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HAEMOSPOROZOAN PARASITES FOUND IN BIRDS IN PENINSULAR MALAYSIA, SINGAPORE, SARAWAK AND JAVA

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ABSTRACT. – Fifty-one species of the haemosporidian genera: *Haemoproteus*, *Leucocytozoon* and *Plasmodium* and a sporozoite of *Lankesterella* from the blood of birds trapped in Peninsular Malaysia, Singapore, Sarawak and Java are described and taxonomically evaluated. Five new species are described: *Haemoproteus alcippe*, type host *Alcippe perracensis*; *H. copsychi*, type host *Copsychus malabaricus*; *H. obtusus*, type host *Garrulax mitratus*; *H. tenuis*, type host *Stachyris nigricollis* and *Plasmodium* (*Giovannolaia*) *ninoxi*, type host *Ninox scutulata*. *Haemoproteus rhipiduri* Bennett, Bishop & Peirce 1991, *Leucocytozoon pittae* Bennet & Peirce, 1992 and *L. pycnonoti* Bennett, Earle & Peirce, 1992 are found to be valid species.

KEY WORDS. – *Haemoproteus*, *Leucocytozoon*, *Plasmodium*, *Lankesterella*, birds, Peninsular Malaysia, Singapore, Sarawak, Java.

INTRODUCTION

Interest in blood parasites in the birds of Southeast Asia dates back to the early 20th century and probably started with the studies of Mathis & Leger (1911) in Tonkin. Species descriptions of avian haemoparasites that were published by these authors and by de Mello in India from 1916 to 1937 are still valid among the species listed from South and Southeast Asian birds. A major survey of blood parasites of both resident and migrant bird species was carried out by McClure et al. during the period from 1963 to 1971 at various sites in India, Nepal, Japan, Korea, Taiwan, Hong Kong, Thailand, Malaysia, Indonesia and the Philippines. The report published by these authors in 1978 included important data on their prevalence as well as geographical and seasonal distribution. However, the collected parasites were identified mostly to generic level and the descriptions of mentioned species were not provided. Slides deposited in the International Reference Centre for Avian Haematozoa, (IRCAH) now in the Queensland Museum, Australia, were a source for subsequent taxonomic studies by Bennett and his co-workers (see listed references cited here). Many of these studies were included in the comprehensive monograph of Valkiunas (1997) (English translation, 2005) and Laird's (1997) contribution on the *Plasmodium* infecting South and East Asian avian hosts. The aims of our study carried out between 1998 to 2003 was to provide a taxonomic and quantitative account on the blood parasitofauna (Haemosporidia and Haemococcidia) of birds from several study sites in Southeast Asia: in Peninsular Malaysia, Singapore, Sarawak and Java. In our first communication (Paperna et al., 2005) we provided a compresensive checklist of all hematozooans found in the study and examined quantitatively by location and habitat each parasite's prevalence and relative of abundance. In the present communication we provide identifications, descriptions and a taxonomic re-evaluation of the species of haemosporidians and *Lankesterella* species recovered from the examined birds.

MATERIALS AND METHODS

Birds were collected in mist nets in Peninsular Malaysia, Singapore, Sarawak and Java. The description of the collection sites and the number of examined bird specimens and species are as follows:

1. Peninsular Malaysia:
   a. Pasoh forest reserve (2°59'N 102°19'E), 1998 – 94 birds, 38 species (hereafter "Pasoh").
   b. The highlands: Cameron Highlands, 2002, 2003 (including Gunung Brinchang), 04°30'40.96"N

101°24'35.76"E, see McClure et al. 1978) − 141 birds, and Fraser's Hill (3°42'N 101°44'E see Lee et al., 2005)–198 birds, total 329 birds, 55 species.

c. Johor, 2003–Bekok (2°20'50.4"N 103°09'24.6"E) and Belumut (2°03'54"N 103°31'34.2"E): lowland primary and secondary forest–170 birds, 38 species (hereafter: "Johor").

2. Singapore, 1998–two forests at the central water catchment area (Nee Soon and MacRitchie 1°22'N 103°48'E, Sodhi, 2002)–168 birds, 54 species; from urban locations (2001) house crow *Corvus splendens* − 30 and common myna (*Acridotheres tristis*)–10 birds. Feral pigeons (*Columba livia*)–126 birds from urban/semi-urban locations were studied earlier, in 1968 (Paperna & Smallridge, 2002).

3. Sarawak (East Malaysia): May and Jun.1998:
   a. Matang Wildlife Sanctuary (1°40'N 110°00'E) and Gunung Gading National Park (1°48'N 109°52'E)–primary and secondary forest–76 birds, 29 species (hereafter: "Sarawak"). See Sodhi (2002) for details.

4. Java (Indonesia): 2001, 2002:
   Linggo Asri (7°00'N 109°30'E) − lowland and mountain primary and secondary forest (hereafter: "Lingo")–155 birds, 25 species, see Sodhi et al. (2005) for details.

A numbered metal ring and a uniquely coloured band were attached to the tarsus of each collected bird, and morphometric and morphological data were recorded. The brachial vein of the bird was pierced by a fine sterile needle. The blood was withdrawn into a heparinized hematocrit capillary and smeared on a clean glass slide. The bird was then released. Air dried blood smears were fixed with absolute methanol and stained with 12% Giemsa (in pH 7.4 phosphate buffer). Slides were processed in the laboratory up to several months after collection. Long delays compromised the stain quality of some slides. Some, with extreme haemolysis, had to be discarded; in some, the parasites had lost the stain's polychromatic quality which made their diagnosis more difficult. In describing and measuring species of *Haemoproteus*, the degree of displacement of the erythrocyte's nucleus ("Nuclear Displacement Ratio" or NDR) was calculated following the equation of Bennett & Campbell (1972):

$$NDR = 2X/(X + Y)$$

X = distance between the erythrocyte periphery (wall) and its nucleus;
Y = distance between the erythrocyte periphery (wall) and its nucleus on the infected side.

All measurements were made in µm and are given as mean ± standard deviation. Where relevant total parasitaemia: (% infected erythrocytes) were calculated from the blood smears. Positive blood smears, including syntypes, marked by the bird-host code will be deposited in the Zoological Reference Collection (ZRC) of the Raffles Museum of Biodiversity Research, National University of Singapore (NUS).

RESULTS

The recovered parasites are listed according to their host species or grouped under their host families. Bird-host code numbers are noted after the parasite's name.

Acridotheres tristis (L.) (Sturnidae)

Haemoproteus cf. *pastoris* Mello, 1935
(Fig. 1) (Table 1)

Locality. **–** Singapore, Jul.2001. One bird, caged for an unknown period was infected. A further 10 trapped free ranging individuals were negative.

Type host. **–** *Sturnus roseus* (India) (redescribed by Bishop & Bennett, 1990; Valkiunas & Iezhova, 1993).

The total parasitaemia in the infected bird was 33.3%, 37.3%; with trophozoites (or premature) 28.3%; gametocytes 5%; and approximately 14% double infections. The ratio of micro- to macrogametocytes was 1:4.

Description. **–** Both micro- and macrogametocytes at full differentiation, even when not occupying the entire volume of the erythrocyte, distort the erythrocyte and displace the nucleus. Some also completely encircle the erythrocyte nucleus. The infected erythrocyte either rounds up or elongates. The erythrocytes become enlarged when infected by trophozoites and young gametocytes (Table 1). The pigment granules (numbering 20–30) are conspicuous. The macrogametocyte nucleus is large (larger than in *H. pastoris* and *H. kairullaevi*, Valkiunas & Iezhova, 1993).

Remarks. **–** *Haemoproteus pastoris* has been reported from many species of Sturnidae (Bishop & Bennett, 1990) but *Hae. kairullaevi* has been found only in *Acr. tristis* (in Kazakhestan, Valkiunas & Iezhova, 1993). Although the

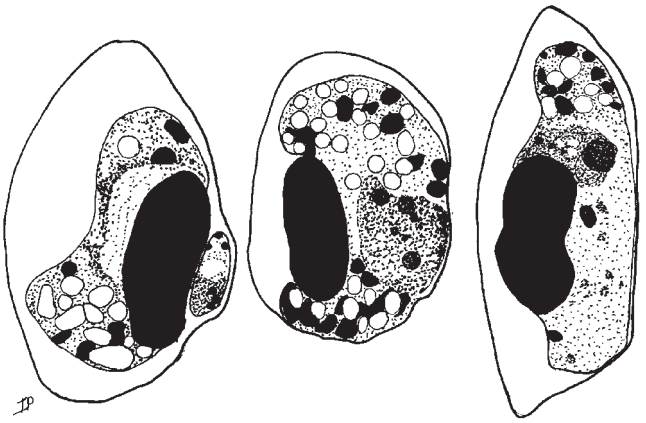

Fig. 1. *Haemoproteus* cf. *pastoris* from *Acridotheres tristis*, Singapore (from left: micrgametocyte and two macrogametocytes).

Table 1. Measurements of *Haemoproteus* cf. *pastoris* Mello, 1935, from *Acridotheres tristis* and of *Haemoproteus alcippae*, new species, from *Alcippe peracensis* in Malaysia. Values in angle brackets for *H.* cf. *pastoris* are for the stumpy form.

Parameter	*H.* cf. *pastoris*	*H. alcippae*
Uninfected erythrocytes	n = 12	n = 16
Length	11.8 ± 0.34	11.5 ± 0.69
Width	5.2 ± 0.54	6.3 ± 0.47
Nucleus length	5.2 ± 0.31	5.6 ± 0.52
Nucleus width	2.0 ± 0.19	2.7 ± 0.22
Erythrocytes with trophozoites.	n = 9	
Length	12.2 ± 0.84	
Width	4.4 ± 0.54	
Nucleus length	5.1 ± 0.50	
Nucleus width	2.0 ± 0.15	
Erythrocytes with macrogametocytes	n = 13	n = 21
Length	12.2 ± 2.13	13.5 ± 1.1
Width	5.8 ± 1.24	6.2 ± 0.65
Nucleus length	5.5 ± 0.85	5.4 ± 0.42
Nucleus width	2.1 ± 0.33	2.5 ± 0.41
NDR (range)	0.43 ± 0.20	0.72 ± 0.16 (0.36–0.95)
Macrogametocytes	n = 13	n = 22
Length [cross]	12.4 ± 1.95 [9.9 ± 0.62]	13.05 ± 1.42 [10.9 ± 0.82]
Width	3.3 ± 2.20	1.32 ± 0.29
Nucleus length	3.0 ± 0.33	2.36 ± 0.53
Nucleus width	2.3 ± 0.56	1.2 ± 0.33
Erythrocytes with microgametocyte	n = 3	n = 14
Length	12.2 ± 0.36	13.7 ± 0.95
Width	6.9 ± 0.95	5.6 ± 0.82
Nucleus length	5.8 ± 0.33	5.2 ± 0.49
Nucleus width	1.8 ± 0.03	2.4 ± 0.34
NDR	0.45 ± 0.18 (0.27–0.63)	0.64 ± 0.19 (0.2–0.89)
Microgametocytes	n = 3	n = 14
Length (range) [cross]	11.1 ± 2.05 (9.1–113.2)	12.7 ± 1.22 [10.7 ± 0.71]
Width	1.25 ± 0.15	1.40 ± 0.57
Nucleus length	4.2 (n = 1)	
Nucleus width	0.8 (n = 1)	

fully grown gametocytes of *Hae. pastoris* from *Stu. roseus* occupy the entire space between the erythrocyte wall and nucleus, they do not encircle the nucleus and only moderately displace the erythrocyte nucleus (by approximately 0.7 NDR compared to approximately 0.45 in the presently described material). Immature or not fully differentiated gametocytes, which produce projections at their lateral ends, were not seen in similar stage gametocytes in *Acr. tristis*.. The number of pigment granules (11), is fewer than in the presently described specimens. Gametocytes of *Hae. kairullaevi* demonstrate a very different appearance; they occupy a smaller part of the erythrocyte and some are clearly detached from the erythrocyte wall. The infected erythrocyte nucleus remains intact and the nucleus is only slightly displaced (0.9 NDR). They contain approximately 10 pigment granules.

