliferation (almost 200) of species names and/or descriptions, many of which are inadequate by modern standards (Bennett *et al.* 1982).

As life-cycles of various species became known and experimental cross-transmissions were carried out, the 'one host species - one parasite species' philosophy was seriously questioned. Experimental work (summarized by Bennett *et al.* 1985) demonstrated that species of *Haemoproteus* were transmitted primarily by members of the Ceratopogonidae (seven of the 11 species for which the life cycle and/or vectors are known) and that parasites were host-family or host-subfamily specific (Bennett *et al.* 1982, Atkinson 1986), but not species specific. This host-family (subfamily) specificity is used in conjunction with the gametocyte's morphology in the identification of *Haemoproteus* spp. until experimental work can confirm the

validity of such species (Bennett and Peirce 1988).

Levine (1980) places the family Haemoproteidae, containing the genus *Haemoproteus* Kruse, 1890 in the Suborder Haemosporina Danilewsky, 1885 of the Phylum Apicomplexa Levine, 1980. The genus includes about 113 species of parasitic protozoa of birds (Bennett and Peirce 1988). Bennett and Peirce (1988) discussed the morphological forms of the avian haemoproteids and presented a check-list of 113 species, many of which have been recently redescribed by Bennett and his colleagues. *Haemoproteus* species have a heteroxenous life cycle, undergoing schizogony in the vertebrate host and sporogony in the invertebrate host which acts as the vector for the transmission of the parasite from one bird to another. For most species of *Haemoproteus*, there is little evidence of morbidity or mortality associated with infection (Bennett *et al.* 1982, 1988). However, pathogenicity has been demonstrated in *H. meleagridis* of turkeys (Atkinson 1986) and doves (Bennett pers. comm.), and has recently been implicated in *Haemoproteus galli*, schizonts of which may have been misidentified as *Arthrocystis* by Levine *et al.* (1970) and which cause extreme lesions in heart muscle (Bennett, pers. comm.).

Life cycle

The life cycles of those species studied have a schizogonic stage in the lungs, heart, kidneys, liver and other internal organs of the bird host (Bennett *et al.* 1965, Desser and Bennett in press). Sporozoites, when inoculated into the peripheral blood by the vector, enter these internal organs, and each develops into a schizont.

Schizogonic development may take 5-17 days after sporozoite - inoculation. Each schizont produces a number of merozoites. Initially, these merozoites continue the tissue stage (each producing another schizont, recurrent cycles producing 'first-' and/or 'second-generation' schizonts). Eventually, some merozoites enter erythrocytes, and each forms either a macrogametocyte (female) or a microgametocyte (male). Maturation of a merozoite usually requires 4-6 days (Desser and Bennett, in press). The prepatent period averages 14 days for most species. Macrogametocytes and microgametocytes are picked up via a blood meal by the vector to begin the sporogonic stage. The vectors for only 10 species are known, eight of which are biting midges of the genus *Culicoides* (Ceratopogonidae). Louse flies of the Hippoboscidae are thought to be vectors of the other species. However, for these species, there is now circumstantial evidence which suggests that *Culicoides* are also involved and that hippoboscids are unusual vectors (Desser and Bennett in press).

After the gametocyte-infected blood is ingested, the macrogametes are formed inside the macrogametocyte and the microgametes are rapidly released inside the midgut by a process termed exflagellation. The macrogamete is fertilized by the microgamete to form a zygote which develops into a ookinete. The ookinete penetrates the midgut epithelium to the basement membrane of the gut and encysts there to form an oocyst. Sporozoites are formed (usually about 16) within the oocyst and released throughout the body of the vector. Some accumulate in the salivary glands and are transmitted to another host via a blood meal, continuing the cycle

when the sporozoites enter the various organs from the peripheral blood. Depending upon the species of *Haemoproteus* and the ambient temperature at which the vectors were held, the sporogonic cycle may take a minimum of 7-12 days (Khan and Fallis 1969).

Haemoproteus spp. infections result in a prolonged parasitaemia and in temperate regions, intensity increases before decreasing to a lower chronic level. Often this stage reveals only a few circulating gametocytes. Cycling with the onset of the reproductive cycle in the host birds is a phenomenon of relapse in which presumably hormonal changes and stress cause an increase in intensity of infection with an increase in the numbers of gametocytes (Bennett and Cameron 1974).

Morphology

Only the gametocytes of *Haemoproteus* are seen in the peripheral blood of the avian host. Macrogametocytes (female) and microgametocytes (male) occur in erythrocytes, with few species having distinctive features. Bennett and Peirce (1988) classified all described species as one of five morphological forms. Gametocytes of most species form either a small or large yoke or 'halteridium' around the erythrocyte nucleus (micro-halteridial and halteridial forms), while others completely encircle it (circumnuclear). There is also a broad cylindrical form which often enucleates the host cell (rhabdosomal), and a rarer disc-shaped form (discosomal). For most species the gametocyte is the only known stage. The identification and rearing of both vectors and host birds present tremendous challenges for life cycle

studies (Atkinson 1986) and classification for *Haemoproteus* species has been based primarily on host taxonomy (Bennett and Peirce 1982). For many species it was recognized that future studies might determine that they were not distinct biological species, and would then fall into synonymy with previously described species.

The morphological characteristics of the gametocytes that have been used to differentiate species of the same basic form are: gametocyte outline, size and shape, hypertrophy, nuclear displacement ratio (NDR), the number, size and placement of pigment granules, presence of volutin granules, and others (Helmy Mohammed 1958, Bennett and Campbell 1972, Bennett *et al.* 1984, 1985, 1988, Greiner *et al.* 1977). Variability in mensural characters has been viewed as natural variation due to host, geographic location or seasonal differences (Bennett *et al.* 1984, Bennett *et al.* 1987).

Taxonomic study of *Haemoproteus*

Although the use of dried blood smears is a valuable diagnostic tool for haemoproteid study, there are limitations which restrict quantitative study of the characters commonly used in taxonomic analysis. The material is subject to artifacts of preparation (Bennett and Campbell 1975), which often cause variability that dominates such analyses. Several factors can affect the appearance of the gametocyte.

One of the difficulties in taxonomic study of blood parasites is with blood smear material taken from dead birds (Bennett and Peirce 1988). *Post mortem* changes include the gametocytes rounding up and/or popping out of the infected

erythrocyte. This actually simulates the first stages of gametogenesis, which normally occurs in the gut of the vector after ingestion. At least two species of 'globular type' *Haemoproteus* have been described from *post mortem* material and have since been synonymized with halteridial species upon studies of suitable material (White and Bennett 1979, Bishop and Bennett 1989). Material from dead birds was examined in the current study, and rounding up and popping out was observed and attributed to these *post mortem* changes (Plate A, Figure 1).

Blood which is slow drying, either because it was very thickly smeared (ideally smears should be one layer of cells), or due to extremely humid conditions, can also cause similar artifacts. Parasites near smear peripheries may then tend to be normal while those near the centre may be rounded as with *post mortem* blood (Bennett, Gabaldon and Ulloa 1982). Delayed or improper fixing and staining also can have effects. Often the parasite's nuclear material condenses and shows deeply stained spots. Observations of such characters, along with those of the normal uninfected erythrocytes were useful in determining if slow-drying was a factor in the appearance of the parasites.

Excess mechanical pressure on the microscope slide when the smear is made distorts and sometimes ruptures cells. When uninfected erythrocytes are distorted in this way, the exact shape and size of the parasites are likely to have been similarly altered. Even without excess pressure, at the outer edges of the blood smear the parasites are often broader and larger than those in more central areas. They also

PLATE A

Figure 1. Microgametocyte of *H. chloris*, initiating exflagellation

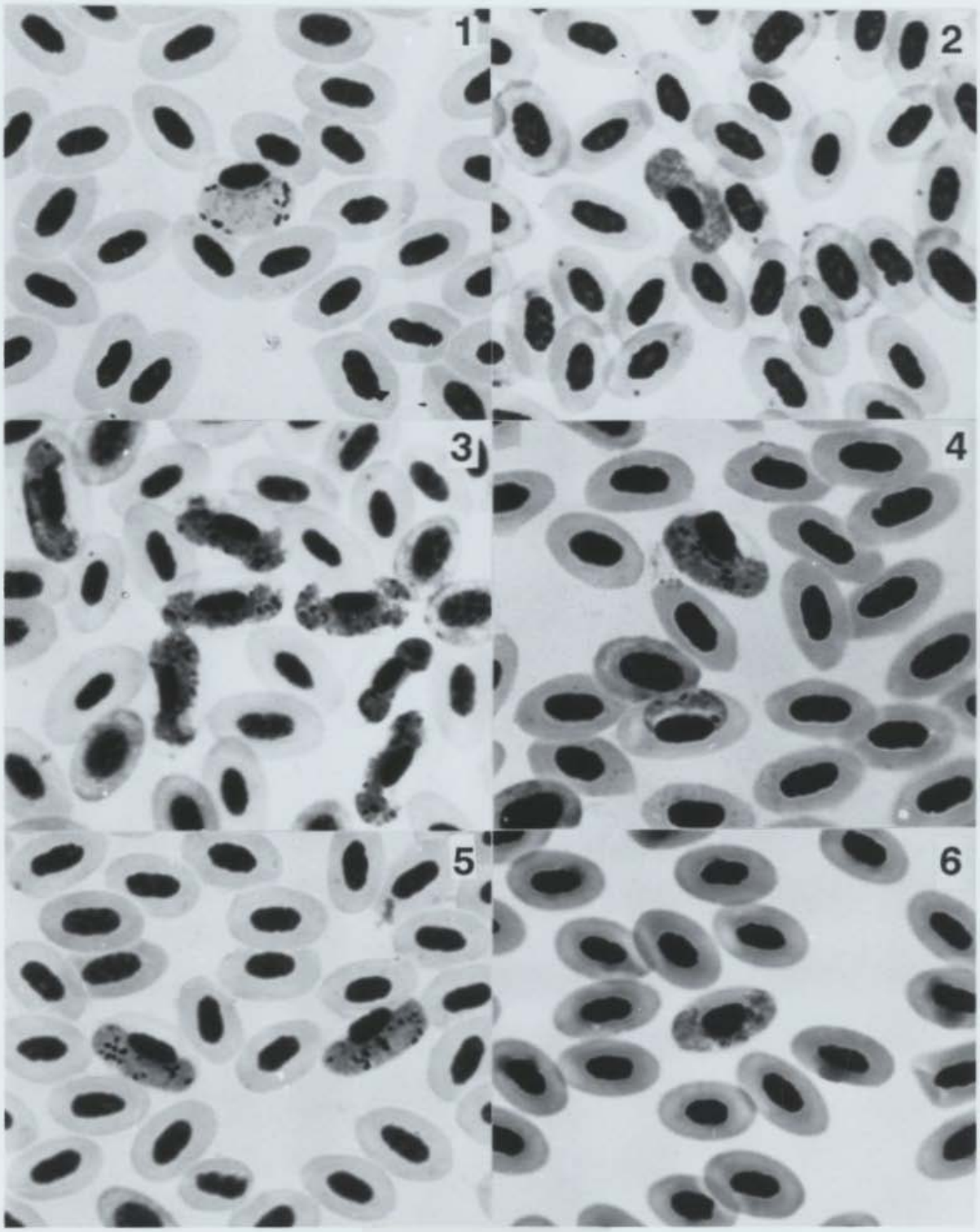
Figure 2. Macrogametocyte of *H. quiscalus* near smear periphery

Figure 3. Gametocytes of *H. coatneyi*

Figure 4. Macrogametocytes of *H. chloris* displacing nucleus

Figure 5. Macrogametocytes of *H. paruli*

Figure 6. Macrogametocyte of *H. quiscalus*


1
2
3
4
5
6
20µm

appear to cause more displacement of the erythrocytic nucleus (Plate A, Figure 2). Sometimes the observation of 'fat' parasites result from mechanical factors, as those forms are usually seen on the smear margins, and smaller halteridial gametocytes in the middle of the smear, and care must be taken to distinguish artifacts of the slide preparation with true nuclear displacement. Comparison with normal uninfected erythrocytes near the infected cells can often help in this determination. In addition to physical factors affecting the appearance of parasites, other influences include the age of the host bird, whether it is a chronic, relapse, or a new infection, and the developmental stage and intensity of the infection itself. As the material used in this study was obtained from wild caught naturally-infected birds, it is difficult to follow an infection through from immature to mature stages. Reinfection may be expected to occur throughout the main transmission season, and it was therefore not possible to separate gametocytes of single origin as would be possible for birds in captivity. There was sufficient material for only a few host bird species for effective evaluation of some of these factors, and these observations are included in the respective species descriptions.

TAXONOMIC REVIEW

FRINGILLIDAE

Fringillinae

***Haemoproteus fringillae* Labbé 1894**

Type Host: *Fringilla coelebs* Linnaeus [Chaffinch]

Type Locality: Bramley Hants, England

Immature gametocyte (Plate 1, Fig 1): Youngest forms seen initiate growth near the middle of erythrocyte, rarely near poles.

Macrogametocyte (Plate 1, Figures 2,4-5; Table 2): Halteridial parasite of medium to large size, occupying 60-70% of the erythrocyte-parasite complex, not causing host-cell hypertrophy; cytoplasm finely granular, staining moderate-blue with Giemsa's stain; margin of parasite entire and usually appressing the host cell nucleus, but not always the central periphery of the host cell; ends of parasite usually rounded, not always touching poles of erythrocyte, nor with symmetrical curves around the erythrocyte nucleus; host cell nucleus not usually displaced laterally (NDR = 0.96); pigment granules round to oval, often large and rod-shaped (up to 1μm in diameter), yellow-brown, averaging 13 (ranging 8-25), usually randomly distributed throughout the cytoplasm; volutin rarely seen; parasite nucleus compact, round to elongate oval, staining pale pink with Giemsa's stain, terminal to sub-terminal in position,

PLATE 1

Haemoproteus fringillae

Figure 1. immature gametocyte

Figure 2. immature macrogametocyte, with 'dip'

Figure 3. microgametocyte

Figure 4. macrogametocyte, large pigment granules

Figure 5. macrogametocyte

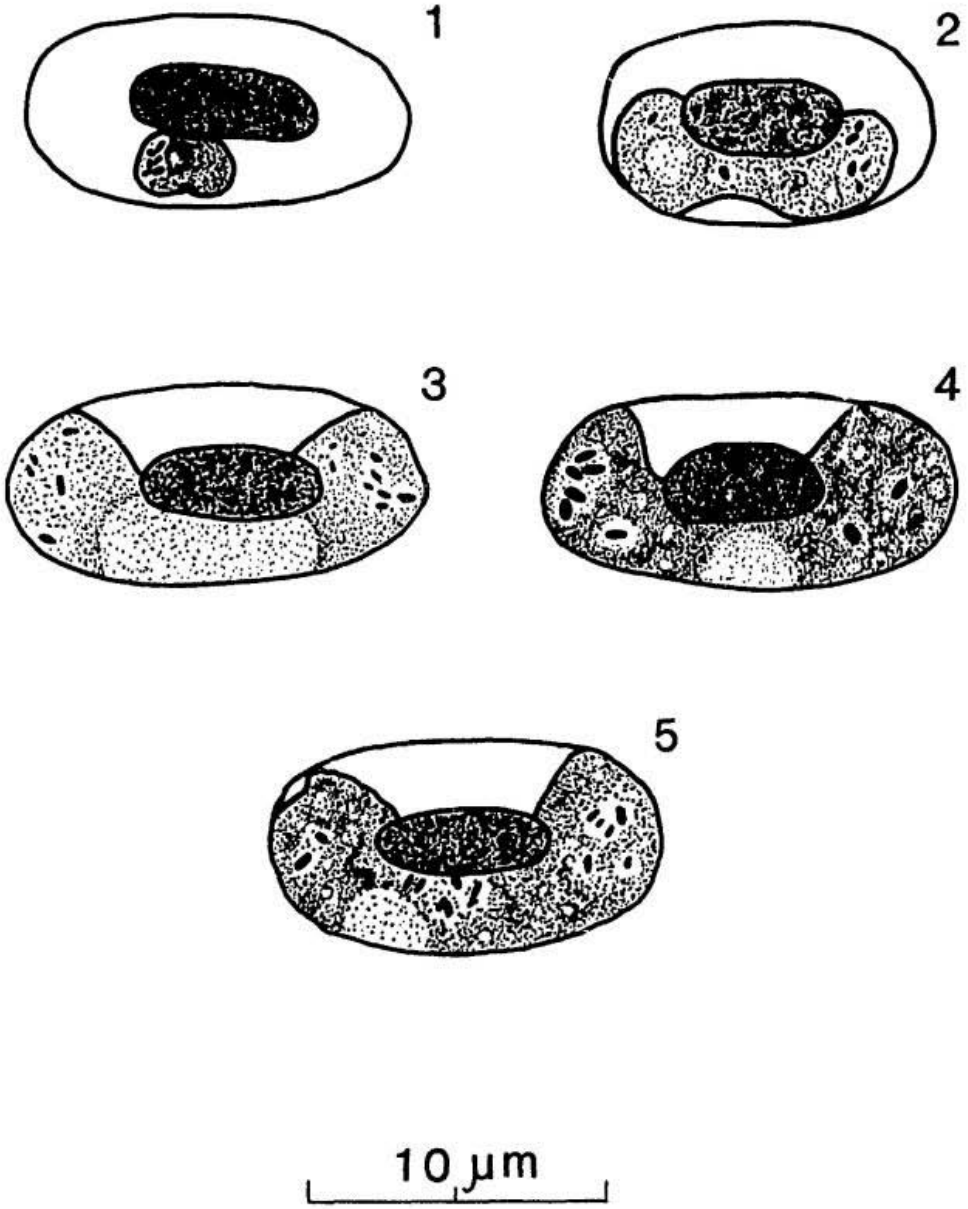

1
2
3
4
5
10 µm

TABLE 2. Morphometric parameters of the haemoproteids of the Fringillidae and Emberizidae.