Conspecificity of *Haemoproteus* from Singapore *Acr. tristis* with *Hae. pastoris* is uncertain, and a more aged gametocytes can assume a gravid shape. Since infected blood from only one bird is available, we prefer to defer our conclusion until more data become available.

Aegithina tiphia (L.) (Aegithinidae)

Haemoproteus aegithinae de Mello, 1935
(Fig. 2)

Locality. – Indonesia: Java, Lingo lowland secondary forest, Jun.2001. In one bird, very low infection; three microgametocytes and one macrogametocyte were found.

***Type host.* –** *Aegithinia tiphia* (India).

***Description.* –** Macrogametocyte – 13.2 (cross 9.7) × 1.1, nucleus 1.1 × 0.88; infected erythrocyte − 11.2 × 6.4, nucleus 4.8 × 1.98, n = 1; microgametocytes – 10.3–10.6 (cross: 9.7–10.3) × 1.5–2.4, n = 2; infected erythrocyte – 10.8–11.2 × 5.9–6.6; nucleus − 4.2–5.2 × 2.0–2.4. NDR of all infected erythrocytes: 0.6. The non-infected erythrocytes are 10.1 ± 0.58 × 6.51 ± 0.4, with nucleus 4.6 ± 0.27 × 2.9 ± 0.17, n = 6.

Measurements made by Bennett & Peirce (1990) and Valkiunas (1997) are: macrogametocytes – 15.1 ± 1.3 × 2.7 ± 1.6, with nucleus 2.5 ± 0.6 × 1.5 ± 0.4; infected erythrocyte–13.2 ± 0.8 × 7.3 ± 0.6, with nucleus 5.7 ± 0.6 × 2.2 ± 0.2 ; microgametocyte–12.3 ± 4.7 × 2.8 ± 0.3; infected erythrocytes- 12.7 ± 2.7 × 7.2 ± 0.5, with nucleus 5.8 ± 0.5 × 2.0 ± 0.4; NDR: 0.8 ± 0.1.

***Remarks.* –** The gametocytes closely adjoin the erythrocyte nucleus and embrace it, but do not surround it; its borders remain partly removed from the erythrocytic wall. Fully-grown gametocytes as reported by Bennett & Peirce (1990) tightly adhere to the erythrocyte wall and completely fill the erythrocyte space. The micro- and macrogametocytes of *Aeg. tiphia* from Java, as well as the infected and non-infected erythrocytes, are smaller than in the type host with NDR 0.6 rather than 0.8 as previously reported. The pigment granules in the observed macrogametocyte were fine and few, aggregated with a volutin granule around two vacuoles. In the microgametocytes, the pigment granules both coarse and fine, number over 20 and (in two out of three) occur mainly along the rims.

Leucocytozoon sp. 1
(Fig. 3)

***Locality.* –** Indonesia: Java, Lingo lowland secondary forest, Jun.2001. In one bird, one specimen (a macrogametocyte) was found.

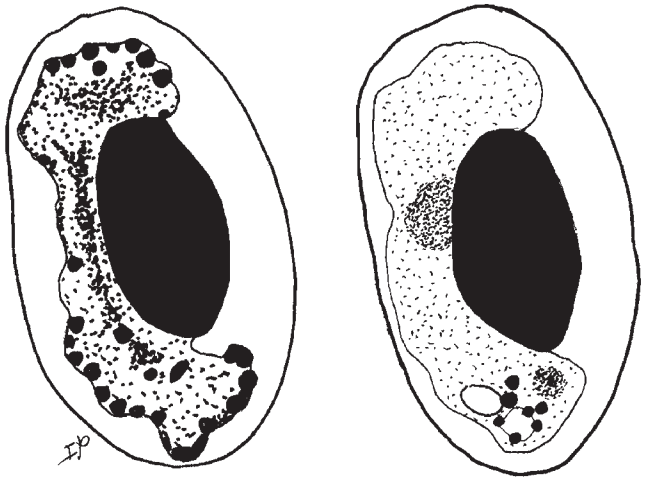

Fig. 2. *Haemoproteus aegithinae* from *Aegithina tiphia*, Java (from left: microgametocyte and macrogametocyte).

***Description.* –** Size: 12.10 × 10.56; nucleus: 5.06 × 2.64; periphery 35.2, host nucleus length: 14.3, embracing 40% of the gametocyte.

***Remarks.* –** McClure et al. (1978) reported *Leucocytozoon* sp. in *Aeg. tiphia* from Palawan, India and Thailand. Records from other Irenidae include *Leu. enriquesi* de Mello, 1936 and *Leu. chloropsidis* de Mello, 1935 which were synonymised by Valkiunas [1997 (2005)] with *Leu. fringillinarum* Woodcock, 1910.

***Aethopyga saturata* (Hodgson) (Nectariniidae)**

Leucocytozoon sp. 2

***Locality.* –** Malaysia: Cameron Highlands, Nov.2002. Found in one bird, a few gametocytes.

***Description.* –** The macrogametocytes, are all round and 11.4 ± 0.64 × 8.8 ± 0.52 in size, with 2.9 ± 0.6 × 2.2 ± 0.2 nucleus (n = 4). The nucleolus is marginal and not very distinct. The deep-blue staining cytoplasm contains variable size vacuoles. The 21.4 ± 3.3 host-cell nucleus encloses 66 ± 11.0% of the macrogametocyte 32.1 ± 1.0 perimeter. The microgametocytes (n = 3) are 10.6 ± 1.9 × 6.8 ± 1.3 in size. The pink cytoplasm contains a few large vacuoles and a denser staining core, apparently the nuclear component. The 20.6 ± 2.5 host-nucleus encloses 75 ± 2.1% of the microgametocyte 28.1 ± 3.1 perimeter.

***Remarks.* –** *Leucocytozoon* sp. was reported from the same host by McClure et al. (1978). The extent of enclosure of the gametocyte by the host-cell nucleus places this *Leucocytozoon* among the *Leu. major*-like species as defined by Valkiunas

Fig. 3. *Leucocytozoon* sp. 1 from *Aegithina tiphia*, Java (macrogametocyte).

[1997 (2005)]. The other *Leucocytozoon* (*Leu*. sp. 4) found in a Nectariniid bird (*Arachnothera longirostra*) is apparently a different species as the host-cell encloses only 47–48% of the gametocytes (closer to *Leu. fringillinarum*-type species) and the macrogametocyte cytoplasm contains many dark granules.

***Alcippe peracensis peracensis* Sharpe (Timaliidae)**

Haemoproteus alcippae, new species
(Fig. 5) (Table 1)

***Locality.* –** Malaysia: Fraser's Hill, through 2002 and 2003.

***Material examined.* –** Thirty-one birds were examined from Aug. to Dec.2002 and 39 more from Mar. to Aug.2003 from Fraser's Hill and Cameron Highlands in Peninsular Malaysia. All the infected birds were from Fraser's Hill: 28 out of 42 (67%); none of the 39 examined birds from Cameron Highlands were found to be infected. Infection was found in birds caught during May, Jul., Aug., Oct. and Nov. Infection intensity was variable but frequently high, up to 2–3% parasitaemia (for quantitative details see Paperna et al., 2005)

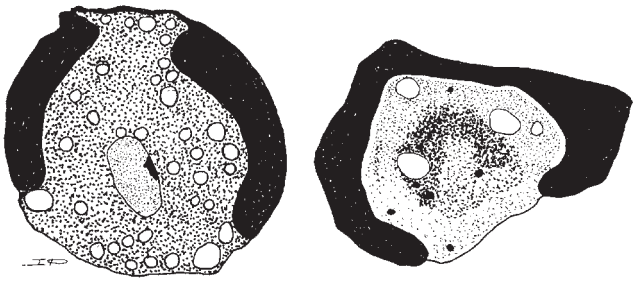

Fig. 4. *Leucocytozoon* sp. 2 from *Aethopyga saturata*, Malaysia (from left: macrogametocyte and microgametocyte).

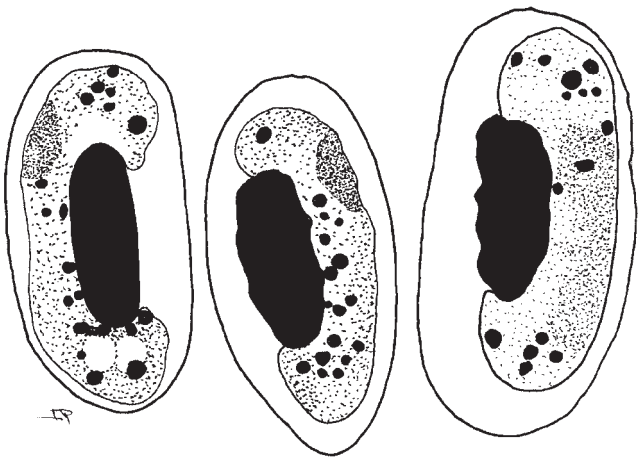

Fig. 5. *Haemoproteus alcippe* from *Alcippe peracensis*, Malaysia (from left: two macrogametocytes and microgametocyte).

***Description.* –** The infected erythrocyte is somewhat elongate, with gametocytes that are slender and barely to moderately displace the erythrocyte nucleus, only slightly bending over the edges of the erythrocyte nucleus and not reaching the erythrocytes' lateral or distal ends. Both gametocytes are moderately pigmented, but in some birds the detected gametocytes contain more numerous larger grains, which sometimes assemble into a line. The macrogametocyte nucleus is off-center, sometimes big enough to adjoin both the host nucleus and the parasite's outer membrane. The cytoplasm stains pale blue. In many microgametocytes, the nucleus is indistinguishable from the reddish cytoplasm, although sometimes it can be seen as an elongate ribbon extending along half or two-thirds of the gametocyte. In only one instance, a gametocyte (a microgametocyte) produced wall extensions.

***Etymology.* –** Named after the generic name of the parasite's host.

***Remarks.* –** *Haemoproteus alcippe* gametocytes are slender and do not fill the entire volume of the erythrocyte up to its distal tips, as do the robust species infecting the Sylviidae (*Hae. belopolski* Valkiunas, 1989, and *Hae. wenyoni*) and Timalliidae (*Hae. timalli*), which fill the erythrocyte and embrace a good part, or the entirety, of the erythrocyte nucleus. Gametocytes of *Hae. aegithinae*, which infect *Aeg. tiphae* in Southeast Asia, extend throughout the length of the erythrocyte, but leave lateral spaces when not gravid. *Haemoproteus fallisi* Bennett & Campbell, 1972, *Hae. minutus* Valkiunas & Iezhova, 1992, and *Hae. copsychi* which, like *Hae. alcippae* are shorter than the erythrocyte, only slightly embrace the erythrocyte nucleus or end bluntly. *Haemoproteus fallisi* and *H. minutus* fill the space between the erythrocyte nucleus and its outer border, while *Hae. copsychi* like *Hae. alcippae* do not reach the lateral rims of the erythrocyte. *Haemoproteus fallisi* and *Hae. copsychi* displace the erythrocyte nucleus conspicuously, *H. alcippae* moderately or slightly, while *Hae. fallisi*, *Hae. minutus* and *Hae. aegithinae* barely displace the erythrocyte nucleus. Wall projections found in all the abovementioned species were absent or exceptional in *Hae. alcippae* and *Hae. copsychi*. *Haemoproteus copsychi* also differs from *Hae. alcippae* in having the macrogametocyte nucleus in a median position, which is distal in the latter.

Haemoproteus cf. *copsychi*
(Table 2)

***Locality.* –** Malaysia: Fraser's Hill, Feb.2002, found in one bird.

***Description.* –** The gametocytes resemble *H. copsychi* new species (see vide) they are short, with their ends only slightly extending beyond the erythrocyte nucleus; they end bluntly, closely applied to, and some slighly bend around the host cell margins. They cause the erythrocyte to swell and usually moderate to extreme displacement of its nucleus (NDR–macrogametocytes: 0.45 ± 0.17; microgametocytes

Table 2. Measurements of *Haemoproteus* cf. *copsychi* from *Alcippe perracensis*.

Parameter	Macrogametocytes	Microgametocytes
Infected erythrocytes	n = 4	n = 4
Length	13.0 ± 1.1	13.0 ± 2.2
Width	7.5 ± 1.0	8.1 ± 1.6
Nucleus length	5.9 ± 0.5	5.9 ± 0.5
Nucleus width	2.2 ± 0.5	2.5 ± 0.5
NDR	0.45 ± 0.17	0.52 ± 0.31
Gametocytes	n = 4	n = 4
Cross length	9.9 ± 1.25	9.9 ± 2.3
Width	3.2 ± 0.7	3.5 ± 0.6
Nucleus length	3.1 ± 0.3	
Nucleus width	1.6 ± 0.45	

0.52 ± 0.31). The pigment granules (numbering 10–21), are round and variable in size. The macrogametocyte cytoplasm stains blue, with the nucleus in a median or close to median position. The microgametocyte stains pink and occasionally forms amoeboid rims.

***Remarks.* –** Gametocytes are stout and cause considerable displacement of the erythrocyte nucleus and disfiguration of the erythrocyte. They are reminiscent of *Hae. copsychi*, new species described from the turdiid *Copsychus malabaricus* from Sarawak.

Leucocytozoon sp. 3
(Fig. 6)

***Locality.* –** Malaysia: Cameron Highlands, Sep.2002, Aug.2003; Fraser's Hill, Feb., Jul.2003. Found both in Fraser's Hill and Cameron Highlands in 6% and 7.7%, respectively, of the examined *Alc. peracensis* in 2002 and 2003 collections, respectively (Paperna et al., 2005).

***Description.* –** All the gametocytes are round. The macrogametocyte mean size is 11.16 ± 1.56 × 8.22 ± 1.30 (n = 18; the largest seen is 14.3 × 8.03), and their blue staining cytoplasm contains moderate number of vacuoles, deep-staining small condensations and 4.12 ± 1.08 × 2.54 ± 0.53 nucleus with central or off-centre karyosome. The host-cell nucleus occupies 18.7 ± 4.31 (61 ± 16%, with a range of 38–76%) of the macrogametocyte perimeter of 31.8 ± 3.9. One monocyte contained a young macrogametocyte. The few (four) microgametocytes found are 10.7 ± 1.84 × 8.03 ± 1.1, with a rose-staining cytoplasm and obliterated nuclear details. The host-cell nucleus occupies 14.7 ± 2.54 (45 ± 7%, with a range of 40–53%) of the microgametocyte perimeter of 32.3 ± 1.3.

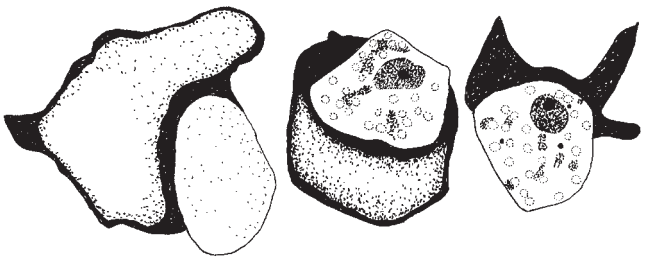

Fig. 6. *Leucocytozoon* sp. 3 from *Alcippe peracensis*, Malaysia (from left: microgametocyte and two macrogametocytes).

***Remarks.* –** The relationship between the host cell nucleus and the gametocyte varies from 38% to 78% and thus partly corresponds with Valkiunas [1997 (2005)] definition of *Leu. majoris*, i.e. the host-cell nucleus-gametocyte relationship is "more than half its perimeter", while the others fit with his definition of *Leu. fringillinarum*, "less than half its perimeter". The apparent wide variation in host-cell nucleus dimensions casts doubts on the validity of the host-nucleus structure as a differentiating character. This leaves us with no other reliable character for differentiating species of *Leucocytozoon*. At the same time, it questions the validity of such all inclusive species as *Leu. majoris* and *Leu. fringillinarum* as suggested by Valkiunas [1997 (2005)].

Plasmodium (*Haemamoeba*) sp.

***Locality.* –** Malaysia: Fraser's Hill, Jul.2003.

***Remarks.* –** Five macrogametocytes and three microgametocyte occurred in swollen erythrocytes with laterally- or distally-displaced nuclei, with one microgametocyte extending numerous projections. Schizogonic stages were not observed.

***Alophoixus bres* (Lesson)**

***Remarks.* –** See Pycnonotidae (page 21).

Arachnothera longirostra (Latham) **(Nectariniidae)**

Leucocytozoon sp. 4.
(Fig. 7)

***Locality.* –** Malaysia: Cameron Highlands, Sep. and Nov. 2002.

***Description and remarks.* –** All the gamerocytes are round and the macrogametocytes are 12.2 ± 1.8 × 9.1 ± 1.0 in size (n = 6), with a usually oval nucleus 3.7 ± 0.9 × 2.0 ± 0.4 and a distinct nucleolus; the single microgametocytes was 11.2 × 10.0 in size. The dense blue-staining macrogametocyte cytoplasm contains a few vacuoles and moderate number of round black-staining corpuscles. The pink-staining microgametocyte cytoplasm shows faint outlines of the nucleus. In the macrogametocyte, the 16.1 ± 2.9 host nucleus occupies 47% ± 11.06 of its 34.5 ± 3.9 perimeter and in the microgametocyte, the 15.4 host nucleus occupies 48% of the microgametocyte's 32.2 perimeter.

The host nucleus degree of embracing in this *Leucocytozoon* corresponds with neither *Leu. fringillinarum* nor *Leu. majoris* structural schemes.

Chalcophaps indica (L.) **(Columbidae)**

Haemoproteus cf. *turtur* Covaleda, Ortega, Gallego & Berenguer, 1950

***Locality.* –** Malaysia: Cameron Highlands, Nov.2002; and Sarawak.

***Type host.* –** *Streptopelia turtur* (Spain).

***Remarks.* –** Found in one bird from Peninsular Malaysia and one from Sarawak; very scant infection. A premature macrogametocyte (9.5 × 1.5 with 2.5 × 1.1 nucleus) has wavy surface and closely apposes the erythrocytic nucleus, features, which conform to that reported in premature *Hae. turtur*. Infected erythrocyte is slightly distended (NDR = 0.77).

Columba livia Gmelin (Columbidae) – feral pigeon.

Haemoproteus columbae Kruse, 1890

***Locality.* –** Singapore, see Paperna & Smallridge (2002).

Copsychus malabaricus (Scopoli) (Turdidae).

Haemoproteus copsychi, new species
(Fig. 8) (Table 3)

***Locality.* –** Malaysia: Sarawak.

***Description.* –** Found only in mature erythrocytes. Gametocytes are closely applied to the host cell nucleus, causing slight swelling in the erythrocyte as well as moderately or extremely displacing its nucleus (NDR–macrogametocytes: < 0.2, microgametocytes: 0.15, 0.40, 0.78). The ends of the gametocytes slightly or moderately extend beyond the erythrocyte nucleus, ending bluntly and only occasionally gripping the host nucleus. The macrogametocyte cytoplasm stains deep-blue and is coarsely granular. The nucleus is pink-staining, discrete and in a median position. The pigment granules, either small (fragmented) and numerous (< 25) or fewer and larger (> 10), usually of mixed sizes (15–20), are more often aggregated at the distal ends and adjoined by a few vacuoles. The microgametocyte cytoplasm stains blue, while the large nucleus occupies the major volume of the cell. The pigment granules are located at the gametocyte extremities and accompanied by one or two vacuoles. They are either coarse (approximately 10) or fine (15–20). The juvenile stages were not found.

***Etymology.* –** Named after the generic name of the parasite's host.

***Remarks.* –** *Haemoproteus copsychi* differs from *Hae. alcippe* found in sylviid birds in considerably displacing the erythrocyte nucleus. Bennett & Campbell (1972) reported *Hae. fallisi* from *Copsychus malabaricus*. These authors considered species of *Haemoproteus* found in blood of various species from the Turdidae family from both Holarctic regions (North America and Eurasia) and from the tropics (SE Asia) to be conspecific with *Hae. fallisi*. They acknowledge considerable variations in the dimensions of parasites as well as the infected erythrocytes. The differences between the presently described species and *Hae. fallisi* as described from different species from the Turdidae are as follows: in *Hae. copsychi*, the host erythrocyte nucleus is radically displaced. The surface of the gametocytes do not form amoeboid extensions or invaginations. The macrogametocyte nucleus is in a median rather than in a subterminal position. With only few exceptions (one microgametocyte), the gametocytes

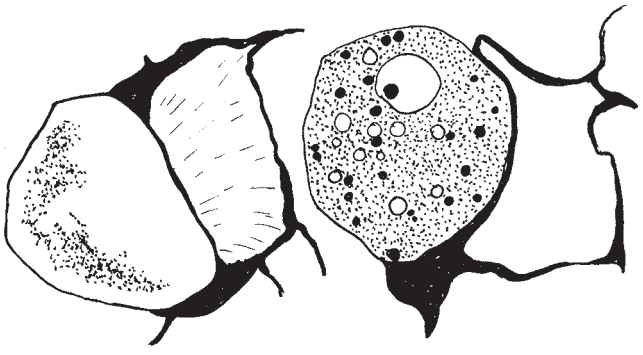

Fig. 7. *Leucocytozoon* sp. 4. from *Arachnothera longirostra*, Malaysia (from left: microgametocyte and macrogametocyte).

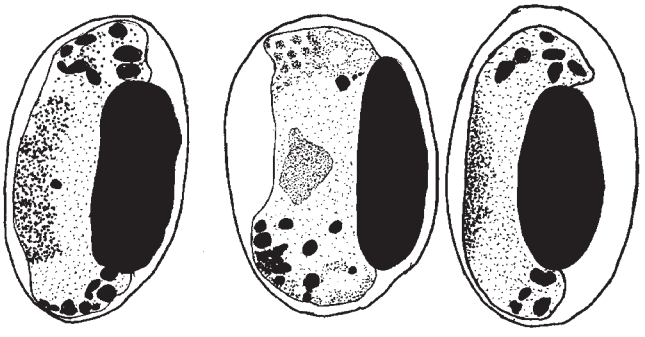

Fig. 8. *Haemoproteus copsychi* from *Copsychus malabaricus*, Sarawak (from left: microgametocyte, macrogametocyte and microgametocyte).

Table 3. Measurements of *Haemoproteus copsychi*, new species, from *Copsychus malabaricus* in Sawarak.