	H. fringillae	*H. coatneyi* n. sp.	*H. mazzai*	*H. chloris*
Uninfected erythrocyte	N = 45	N = 135	N = 111	N = 70
length	12.6 (.87)*	11.9 (.81)	11.6 (.85)	11.6 (.75)
width	6.2 (.32)	6.2 (.57)	6.5 (.46)	6.2 (.55)
area	62.5 (4.4)	59.2 (7.4)	59.8 (6.2)	58.5 (7.6)
Uninfected erythrocyte nucleus	N = 45	N = 135	N = 111	N = 70
length	5.8 (.45)	5.5 (.50)	5.0 (.59)	5.5 (.40)
width	2.5 (.24)	2.4 (.27)	2.2 (.29)	2.5 (.25)
area	12.0 (1.4)	11.0 (1.8)	9.1 (1.6)	11.3 (1.6)
Erythrocyte infected by macrogametocyte	N = 75	N = 150	N = 159	N = 86
length	13.0 (.91)	12.3 (.94)	12.8 (.95)	12.7 (.63)
width	6.1 (.42)	6.2 (.70)	6.4 (.51)	6.5 (.65)
area	64.8 (6.5)	63.4 (8.7)	66.7 (6.3)	67.2 (6.6)

TABLE 2 (cont'd). Morphometric parameters of the haemoproteids of the Fringillidae and Emberizidae.

	H. fringillae	*H. coatneyi* n. sp.	*H. mazzai*	*H. chloris*
Infected erythrocyte nucleus	N = 75	N = 150	N = 159	N = 86
length	5.4 (.52)	5.4 (.46)	5.0 (.65)	5.5 (.67)
width	2.3 (.25)	2.3 (.39)	2.3 (.28)	2.5 (.36)
area	10.5 (1.5)	10.6 (2.1)	9.4 (1.7)	11.6 (2.6)
Macrogametocyte	N = 75	N = 150	N = 159	N = 86
length	16.1 (.80)	16.5 (3.4)	14.4 (1.2)	15.4 (1.4)
width	2.0 (.38)	2.0 (.88)	2.4 (.53)	2.7 (.67)
area	41.7 (4.8)	39.4 (7.9)	42.0 (5.7)	44.5 (5.1)
% Area of erythrocyte-parasite complex	64.4	62.1	63.1	66.5
Macrogametocyte nucleus	N = 75	N = 149	N = 159	85
length	2.0 (.41)	2.4 (.60)	2.6 (.54)	2.4 (.52)

TABLE 2 (cont'd). Morphometric parameters of the haemoproteids of the Fringillidae and Emberizidae.

	H. fringillae	*H. coatneyi* n. sp.	*H. mazzai*	*H. chloris*
width	1.9 (.40)	2.1 (.48)	2.1 (.37)	2.0 (.57)
area	3.3 (.69)	4.4 (1.6)	4.6 (.88)	4.1 (1.2)
% Area of gametocyte	8.0	11.3	11.1	9.3
Pigment granules - avg.	12.8 (3.0)	11.6 (2.9)	10.5 (2.2)	12.5 (3.0)
range	8-21	7-20	6-17	6-21
Nuclear displacement ratio	.95 (.15)	.78 (.20)	.74 (.18)	.66 (.20)
Erythrocyte infected by microgametocyte	N = 27	N = 15	N = 34	N = 10
length	12.5 (.63)	11.6 (.55)	12.3 (.82)	12.7 (.73)
width	6.1 (.63)	5.9 (.51)	6.5 (.46)	6.1 (.44)
area	63.6 (9.3)	57.1 (7.0)	64.8 (5.3)	63.9 (6.2)

TABLE 2 (cont'd). Morphometric parameters of the haemoproteids of the Fringillidae and Emberizidae.

	H. fringillae	*H. coatneyi* n. sp.	*H. mazzai*	*H. chloris*
Infected erythrocyte nucleus	N = 27	N = 15	N = 34	N = 10
length	5.5 (.48)	5.4 (.33)	4.6 (.47)	5.2 (.57)
width	2.3 (.24)	2.0 (.24)	2.3 (.28)	2.3 (.24)
area	10.7 (1.3)	9.2 (1.3)	8.7 (1.6)	10.1 (1.6)
Microgametocyte	N = 27	N = 15	N = 34	N = 10
length	16.3 (1.3)	15.3 (.78)	14.2 (1.2)	16.9 (1.5)
width	2.0 (.39)	2.0 (.83)	2.9 (.73)	2.6 (.63)
area	41.0 (7.6)	37.9 (9.1)	43.9 (4.3)	46.5 (5.9)
% Area of erythrocyte - parasite complex	64.3	65.7	67.9	72.7
Microgametocyte nucleus	N = 27	N = 15	N = 34	N = 10
length	6.4 (.69)	6.7 (.88)	6.6 (.97)	6.8 (1.5)

TABLE 2 (cont'd). Morphometric parameters of the haemoproteids of the Fringillidae and Emberizidae.

	H. fringillae	*H. coatneyi* n. sp.	*H. mazzai*	*H. chloris*
width	1.8 (.69)	1.8 (.46)	2.6 (.39)	2.5 (.58)
area	11.1 (2.6)	12.0 (3.1)	15.3 (2.4)	18.8 (6.8)
% Area of gametocyte	27.1	31.8	34.9	39.4
Pigment granules	13.8 (3.0)	9.7 (1.8)	11.7 (2.7)	11.2 (1.8)
range	9-21	7-14	7-17	9-14
Nuclear displacement ratio	.94 (.13)	.72 (.21)	.68 (.16)	.67 (.17)

Linear measurements are given in μm, area measurements in μm^2.

*Standard deviations given (in parentheses) below means.

occupying 8 % of parasite, usually adjoining host cell margin.

Microgametocyte (Plate 1, Fig. 3; Table 2): Halteridial parasite of moderate to large size, not usually causing hypertrophy; cytoplasm finely granular, staining lighter than macrogametocyte with Giemsa's stain; pigment granules round to oval, sometimes rod-shaped, yellow-brown, averaging 14 (ranging 8-21); volutin rarely seen; parasite nucleus large, diffuse, staining very pale pink with Giemsa's stain, occupying 27% of the gametocyte area.

Geographic Range: United Kingdom, Czechoslovakia, Lithuania, Norway, Portugal, France, Spain, and presumably throughout the geographic range of the Fringillidae.

Basis of redescription:

Neohapantotype: It is not known if Labbé designated any hapantotype material. The neohapantotype should be from the same host and locality as the original but if no suitable material is available from either of these, a specimen from the nearest locality and closest related species may be designated as the neohapantotype (ICZN 1985). Blood smears from the type host and locality were of poor quality and were not suitable for neohapantotype designation. In the absence of the original material, the blood film # 92411 from *Fringilla coelebs*, collected by Peirce at Bramley, Hants, U.K. on June 28, 1981, is designated as the neohapantotype of *H. fringillae*.

Paraneohapantotype: From *Fringilla coelebs*, Blood film # 67603 collected by J. Kucera on 21 May, 1975, Prague, Czechoslovakia.

Additional Host Records: Appendix A.

Comments: Labbé (1894) described a variety of *Halteridium Danilewskyi*, which he stated was very common in the blood of the chaffinch *Fringilla coelebs*. The description, which included colour plates but no measurements, was of a small halteridial parasite (occupying less than 50% of the infected cell area) which sometimes had a tendency to surround the nucleus, with indentations along the cell margins. It was later raised to specific status by Woodcock in 1910, who listed it as *Halteridium fringillae* (Labbé). According to Article 51(c) (i) of the ICZN this is only a change in rank within the species groups and therefore did not require the use of parentheses with the authority.

It is difficult to determine when *Halteridium* was synonymized with *Haemoproteus*, and when the designation *Haemoproteus fringillae* (Labbé) became correct. *Haemoproteus* was first described by Kruse in 1890, and as early as 1904 Schaudinn recognized *Haemoproteus* as the valid genus, but for years the names were used interchangeably. Coatney (1936) stated that *Halteridium* was one of the synonyms of *Haemoproteus*, and specifically listed *Haemoproteus fringillae* in *Fringilla caelebs* (sic). Since then, the name *H. fringillae* has been published as the halteridial haemoproteid occurring in many avian families other than the Fringillidae, from

which it was originally described (Bennett, Whiteway and Woodworth-Lynas 1982).

In practice, the term *H. fringillae/orizivorae* 'complex' (Peirce 1983) was used to identify the haemoproteids of many host families because of the frequent occurrence of both small halteridial parasites (*'fringillae*-like') and larger, broader parasites similar to *H. orizivorae* of the family Estrildidae. It was difficult to determine whether mixed infections or one pleomorphic species were present. *H. orizivorae* has recently been redescribed and its range redefined (Bennett and Peirce 1991).

Peirce (1984) redescribed *H. fringillae*, and distinguished it from *H. orizivorae* on the basis of smaller size, fewer pigment granules and less displacement of the host cell nucleus. However, the material used in the redescription (but not designated as a neohapantotype) was from *Sylvia borin* from Zambia. This host bird species is in the subfamily Sylviinae of the Muscicapidae. The haemoproteids of this family have recently been reviewed and the *Haemoproteus* species occurring in the Sylviinae described as *H. sylvae* (Bennett *et al.* 1991).

In 1916, de Mello and Braz de Sa described *Haemoproteus moruony* from *Copsychus saularis* (a member of the thrush subfamily Turdinae of the Muscicapidae). Bennett and Campbell (1972) synonymized (*in partim*) *H. moruony* with *H. fringillae* based on the earlier description and figures. However the haemoproteids of the thrushes have recently been reviewed and redescribed, with the haemoproteid species occurring in the subfamily Turdinae referred to *H. fallisi* (Bennett *et al.* 1991).

In view of the host family and subfamily specificity experimentally

demonstrated for a number of species of *Haemoproteus*, and the results of this study, assigning *H. fringillae* to such a broad range of hosts is probably in error. This species should be limited to the Fringillidae until experimental evidence clearly indicates a wider host spectrum. In this study, *H. fringillae* was identified in *Fringilla coelebs* and *F. montifringilla*. No material was available from *F. teydea*, the only other representative of this family. *Haemoproteus fringillae* is herein redescribed with neohapantotype and paraneohapantotype slides designated.

Haemoproteus fringillae is a medium sized halteridial haemoproteid which typically neither deforms the host erythrocyte in any way, nor displaces its nucleus, and which occupies approximately 65% of the erythrocyte - parasite complex. The nuclei of both macrogametocyte and microgametocyte are typically smaller than that of other haemoproteids in related host families (Table 2). The variability in pigment granule size and number is comparable with that seen in other species.

EMBERIZIDAE

Emberizinae

Nomen nudum: *Haemoproteus emberiza*

H. emberiza has been variously listed in the Emberizinae, by Zeiniev (1975), Musaev and Zeiniev (1977), and Subkhanov and Mirzobakhadurov (1976) who attributed the species to Berson (1964). Berson, however does not cite this parasite species in his paper, and there is no description of the species. Peirce and Bennett (1979), in describing examples of problems arising in the past in Russian literature, designated *H. emberiza* as a *nomem nudum*.

Haemoproteus coatneyi n. sp.

Type Host: *Zonotrichia albicollis* (Gmelin) [White-throated sparrow]

Type Locality: Gander, Newfoundland, Canada

Immature gametocyte (Plate 2, Figures 1-2): Youngest forms seen usually initiate growth lateral to erythrocyte nucleus, although polar positions are sometimes found; parasites small dumbbell-like or sausage shaped and usually appress the host cell nucleus; margins usually entire with ameboid edges common only in intense infections.

Macrogametocyte (Plate 2, Figure 4-7; Table 2): Halteridial parasite of medium to