Parameter	Data
Uninfected erythrocytes	n = 9
Length	12.4 ± 0.68
Width	6.9 ± 0.52
Nucleus length	5.7 ± 0.41
Nucleus width	2.5 ± 0.24
Macrogametocyte	n = 5
Length	8.5 ± 1.15
Width	3.1 ± 0.39
Nucleus length	2.7 ± 0.75
Nucleus width	1.7 ± 0.37
Microgametocyte	n = 3
Length	9.4 ± 0.5
Width	2.5 ± 0.26
Nucleus length	5.2 ± 0.66
Nucleus width	1.6 ± 0.54
Infected erythrocytes with macrogametocyte	n = 5
Length	10.5 ± 2.87
Width	6.2 ± 0.68
Nucleus length	6.2 ± 0.42
Nucleus width	2.4 ± 0.24
Infected erythrocytes with microgametocyte	n = 3
Length	11.2 ± 3.20
Width	5.1 ± 2.11
Nucleus length	6.7 ± 1.63
Nucleus width	2.2 ± 0.20

end bluntly and do not embrace the erythrocyte nucleus. Gametocytes reported by Bennett & Campbell (1972) from *Copsychus malabaricus* are considerably larger (13.9 ± 0.8 × 3.0 ± 0.5), cause an elongation rather than a swelling of the erythrocyte (infected: 14.3 × 7.3, non-infected 13.0 × 8.2) and displace the erythrocyte nucleus to a lesser extent (NDR = 0.64 ± 0.26).

Plasmodium (*Haemamoeba*) sp.

Locality. – Malaysia: Sarawak.

Description and Remarks. – Some erythrocytes contained round macrogametocytes, 5.0–5.7 × 4.4–4.8, with blue-staining cytoplasm containing 9–13 coarse pigment granules and a 1.7–2.6 × 0.7–2.2 red-staining nucleus. The erythrocytes 11.6–15.2 × 7.0–9.5 are distorted, with extremely laterally displaced 5.6–6.8 × 1.8–2.2 nuclei. These are less likely to be aged *H. copsychi*, found in the same host.

Corvus splendens Vieillot (Corvidae)

Leucocytozoon sakharoffi Sambon, 1908
(Fig. 9)

Locality. – Singapore: urban zone, 2001.

Type host. – *Corvus corax* L., Russia.

Description. – The macrogametocyte is rounded, 11.62 × 9.1 in size, with a central nucleus: 5.6 × 3.08 and an indistinct nucleolus, two-thirds enclosed by the host cell nucleus forming a 14 long, 1.96 wide arch, split into two segments, and by an arch of 12.6, 3.22 wide, of host-cell cytoplasm. The microgametocyte is round, 10.92, 11.62 × 9.1, 9.1 in size with faint blue cytoplasm and a distinct central nuclear red zone 7.42, 5.6 × 4.48, 3.08. The host nucleus, 14 long, encloses half the of the microgametocyte circumference, its exterior rim with or without undulations. Arching host-cell cytoplasm, 4.06 wide, encloses the host cell nucleus.

Remarks. – Blood films from 21 house crows and visceral (liver, kidney and spleen) imprints from 30 crows shot by the municipal authority revealed one infected crow, with one macrogametocyte and two microgametocytes, and another with a juvenile stage in a monocyte.

Leucocytozoon sakharoffi macrogametocyte measurements according to Bennett & Peirce (1992) from *Cor. cornix* from St. Albans, UK (n = 35) are: length–12.6 ± 1.3; width 10.9 ± 1.0, nucleus length – 3.8 ± 0.8, width 2.5 ± 2.1, host nucleus length: 29.8 ± 3.2. There are some structural differences between the specimens from *Cor. splendens* and *Leu. sakharoffi* from *Cor. cornix* as illustrated in Valkiunas [1997 (2005)], which however are unlikely to suggest interspecific divergence.

Lankesterella sp.

***Locality.* –** Singapore: urban zone, 2001.

***Description.* –** Sporozoite stages of *Lankesterella* sp. were found, one inside an erythrocyte and one free in the liver smear. The sporozoites (6.0 × 1.2 in size) were recognized by their conspicuous, blue-staining refractile body.

***Remarks.* –** Baker et al. (1997) confirmed early reports of Lainson (1958) and Dissaniake (1967) on the presence of species of *Lankesterella* in birds, which produced visceral gamogonies, and sporogonies yielding circulating sporozoites. *Lankesterella* spp. coexists with infections of extra-intestinal merogonic stages of *Isospora*, also called *Atoxoplasma* Garnham, 1950. This led to considerable nomenclatural confusion: denial of the existence of the sporozoite yielding *Lankesterella* and application of the name *Lankesterella* to the isosporan visceral infection (*Atoxoplasma*) (Lainson, 1959; Box, 1970, 1981).

Eurylaimus javanicus Horsfield (Eurylaimidae)

Lankesterella ? sp.

***Locality.* –** Lingo lowland secondary forest, Java 9.7.01, (one case, inside an erythrocyte).

Remarks.* –** See ***Remarks on *Lankesterella* from *Corvus splendens*)

Ficedula solitaria (Muller) (Muscicapidae)

Haemoproteus pallidus Valkiunas & Iezhova 1991 (Fig. 10)

***Locality.* –** Malaysia: Fraser's Hill, May 2003. In one out of 16 specimens examined in 2003, none in 11 examined in 2002.

***Type species.* –** *Ficedula hypoleuca* (Pallas), Baltic region.

***Description.* –** Observed infection in *Fic. solitaria* was scanty, so detected cells were few. An early invaded erythrocyte was observed (10.2 × 6.0 with 5.3 × 7.2 nucleus and NDR = 1.0) with 4 trophozoites, 4.3–6.3 × 1.3–2.0 in size, each with a large posterior vacuole, half the size of the trophozoite; one erythrocyte (12.2 × 6.3) with a elongate macrogametocyte (23.8 long, 2.2, wide) folded around the 5.3 × 2.8 erythrocyte nucleus (NDR = 0.85); another erythrocyte (10.6 × 5.7) completely occupied by a macrogametocyte with a very displaced host cell nucleus (5.3 × 2.4, NDR = 0.30) and an erythrocyte almost completely invaded by a large microgametocytic plasmodium (11.4 × 6.4). Both macrogametocytes and microgametocytes contain nuclear masses, which do not suggest if it is a single or merged nuclei. Uninfected erythrocytes are 10.3 ± 0.84 × 6.2 ± 0.33 with 5.8 ± 0.53 × 2.6 ± 0.31 nucleui (n = 8).

***Remarks.* –** Valkiunas [1997 (2005)] describes two forms of *Hae. pallidus* infection: single and multiple. In the single infection the gametocyte grips the erythrocyte nucleus on one side but never totally embraces it; in a multiple infection the erythrocyte is invaded by several gametocytes, two of which grow and merge into a common plasmodium which encloses the host-cell nucleus.

***Garrulax* (Timaliidae)**

Haemoproteus timalus Bennett, Bishop & Peirce, 1991 ***(***Table 4)

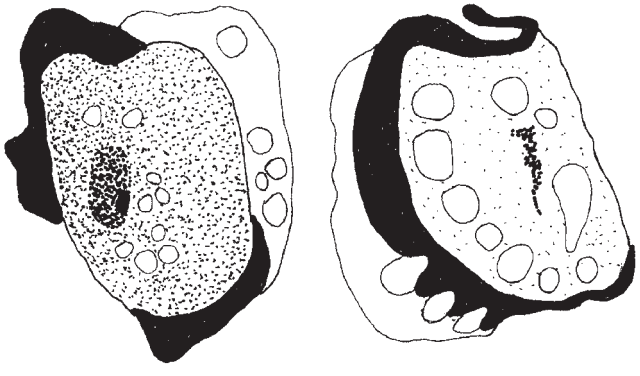

Fig. 9. *Leucocytozoon sakharoffi* from *Corvus splendens*, Singapore (from left: macrogametocyte and microgametocyte).

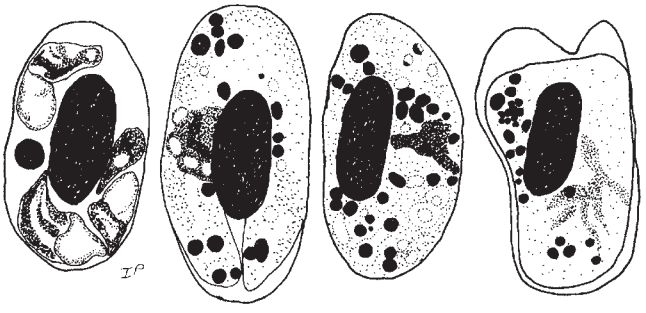

Fig. 10. *Haemoproteus* cf. *pallidus* from *Ficedula solitaria*, Malaysia (from left: multiple juvenile infection; elongated macrogametocyte folded around the host nucleus, seemingly merged gametocytes with conspicuous macrogametocyte nucleus; same but with conspicuous microgametocyte features.

Table 4. Measurements from *Haemoproteus timalus* from *Garrulax erythrocephalus* and *G. mitratus* compared with *H. obtusus*, new species from *G. mitratus*.

Parameter	*H. timalus* ex *G. erythrocephalus*	*H. timalus* ex *G. mitratus*	*H. obtusus*, new species, ex *G. mitratus*
Uninfected erythrocytes	n = 11	n = 9	
Length	11.9 ± 0.45	12.2 ± 0.63	
Width	6.9 ± 0.80	6.1 ± 0.53	
Nucleus length	5.0 ± 0.49	5.5 ± 0.48	
Nucleus width	3.0 ± 0.23	2.3 ± 0.65	
Erythrocytes with macrogametocytes	n = 11	n = 12	n = 11
Length	13.0 ± 0.73	14.0 ± 0.87	13.9 ± 0.81
Width	7.3 ± 0.82	5.7 ± 0.75	6.7 ± 0.96
Nucleus length	4.8 ± 0.51	5.1 ± 0.52	5.5 ± 0.51
Nucleus width	3.0 ± 0.63	2.3 ± 0.46	2.5 ± 0.22
NDR (range)	0.71 ± 0.21 (0.33–1.0)	0.61 ± 0.16 (0.33-0.86)	0.87 ± 0.14
Macrogametocytes	n = 10	n = 12	n = 11
Length [cross]	15.8 ± 1.69 [12.4 ± 1.11]	12.3 ± 1.23 [10.6 ± 0.45]	9.2 ± 0.43
Width	2.5 ± 0.67	1.7 ± 0.38	2.2 ± 0.31
Nucleus length	3.7 ± 0.71	2.4 ± 0.42	2.4 ± 0.45
Nucleus width	2.4 ± 0.15	1.7 ± 0.27	1.6 ± 0.38
Erythrocytes with microgametocyte	n = 11	n = 12	n = 7
Length	13.0 ± 1.07	14.1 ± 0.80	14.0 ± 0.75
Width	6.6 ± 0.86	6.1 ± 0.59	7.2 ± 0.81
Nucleus length	4.7 ± 0.34	5.2 ± 0.38	5.0 ± 0.41
Nucleus width	2.8 ± 0.47	2.1 ± 0.13	2.6 ± 0.24
NDR (range)	0.64 ± 0.22 (0.32–0.94)	0.78 ± 0.13 (0.53–1)	7.4 ± 0.19
Microgametocytes	n = 10	n = 12	n = 7
Length [cross]	13.3 ± 1.00 [11.0 ± 0.21]	12.3 ± 0.95 [10.8 ± 0.64]	8.9 ± 0.67
Width	2.1 ± 0.42	1.5 ± 0.49	2.2 ± 0.51
Nucleus length	(5.5–8.8)		5.3 ± 0.22
Nucleus width	(1.3–2.0)		1.7 ± 0.51

Garrulax erythrocephalus (Vigors)

Locality. – Malaysia: Fraser's Hill, Aug. and Dec.2002; Cameron Highlands, Feb. and Jul.2003.