PLATE 2

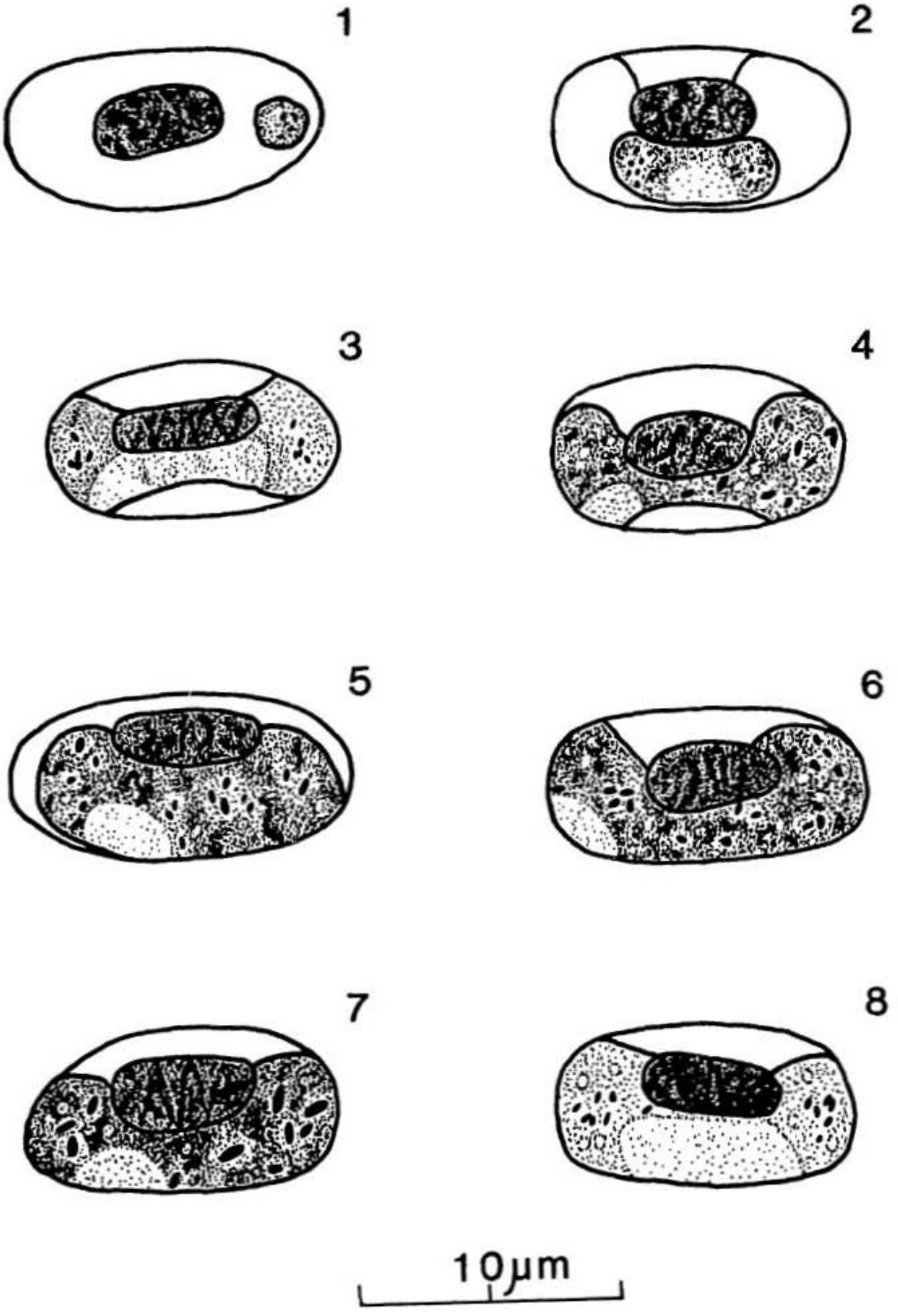
Haemoproteus coatneyi **n. sp.**

Figure 1-2. immature gametocytes

Figures 3. microgametocytes

Figure 4-7. macrogametocytes

Figure 8. microgametocyte


1
2
3
4
5
6
7
8
10µm

large size, dumbbell-shaped, or broadly halteridial, occupying 55-70% of the host erythrocyte - parasite complex; hypertrophy of infected cell area variable, from 2-25%, sometimes displacing the erythrocyte nucleus, usually only in sausage-shaped forms (NDR ranges from 0.5 to 1.0) (Plate 2, Figures 5,7); cytoplasm granular, staining moderate blue with Giemsa's stain; margins entire and usually rounded; gametocyte usually appressed to the erythrocyte nucleus, but frequently the outer edge does not appear to extend to the outer periphery of the erythrocyte, causing a 'dip' and giving a bilobed or dumbbell appearance (Plate 2, Figure 4); pigment granules, when visible, appear either large and rod-shaped, small and ovoid, or irregular, yellow to dark brown, averaging 9-13 (ranging 9-21), usually distributed randomly throughout the cytoplasm, but in some hosts (especially *Pipilo* spp. and *Sporophila* spp.) are paired; volutin granules not usually seen; parasite nucleus round to broadly triangular, terminal to subterminal in position, occupying 10-16% of the gametocyte area; multiple infections of 2-4 parasites in intense infections (2 most common of multiple infections).

Microgametocyte (Plate 2, Figures 3,8; Table 2): Halteridial parasite of medium to large size, occupying 66% of the host erythrocyte - parasite complex; hypertrophy of erythrocyte variable, rarely displacing the erythrocyte nucleus; cytoplasm finely granular, staining only lightly with Giemsa's stain; margins entire and usually rounded; pigment granules small to medium and ovoid or irregular, often clumped at poles of parasite; volutin granules not usually seen; parasite nucleus large and

diffuse, often not distinguishable from the cytoplasm, staining pale pink with Giemsa's stain, occupying 32% of the parasite area.

Geographic range: North and South America, Palearctic, Africa, India, Asia, presumably throughout the range of the Emberizinae.

Hapantotype: Blood film # 79654 from *Zonotrichia albicollis*, collected by J. Burry Caines at Gander, Newfoundland on August 18, 1979.

Parahapantotypes: Blood film # 30671 from *Passerella iliaca*, collected by G.F. Bennett at Pickavance Creek, Newfoundland, Canada on June 14, 1972; from *Zonotrichia capensis*, # 46137 collected by R.W. McFarlane at Arica, Chile on April 28, 1973, # 76654 collected by O. Souza Lopes at Itapetininga, Brazil on April 3, 1969, # 97246 collected by A. Gabaldon at Merida, Venezuela on September 4, 1980; # 97846 from *Zonotrichia albicollis*, collected by C. Kirkpatrick at Mercer County, New Jersey on May 5, 1985; # 113646 from *Passerella iliaca*, collected by P.E. Super at Point Reyes Peninsula, California on September 30, 1989.

Additional records: Appendix A.

Comments: Haemoproteids were first discovered in the blood of North American sparrows of the genus *Melospiza*, by Opie in 1898. Among others, Novy and

MacNeal (1905) observed them in *Melospiza* and *Spizella*, and Manwell and Herman (1935) listed them in *Passerculus, Junco, Spizella, and Melospiza*. However, due in part to poor descriptions and the variability observed, most authors were reluctant to identify the species of *Haemoproteus*, and identified them simply as *H.* sp. (Manwell 1955, Bennett *et al.* 1982). Various studies have referred the names *Haemoproteus fringillae*, *H. orizivorae* or *H. fringillae/orizivorae* complex to those haemoproteids having the same basic halteridial form (Bennett *et al.* 1982, Peirce 1983,1984). These designations have been made for haemoproteids of many hosts including the Emberizinae in the absence of comprehensive studies of the parasites across wide host and geographic ranges. Some parasites were medium-sized halteridial forms, often appearing bilobed. Others were larger, broader and often displaced the erythrocytic nucleus. The number and size of pigment granules were variable. Whether there were indeed two separate species was confounded by the frequent occurrence of both types in any one blood smear.

Material from 25 host species across a wide geographic range examined in the current study (Appendix A) revealed that there was variability in the shape of the haemoproteids in this subfamily, and that pigment in mature gametocytes varied from a few (7-10) large granules to several (17-20) small or medium granules. In many smears, the pigment was not very distinguishable and there were both parasites with small pigment granules as well as those with large elongate rod-shaped granules, and indeed many with both sizes. There was no consistent pattern of pigment granule size and number with the overall morphology. Also, in many cases there were

specimens of both the dumbbell type and the broader halteridial type regardless of whether smear artifacts were believed to be present. In any one smear, there was not always a clear distinction of infection with a dumbbell shape (with a 'dip') (Plate 2, Figure 4) and that with a large broader form (Plate 2, Figures 5-7) but rather a continuum existed (Plate A, Figure 3).

Smears from individual birds taken at different times showed no pattern of the occurrence of one type or the other. For example, one *Zonotrichia albicollis* from Newfoundland showed an infection of almost all dumbbell forms in late May (pre-transmission season, therefore probably a relapse infection). One week later both dumbbell (some with 'dips') and broader forms were seen, and two weeks later (mid-June) only broad forms were present. Another *Z. albicollis*, from New Brunswick, showed the reverse pattern in three captures beginning in early June. Whether or not progressive development of gametocytes results in such observations can only be determined by life cycle studies where birds are not subject to reinfection as they are in the field. In any case, throughout the whole host and geographic range examined, there was frequent though not totally consistent occurrence of the 'dip'. It was especially pronounced in South American specimens (especially in *Zonotrichia capensis*) where the parasites were fairly small compared to some from North America. Sometimes it appeared that the cytoplasm simply did not stain in the central portion of the parasite, but in other cases, a distinct cell membrane could be seen. Often, '*fringillae* type' parasites can be seen on one particular section of the smear, and the '*orizivorae* type' on another. The fact that this did not occur in just

a few isolated cases points to either two species transmitted by the same vector, or one morphologically variable species.

Culicoides crepuscularis and C. sphagnumensis have been identified as containing sporozoites of the haemoproteid found in North American sparrows of the genus *Zonotrichia* (Fallis and Bennett 1961). Khan and Fallis (1969) described the schizogonic stages in lung tissue of *Zonotrichia albicollis*. However, the species was identified as *H. fringillae*. In view of the current study's findings and in accordance with the currently accepted family/subfamily specificity (Bennett and Peirce 1988) this misidentifed species was almost certainly *Haemoproteus coatneyi*.

Haemoproteus coatneyi n. sp. is herein proposed and described as a new species found in the subfamily Emberizinae of the Emberizidae, and hapantotype and parahapantotype slides designated. The specific name is in honour of the late G. Robert Coatney, in recognition of his contribution to the study of haematozoa of North American passerines.

EMBERIZIDAE

Cardinalinae

***Haemoproteus mazzai* Parodi and Niño, 1927**

Synonym: *Haemoproteus hedymelis* Coatney and Roudabush, 1937

Type Host: *Pheucticus aureoventris* d'Orbigny and Lafresnaye [Black-backed grosbeak]

Type Locality: Louisiana, U.S.A.

Immature gametocyte (Plate 3, Figures 1-2): Youngest forms seen lateral or medial to the host erythrocyte nucleus, or rarely, at either pole; gametocyte usually grows with membrane appressed to the host cell nucleus, developing from small ovoid forms to thin banana-shapes to thickened sausage-shaped forms; margin amoeboid or entire.

Macrogametocyte (Plate 3, Figures 3-5; Table 2): Halteridial parasite of medium to large size, sausage-shaped or broadly halteridial, occupying 60-70 % of the host erythrocyte-parasite complex; hypertrophy in area variable, (5-25%); displacing the nucleus in some cases (usually about half); cytoplasm finely granular, occasionally vacuolate, staining moderate blue with Giemsa's stain; margins entire or with indentations at ends, appearing amoeboid or square, especially in those not quite

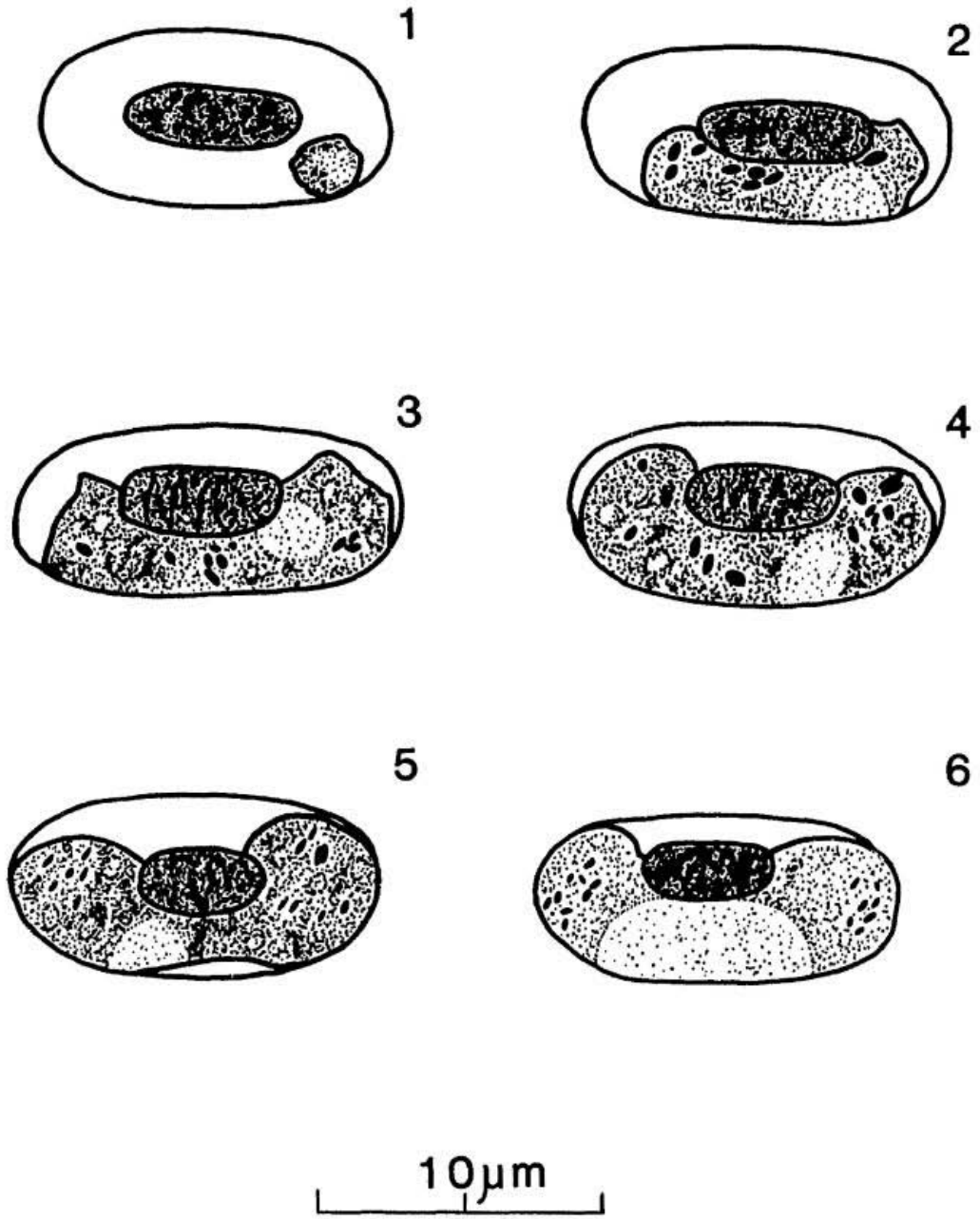
PLATE 3

Haemoproteus mazzai

Figure 1-2. immature gametocytes

Figures 3-5. macrogametocytes

Figure 6. microgametocyte


1
2
3
4
5
6
10μm

fully mature; ends of parasites often not reaching poles of host erythrocyte, usually touching cell nucleus but not always cell periphery; pigment granules large and rod-shaped, or small and ovoid, parasites with both sizes seen in the same smear, yellow to dark yellow-brown, averaging 11-14 (ranging 7-16) distributed randomly throughout the cytoplasm, sometimes paired or in small clumps; volutin granules seen only in parasites of a *Cardinalis phoeniceus* from Venezuela; parasite nucleus round or more rarely broadly triangular, medial to sub-medial in position, but occasionally terminal, located on the outer margin of the parasite, rarely appressed to the nucleus; occupying 12% of the parasite area; multiple infections (1-2 gametocytes) of the same erythrocyte seen in intense infections, usually on opposite sides of the host cell nucleus.

Microgametocyte (Plate 3, Figure 6; Table 2): Halteridial parasite of medium to large size, occupying 60-70% of the host erythrocyte - parasite complex; cytoplasm finely granular, staining only lightly with Giemsa's; ends usually rounded and margin entire but sometimes amoeboid; pigment granules usually small and ovoid, even in those hosts where macrogametocytes have mostly large pigment granules, polar in distribution, averaging 10-13 per parasite; parasite nucleus large and diffuse, staining very pale pink with Giemsa's stain, occupying approximately 35% of the parasite area; volutin granules seen in parasites of a *Cardinalis phoeniceus* from Venezuela.

Geographic range: New Brunswick, Canada; California, Maryland, New Jersey,

U.S.A.; El Salvador; Jamaica, Venezuela and presumably throughout the entire range of the subfamily Cardinalinae.

Basis of redescription:

Neohapantotype: In the absence of suitable material from the original type host and locality, Blood film # 103795 from *Cardinalis cardinalis*, collected by M. Garvin at Baton Rouge, Louisiana, U.S.A. on May 16, 1988 is designated as the neohapantotype of *Haemoproteus mazzai*.

Paraneohapantotypes: From *Pheucticus ludovicianus*: Blood film # 57493, # 60293, # 60384, # 60385, collected by G.F. Bennett at Tantramar Marsh, New Brunswick, Canada on August 5, 1976, June 29, 1977, July 5, 1977 and July 5, 1977, respectively; # 98013, collected by C. Kirkpatrick at New Jersey, U.S.A. on May 11, 1986; # 113671, from *Pheucticus melanocephalus*, collected by P.E. Super at Point Reyes, California, U.S.A. on May 3, 1990.

Additional records: Appendix A.

Comments: Parodi and Niño (1926) described, and later (1927) named *Haemoproteus mazzai* from both stained and fresh blood preparations and lung tissue stages found in *Pheucticus aureoventris* from northern Argentina. No hapantotype material was designated. The authors described the immature gametocytic forms

as "more or less globular or in the shape of small bananas" and the mature parasites as "widened halteridial forms with numerous granules of pigment..." which sometimes caused nuclear displacement, and eventually ruptured the host cell. They did not give specific pigment granule counts but stated they were "irregular of form, at times distributed around the nucleus and at other times at the extremities of the parasite". Their plates and figures indicated a broadly halteridial or sausage-shaped parasite similar to those seen in the current study. The figures showed fairly large pigment granules, numbering from 8-14. The description included that of schizonts in endothelial cells of lung alveoli. However, the statement of finding merozoites in leucocytes as well as the endothelial cells, and "numerous melanic monocytes" is confusing. These findings must be in error as merozoites of *Haemoproteus* are not found in blood cells other than erythrocytes. They described the development of the parasite as being similar to that of *H. orizivorae* and *H. columbae*.

Coatney and Roudabush (1937) described, from *Pheucticus ludovicianus*, a halteridial haemoproteid which they called *Haemoproteus hedymelis*, and distinguished it from *H. mazzai* by the former's extreme nuclear displacement and tendency to become round and burst out of the host cell. This rounding and 'bursting out' of the gametocyte was likely either the typical *post mortem* changes that occur in haemoproteids or the result of slow-drying blood, and are considered of no taxonomic consequence (White and Bennett 1979, Bishop 1989). Coatney and Roudabush described *H. hedymelis* as generally having smooth rounded ends, usually touching the host cell nucleus, but not always the cell periphery. The

macrogametocytes usually caused some nuclear displacement while the microgametocytes did only in about half the cases. The pigment granules were elliptical to rod-shaped, ranging from 8-12 (average 9). From the description and figures given in both descriptions, it is clear that they are the same species. Examination of material from *Pheucticus* and *Cardinalis* confirmed the occurrence of one species in this subfamily, with a pleomorphic form. By the Principle of Priority (Article 23 (a) of the ICZN), *H. mazzai* Parodi and Niño 1927 is the valid species name. *H. hedymelis* Coatney and Roudabush 1937 is hereby declared a synonym of *H. mazzai*.

The material examined in this study from this subfamily was from three host species from a variety of locations; the subfamily is limited to North and South America. *Haemoproteus mazzai* exhibited a broad range of size and shape and is fairly typical of the moderate to large halteridial haemoproteid. The inconsistency of gametocyte outline, nuclear displacement and pigment granule size were presumed to be the result of natural variation, as any single blood smear showed a variety of forms. Although other South American species of this avian subfamily have been examined for blood parasites (Woodworth-Lynas *et al.* 1988), there are no other records of *Haemoproteus* (Bennett *et al.* 1982). The host species and geographical locations from which *H. mazzai* was found in the current study are given in Appendix A. *Haemoproteus mazzai* is herein redescribed as the haemoproteid species found in the Cardinalinae of the Emberizidae, and neohapantotype and paraneohapantotype slides are designated.

EMBERIZIDAE

Carduelinae

Nomina nuda: *Haemoproteus loxiae* Tartakovskii, 1913

Haemoproteus acanthis Musaev and Zeiniev, 1977

In 1913 at a laboratory exhibition in Petrograd (Leningrad), Tartakovskii described and illustrated with tables and watercolour pictures, five species of *Haemoproteus*. Among these was *Haemoproteus loxiae* from *Loxia curvirostra*. The proceedings from the exhibition were published, but they did not contain any of the illustrations or numerical data. The material, stored in the laboratory's archives, was used as fuel in the siege of Leningrad during World War II (Peirce and Bennett 1979). Therefore, it is not possible to compare the pictures with any subsequent material from members of this subfamily. Tartakovskii's text does not meet the basic requirements of the International Code of Zoological Nomenclature (ICZN 1985) for species designation, and Peirce and Bennett (1979) declared the species to be a *nomen nudum*.

Musaev and Zeiniev (1977) listed *Haemoproteus acanthis* as a parasite of *Acanthis cannabina*. However, they did not give any description or illustrations, and in fact spelled the specific name differently when they listed it in text (*H. acanthies*). Again, this does not meet the requirements of the ICZN as a species description, and therefore *H. acanthis* was declared a *nomen nudum* by Peirce and Bennett in 1979.

Haemoproteus chloris Covaleda Ortega and Gállego Berenguer, 1950

Synonyms: *Haemoproteus globulosus* C. Ortega and G. Berenguer, 1950

Haemoproteus macropigmentatus C. Ortega and G. Berenguer, 1950

Haemoproteus serini Levine and Campbell, 1971

Haemoproteus tartakovskyi Valkiūnas, 1986

Type Host: *Carduelis chloris* (Linnaeus) [European greenfinch]

Type Locality: Malzeville, France

Immature gametocyte (Plate 4, Figure 1): Youngest forms seen lateral or medial to the host erythrocyte nucleus, rarely at pole; margin amoeboid or entire.

Macrogametocyte (Plate 4, Figures 2-5; Table 2): Halteridial parasite ranging from a large broadly sausage-shape or a medium-sized dumbbell shape, occupying 60-75% of the host erythrocyte-parasite complex, at times causing 5-10% hypertrophy in area, especially in North American hosts; displacing the nucleus in some cases and often causing atrophy of the erythrocyte nucleus; cytoplasm granular, often vacuolate, staining moderate blue with Giemsa's stain; margins entire and rounded although sometimes with indentations at ends, appearing 'squarish'; pigment granules usually large, often rod-shaped, or small and ovoid, often both sizes in one gametocyte, yellow to dark yellow-brown, averaging 14 (ranging 9-25 with host and geographic

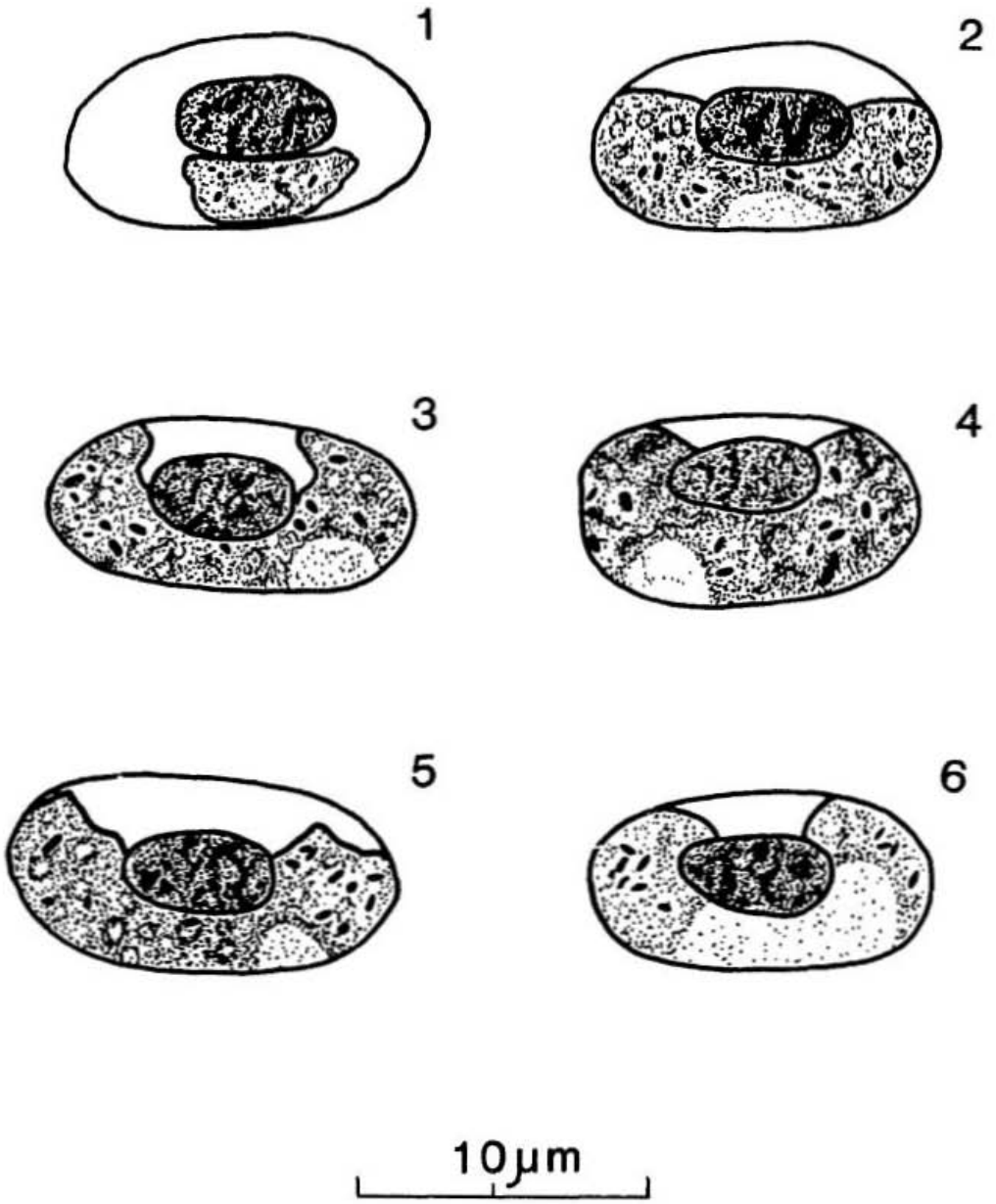
PLATE 4

Haemoproteus chloris

Figure 1. immature gametocyte

Figures 2-5. macrogametocytes

Figure 6. microgametocyte


1
2
3
4
5
6
10μm

variation), distributed randomly throughout the cytoplasm, and more rarely clumped; volutin granules not usually seen; parasite nucleus round to ovoid or broadly triangular, medial to sub-medial in position and usually located on the outer margin of the parasite, occupying 9% (ranging 5-12%) of the parasite area; multiple infections (1-4 gametocytes) of the same erythrocyte seen in intense infections, sometimes on the same side of the host cell nucleus, (seen most often in *Loxia* and *Acanthis* spp.) causing extreme nuclear rotation and/or displacement.

Microgametocyte (Plate 4, Figure 6; Table 2): Halteridial parasite of medium to large size, occupying 73% of the host erythrocyte - parasite complex; cytoplasm finely granular, staining only lightly with Giemsa's stain; ends usually rounded and margin entire but sometimes amoeboid or squarish; pigment granules usually large and rod-shaped but also small and ovoid, usually clumped near the poles, averaging 11-14 per parasite; volutin granules not usually seen; parasite nucleus large and diffuse, staining pale pink with Giemsa's stain, occupying approximately 30% of the parasite area.

Basis of re-description:

Neohapantotype: It is not known if Covaleda Ortega and Gállego Berenguer (1950) designated hapantotype material, or whether their original collection is intact. According to the ICZN, the neohapantotype should be from the same host and locality as the original but if no suitable material is available from either of these,

a specimen from the nearest locality and the closest related species may be designated as the neohapantotype. No suitable material from the type host and locality was available for study or designation. In the absence of the original material, Blood film # 68217, from *Carduelis carduelis*, collected by J. Blancou at Malzeville, France on September 6, 1978 is hereby designated as the neohapantotype of *Haemoproteus chloris*.

Paraneohapantotypes: Blood film # 21924 from *Loxia curvirostra*, collected by G.F. Bennett at Pickavance Creek, Newfoundland, Canada on June 18, 1971; # 58131 from *Carduelis chloris*, collected by M.A. Peirce at England on May 21, 1965; # 107373 from *Acanthis flammea*, collected by G. Seutin at Churchill, Manitoba, Canada on June 24, 1989.

Additional host records: Appendix A.

Geographic Range: North America, Europe, Asia, Africa and presumably throughout the entire range of the subfamily Carduelinae of the Emberizidae.

Comments: Covaleda Ortega and Gállego Berenguer (1950) described three species of haemoproteids from members of the genus *Carduelis*. *Haemoproteus globulosus* was described as a halteridial parasite that when mature took on a globular form, displacing the host cell nucleus to one margin and causing great hypertrophy. The

description was based solely on one positive blood smear and from the description and figures was likely the result of using blood from a dead bird or from slow drying of the smear, two conditions which are known to cause such artifacts (Bennett et al. 1975, White and Bennett 1979). These forms represent the initiation of gamete formation that would normally occur upon ingestion by a susceptible vector. The fact that 'immature' halteridial forms were seen in the smear further supports this view. Peirce (1983) also believed this to be the case but did not synonymize the name of the species. Also in 1950, Covaleda Ortega and Gállego Berenguer described a similar globular species occurring in owls. This species was also presumed to be described from *post mortem* material causing changes in the gametocyte and has since been synonymized (Bishop and Bennett 1989). Considering this, and because the presumed infection was found in only one bird, *H. globulosus* is hereby declared a synonym of *H. chloris*.

Covaleda Ortega and Gállego Berenguer (1950) also described *Haemoproteus macropigmentatus* from one smear from *Carduelis carduelis*. The parasite was described as being halteridial with voluminous appearance which causes slight displacement and rotation of the erythrocyte nucleus. They described the pigment as large oval-rounded dark violet granules, sometimes surpassing 1 μm and numbering 7-11 in macrogametocytes, and based their diagnosis largely on these characteristics. It appears that they confused volutin granules (which are purple-red in color), a fairly variable characteristic of some *Haemoproteus* species (often within an individual host bird) with true hemazoin pigment granules which are yellow-brown

(Bishop 1989, Bennett and Peirce 1989). Volutin was only rarely observed in the cardueline material in this study. All other characterisitics of this described specimen were the same as those of the basic halteridial parasites seen in the others of this subfamily. *H. macropigmentatus* is hereby declared a synonym of *H. chloris*.

Valkiūnas (1986) described *H. tartakovskyi* from *Loxia curvirostra* in Lithuania as the first 'enucleator' type haemoproteid described from the passerines. The immature parasites are comparable in both size and shape to the halteridial form seen in other members of the Carduelinae. The major difference was the occurrence of some gametocytes which displace the nucleus, and sometimes causing rotation of the nucleus. As well, some occasionally enucleated the infected erythrocyte. These characteristics were seen in the current study in material from *Loxia* and *Acanthis* in North America, although enucleating forms were not as frequent as in Valkiūnas' material. In addition, peripheral blood smears from any bird species often contain a few specimens that show similar nuclear displacement and/or rotation, usually at the periphery of the smear. These are probably caused by excess pressure on the blood as it is smeared on the microscope slide. Other recognized enucleator types (*H. enucleator*, *H. bennetti*) show a frequent occurrence of the displaced and enucleated specimens. In *H. bennetti*, the percentage of parasitized enucleated cells varies up to 96% (Greiner *et al.* 1977). In specimens of carduelines from North America, the occurrence of enucleated cells is minimal (<2%). Several slides of *H. tarkakovskyi* in *Loxia curvirostra*, from Lithuania (including a parahapantotype slide) were examined in this study. The parasite was generally large and often showed

extreme nuclear displacement, and there were instances of enucleation. However, in many cases, multiple infection, seen often in intense infections, caused the displacement. Two or more immature gametocytes initiating growth on the same side of the nucleus resulted in displacement and rotation (Plate A, Figure 4). This could be mistaken for true displacement caused by one gametocyte in some cases where differentiation of the parasite membrane was difficult. At this time, until experimental evidence can confirm the existence of a different species, the haemoproteid occurring in Lithuania would be better considered a geographic variant of a single, pleomorphic species. *H. tarkakovskyi* is hereby declared a synonym of *H. chloris*.

Sergent and Sergent (1948) described a *Haemoproteus* species from a canary (*Serinus canaria*) that was held in captivity in Algiers, Algeria, in the same area as Algerian sparrows (family Passeridae) from which *H. wenyoni* Sergent and Sergent 1948 was described. This *Haemoproteus* was similar in appearance to *H. wenyoni* and although Sergent and Sergent described it separately, they did not give it a name. Levine and Campbell (1971) assigned the name *H. serini*, based upon the parasite's occurrence in a separate genus. They did not redescribe the species, however. The name *H. serini* thus dates from 1971, while the description is from 1948. The haemoproteid examined in this study from canaries was considered the same as *H. chloris*, which holds precedence according to the Principles of Priority of the ICZN. Therefore, *H. serini* is synonymized with *H. chloris*.