Garrulax mitratus (Muller)

Locality. – Malaysia: Fraser's Hill, Aug.2002 and Jul.2003.

Remarks. – *Haemoproteus timalus* has been recorded, in addition to the African origin type host species *Turdoides rubiginosus*, from Southeast Asian timaliid hosts including *Garrulax* spp. [Bennett et al., 1991; Valkiunas, 1997 (2005)]. The gametocytes recovered from the timaliid *Pellorneum capistratum* from Sarawak and Java, however, conform better than those from *Garrulax* spp. with the type description. The gametocytes embrace the erythrocyte nucleus and fill the entire space between the nucleus and erythrocyte wall.

Contrary to the type description by Bennettt et al. (1991), who reported the presence of "amoeboid outlines" (projections) also in fully mature specimens, the gametocytes from *Garrulax* spp. rarely extend wall projections, and only in the younger specimens. The infected erythrocyte becomes enlarged as previously reported, whereas the host-cell nucleus is frequently considerably displaced (NDR approximately 0.6, with the exception of a microgametocyte-infected *Gar. mitratus* erythrocyte, which is approximately 0.8, comparable with 0.8 in the type material and 0.76–0.87 of *Pellorneum capistratum* infections). The pigment granules, numbering about 10–11, are robustly-elongate and of medium size, as in the other described *Hae. timalus*.

Haemoproteus obtusus, new species
(Fig.11) (Table 4)

Garrulax mitratus

Locality. – Malaysia: Cameron Highlands, Dec.2002 (Type).

Table 5. Measurements of *Leucocytozoon* sp. 5 from *Garrulax leucolophus* and *G. erythrocephalus*.

Parameters	ex *G. leucolophus*	ex *G. erythrocephalus*
Macrogametocytes:	n = 13	n = 3
Length	11.6 ± 1.49	12.4 ± 1.68
Width	8.7 ± 1.30	8.2 ± 1.63
Nucleus length	3.1 ± 0.37	4.3 ± 0.70
Nucleus width	2.3 ± 0.38	2.3 ± 0.74
Perimeter	31.6 ± 3.85	32.3 ± 2.54
Host-cell nucleus	23.2 ± 5.03	18.7 ± 4.67
% cover	73.4 ± 11.57	(50–62 ~ 99)
Microgametocytes:	n = 8	
Length	10.8 ± 1.74	
Width	7.8 ± 1.72	
Perimeter	30.8 ± 1.66	
Host-cell nucleus	25.1 ± 2.65	
% cover	81.5 ± 7.13	

Garrulax erythrocephalus

***Locality.* –** Malaysia: Cameron Highlands, Dec.2002.

***Description.* –** The gametocytes are short, stout (Table 5), end bluntly, loosely appose the host-cell nucleus, do not embrace it and usually closely apply to the erythrocyte pellicle. They occasionally displace the host-cell nucleus. No wall projections or amoeboid out growths are formed. The macrogametocyte cytoplasm stains faint-blue and the nucleus is distal or sub-distal. The microgametocyte nucleus is scattered. The medium and small size pigment granules, numbering 15–20, are accompanied by variable numbers of volutin granules, aggregated on both distal margins, and sometimes also in the middle zone. The juvenile stages develop attached to the erythrocyte's margins and in detachment from the host nucleus.

***Etymology.* –** Named for its blunt shape.

***Remarks.* –** This blunt *Haemoproteus* is reminiscent of *Hae. fallisi* Bennett & Campbell, 1972, *Hae. minutus* Valkiunas & Iezhova 1992 and *Hae. copsychi*, presently described. In mixed infections with *Hae. timalus*, or in specimens damaged due to haemolysis, this species cannot be readily differentiated from premature *Hae. timalus*. *Haemoproteus minutus* as well as *Hae. fallisi* and *Hae. timalus* juveniles develop attached to the nucleus; in *Hae. copsychi*, the macrogametocyte nucleus is central. Some *Hae. fallisi and Hae. minutus* form wall projections and also in *Hae.* cf. *copsychi* from *Alc. peracensis* one microgametocyte is seen to produce wall projections.

Fig. 11. *Haemoproteus obtusus* from *Garrulax mitratus*, Malaysia (from left: microgametocyte and two macrogametocytes).

Leucocytozoon sp. 5
(Fig. 12) (Table 5)

Garrulax leucolophus (Hardwicke)

***Locality.* –** Malaysia: Fraser's Hill, Aug.2002.

Garrulax erythrocephalus

***Locality.* –** Malaysia: Cameron Highlands, Dec.2002.

***Description.* –** A round type, the host cell nucleus encloses 73 ± 12% of the macrogametocyte perimeter and 81 ± 7% of the microgametocyte perimeter. The macrogametocyte nucleus is usually central and the karyosome is distinct, while the cytoplasm contains some vacuoles and dense granules.

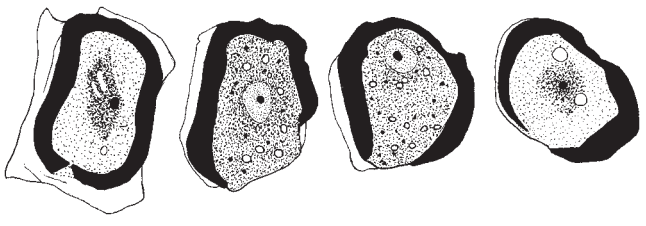

Fig. 12. *Leucocytozoon* sp. 5 from *Garrulax leucolophus*, Malaysia (from left: microgametocyte, two macrogametocytes and a microgamettcyte).

The microgametocyte cytoplasm contains a few vacuoles and a diffuse nuclear mass with a central large pink-staining granule (Fig. 12).

***Remarks*. –** Valkiunas [1997 (2005)] synonymized *Leucocytozoon* spp. from passeriform birds, enclosed by over half by the host-cell nucleus with *Leu. majoris*. In both *Leu. majoris* from the type host genus *Parus* as well as of host from other families included in *Leu. majoris*, notably Timaliidae (as the presently discussed), the host-cell nucleus covers over 75% of the gametocyte periphery (Bennett & Peirce, 1992). Since the coverage of the parasite by the host-cell nucleus is the cardinal character for specific differentiation, it remains to examine the validity of such an inclusive species, as proposed by Valkiunas, 1997/2005 which infects a wide range of non-related hosts, of diverse geographical origin (see also remarks to *Leucocytozoon* sp. 3).

Heterophasia picadoides (Hodgson) (Timaliidae)

Haemoproteus alcippae, new species

***Locality.* –** Malaysia: Fraser's Hill, May 2003.

***Type host.* –** *Alcippe peracensis* (Malaysia).

***Remarks*. –** Low infection was observed, the two microgametocytes and one macrogametocyte measured, conform in their structure and measurements with those from the type host, as well as in their impact on the infected erythrocyte (NDR–macrogametocytes: 0.71, microgametocyte 0.83, 0.95).

Leucocytozoon sp. 6

***Locality.* –** Malaysia: Fraser's Hill, May 2003.

***Description and Remarks.* –** A total of four macrogametocytes were found in the blood films, some with the host nuclei disrupted. The macrogametocyte periphery ranges from 24 to 39, while the nuclei are 2.8–4.9 × 1.26–3.5. The host nucleus covers 84–86% of the macrogametocyte diameter, i.e. conforming with the *Leu. majoris*-like species, sensu Valkiunas [1997 (2005)].

Lacedo pulchella (Horsfield) (Alcedinidae)

Haemoproteus halcyonis de Mello , 1935
(Table 6)

***Locality.* –** Malaysia: Pasoh, 1998; Johor, Malaysia, 2003.

***Type host.* –** *Halcyon smyrnensis* (L.) (India).

***Description*. –** Robust gametocytes are observed, which gradually expand and occupy the greater volume of the erythrocyte, while displacing the nucleus (NDR from 0.72 to 0.08). Most gametocytes embrace the displaced nucleus but only few also grip it; a few gametocytes embrace completely the erythrocyte nucleus. The macrogametocyte nucleus usually in off-centre position, but is occasionally central. The young stages attach to the erythrocyte wall rather than to its nucleus. Small and medium pigment granules are numerous (> 30).

***Remarks.* –** Bennett & Campbell (1973) described the same species from *Hal. chloris* in Malaysia, reporting among 10% of the gametocystes wavy undulations on their outer surface as well as that apposing the ertythrocyte nucleus. They suspected these undulations to be artefacts. No such gametocytes has been noticed in the presently studied considered heavy infection. From *Hal. smyrnensis* second species, *Hae. fuscae* (Mello & Fonseca, 1937) Bennett & Campbell, 1973 was described. This species likewise fills the entire volume of the erythrocyte, sometimes encircles the nucleus and lacks the surface undulations. Unlike in *Hae. halcyonis*, in *Leu. fuscae* the erythrocyte nucleus is barely displaced (NDR = 0.9).

***Lanius* (Laniidae)**

Haemoproteus lanii Mello, 1936
(Table 6)

Lanius tigrinus Drapiez

***Locality.* –** Singapore: Nee Soon, 1998,

Lanius cristatus Rüppell

***Locality.* –** Malaysia: Cameron Highlands, Sep.2002.

***Type host.* –** *Lanius schach*, India. In *Lan. tigrinus* infection was intensive, comprising 70% macrogametocytes, 19.5% microgametocytes and 10.5 % immature gametocytes. In *Lan. crystatus* infection was scanty, only four macro- and one microgametocytes found. The gametocytes were 17.0–19.8 (cross 11.7–12.6) × 2.2–2.9 in size, and like in other hosts cause infected erythrocytes to expand (12.1–13.3 × 5.2–5.7 vs. uninfected 10.7 ± 0.41 × 6.5 ± 0.53) and displace the nucleus (NDR = 0.56–0.71).

***Remarks.* –** Conforms to previous descriptions of *Hae. lanii* [from *Lan. cullerio*, Kurian Spit, in Valkiunas, 1990 and 1997 (2005)]. Gametocytes form some projections on their surface and in shape become gradually compact-stumpy as they age. They tightly embrace the erythrocyte nucleus, but appear never to completely enclose the nucleus, as described in the infections in other hosts. The macrogametocytes and particularly microgametocytes often radically displace the nucleus [not so evident in earlier described infections, e.g. Valkiunas, 1997 (2005)]. The macrogametocyte nucleus is median and apposed to the erythrocyte nucleus. The early gametocytes are located closer to the erythrocyte wall than the nucleus. With subsequent growth, they adjoin the erythrocyte nucleus. The pigment granules are medium and large in size,

Table 6. Comparison of *Haemoproteus halcyonis* dimensions in *Lacedo pulchella* from Singapore and Malaysia, and measurements taken of *Haemoproteus lanii* in *Lanius tigrinus*, Singapore.

Parameters	*Hae. halcyonis* (ex *L. pulchella*, Singapore)	*Hae. halcyonis* (ex *L. pulchella*, Malaysia)	*H. lanii* (ex *Lanius tigrinus*)
Uninfected erythrocytes	n = 10		n = 20
Length	12.1 ± 0.66		12.3 ± 0.72
Width	7.6 ± 0.58		7.0 ± 0.39
Nucleus length	6.6 ± 0.38		5.7 ± 0.39
Nucleus width	2.9 ± 0.14		2.6 ± 0.21
NDR	0.96 ± 0.03		0.94 ± 0.10
Erythrocytes with macrogametocytes	n = 11	n = 8	n = 19
Length	14.7 ± 1.13	14.6 ± 1.14	12.9 ± 0.79
Width	7.0 ± 1.44	7.8 ± 0.68	7.1 ± 0.56
Nucleus length	6.4 ± 0.51	6.3 ± 0.56	5.5 ± 0.56
Nucleus width	2.9 ± 0.33	2.6 ± 0.48	2.1 ± 0.27
NDR (range)	0.36 ± 0.15	0.38 ± 0.22	0.65 ± 0.21 (0.33–1.00)
Macrogametocytes	n = 11	n = 8	n = 19
Length [cross]	15.5 ± 1.93 [14.0 ± 0.98]	15.6 ± 1.60 [13.6 ± 2.02]	16.1 ± 2.93 [12.1 ± 1.11]
Width	3.8 ± 0.58	3.9 ± 0.39	2.8 ± 0.89
Nucleus length	2.9 ± 0.88	3.8 ± 0.63	2.8 ± 0.77
Nucleus width	2.8 ± 0.57	2.9 ± 0.33	2.2 ± 0.69
Erythrocytes with microgametocyte	n = 10	n = 8	n = 17
Length	15.3 ± 0.90	15.4 ± 1.10	12.7 ± 1.06
Width	8.1 ± 1.65	8.8 ± 0.92	7.5 ± 0.74
Nucleus length	6.7 ± 0.47	6.2 ± 0.31	5.7 ± 0.49
Nucleus width	2.4 ± 0.42	2.9 ± 0.69	3.1 ± 3.04
NDR (range)	0.35 ± 0.19	0.41 ± 0.19	0.54 ±0.29 (0.09–0.95)
Microgametocytes	n = 10	n = 8	n = 17
Length [cross]	19.8 ± 2.52 [14.9 ± 1.14]	15.6 ± 1.10 [14.5 ± 1.04]	14.5 ± 2.41 [11.9 ± 0.81]
Width	4.5 ± 0.86	4.03 ± 0.54	3.7 ± 1.05
Nucleus length			6.3 ± 0.95
Nucleus width			2.9 ± 1.14

are fewer and larger than in past described infections, and become consolidated within a pigment dust enclave, where they may remain aggregated in some gametocytes.

Plasmodium (*Haemameoba*) sp.

Lanius tigrinus

***Locality.* –** Malaysia: Pasoh, 1998; Singapore: Nee Soon, 1998.

***Description.*–**Available blood films were faded. The infected erythrocytes are distorted with a displaced laterally or distally nucleus. They contain either a schizont, with 5–12 nuclei, or one to two usually rounded gametocytes (4.8 ± 1.2 × 3.44 ± 1.07; range 3.3–5.94 × 2.2–5.06) with a few (one to five), sometimes aggregated coarse pigment granules, and outlines of one or two vacuoles. The pigment granules in some trophozoites are aggregated, or encircle the vacuole; the faded state of the stain obscures other details. Infected erythrocytes are 12.7 ± 0.91 × 7.1 ± 0.91 with 5.72 ± 0.39 × 2.3 ± 0.30 nuclei.

***Remarks.* –** Laird (1997) lists *Lanius* spp. among the commonest hosts of *Pla.* (*H.*) *matutinum* (Huff, 1937) Coradetti et al., 1960 in SE Asia. Originally isolated from *Turdus migratorius* in North America, most of the descriptions were made from infections in experimental hosts. The redescription (Corradetti et al., 1960) from the European host, *Turdus iliacus*, as cited by Laird, also incorporates data from experimental hosts. Neither the faded state of our specimens, nor Laird's description and illustrations, including of the infection from *Lan. cristatus*, can provide an unambiguous identification of the *Plasmodium* species found.

Leiothrix argentauris (Hodgson) (Timaliidae)

Haemoproteus timalus Bishop, Bennett & Peirce, 1991

***Locality.* –** Malaysia: Fraser's Hill, May 2003.

***Type species.* –** *Turdoides rubiginosus* (Africa).

***Description and remarks.* –** The gametocyte lacks the projections described in the type material (from the African host, see comments to *Hae. timalus* from *Garrulax* spp.). The erythrocytes infected by macrogametocytes are 13.6 ± 0.61 × 5.7 ± 0.52 in size, with 5.7 ± 0.54 × 2.1 ± 1.15 nucleus and NDR 0.79 ± 0.06. The microgametocyte-infected erythrocytes are 13.8 ± 0.46 × 6.1 ± 0.32 in size, with 5.5 ± 0.65 × 2.4 ± 0.28 nucleus and NDR 0.78 ± 0.16. The macrogametocytes are 11.6 ± 1.48 (cross: 10.5 ± 0.52) × 1.2 ± 0.38 in size and 2.7 ± 0.84 × 1.5 ± 0.45 nucleus; their distal ends are expanded; the nucleus is located in this distal part. The microgametocytes are 11.2 ± 0.44 (cross 10.8 ± 0.50) × 1.5 ± 0.27 in size with inconspicuous nucleus. The pigment granules in both gametocytes number six to eleven; some are robust/large and often clumped into one to two aggregates.

Leucocytozoon sp. 7
(Fig. 13)

***Locality.* –** Malaysia: Cameron Highlands, Sep.2002 and Jun.2003.

***Description.* –** In each was found one macrogametocyte 8.7 × 7 and 11.9 × 6.3 in size, and of a perimeter of 25.2 and 30.8, respectively. The host cell nuclei (23 and 29) enclose 92 and 93% of the plasmodium, respectively. The cytoplasm contains a few vacuoles and some granules.

***Remarks.* –** The tight embracing by the host nucleus is reminiscent of the "*Leu. majoris*" -like *Leucocytozoon* (sp. 5) from species of *Garrulax*, another member of Timaliidae.

Lonchura fuscans (Cassin) (Estrildidae)

Haemoproteus orizivorae Anschutz, 1909
(Table 7)

***Locality.* –** Malaysia: Sarawak.

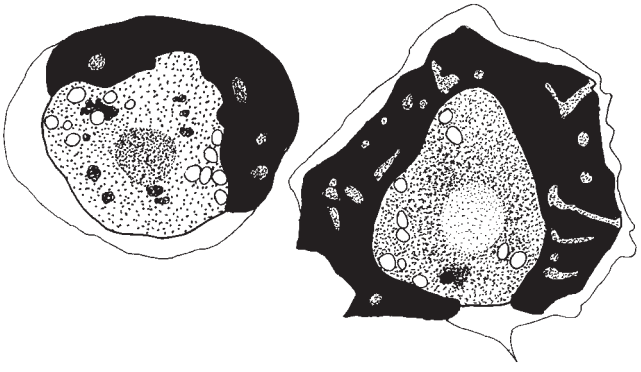

Fig. 13. *Lecocytozoon* sp. 7, macrogametocyte, from *Leiohtrix argentauris* (right), *Leucocytozoon* sp. 10, macrogametocyte from *Oriolus cruentus* (left), Malaysia.

***Type host.* –** *Lonchura orizivora* (L.) imported to Buenos Aires (Anchultz 1909); later findings: *Lon. orizivora*, West Java, *Lon. punctata*, Bangkok, *Lon. malabarica*, Gujarat State India (Bennett & Peirce, 1991).

***Remarks.* –** The gametocytes grow around the nucleus of the host erythrocyte, but never enclose it completely. Fully-grown gametocytes fill the erythrocyte's entire space by displacing its nucleus. Growing gametocytes initially adhere to the nucleus and contain approximately 20 small to medium-sized pigment granules. The macrogametocyte cytoplasm is granular and consists of minute vacuoles; the macrogametocyte nucleus is conspicuously large [not mentioned in Valkiunas, 1997 (2005), but shown in his Figures].

Luscinia cyane (Pallas) (Muscicapidae)

Haemoproteus wenyoni Mello, Sa,
Sousa Dias & Noronha, 1916.
(Table 7)

***Locality.* –** Malaysia: Johor, 2003.

***Type host.* –** *Orthotomus sutorius* (India).

***Remarks.* –** The gametocytes extend alongside the erythrocyte nucleus, with a slight adherence. Compared with the mild nuclear displacement reported in the type material from the type displacement of the nucleus varies from extreme to negligible (NDR 0.27–1.0 in macrogametocyte and 0.11–0.75 in microgametocyte-infected cells). Both gametocytes otherwise conform with the type description and our description from a host congeneric to the type host (*Ort. sepium*, see vide). The pigmented granules number 14–20 (20–23 in the type) and are round and of moderate size. It is noteworthy that *H. wenyoni* parasitizes bird hosts of the Families Sylviidae and Timaliidae (also regarded as a subfamily of Sylvidae). Being found in a host of the family Muscicapidae may demonstrate a case of host switching (see Bensch et al., 2000).

Malacopteron **(Timaliidae)**

Haemoproteus wenyoni Mello, Sa, Sousa,
Dias & Norontha, 1916
(Table 8)

Malacopteron albogulare (Blyth); Malaysia: Sarawak.

Malacopteron cinereum Eyton; Indonesia : Java, Lingoasri mountain primary forest, 2002.

Malacopteron magnirostre (Moore); Malaysia: Pasoh, 1998; Johor, 2003.

***Type host.* –** *Orthotomus sutorius* (Nova Goa, India).

Table 7. Comparison of measurements of *Haemoproteus orizivorae* from *Lonchura fuscans* and measurements for *Haemoproteus wenyoni* from *Luscinia cyane*.

Parameters	*Hae.orizivorae* (from *Lonchura fuscans*)	*Hae.wenyoni* (from *Luscinia cyane*)
Uninfected erythrocytes	n = 7	n = 6
Length	11.4 ± 1.14	12.2 ± 0.89
Width	6.2 ± 0.65	7.2 ± 0.79
Nucleus length	5.2 ± 0.10	5.3 ± 0.53
Nucleus width	2.3 ± 0.34	2.2 ± 0.33
Infected erythrocytes with macrogametocyte	n = 15	n = 5
Length	11.8 ± 0.57	14.1 ± 0.62
Width	6.1 ± 0.62	5.6 ± 0.68
Nucleus length	5.0 ± 0.42	5.32 ± 0.40
Nucleus width	2.0 ± 0.27	2.1 ± 0.23
NDR	0.3 ± 0.20	0.65 ± 0.27
Macrogametocyte	n = 15	n = 5
Length [cross]	15.1 ± 1.95 [11.6 ± 0.57]	12.8 ±2.17 (max. 16.5) [12.1 ± 0.81]
Width	3.42 ± 0.50	2.3 ± 0.37
Nucleus length	3.2 ± 0.62	2.5 ± 0.30
Nucleus width	2.8 ± 0.5	2.0 ± 0.10
Infected erythrocyte with microgametocyte	n = 2	n = 5
Length	12.3,13.4	13.9 ± 0.49
Width	6.4, 7.5	6.1 ± 0.74
Nucleus length	5.5, 7.7	5.4 ± 0.13
Nucleus width	2.2, 3.5	2.0 ± 0.09
NDR	0.09, 0.09	0.55 ± 0.26
Microgametocyte	n = 2	n = 5
Length	13.4, 19.8	14.5 ± 1.63
[cross]	[12.3, 13.4]	[12.7 ± 1.02]
Width	4.2, 3.3	2.8 ± 0.09
Nucleus length		6.8
Nucleus width		1.5

***Remarks.* –** Infection was scanty in all hosts found infected. All detected gametocytes conform in shape and dimensions and their impact on the infected erythrocytes. There are some discrepancies in size, but not in shape, from the ones described from the type host, *Ort. sutorius*. The pigment load is scantier or even absent (an artefact?) in some gametocytes from *Malacopteron*. The erythrocyte sizes given for *Ort. sutorius* (by Bennettt et al., 1991) are somewhat larger than in our data for both species of *Malacopteron* and *Ort. sepium* (callibration error?). See vide in *Ort. sepium* for more detailed description and comparative dimensions.

Leucocytozoon sp. 8
(Fig. 14)

Malacopteron magnum Eyton; Malaysia: Sarawak. Both examined birds were infected.