Haemoproteus chloris is a halteridial haemoproteid with a broad geographic

and host range. In the material studied, it exhibited a highly pleomorphic form, ranging from a broadly fat sausage shape to a medium-sized halteridial parasite. While the smaller halteridial shape did not decidedly displace the host cell nucleus, but rather enveloped it, the larger sausage shape often displaced the nucleus towards the periphery of the cell. Often forms of the entire range were seen in any one blood smear from any one bird.

In most of the material examined, there were usually parasites with either few large rod-shaped pigment granules or small ovoid ones. However, there were specimens in all bird genera and geographic areas with both sizes of pigment granules within the same gametocyte (Plate A, Figure 5). There was no consistency in the relationship of parasite size and shape with other generally used characters such as pigment number, margin outlines or degree of nuclear displacement. The basic trend of larger ratio of parasite to parasite-erythrocyte complex area with more nuclear displacement was the same for all within the subfamily, as might be expected in sampling parasites at various stages of growth and development.

The frequent occurrence of specimens in a single smear of both dumbbell shaped gametocytes and fatter halteridial gametocytes which are not attributable to smear artifacts lends support for one highly morphologically variable species within this subfamily. Considering the large number of host bird species (125) within this subfamily and the large geographical range (four continents) in which they occur, this not surprising, and may illustrate a still-evolving species. Life cycle cross-transmission studies may reveal whether such geographical and/or host induced differences occur

at the species level.

Haemoproteus chloris is herein redescribed as the single haemoproteid species found in the Carduelinae of the Emberizidae, and neohapantotype and paraneohapantotype slides are designated. The specific name is emended from *chloriis* to *chloris* in accordance with Article 34 (b) of the ICZN (1985). The species is pleomorphic and may represent a complex of a still-evolving species.

PARULIDAE

Parulinae

Haemoproteus paruli **n. sp.**

Type Host: *Dendroica coronata* (Linnaeus) [Yellow-rumped warbler]

Type Locality: Gander, Newfoundland, Canada

Immature gametocyte (Plate 5, Figure 1): Youngest forms seen initiate growth lateral to host erythrocyte nucleus, usually near middle of nucleus; Margins entire.

Macrogametocyte (Plate 5, Figures 2-3; Table 3): Halteridial parasite of medium to large size, occupying ~70% of the host-erythrocyte complex; hypertrophy of cell area variable, ranging from 2-23%, displacing the host cell nucleus on occasion; cytoplasm finely granular, staining moderate blue with Giemsa's stain; margins entire and usually rounded although can sometimes be squared; pigment granules medium sized, usually ovoid, although can be rod-like, yellow to dark-brown, averaging 14 (ranging from 7-25), distributed randomly throughout the cytoplasm; volutin not seen; parasite nucleus round to broadly triangular, subterminal to terminal in position, occupying 10% of the gametocyte area; multiple infections (1-4) parasites seen in intense infections.

Microgametocyte (Plate 5, Figures 4-5, Table 3): Halteridial parasite of medium to

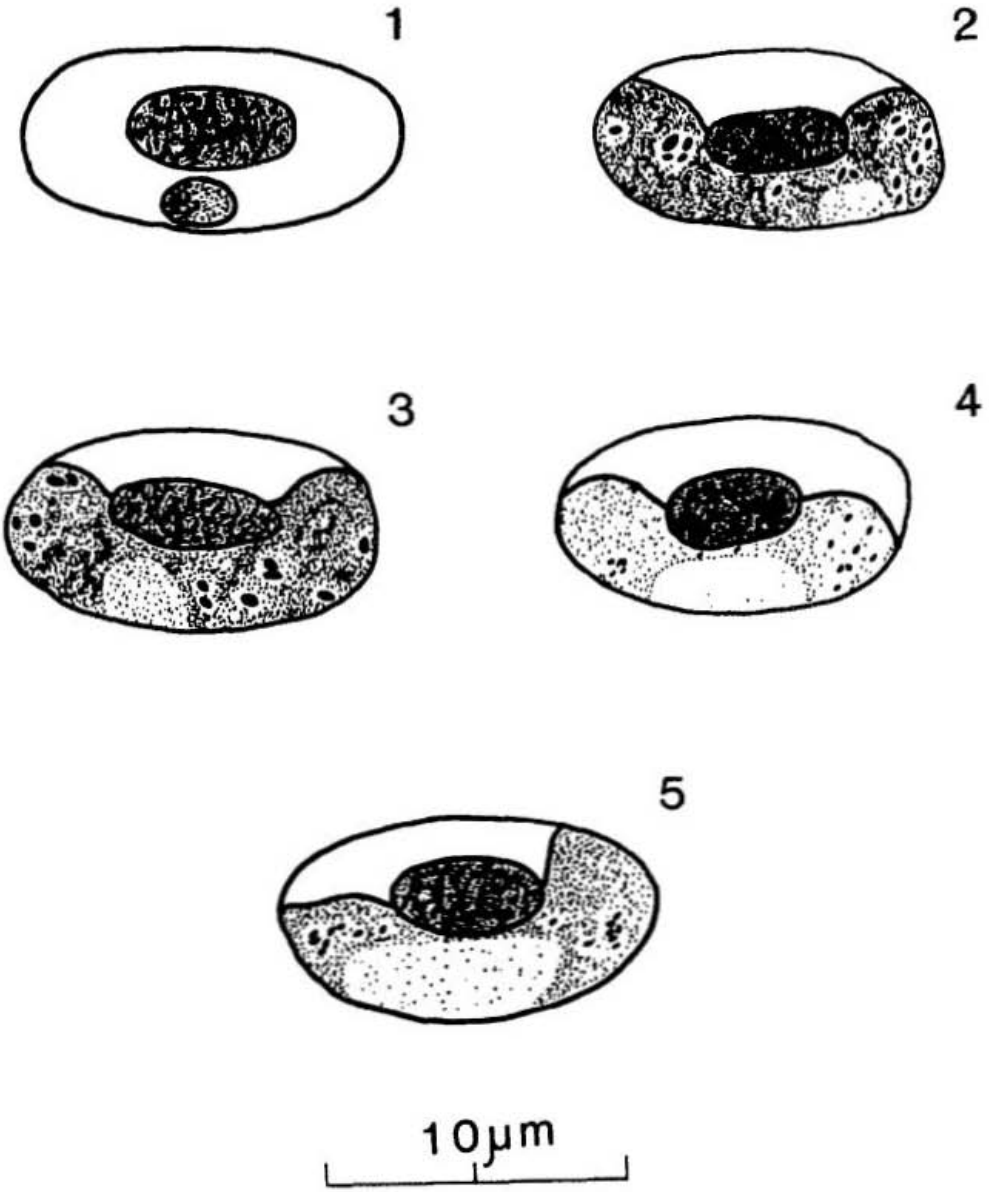
PLATE 5

Haemoproteus paruli n. sp.

Figure 1. immature gametocyte

Figures 2-3. macrogametocytes

Figure 4-5. microgametocytes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10μm

TABLE 3. Morphometric parameters of the haemoproteids of the Parulidae, Thraupidae and Icteridae.

	H. paruli n. sp.	*H. coereba* n. sp.	*H. thraupi* n. sp.	*H. quiscalus*
Uninfected erythrocyte	N = 115	N = 45	N = 140	N = 95
length	11.6 (.89)*	11.6 (.97)	11.7 (.73)	11.7 (.72)
width	6.3 (.43)	6.2 (.47)	6.7 (.52)	6.7 (.60)
area	58.9 (5.4)	57.4 (7.4)	62.8 (6.7)	62.2 (6.1)
Uninfected erythrocyte nucleus	N = 115	N = 45	N = 140	N = 95
length	5.2 (.56)	5.3 (.51)	5.1 (.51)	5.3 (.54)
width	2.4 (.22)	2.2 (.39)	2.1 (.38)	2.3 (.30)
area	10.5 (1.4)	9.6 (2.2)	8.8 (2.3)	10.1 (2.0)
Erythrocyte infected by macrogametocyte	N = 222	N = 45	N = 150	N = 100
length	12.7 (.75)	13.3 (.59)	12.8 (1.0)	12.7 (.79)
width	6.3 (.41)	6.4 (.48)	6.5 (.72)	6.7 (.57)
area	65.1 (4.7)	70.2 (6.5)	68.5 (10.7)	69.6 (7.1)

TABLE 3 (cont'd). Morphometric parameters of the haemoproteids of the Parulidae, Thraupidae and Icteridae.

	H. paruli n. sp.	*H. coereba* n. sp.	*H. thraupi* n. sp.	*H. quiscalus*
Infected erythrocyte nucleus	N = 222	N = 45	N = 150	N = 100
length	5.4 (.52)	5.4 (.45)	5.1 (.55)	5.1 (.57)
width	2.3 (.23)	2.3 (.39)	2.1 (.44)	2.4 (.36)
area	10.4 (1.3)	10.5 (1.5)	8.7 (2.5)	10.1 (2.3)
Macrogametocyte	N = 222	N = 45	N = 150	N = 100
length	15.4 (1.0)	15.1 (1.2)	13.0 (1.6)	15.1 (1.7)
width	2.3 (.44)	2.8 (.73)	3.0 (.63)	2.5 (.45)
area	41.9 (4.4)	48.8 (8.0)	42.0 (7.8)	43.1 (6.1)
% Area of erythrocyte-parasite complex	64.5	69.2	62.2	62.4
Macrogametocyte nucleus	N = 222	N = 45	N = 150	100
length	2.5 (.37)	2.7 (.57)	2.6 (.46)	2.2 (.66)

TABLE 3 (cont'd). Morphometric parameters of the haemoproteids of the Parulidae, Thraupidae and Icteridae.

	H. paruli n. sp.	*H. coereba* n. sp.	*H. thraupi* n. sp.	*H. quiscalus*
width	1.8 (.33)	2.2 (.45)	2.0 (.36)	2.1 (.37)
area	4.2 (.95)	4.9 (1.1)	4.1 (.98)	3.8 (1.1)
% Area of gametocyte	10.0	10.3	10.0	8.9
Pigment granules - avg.	13.8 (2.1)	11.6 (2.2)	13.3 (3.0)	12.2 (3.1)
range	8-20	9-14	7-20	7-24
Nuclear displacement ratio	.84 (.21)	.65 (.27)	.64 (.28)	.84 (.14)
Erythrocyte infected by microgametocyte	N = 32	N = 10	N = 36	N = 35
length	12.3 (.79)	12.9 (.88)	12.8 (.83)	12.6 (.98)
width	6.7 (.39)	5.9 (.42)	6.5 (.67)	6.8 (.66)
area	66.5 (5.2)	61.4 (5.7)	69.1 (9.0)	68.6 (8.6)

TABLE 3 (cont'd). Morphometric parameters of the haemoproteids of the Parulidae, Thraupidae and Icteridae.

	H. paruli n. sp.	*H. coereba* n. sp.	*H. thraupi* n. sp.	*H. quiscalus*
Infected erythrocyte nucleus	N = 32	N = 10	N = 36	N = 35
length	5.0 (.31)	5.1 (.29)	5.1 (.50)	5.3 (.68)
width	2.3 (.29)	2.5 (.25)	2.1 (.34)	2.4 (.41)
area	9.7 (1.2)	10.8 (.98)	8.9 (1.6)	10.8 (2.6)
Microgametocyte	N = 32	N = 10	N = 36	N = 35
length	15.7 (1.2)	14.1 (1.0)	13.4 (1.4)	15.1 (1.6)
width	2.8 (.36)	1.9 (.32)	3.0 (.71)	2.5 (.38)
area	45.7 (4.9)	37.3 (5.2)	43.9 (8.3)	41.3 (6.2)
% Area of erythrocyte - parasite complex	68.7	60.8	63.9	60.6
Microgametocyte nucleus	N = 32	N = 8	N = 36	N = 35
length	7.3 (1.1)	5.3 (.31)	5.4 (.83)	6.0 (.87)

TABLE 3 (cont'd). Morphometric parameters of the haemoproteids of the Parulidae, Thraupidae and Icteridae.

	H. paruli n. sp.	*H. coereba* n. sp.	*H. thraupi* n. sp.	*H. quiscalus*
width	2.4 (.33)	1.8 (.30)	1.7 (.96)	1.6 (1.1)
area	15.9 (3.7)	9.0 (1.2)	9.9 (2.2)	12.5 (3.2)
% Area of gametocyte	34.5	24.3	22.7	30.7
Pigment granules	15.0 (3.7)	12.5 (1.7)	13.9 (3.2)	11.9 (3.4)
range	10-20	11-15	8-18	7-24
Nuclear displacement ratio	.71 (.12)	.87 (.24)	.61 (.26)	.86 (.12)

N = number measured. Linear measurements in μm, area measurements in μm^2.

*Standard deviations given (in parentheses) below means.

large size, occupying approximately 70% of the erythrocyte-complex area, hypertrophy of the erythrocyte variable; occasionally displacing the host cell nucleus slightly; cytoplasm finely granular, staining only lightly with Giemsa's stain; ends usually rounded and margin entire; pigment granules small to medium-sized and ovoid, usually clumped near the poles, averaging 15 per parasite; volutin granules not seen; parasite nucleus large and diffuse, staining pale pink with Giemsa's, occupying 34% of the gametocyte area.

Geographic range: Nearctic and Neotropical regions, throughout the geographic range of the Parulidae.

Hapantotype: Blood film 87334 from *Dendroica coronata*, collected by J. Burry Caines at Gander, Newfoundland on June 2, 1981.

Parahapantotypes: Blood film # 56347 from *Dendroica petechia*, collected by G.F. Bennett at Tantramar Marsh, New Brunswick on August 3, 1976; # 60080 from *Dendroica coronata*, collected by G.F. Bennett at Tantramar Marsh, New Brunswick on June 4, 1977; # 89186 from *Dendroica coronata* by J. Burry Caines at Gander, Newfoundland on July 22, 1981; # 90230 from *Dendroica petechia* collected by J. Burry Caines at Gander, Newfoundland on June 18, 1982.

Additional records: Appendix A.

Comments: No haemoproteid species have been described from this subfamily to date, although haemoproteids have been identified for many years in members of this subfamily (North American wood warblers). As in other cases, most studies have listed them as either as *Haemoproteus sp.* or referred to them as *H. fringillae/orizivorae* (Bennett *et al.* 1982). In the current study, haemoproteids were identified in many species of the subfamily, from North to South America (Appendix A), but were more common in certain genera, such as *Dendroica* spp. This differential prevalence could be caused by host immune responses or be due to ecological factors such as habitat stratification (Greiner *et al.* 1975).

The forms seen in the current study were typical halteridial haemoproteids, ranging from small dumbbell shapes to broader fuller ones with few other distinguishing characters. Pigment granules ranged from 8 to 20 or more in mature cells. In general, gametocyte characters varied somewhat with host bird species and geographic location, although there was no pattern in these differences. The degree of host cell deformation varied, but gross changes in erythrocyte size or shape were not usually evident.

Haemoproteus paruli n. sp. is described as the halteridial haemoproteid found in the subfamily Parulinae of the Parulidae, and hapantotype and parahapantotype slides are designated. The specific name refers to the host family name.

PARULIDAE

Coerebinae

Haemoproteus coereba **n. sp.**

Type Host: *Coereba flaveola* (Linnaeus) [Bananaquit]

Type Locality: Green Hills, Jamaica

Immature gametocyte: (Plate 6, Figure 1). Youngest forms seen usually initiate growth near poles of erythrocyte; margin usually entire and ends rounded.

Macrogametocyte: (Plate 6, Figure 2; Table 3). Halteridial parasite of large size, occupying 70-75% of the erythrocyte-parasite complex, causing host-cell hypertrophy of up to 30%; cytoplasm finely granular, staining moderate-blue with Giemsa's stain; parasite margin entire, appressing the host cell nucleus; ends of parasite usually rounded, sometimes pointed, giving a 'hooked' appearance; host cell displaced laterally in some cases (NDR = 0.65); pigment granules round to oval, often large, yellow-brown, averaging 12, (range 8-16) sometimes scattered but more often in polar clumps; parasite nucleus compact, round to elongate oval, occupying 10% of parasite, usually adjoining host cell margin.

Microgametocyte: (Plate 6, Figure 3; Table 3). Halteridial parasite of large size, occupying 70% of the host-erythrocyte complex, hypertrophy in erythrocyte area less

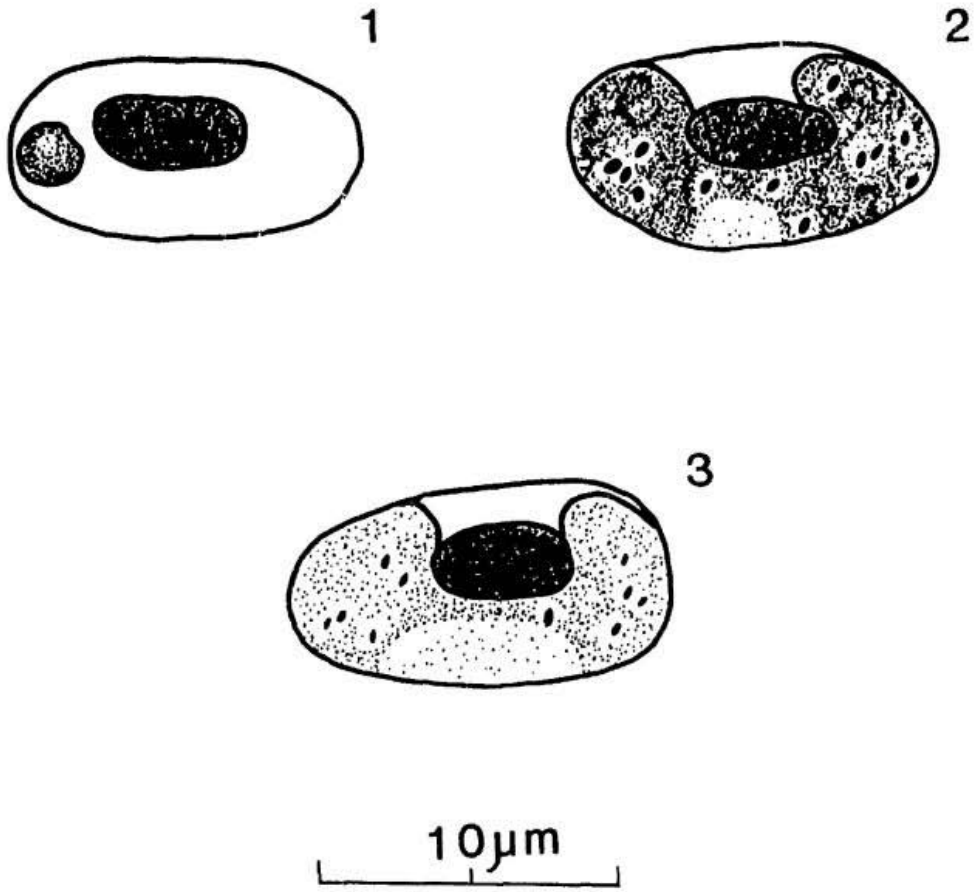
PLATE 6

Haemoproteus coereba n. sp.

Figure 1. immature gametocyte

Figure 2. macrogametocyte

Figure 3. microgametocyte


1
2
3
10µm

than 10%; cytoplasm finely granular, staining only lightly with Giemsa's stain; erythrocyte nucleus not usually laterally displaced; pigment granules average 12 (range 11-15); volutin not seen; parasite nucleus large, diffuse, often not differentiable from the cytoplasm, occupying approximately 24% of the parasite area.

Geographic Range: Jamaica, Puerto Rico and potentially throughout the entire range of the monotypic subfamily Coerebinae.

Hapantotype: Blood film # 62976, from *Coereba flaveola*, the Bananaquit, collected by H. Witt, at Green Hills, Jamaica on April 8, 1978.

Parahapantotypes: From *Coereba flaveola*, blood film # 103801, collected by M. Garvin at Puerto Rico on October 31, 1988; # 59647 collected by H. Witt at Malvern, Jamaica on April 17, 1977; # 80560 collected by R. Sutton at Treasure Beach, Jamaica on February 23, 1981.

Comments: This species of *Haemoproteus* is one of the large halteridial forms with few other distinguishing characteristics. Both male and female gametocytes occupy a relatively large portion of the host-erythrocyte area and cause hypertrophy of the host cell, more so in the Jamaican birds than the Puerto Rico specimens. The gametocytes usually initiate growth near the poles of the host cell, and are rarely ameboid at any stage of gametocyte development.

Haemoproteus coereba n. sp. is described as the haemoproteid found in the genus *Coereba* of the Coerebinae.

THRAUPIDAE

***Haemoproteus thraupi* n. sp.**

Type Host: *Thraupis sayaca* (Linnaeus) [Sayaca tanager]

Type Locality: Guaratuba, Brazil

Immature gametocyte (Plate 7, Figure 1): Youngest forms seen initiate growth lateral to host erythrocyte nucleus, usually near middle of nucleus, but sometimes closer to poles; margin entire or ameboid.

Macrogametocyte (Plate 7, Figures 2-4; Table 3): Halteridial parasite of medium to large size, sausage shaped or more rarely dumbbell shaped, occupying 50-70% of the host-erythrocyte complex; hypertrophy of cell area variable, from -15% (atrophy) to 27%; nuclear displacement variable, usually more so in large sausage shaped gametocytes; hypertrophy of cell nucleus variable; cytoplasm granular, sometimes vacuolate, staining moderate blue with Giemsa's stain; margins usually entire and ends rounded, but sometimes ends slightly ameboid; pigment granules when visible small to medium size, usually ovoid, yellow to dark brown, averaging 13 (ranging 7-21), usually scattered but sometimes paired or clumped; volutin granules seen only in a few gametocytes in two South American hosts; parasite nucleus round to ovoid or broadly triangular, medial to sub- medial in position, occupying 10% of the parasite area.

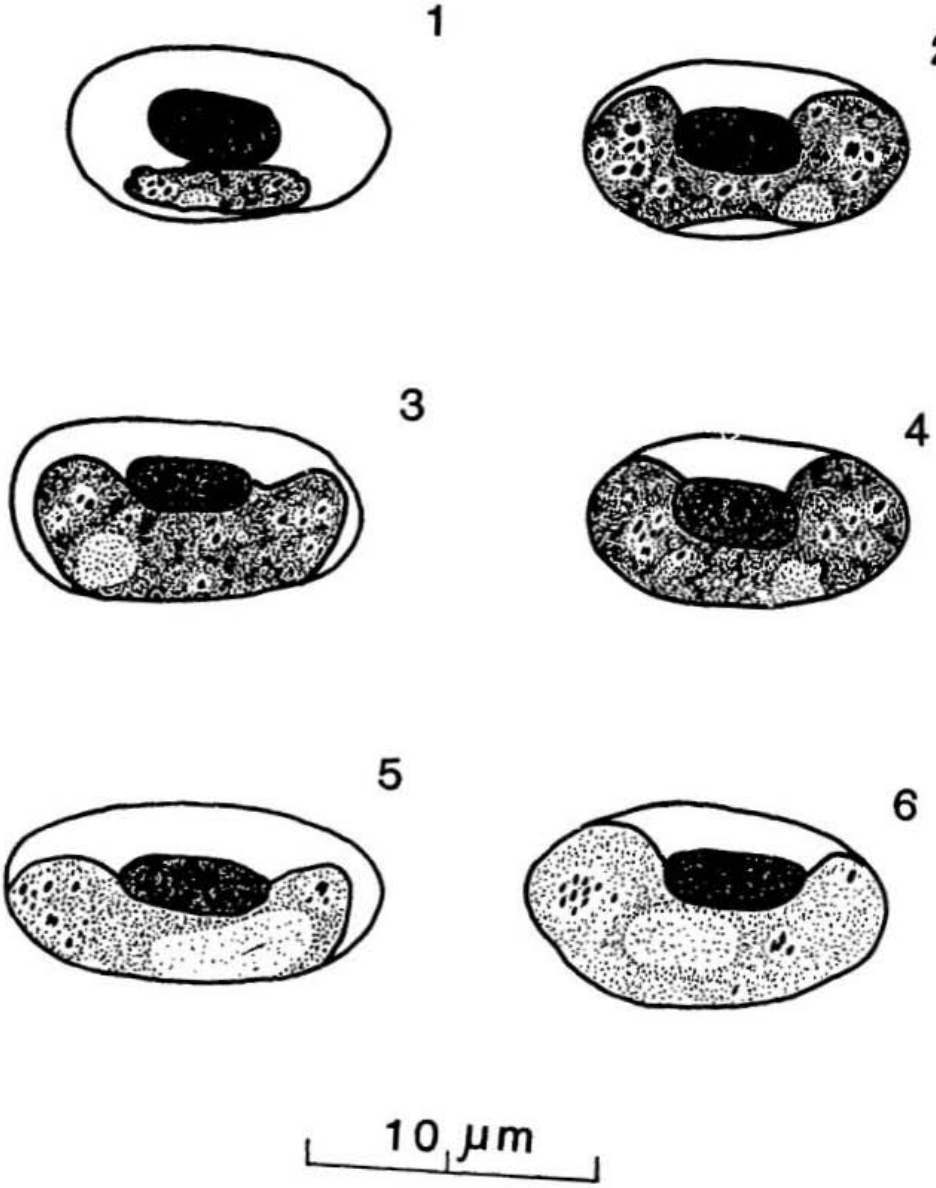
PLATE 7

Haemoproteus thraupi n. sp.

Figure 1. immature gametocyte

Figures 2-4. macrogametocytes

Figures 5-6. microgametocytes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10 µm

Microgametocyte (Plate 7, Figures 5-6; Table 3): Halteridial parasite of medium to large size, dumbbell to sausage shaped, occupying 50-70% of the host-parasite complex; nuclear displacement variable; cytoplasm finely granular, staining only very lightly with Giemsa's stain; ends usually rounded and margin entire in dumbbell shaped gametocytes, but sometimes ends ameboid in sausage-shaped parasites; pigment granules yellow-brown, ovoid, averaging 14 (range 8-18), usually concentrated at poles and sometimes clumped; volutin granules seen only in two South American hosts, at gametocyte poles, and when present obscure true pigment granules; parasite nucleus large and diffuse, staining pale pink with Giemsa's stain, occupying approximately 23% of the parasite area.

Geographic range: North and South America.

Hapantotype: Blood film # 82278, from *Thraupis sayaca*, collected by O. Souza Lopes at Guaratuba, Brazil on August 23, 1970.

Parahapantotypes: From *Dacnis cayana*, collected by O. Souza Lopes, blood film # 33258, Guaratuba, Brazil on July 13 1972, # 44153 Guaratuba, Brazil, on August 23 1970; from *Thraupis sayaca*, blood film # 81225, Itapetininga, Brazil on November 11 1968, # 81251, Itapetininga, Brazil on November 25 1968, # 85584, Guaratuba, Brazil on December 18 1974, # 86678, Iguape, Brazil on October 24 1975; # 114561 from *Piranga rubra*, collected by M. Garvin, Baton Rouge, Louisiana

on April 28 1988.

Additional Host Records: Appendix A.

Comments: Haemoproteids have been identified in the tanager family Thraupidae either as *Haemoproteus sp.* or *H. fringillae/orizivorae* (White et al. 1978, Bennett et al. 1982, Woodworth-Lynas et al. 1989). This haemoproteid species exhibits much the same pleomorphism as seen in those of many other passeriform families, with basic forms ranging from a broad sausage-shaped halteridial parasite which often displaces the host erythroctye nucleus to a smaller dumbbell-shaped form with less displacement. As with other similar species, some gametocytes, especially the dumbbell forms, tend to draw away from the periphery of the host cell at the central portion (Plate 7, Figure 2).

Haemoproteus thraupi n. sp. is described as the haemoproteid found in the Thraupidae, and hapantotype and parahapantotype slides are designated. The haemoproteid found in this family is similar to that found in the Emberizinae and the Parulinae, with sometimes an even more pronounced size difference between the dumbbell and broader halteridial forms. Future studies may reveal a single species. At this time, however, following the accepted trend of family/subfamily specificity for haemoproteids, it is described here as a separate species. The specific name refers to the avian host family name.

ICTERIDAE

Icterinae

Haemoproteus quiscalus Coatney and West, 1938

Type Host: *Quiscalus quiscula* (Linnaeus) [Common grackle]

Type Locality: Peru, Nebraska, U.S.A.

Immature gametocyte (Plate 8, Figure 1): Youngest forms seen usually initiate growth lateral to erythrocyte nucleus, but sometimes are near poles of cell; smallest forms are nearly round, larger ones are broadly halteridial or sausage shaped and usually appress the host cell nucleus; parasite margins entire or ameboid; pigment usually small and clumped.

Macrogametocyte (Plate 8, Figure 2-5; Table 3): Halteridial parasite of medium to large size, often broadly so, or sausage shaped, occupying from 65-70% of the host erythrocyte - parasite complex, not causing hypertrophy of the infected erythrocyte or nuclear displacement; cytoplasm granular, staining moderate blue with Giemsa's stain; margins usually entire but can be ameboid, gametocyte does not always reach erythrocyte poles, nor does it always appress erythrocyte nucleus at its poles (Plate 8, Figures 3,4), occasionally parasite does not appress erythrocyte margin near middle of cell, appearing to 'dip' in as in *H. coatneyi* of the Emberizinae (Plate 8, Figure 2); pigment granules vary from small to large rod shaped and average 12 (range 7-24),

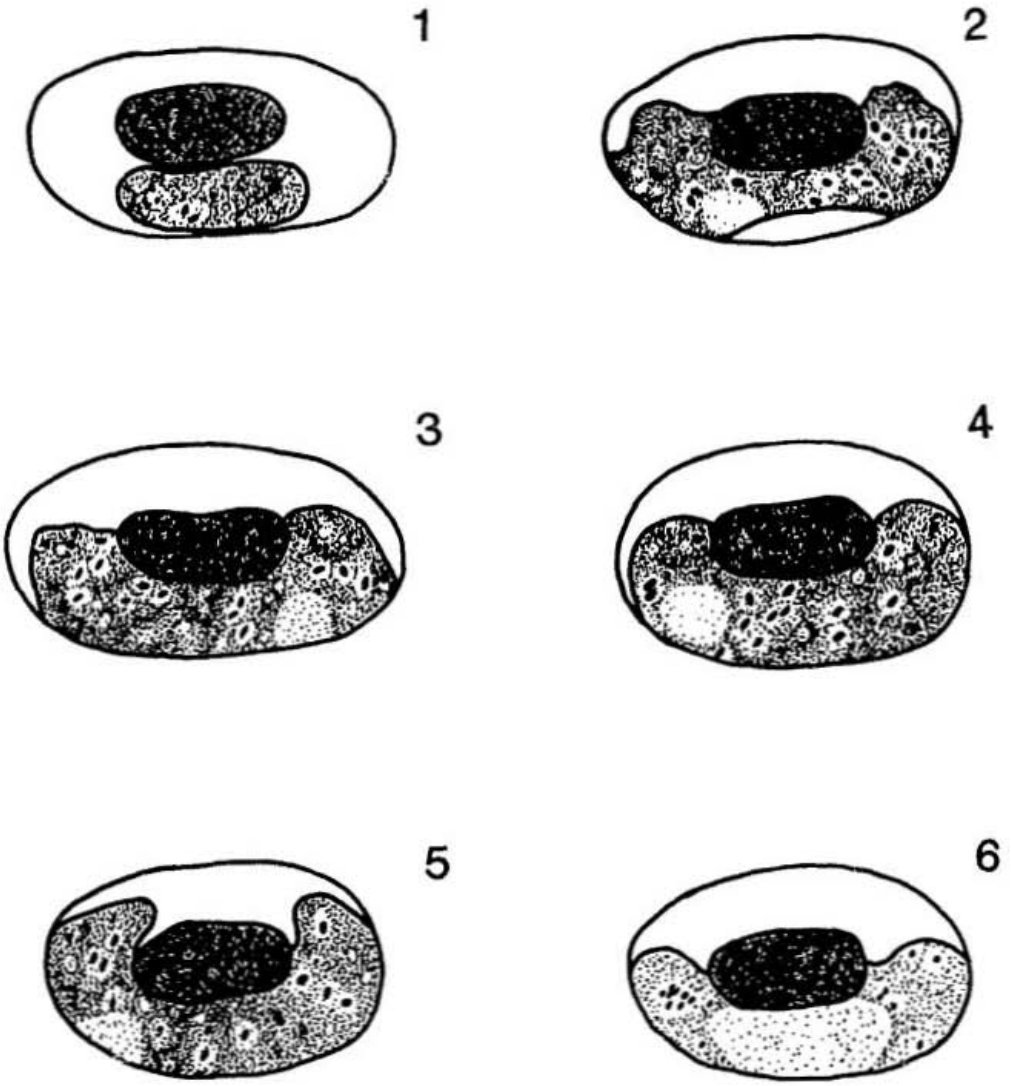
PLATE 8

Haemoproteus quiscalus

Figure 1. immature gametocyte

Figure 2-5. macrogametocytes

Figure 6. microgametocyte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6
10 µm

distributed randomly throughout the cytoplasm but also clumped; volutin granules not seen; gametocyte nucleus generally appears triangular, but round ones are frequent, usually subterminal in position, occupying 7% of the gametocyte area; multiple infections of 2-4 parasites seen in intense infections.