***Description.* –** All gametocytes are of the round morph. The macrogametocytes have a mean size 9.8 ± 1.35 × 8.1 ± 1.23 (n = 8), with a circumference of 28.9 ± 3.16. The cytoplasm contains moderate number of small vacuoles. The nucleus' mean size is 3.6 ± 0.69 × 2.6 ± 0.34, with a marked central or off-centre karyosome. The host-cell nucleus on the average encloses 48% (± 23.5%) of the parasite periphery, but it occurs with a wide range of cupping from 15% (cup-shaped) to 67%. The microgametocytes are few (n = 2), 8.8, 13.3 × 7, 4.9, and the nuclear region, occupying either the centre, or one side, stains more intensively. The host cell nucleus encloses 83% to 90% of the 29 to 38 long circumference of the microgametocyte.

***Remarks.* –** In the same blood films, macrogametocytes are covered from 15% to 67% by the host-cell nucleus ranged from "*Leu. fringillinarum*" to "*Leu. majoris*" morphological characteristics [sensu Valkiunas, 1997(2005)], while all the few microgametocytes found are reminiscent of *Leu. majoris* (with a cover of 83–90%). This could suggest the presence of two co-existing species, but more likely it questions (as stated elsewhere) the validity of the host-nucleus cover as a taxonomic differentiating character.

Table 8. Measurements taken from *Haemoproteus wenyoni*-infected *Malacopteron albogulare*, *M. cinereus* and *M. magnirostris*.

Parameter	*M. albogulare* (MCW11-Sarawak)	*M. cinereus* (A99-Java)	*M. magnirostris* (P98003-Malaysia)
Uninfected erythrocytes	n = 10	n = 8	n = 12
Length	10.9 ± 0.6	10.4 ± 0.43	11.43 ± 0.37
Width	6.4 ± 0.43	6 ± 0.55	7.05 ± 0.36
Nucleus length	4.9 ± 0.27	5.3 ± 0.54	5.7 ± 0.44
Nucleus width	2.4 ± 0.13	2.25 ± 0.25	2.3 ± 0.24
NDR			0.95 ± 0.05
Erythrocytes with macrogametocytes	n = 1	n = 5	n = 4 (or mic.)*
Length	12.6	11.6 ± 0.69	12.56 ± 0.54
Width	6.6	6.16 ± 0.36	6.96 ± 0.76
Nucleus length	4.8	5.6 ± 0.52	5.21 ± 0.18
Nucleus width	2.5	1.9 ± 0.65	2.2 ± 0.37
NDR	1	0.8 ± 0.17	0.7 ± 0.17
Macrogametocytes	n = 1	n = 5	n = 4 (or mic.)*
Length [cross]	14 [11.8]	14.6 ± 0.78 [11.32 ± 0.98]	12.74 ± 0.93 [11.55 ± 0.18]
Width	2.1	2.6 ± 0.64	2.7 ± 1.07
Nucleus length	1.96	2.7 ± 0.66	5.3 (*) = micr. ?
Nucleus width	1.3	3.1 ± 0.84	1.4 (*)
Erythrocytes with microgametocyte	n = 2	n = 1	
Length	11.9, 13	10.5	
Width	5.9, 8.3	6.4	
Nucleus length	4.8, 5.1	5.04	
Nucleus width	2.2, 2.6	2.1	
NDR	0.89, 0.59	0.95	
Microgametocytes	n = 2	n = 1	
Length [cross]	12.6, 13.2 [10.2,11.9]	15.4 [10.5]	
Width	1.5, 2	3.1	
Nucleus length	6.2, 7.3	5.2	
Nucleus width	1.6, 1.8	2.7	

*Faded staining did not allow differentiation into macro- and microgametocytes.

Plasmodium cf. *rouxi* Sergent, Sergent & Catanei, 1928.

Malacopteron magnum Eyton; Malaysia: Sarawak.

***Description.* –** The studied blood film contained only schizogony stages with scanty cytoplasm, with up to four nuclei and often in cross configuration (27 × 31). The cytoplasm is void of neither a globule nor a vacuole. The infected erythrocyte is unaltered and the schizont is detached from both the erythrocyte rim and its nucleus.

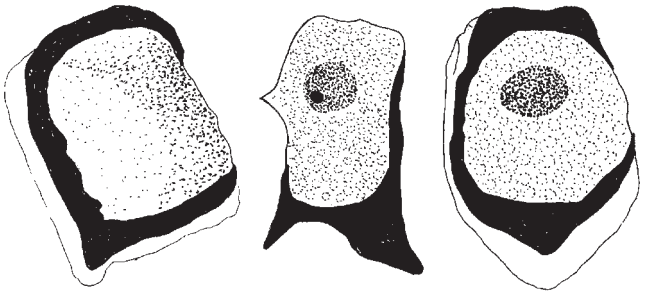

Fig. 14. *Leucocytozoon* sp. 8 from *Malacopteron magnum*, Sarawak (from left: microgametocyte and two macrogametocytes).

***Remarks.* –** This *Plasmodium* is reminiscent of *Pla.* rouxi, described from *Passer hispaniolensis* in Algeria (Sergent et al. 1928). Absence of a globule and differences in host and geographic location however suggests this *Plasmodium* to be a distinct species from *Pla. rouxi*.

Megalaima oorti (Muller) (Capitonidae)

Haemoproteus xantholaemae Zargar, 1945
(Table 9)

***Locality.* –** Malaysia: Fraser's Hill, Jul.2003.

***Type host.* –** *Megalaima haemacephala* (India).

***Remarks.* –** Four species of *Haemoproteus* were described

Table 9. Measurements of *Haemoproteus xantholaemae* from *Megalaima oorti* and of *Haemoproteus wenyoni* from *Orthotomus sepium.*

Parameters	*Hae. xantholaemae* (from *Megalaima oorti*)	*Hae. wenyomi* (from *Orthotomu sepium*)
Uninfected erythrocyte	n = 7	n = 24
Length	12.6 ± 0.79	11.39 ± 0.39
Width	7.0 ± 0.51	6.72 ± 0.54
Nucleus length	6.4 ± 0.45	5.8 ± 0.4
Nucleus width	2.9 ± 0.26	2.8 ± 0.33
Infected erythrocyte with macrogametocyte	n = 11	n = 23
Length		13.1± 0.94
Width	14.8 ± 0.93	7.0 ± 0.94
Nucleus length	7.0 ± 0.91	5.6 ± 0.4
Nucleus width	5.6 ± 0.38	2.5 ± 0.3
NDR	2.7 ± 0.38	0.71 ± 0.27
	0.58 ± 0.20	
Macrogametocyte	n = 11	n = 23
Length [cross]	14.3 [13.3 ± 1.62]	16.4 ± 1.23 [12.3 ± 0.6]
Width	2.2 ± 0.44	2.7 ± 0.51
Nucleus length	4.8 ± 0.92	3.2 ± 0.62
Nucleus width	1.7 ± 0.70	2.4 ± 0.53
Infected erythrocyte with microgametocyte	n =11	n = 11
Length	14.3 ± 0.76	12.7 ± 1.0
Width	7.0 ± 0.42	6.5 ± 0.9
Nucleus length	5.7 ± 0.52	5.5 ± 0.38
Nucleus width	2.8 ± 0.34	2.45 ± 0.34
NDR	0.66 ± 0.11	0.69 ± 0.11
Microgametocyte	n = 10	n = 11
Length [cross]	12.1–17.6 [12.0 ± 0.76]	16.7 ± 2.8 [11.8 ± 0.6]
Width	1.8 ± 0.57	2.6 ± 0.6
Nucleus length	5.9–7.7	7.1 ± 0.5
Nucleus width	1.1–1.1	2.1 ± 0.7

from species of the genus *Megalaima*. The species *Hae. xantholaemae* conforms best with the gametocytes found in *Meg. oorti*. McClure et al. (1978) found no parasites in *Meg. oorti.* It is entirely distinct from *Hae. bilobata*. Fully differentiated *Hae. cornuata* tightly adheres to the erythrocyte nucleus, while *Hae. thereicerycis, Hae. xantholaemae* and the presently described species lie parallel to the host-cell nucleus or only slightly grips it. In *Hae. thereicerycis,* the host-cell nucleus is displaced to the erythrocyte wall, and in some, to the extreme of bulging out from the erythrocyte perimeter. In this species and in *Hae. cornuata* some gametocytes are distinctly distanced from the host nucleus (artefact?). The nucleus of some of the presently studied macrogametocytes is bilobated or scattered, but not mentioned in previous descriptions. The number of pigment granules is 12–18.

Napothera brevicaudata (Blyth) (Timaliidae)

Leucocytozoon sp. 9

Locality. – Malaysia: Cameron Highlands, 2002.

Description. – Only two macrogametocytes are found, 10.1 × 8.8 and 11.3 × 7 in size, with 3.5 × 2.7–2.8 nuclei (karyosome not visible). Their periphery 30.1, 30.8 is covered by 18.9 (63%) and 25.2 (82%) of the host cell-nucleus.

Oriolus cruentus Robinson & Kloss (Oriolidae)

Leucocytozoon sp. 10
(Fig. 13)

Locality. – Malaysia: Fraser's Hill, Aug.2001.

Description. – One macrogametocyte found, 7.3 × 6.9 in size, 23.8 perimeter, and 2.8 × 2.4 nucleus with visible karyosome. The cytoplasm contains vacuoles. The 12.6 host-cell nucleus covers 53% of the gametocyte.

Remarks. – Entirely different from *Leucocytozoon* sp. found in vagrant *Ori. oriolus* in Israel (Paperna, unpublished data).

***Orthotomus* (Sylviidae)**

Haemoproteus wenyoni Mello, Sa, Sousa, Dias et Noronha, 1916
(Table 9)

Orthotomus sepium Horsfield

***Locality.* –** Indonesia: Java, Lingo lowland secondary forest, Jun.2002 and Jul.2001; Lingo mountain secondary forest, Jul.2001. In one bird heavy infection, including trophozoites.

***Type host.* –** *Orthotomus sutorius* (Nova Goa, India).

***Remarks.* –** The gametocytes conform in shape and approximate in size with the type specimens from Gujarat, as reported by Valkiunas [1997 (2005)]. The gamtocytes, likewise, grow around the erythrocyte's nucleus, but do not enclose it and reach both the erythrocyte's nucleus and wall. Premature gametocytes partly adjoin the erythrocyte wall or even its nucleus. Gametocytes only slightly or moderately displace the erythrocyte nucleus, but to a lesser extent than in the type specimens. The gametocytes only slightly (to moderately) displace the erythrocyte nucleus (NDR means 0.68–0.80); but a few, apparently aged, markedly displace the nucleus (NDR 0.1 to 0.6). In having larger and more numerous pigment granules, rather than smaller and fewer, presently found *Hae. wenyoni* are reminiscent of *Hae. belopolskyi*, infecting Sylviidae in western Eurasia (Bennett et al., 1991; Valkiunas, 1997). Some gametocytes (chiefly from LS062) extend spiked extentions, reminiscent of configurations reported from *Hae. timalus* (see vide) and *Hae. belopolskyi*.

Leucocytozoon sp. (juvenile)

Orthotomus sericeus Temm.

***Locality.* –** Malaysia: Sarawak. One juvenile observed in a monocyte (not measured).

Leucocytozoon sp. 11

Orthotomus sutorius (Pennant)

***Locality.* –** Malaysia: Cameron Highlands, Jun.2003. One macrogametocyte found, 12.8 × 9.2 in size with a 4.8 × 3.3 nucleus, a periphery of 36.3 covered by 23.1 (64%) host-cell nucleus. The cytoplasm contains a few vacuoles.