Microgametocyte (Plate 8, Figure 6; Table 3): Halteridial parasite of medium to large size, occupying 61% of the host erythrocyte - parasite complex; hypertrophy variable but rarely extreme; cytoplasm finely granular, staining lighter than macrogametocyte with Giemsa's stain; pigment granules small, round to oval, yellow-brown, averaging 12 (ranging 7-24), usually polar and sometimes clumped; volutin not seen; parasite nucleus large and diffuse, staining only pale pink and often not visible, occupying approximately 31% of the gametocyte area.

Geographic range: Identified in North and South America, and presumably throughout the geographic range of the subfamily Icterinae of the Icteridae.

Basis of redescription:

Hapantotype: Parahapantotype material of *H. quiscalus* of Coatney and Roudabush (2 slides from one host bird) was available through the collection of R.M. Stabler. It is not known if the material from this bird was designated as 'type' or 'paratype'. Two slides from *Quiscalus quiscula* in Peru, Nebraska, collected on June 22, 1937 by Coatney and West (1938) are currently in the collection of the IRCAH as Accession

numbers 45247 (I) and (II). Blood film number 45247 (I) is hereby designated as the hapantotype of *Haemoproteus quiscalus.*

Parahapantotype: Blood film # 45247 (II) from *Quiscalus quiscula*, collected by G.R. Coatney and E. West at Peru, Nebraska on June 22, 1937.

Additional Material: # 98086 from *Agelaius phoeniceus*, collected by P. Weatherhead at Lake Opinicon, Ontario, Canada on June 2, 1987; # 99443 from *Quiscalus quiscula*, collected by C. Kirkpatrick at Urbana, Illinois, U.S.A. on May 21, 1987.

Additional records: Appendix A.

Comments: *Haemoproteus quiscalus* was observed as generally a medium to large halteridial parasite which tended to surround the host cell nucleus but did not commonly distort the host erythrocyte. Often the parasite did not appress the cell nucleus at its poles, giving a somewhat 'hooked' appearance (Plate A, Figure 6). While this situation was not usual or extreme it was seen in several hosts although not pronounced in the hapantotype material. Pigment granules were smaller and more numerous in cases where parasites had ameboid ends, likely indicating gametocytes were not quite mature.

The hapantotype slide, deposited at the IRCAH, was used in the redescription

of *Haemoproteus quiscalus*. Material from the subfamily Doliconychinae was not suitable for taxonomic purposes and so the haemoproteid found in this subfamily of the Icteridae was identified only as *Haemoproteus* sp.

Haemoproteus quiscalus is herein redescribed from the original blood smear material, with observations and measurements from a wider variety of host species and geographic locations (Appendix A).

SUMMARY

The haemoproteids of the Fringillidae, Emberizidae, Parulidae, Thraupidae and Icteridae (*sensu* Edwards 1986) were reviewed and eight *Haemoproteus* spp. were either described or redescribed. There was considerable similarity of the parasites from various host bird species examined (Appendix A). All are of the basic halteridial or microhalteridial forms which have been described by Bennett and Peirce (1988), and species could not be consistently separated on measurements of morphological characters. In fact, as with some other host families (Bennett *et al.* 1991) without prior knowledge of the host species, it would be difficult to make a species diagnosis. Indeed the situation in the past with the use of the names *H. fringillae* and *orizivorae* illustrates some of the difficulties taxonomists have encountered. For most *Haemoproteus* species previously described from the families studied, there was insufficient information to make quantitative comparisons. In this study several synonymies were declared, based on the variability seen within individuals, host species, and geographic range of the same and different host species. There were characteristics which were more frequent in some subfamilies than in others, and these were identified in separate species descriptions. With the intent to make the taxonomy as useful as possible, together with the presumed host family and subfamily specificity of *Haemoproteus*, it was proposed that only eight species were present.

Haemoproteus species with a wide host and geographic range (eg. those found

in the Carduelinae and Emberizinae) exhibited greater variability than those with more restricted ranges. This was evident from the study of measurements from individual hosts. Comparatively high values of standard deviations for certain variables in parasite species with data pooled from several hosts and/or locations indicate the extreme pleomorphism (Tables 2, 3). The nature of the distribution of the measurement data made this variability difficult to evaluate. The limitations associated with the use of blood smears for taxonomy were recognized, as was the inappropriate reliance on measurements from few specimens. For example, hypertrophy or atrophy of erythrocytes infected by *Haemoproteus* spp. was inconsistent. In two blood smears made at the same time from the same *Quiscalus quiscula* there was significant cell atrophy in one case and hypertrophy in another. Other examples include samples over time of parasites (from the same individuals) which differed in several variables at one time or another. There were many examples of differences in parasite measurements from different hosts. The erratic nature of these differences and the near absence of any real patterns further demonstrates the necessity of qualitative assessment based upon knowledge of the variation in morphological form.

Although the ultimate size of a parasite is presumed to be genetically predetermined, variation in gametocyte morphology may also reflect the ability of a parasite to adjust to differences among host birds, from effects of variable erythrocyte size to differences in host immune response, both on an individual bird and bird species basis. The possible influence of vectors in different geographical locations

is also a consideration. These factors have been suggested for the variability seen in other passeriform host families such as the Vireonidae (Bennett *et al.* 1987).

Identification of true biological species can only be made with life cycle and cross transmission studies. Such studies may well confirm that there is one halteridial species which shows great pleomorphism depending upon the host bird family or subfamily. The trend in recent years followed by Bennett and his colleagues to reduce the number of valid species in declaring several synonymies (Bennett and Peirce 1988) may be indicative of the degree of intraspecific variation in the Haemoproteidae. The current study offered the opportunity to study a wide range of host species and locations for the five families of birds considered, something not logistically possible with many families previously studied. The extent of morphological pleomorphism found within the parasite species described herein supports the idea of a large amount of intraspecific variation. This is not unexpected given the nature of the life cycle and reproductive behaviour of haemoproteids (Manwell 1957). In fact further synonymies might be expected if such extensive study could be applied to other host families. Until then, it is best to acknowledge variability within the haemoproteids of these families of birds, designating a distinct morphologically definable taxon rather than a vague generic reference (Williams *et al.* 1975). Table 4 lists the species of *Haemoproteus* described or redescribed in the current study and their host families and geographic ranges.

Table 4. ***Haemoproteus*** **species of the Fringillidae, Emberizidae, Parulidae, Thraupidae and Icteridae.**[1]

Family	*Haemoproteus* species	Geographic range
FRINGILLIDAE		
Fringillinae	*H. fringillae* (Labbé 1894)	Palearctic
EMBERIZIDAE		
Emberizinae	*H. coatneyi* n. sp.*	Nearctic, Neotropic
Cardinalinae	*H. mazzai* Parodi and Niño 1927	Nearctic, Neotropic,
Carduelinae	*H. chloris* Covaleda Ortega and Gállego Berenguer 1950	Nearctic, Neotropic Palearctic, Asia, Africa
PARULIDAE		
Parulinae	*H. paruli* n. sp.*	Nearctic, Neotropic
Coerebinae	*H. coereba* n. sp.*	Nearctic, Neotropic
THRAUPIDAE		
Thraupinae	*H. thraupi* n. sp.*	Nearctic, Neotropic
ICTERIDAE		
Icterinae	*H. quiscalus* Coatney and West, 1938	Nearctic, Neotropic

[1] Avian classification follows Edwards 1986.
* New species described from material examined in this study.

LITERATURE CITED

Adie, H.A. 1915. The sporogony of *Haemoproteus columbae*. Indian J. Med. Res. 2: 671-680.

American Ornithologists' Union. 1983. Check-list of North American birds. Sixth edition. Allen Press, Inc., Lawrence, Kansas. 877pp.

Aragão, H. de B. 1908. Über den entwicklungsgang und die übertragung von *Haemoproteus columbae*. Arch. Protistenkd. 12: 154-167.

Atkinson, C.T. 1986. Host specificity and morphometric variation of *Haemoproteus meleagridis* Levine, 1961 (Protozoa: Haemosporina) in gallinaceous birds. Can J. Zool. 64: 2634-2638.

Bennett, G.F. 1970. Simple techniques for making avian blood smears. Can. J. Zool. 48: 585-586.

Bennett, G.F., M.A. Bishop and M.A. Peirce. 1991. The species and distribution of the haemoproteids of the avian family Muscicapidae *sensu lato* (Passeriformes). J. Nat. Hist. 25: 23-43.

Bennett, G.F., J.R. Caines and C.B. Woodworth-Lynas. 1987. Avian Haemoproteidae. 24. The haemoproteids of the New World passeriform families Formicariidae, Furnariidae, Mimidae, and Vireonidae. Can. J. Zool. 65: 317-321.

Bennett, G.F., J.R. Caines and M.A. Bishop. 1988. Influence of blood parasites on the body mass of passeriform birds. Journal of Wildlife Diseases 24: 339-343.

Bennett, G.F., J.R. Caines and M.A. Whiteway. 1986. Avian haemoproteidae. 22. The haemoproteids of the New World flycatchers, the Tyrannidae. Can. J. Zool. 64: 774-777.

Bennett, G.F. and M. Cameron. 1974. Seasonal prevalence of avian haematozoa in passeriform birds of Atlantic Canada. Can. J. Zool. 52: 1259-1264.

Bennett, G.F. and A.G. Campbell. 1972. Avian Haemoproteidae. I. Description of *Haemoproteus fallisi* n. sp. and a review of the haemoproteids of the family Turdidae. Can. J. Zool. 50: 1269-1275.

Bennett, G.F. and A.G. Campbell. 1973. Avian haemoproteidae. III. Description of *Haemoproteus fusca* sp. n. and redescription of *Haemoproteus halcyonis* de Mello, 1935, parasites of the kingfisher family Alcedinidae. J. Parasitol. 59:

337-343.

Bennett, G.F. and A.G. Campbell. 1975. Avian Leucocytozoidae. I. Morphometric variation in three species of *Leucocytozoon* and some taxonomic implications. Can. J. Zool. 53: 800-812.

Bennett, G.F. and A.M. Fallis. 1960, Blood parasites of birds in Algonquin Park, Canada and a discussion of their transmission. Can. J. Zool. 38: 261-273.

Bennett, G.F., A. Gabaldon and G. Ulloa. 1982. Avian Haemoproteidae 17. The haemoproteids of the avian family Cracidae (Galliformes); the guans, curassows, and chachalacas. Can. J. Zool. 60: 3105-3112.

Bennett, G.F., P.C.C. Garnham and A.M. Fallis. 1965. On the status of the genera *Leucocytozoon* Ziemann 1898 and *Haemoproteus* Kruse 1890 (Haemosporidida: Leucocytozoidae and Haemoproteidae). Can. J. Zool. 43: 927-932.

Bennett, G.F., E.C. Greiner and A.G. Campbell. 1975. Avian Haemoproteidae. 5. The haemoproteids of the family Threskiornithidae. Can. J. Zool. 53: 634-638.

Bennett, G.F. and M.A. Peirce. 1988. Morphological form in the avian Haemoproteidae and an annotated checklist of the genus *Haemoproteus* Kruse, 1890. J. Nat. Hist. 22: 1683-1696.

Bennett, G.F. and M.A. Peirce. 1989. The haemoproteids of the avian family Phasianidae. Can. J. Zool. 67: 1557-1565.

Bennett, G.F. and M.A. Peirce. 1991. The haemoproteids of the weaver finches (Passeriformes). J. Nat. Hist. 25: 7-22.

Bennett, G.F,, M.A. Peirce and J.R. Caines. 1985. Avian Haemoproteidae. 19. The haemoproteids of the sunbirds (family Nectariniidae) and morphometric variation in *Haemoproteus sequeirae*. Can. J. Zool. 63: 1371-1376.

Bennett, G.F., M.A. Peirce and R.A. Earlé. 1990. The haemoproteids of the shrikes of the avian family Laniidae (Passeriformes). S. Afr. Tydskr. Dierk. 25: 194-198.

Bennett, G.F., M. Whiteway and C. Woodworth-Lynas. 1982. A host-parasite catalogue of the avian haematozoa. Memorial Univ. Nfld. Occas. Pap. Biol. No. 5. 243pp.

Berson, J.P. 1964. Les protozoaires parasites des hématies et du système histiocytaire des oiseaux. Essai de nomenclature. Rev. Elev. Med. vet. Pays trop. 17: 43-96.

Bishop, M.A. 1989. A taxonomic study of the Haemoproteidae (Apicomplexa: Haemosporina) of the avian order Strigiformes. M.Sc. Thesis, Memorial University of Newfoundland. 82pp.

Bishop, M.A. and G.F. Bennett. 1989. The haemoproteids of the avian order Strigiformes. Canadian Journal of Zoology 67: 2676-2684.

von Brand, T. 1966. Biochemistry of Parasites. Academic Press, New York. 429pp.

Campbell, B. and E. Lack. 1985. A Dictionary of Birds. The British Ornithologists's Union. T.& A.D. Poyser, Calton. 670pp.

Clements, J.F. 1974. Birds of the World: A Check List. First edition. The Two Continents Publishing Group Ltd., N.Y. 524pp.

Clements, J.F. 1978. Birds of the World: A Check List. Second edition. The Two Continents Publishing Group Ltd., N.Y. 532pp.

Coatney, G.R. 1936. A check-list and host-index of the genus *Haemoproteus*. J. Parasitol. 22: 88-105.

Coatney, G.R. and R.L. Roudabush. 1937. Some blood parasites from Nebraska birds. Am. Midl. Nat. 18: 1005-1030.

Coatney, G.R. and E. West. 1938. Some blood parasites from Nebraska birds. II. Am. Midl. Nat. 19: 601-612.

Covaleda Ortega, J. and J. Gállego Berenguer. 1950. Hemoproteus aviares. Rev. Iber. Parasitol. 10: 141-185.

Desser, S.S. and G.F. Bennett. The genera *Leucocytozoon, Haemoproteus and Hepatocystis*. *In*: Parasitic Protozoa. Volume III, 2nd edition. J.P. Kreier editor. Academic Press, N.Y. (in press).

Edwards, E.P. 1986. A Coded Workbook of Birds of the World. Volume 2: Passerines. Second edition. Ernest P. Edwards, Sweet Briar, VA. 170pp.

Fallis, A.M. and G.F. Bennett. 1961. Ceratopogonidae as intermediate hosts for *Haemoproteus* and other parasites. Mosquito News 21: 21-28.

Forrester, D.J., E.C. Greiner, G.F. Bennett and M.K. Kigaye. 1977. Avian Haemoproteidae. 7. A review of the haemoproteids of the family Ciconiidae (storks) and descriptions of *Haemoproteus brodkorbi* sp. nov. and *H. peircei* sp. nov. Can. J. Zool. 55: 1268-1274.

Greiner, E.C., G.F. Bennett, E.M. White and R.F. Coombs. 1975. Distribution of the avian haematozoa of North America. Can. J. Zool. 53: 1762-1787.

Greiner, E.C. and D.J. Forrester. 1980. *Haemoproteus meleagridis* Levine 1961: Redescription and developmental morphology of the gametocytes in turkeys. J. Parasitol. 66: 652-658.

Greiner, E.C., A.K. Mandal and N.C. Nandi. 1977. *Haemoproteus bennetti* sp. n. and a review of the haemoproteids from the Picidae (Woodpeckers). J. Parasitol. 63: 651-656.

Helmy Mohammed, A.H. 1958. Systematic and experimental studies on protozoal parasites of Egyptian birds. Vol. II. Cairo University Press. 298pp.

International Code of Zoological Nomenclature. 1985. Third edition. International Trust (in assoc. with the British Museum (Natural History)), London. 338pp.

Khan, R.A. and A.M. Fallis. 1969. Endogenous stages of *Parahaemoproteus fringillae* (Labbé, 1894) and *Leucocytozoon fringillinarum* Woodcock, 1910. Can. J. Zool. 47: 37-39.

Kruse, W. 1890. Ueber blutparasiten. Archiv fuer Pathologische Anatomie und Physiologie und fuer Klinische Medecin 120: 541-559.

Labbé, A. 1894. Recherches zoologiques et biologiques sur les parasites endoglobulaires du sang des vertébrés. Arch. Zool. Exp. Gen. 2: 55-258.

Levine, N.D. 1980. The Committee on Systematics and Evolution of the Society of Protozoologists. A newly revised classification of the Protozoa. J. Protozool. 27: 37-58.

Levine, N.D., P.D. Beamer and J. Simon. 1970. A disease of chickens associated with *Arthrocystis galli* n. g., n. sp., an organism of uncertain taxonomic position. H.D. Srivastava Commen. Vol. 429-434.

Levine, N.D. and G.R. Campbell. 1971. A check-list of the species of the genus *Haemoproteus* (Apicomplexa, Plasmodiidae). J. Protozool. 18: 475-484.

Manwell, R.D. 1955. The blood protozoa of seventeen species of sparrows and

other Fringillidae. J. Protozool. 2: 21-27.

Manwell, R.D. 1957. Intraspecific variation in parasitic protozoa. Syst. Zool. 6: 2-6.

Manwell, R.D. and C.M. Herman. 1935. Blood parasites of birds of the Syracuse (N.Y.) region. J. Parasitol. 21: 415-416.

de Mello, I.F. and L.J. Braz de Sa. 1916. A contribution to the study of Haemoprotozoa in Portuguese India. Indian J. Med. Res. 3: 731-737.

Musaev, M.A. and N.R. Zeiniev. 1977. Nekotorye voprosy sistematiki kroveparazitov ptits roda *Haemoproteus* na primere analiza materialov vtorogo vsesoyuznogo s'ezda. (Questions of the systematics of blood parasites of the genus *Haemoproteus* during the analysis of material of the Second All Union Conference on Protozoology.) Izv. Akad. Nauk. Az. SSR Ser. Biol. Nauk 1: 51-59.

Novy, F.G. and W.J. MacNeal. 1905. On the trypanosomes and bird malaria. Proc. Soc. Exp. Biol. Med. 2: 23-28.

Opie, E.L. 1898. On the Haemocytozoa of birds. J. Exp. Med. 3: 79-101.

Parodi, S.E. and F.L. Niño. 1926. *Haemoproteus* en la sangre periférica del "Pheucticus aureoventris". (Nota previa). Prensa med. Argentina 13: 502-503.

Parodi, S.E. and F.L. Niño. 1927. *Haemoproteus* n. sp. de la reina mora del Norte (*Pheucticus aureoventris* D'Orb. y Lafr.: fringílido.) Bol. Inst. Clin. Quir. 3: 356-359.

Peirce, M.A. 1983. Studies in the taxonomy and ecology of avian haematozoa. Ph. D. Thesis, University of Salford, England. 292pp.

Peirce, M.A. 1984. Haematozoa of Zambian birds. I. General survey. J. Nat. Hist. 18: 105-122.

Peirce, M.A. 1984. Haematozoa of Zambian birds. VI. Haemoproteids of small passerines with particular reference to *Haemoproteus passeris* and the *H. fringillae/orizivorae* complex. J. Nat. Hist. 18: 559-566.

Peirce, M.A. and G.F. Bennett. 1979. Avian haematozoa: some taxonomic and nomenclatural problems arising from the Russian literature. J. Protozool. 26: 357-359.

Peters, J.L. 1968. Check-list of Birds of the World. Volume XIV. Heffernan Press Inc., Worcester, Mass. 433pp.

Peters, J.L. 1970. Check-list of Birds of the World. Volume XIII. Heffernan Press Inc. Worcester, Mass. 443pp.

Schaudinn, F. 1904. Generations-und wirtswechsel bei *Trypanosoma* und *Spirochaete*. Arbeiten aus dem kaiserlichen Gesundheitsamte 20: 387-439.

Sergent, Ed. and Ét. Sergent. 1906. Sur le second hôte de l'*Haemoproteus* (*Halteridium*) du pigeon. (Note préliminaire). C.R. Séances Soc. Biol. Fil. 61: 494-496.

Sergent, Ed. and Ét. Sergent. 1907. Études sur les hématozoaires d'oiseaux. *Plasmodium relictum, Leucocytozoon ziemanni* et *Haemoproteus noctuae, Haemoproteus columbae*, trypanosome de l'hirondelle. Ann. Inst. Pasteur (Paris) 21: 251-280.

Sergent, Ed. and Ét. Sergent. *(in memoriam).* 1948. *Haemoproteus wenyoni* nov. sp. parasite du moineau algérien retrouvé chez des canaris élevés en cage. Arch. Inst. Pasteur Algérie. 26: 394-396.

Sibley, C. and Ahlquist. 1984. The phylogeny and classification of the passerine birds, based on comparisons of the genetic material, DNA. Proc. XVIII Int. Orn. Congr.

Subkhanov, M. and R. Mirzobakhodurov. 1976. Nekotorye vidy kroveparasitov ptits Kirgizii. (In Russian). (Some species of avian blood parasites from Kirgizia). Izv. Akad. nauk Tadzh. SSR, Otd. biol. nauk 2: 108-109.

Tartakovskii, M. 1913. Genus: *Haemoproteus* Kruse. The distribution of red blood cell parasites in Transcausasia (In Russian). Tr. Selsk. Bakteriol. Lab. (St. Petersburg) 4: 420-455.

Valkiūnas, G.A. 1986. *Haemoproteus tartakovskyi* sp. n. (Haemosporidia, Haemoproteidae) is klesta-elovika. (*Haemoproteus tartakovskyi* sp. n. (Haemospiridia, Haemoproteidae) from the crossbill). (In Russian). Parasitologiya (Leningrad) 20: 307-310.

White, E.M. and G.F. Bennett. 1978. Avian haemoproteidae. 9. Description of *Haemoproteus stellaris* n. sp. and a review of the haemoproteids of the swallow family Hirundinidae. Can. J. Zool. 56: 2110-2116.

White, E.M. and G.F. Bennett. 1979. Avian Haemoproteidae. 12. The

haemoproteids of the grouse family Tetraonidae. Can. J. Zool. 57: 1465-1472.

White, E.M., E.C. Greiner, G.F. Bennett and C.M. Herman. 1978. Distribution of the hematozoa of neotropical birds. Rev. Biol. Trop. 26: 43-102.

Williams, N.A., G.F. Bennett and J.L. Mahrt. 1975. Avian Haemoproteidae. 6. Description of *Haemoproteus caprimulgi* sp. nov. and a review of the haemoproteids of the family Caprimulgidae. Can. J. Zool. 53: 916-919.

Woodcock, H.M. 1910. Studies on avian haematozoa. I. On certain parasites of the chaffinch (*Fringilla coelebs*) and the redpoll (*Linota rufescens*). Q.J. Microsc. Sci. 55: 641-740.

Woodworth-Lynas, C.B., J.R. Caines and G.F. Bennett. 1989. Prevalence of avian haematozoa in Sao Paulo State, Brazil. Mem. Inst. Oswaldo Cruz, Rio de Janeiro. 84: 515-526.

Zeiniev, N.R. 1975. Paraziticheskie prosteishie krovi ptits severo-vostochnogo Azerbaidzhana. (In Russian). (Parasitic protozoa in the blood of birds from north-eastern Azerbaidzhan). Izv. Akad. nauk Az. SSR, ser. biol. nauk 4: 86-89.

Appendix A. ***Haemoproteus*** **species found in the host birds examined in the current study. Samples were examined from the locations listed.**

FRINGILLIDAE	***Haemoproteus fringillae*** **Labbé 1894**	
Fringilla coelebs Linnaeus		U.K.; France; Portugal; Czechoslovakia; Lithuania; Norway
Fringilla montifringilla Linnaeus		Norway
EMBERIZIDAE		
Emberizinae	***Haemoproteus coatneyi*** **n. sp.**	
Aimophila ruficeps (Cassin)		CA, U.S.A.
Coryphospingus cucullatus (Müller)		Bolivia
Emberiza citrinella Linnaeus		France
Emberiza flaviventris Stephens		South Africa; Zambia
Emberiza melanocephala Scopoli		Iran
Emberiza schoeniclus (Linnaeus)		France
Emberiza spodocephala Pallas		Korea
Emberiza rutila Pallas		Korea; Thailand
Haplospiza unicolor Cabanis		Brazil
Junco hyemalis (Linnaeus)		NB, NF, ON, Canada; CA, PA, U.S.A.
Melophus lathami (Gray)		India
Melospiza georgiana (Latham)		NB, ON, Canada

Melospiza lincolnii (Audubon)	NB, NF, Canada
Melospiza melodia (Wilson)	NB, NF, Canada; NJ, U.S.A
Passerculus sandwichensis (Gmelin)	NB, NF, QU, Canada
Passerella iliaca (Merrem)	NB, NF, ON, Canada; CA, U.S.A.
Pipilo erythrophthalmus (Linnaeus)	PA, U.S.A.
Pipilo fuscus Swainson	CA, U.S.A.
Pooecetes gramineus (Gmelin)	NB, Canada; MA, U.S.A.
Spizella passerina (Bechstein)	ON, Canada; MA, MD, PA, U.S.A.
Sporophila schistacea (Lawrence)	Bolivia
Zonotrichia albicollis (Gmelin)	NB, NF, ON, Canada; NJ, PA, CT, SC, U.S.A.
Zonotrichia atricapilla (Gmelin)	CA, U.S.A.
Zonotrichia capensis (Müller)	Brazil; Chile; Venezuela
Zonotrichia leucophrys (Forster)	ON, Canada

Cardinalinae ***Haemoproteus mazzai* Parodi and Niño 1927**

Cardinalis cardinalis (Linnaeus)	LA, U.S.A.
Cardinalis phoeniceus Bonaparte	Venezuela
Pheucticus ludovicianus (Linnaeus)	NB, Canada; El Salvador; Jamaica; CT, LA, MD, NJ, U.S.A
Pheucticus melanocephalus (Swainson)	CA, U.S.A.

Carduelinae	***Haemoproteus chloris***	**Covaleda Ortega and Gállego Berenguer 1950**
Acanthis flammea (Linnaeus)	MA, NF, Canada; VT, U.S.A.	
Carduelis carduelis (Linnaeus)	France, Iran	
Carduelis chloris (Linnaeus)	U.K.; Portugal	
Carduelis pinus (Wilson)	BC, NF, Canada	
Carduelis sinica (Linnaeus)	Korea	
Carduelis spinus (Linnaeus)	Norway, U.K.	
Carduelis tristis (Linnaeus)	B.C., Canada; N.J., U.S.A.	
Carpodacus erythrinus (Pallas)	India	
Carpodacus mexicanus (Müller)	CA, U.S.A.	
Carpodacus purpureus (Gmelin)	NB, NF, ON, Canada; CA, U.S.A.	
Coccothraustes coccothraustes (Linnaeus)	Japan	
Coccothraustes icterioides Vigors	India	
Coccothraustes migratorius (Hartert)	Korea	
Loxia curvirostra Linnaeus	NB, NF, Canada; Czechoslovakia; Lithuania	
Loxia leucoptera Gmelin	NB, NF, Canada	
Pinicola enucleator (Linnaeus)	NF, Canada	
Pyrrhula pyrrhula (Linnaeus)	Czechoslovakia	
Serinus atrogularis (Smith)	S. Africa	
Serinus canaria (Linnaeus)	Portugal	

Serinus flaviventris (Swainson)	S. Africa; Korea; India
Serinus gularis (Smith)	S. Africa
Serinus mennelli (Chubb)	Zambia
Serinus mozambicus (Müller)	S. Africa; Zambia

PARULIDAE

Parulinae ***Haemoproteus paruli* n. sp.**

Dendroica coronata (Linnaeus)	NB, NF, ON, Canada
Dendroica petechia (Linnaeus)	NB, NF, ON, Canada
Dendroica striata (Forster)	NB, NF, Canada
Dendroica townsendi (Townsend)	CA, U.S.A.
Dendroica virens (Gmelin)	NB, NF, Canada
Mniotilta varia (Linnaeus)	NF, Canada
Oporornis philadelphia (Wilson)	NF, Canada
Parula americana (Linnaeus)	NB, Canada
Seiurus noveboracensis (Gmelin)	NB, NF, Canada
Vermivora celata (Say)	BC, Canada; CA, U.S.A.
Wilsonia citrina (Boddaert)	NF, Canada; MD, U.S.A.
Wilsonia pusilla (Wilson)	NB, NF, Canada

Coerebinae ***Haemoproteus coereba* n.sp.**

Coereba flaveola (Linnaeus)	Jamaica; Puerto Rico

THRAUPIDAE *Haemoproteus thraupi* **n.sp.**

Chlorothraupis olivacea (Cassin)	Colombia
Dacnis cayana (Linnaeus)	Brazil
Euneornis campestris (Linnaeus)	Brazil
Euphonia pectoralis (Latham)	Brazil
Euphonia violacea (Linnaeus)	Brazil
Pipraeda melanota (Vieillot)	Brazil
Piranga olivacea (Gmelin)	NB, Canada; VT, U.S.A.
Piranga rubra (Linnaeus)	LA, U.S.A.
Spindalis zena (Linnaeus)	Jamaica
Tachyphonus coronatus (Vieillot)	Brazil
Tangara cyanocephala (Müller)	Brazil
Tangara desmaresti (Vieillot)	Brazil
Tangara seledon (Müller)	Brazil
Thraupis cyanoptera (Vieillot)	Brazil
Thraupis palmarum (Wied)	Brazil
Thraupis sayaca (Linnaeus)	Brazil

ICTERIDAE

Icterinae *Haemoproteus quiscalus* **Coatney and West 1938**

Agelaius phoeniceus (Linnaeus)	ON, Canada
Euphagus cyanocephalus (Wagler)	CA, U.S.A.

Icterus galbula (Linnaeus)	NE, PA, U.S.A.
Icterus leucopteryx (Wagler)	Jamaica
Icterus spurius (Linnaeus)	LA, U.S.A.
Molothrus bonariensis (Gmelin)	Brazil
Quiscalus quiscula (Linnaeus)	ON, Canada; AR, IL, LA, U.S.A.

Dolichonychinae *Haemoproteus sp.*

Dolichonyx oryzivorus (Linnaeus)	NB, Canada