Pellorneum capistratum (Temm.) (Timaliidae)

Haemoproteus timalus Bennett, Bishop & Peirce, 1991
(Table 10)

***Locality.* –** Malaysia: Sarawak; Indonesia: Java, Lingo lowland secondary forest, Java; Sep.2001.

***Type host.* –** *Turdoides rubiginosus* (Kenya, East Africa). Additional hosts of *Hae. timalus* in SE Asia are *Garrulax* spp. and *Heterophasia picadoides* (Bennett et al., 1991). Infection in *Pel. capistratum* from Sarawak consisted predominantly of macrogametocytes; the one microgametocyte traced was not measured.

***Remarks.* –** The gametocytes adhere to the erythrocyte nucleus and either fill the entire space between the nucleus and erythrocyte wall or remain partly detached from the wall. Gametocytes from *Pel. capistratum* are more reminiscent of the type material than those from *Garrulax* spp. The seemingly fully-grown gametocytes never reach one or both extremities of the erythrocyte, in the type material this occur only in those not fully grown. Protrusions and spikes shown in the type description also occur in some presently reported macro- and microgametocytes. The macrogametocytes have blue-staining cytoplasm and sometimes disclose densely packed vacuoles. The pigment granules are often fewer than reported in the type material, mostly small and some accompanying a vacuole. Erythrocyte nuclear displacement is the same as in the type material. The growing young gametocytes become attached first to the erythrocyte nuclei.

***Pitta guajana* (Muller) (Pittidae)**

Leucocytozoon pittae **Bennett & Peirce, 1992**
(Fig. 15)

***Locality.* –** Indonesia: Java, Lingo mountain secondary forest, 2001.

***Description.* –** The macrogametocytes are 10.3 ± 0.63 × 8.6 ± 0.50 in size (n = 4) with 3.3 ± 0.55 × 2.7 nucleus, usually with a conspicuous nucleolus enclosed with extended (not cup-shaped) host-cell nucleus, 11.3 ± 2.0 long. The latter encloses 28–48% (38 ± 8.3%) of the gametocytes' circumference, which measures 30 ± 1.9. The macrogametocyte blue-staining cytoplasm is dotted with vacuoles. The two microgametocytes

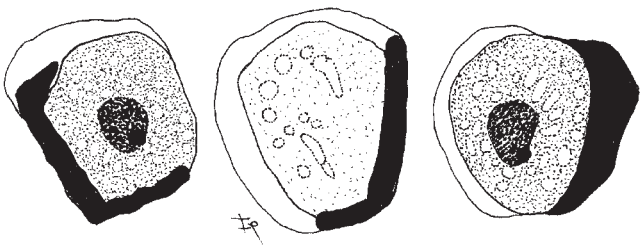

Fig. 15. *Leucocytozoon pittae* from *Pitta guajana*, Java (from right: macrogametocyte, microgametocyte and macrogametocyte).

Table 10. Comparison of measurement of *Haemoproteus timalus* from *Pellorneum capistratum* from Sarawak and Java.

Parameter	ex Java (LSO7-9)	ex Sarawak (MCW14)
Uninfected erythrocytes	n = 14	n = 20
Length	12.0 ± 0.57	10.7 ± 0.49
Width	6.7 ± 0.47	6.6 ± 0.33
Nucleus length	5.5 ± 0.33	5.0 ± 0.42
Nucleus width	3.1 ± 0.25	3.3 ± 0.17
NDR	0.95 ± 0.03	0.95 ± 0.04
Erythrocytes with macrogametocytes	n = 9	n = 6
Length	12.4 ± 0.75	12.5 ± 0.88
Width	6.2 ± 0.54	6.2 ± 0.44
Nucleus length	5.1 ± 0.25	5.3 ± 0.71
Nucleus width	2.7 ± 0.31	2.2 ± 0.19
NDR	0.76 ± 0.19	0.87 ± 0.09
Macrogametocytes	n = 9	n = 6
Length [cross]	11.6 ± 1.56 [9.8 ± 0.72]	11.0 ± 1.44 [10.5 ± 1.14]
Width	1.6 ± 0.43	2.2 ± 0.38
Nucleus length	2.0 ± 0.56	2.6 ± 0.51
Nucleus width	1.5 ± 0.23	1.6 ± 0.50
Erythrocytes with microgametocyte	n = 7	
Length	12.7 ± 0.72	
Width	6.4 ± 0.41	
Nucleus length	5.1 ± 0.39	
Nucleus width	2.8 ± 0.61	
NDR	0.76 ± 0.14	
Microgametocytes	n = 7	
Length [cross]	12.6 ± 1.45 [10.5 ± 0.41]	
Width	2.0 ± 0.27	
Nucleus length	6.3 ± 0.66	
Nucleus width	1.6 ± 0.33	

found are 10.1–10.3 × 8.3–6.4 in size, enclosed with 12.6–15.4 extended host-cell nucleus, which encloses 40 and 50% of the gametocytes' circumference, respectively, which measures 31.

***Remarks.* –** Valkiunas [1997 (2005)] considered *Leu. pittae* (together with many other species) as junior synonym of *Leu. fringillinarum*. Both the macrogametocytes and microgametocytes presently found in *Pit. guajana* are larger and differ distinctly from *Leu. fringillinarum* (described from the type host *Fringilla coelebs*) in being extended and elongated rather than cup-like around the host-cell nuclei. We therefore consider *Leu. pittae* a valid species.

Pomatorhinus hypoleucos (Blyth) (Timaliidae)

Leucocytozoon sp. 12
(Fig. 16)

***Locality.* –** Malaysia: Fraser's Hill, Oct.2002 and Feb.2003.

***Description.* –** Two macrogametocytes were found in each host (n = 4), 9.4 ± 2.29 × 7.1 ± 1.77 in size with a 28.9 ± 4.5 circumference. The cytoplasm is very vacuolated and the nucleus is 2.5 ± 1.09 × 2.1 ± 0.95 in size. The 20.4 ± 4.42 host-cell nucleus covers 70 ± 0.05% of the gametocyte.

Psittacidae

Haemoproteus handai Maqsood 1943
(Table 11)

Cacatua sulphurea (Gmelin)

***Locality.* –** Singapore: urban, free-ranging, 2001.

Loriculus galgulus L.

***Locality.* –** Malaysia: Pasoh, 1998.

***Type host.* –** *Psittacula cyanocephala* (Lahore, Pakistan).

Table 11. Measurements of *Haemoproteus handai* from *Cacatua sulphurea* from Singapore.

Parameter	*Cacatua sulphurea* (Singapore)
Uninfected erythrocytes	n = 14
Length	12.7 ± 0.6
Width	7 ± 0.6
Nucleus length	6.6 ± 0.74
Nucleus width	2.8 ± 0.24
Erythrocytes with macrogametocytes	n = 6
Length	15.6 ± 1.9
Width	8.1 ± 0.51
Nucleus length	6.8 ± 0.53
Nucleus width	2.4 ± 0.22
NDR	0.65 ± 0.19 (0.41–0.85*)
Macrogametocytes	n = 6
Length [cross]	15.4 ±2.41 [13.4 ± 0.5]
Width	3.2 ± 0.7
Nucleus length	3.1 ± 0.61
Nucleus width	3.1 ± 0.45
Erythrocytes with microgametocyte	n = 11
Length	14.96 ± 0.69
Width	7.4 ± 0.22
Nucleus length	6.2 ± 0.47
Nucleus width	6.2 ± 0.47
NDR	0.67 ± 0.16 (0.4–0.9*)
Microgametocytes	n = 11
Length [cross]	18.1 ± 3.24 [13.8 ± 0.53]
Width	2.5 ± 0.65
Nucleus length	~25
Nucleus width	~12

***Remarks.* –** *Cacatua sulphurea* was kept in the Singapore Zoological Gardens veterinary clinic. Initially the infection was moderate, predominantly by microgametocytes (11:4); in the latest checks, two weeks later, there was an onset of a relapse. Two addional specimens of free ranging *Cac. sulphurea* and one *Cac. galerita* from Jurong BirdPark in Singapore were negative. The infection in *Lor. galgulus* was scanty and the stain was faded: only six infected erythrocytes were detected, two with typical *H. handai* microgametocytes (size: 22–24 [cross: 12.7, 14.5] × 1.98–2.42) and four with premature macrogametocytes and young gametocytes.

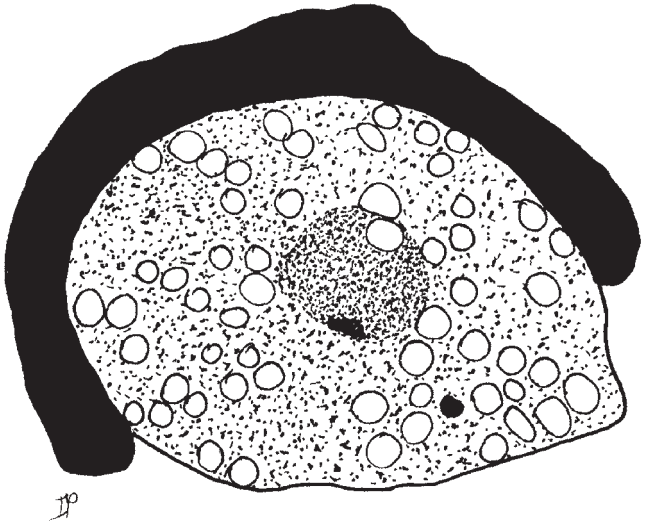

Fig.16. *Leucocytozoon* sp. 12 from *Pomatorhinus hypoleucos*, Malaysia (macrogametocyte).

Both the macro- and microgametocytes exhibit wide morphological diversity. Bennett & Peirce (1986) and Valkiunas [1997 (2005)] mentioned the complete occupation of the erythrocyte as a diagnostic feature, but in the *Cac. sulphurea* blood very few completely invaded erythrocytes were traced. More characteristic to this species are the formation of numerous projections seemingly with aging, in both the macro- and microgametocytes. Projections are absent in premature and seemingly not fully-matured gametocytes. Together with large (aged) gametocytes bearing projection also occur large (aged) gametocytes with smooth surfaces. Gametocytes both with, and without, projections have variable effect on the host cell: all infected erythrocytes become somewhat enlarged, their nuclei either remain in a median position, or become displaced or rotated. The NDR is segregated into two groups: approximately 0.4 and

Table 12. Measurements of *Haemoproteus* spp. from Pycnonotidae.

Parameter	*Hae. otocompsae* (LS2)	*Hae. sanguinis* (LS2)	*Hae. sanguinis* (SO7-9)
Uninfected erythrocytes	n = 12	same	n = 12
Length	11.28 ± 0.12		12.2 ± 0.81
Width	7.20 ± 0.42		7.1 ± 0.41
Nucleus length	5.42 ± 0.29		6.3 ± 0.37
Nucleus width	2.8 ± 0.19		2.9 ± 0.37
Erythrocytes with macrogametocytes	n = 4	n = 5	n = 7
Length	11.56 ± 0.21	12.3 ± 0.42	13.3 ± 0.89
Width	6.76 ± 0.49	6.87 ± 0.61	7.2 ± 0.54
Nucleus length	5.36 ± 0.30	5.28 ± 0.66	5.9 ± 1.22
Nucleus width	2.59 ± 0.23	2.46 ± 0.24	2.8 ± 0.53
NDR	0.72 ± 0.09	0.82 ± 0.17	0.71 ± 0.14 (0.78 ± 0.07)
Macrogametocytes			
Length [cross]	13.11 ± 3.1 [10.51 ± 0.94]	12.98 ± 0.9 [11.1 ± 0.83]	12.4 ± 1.57 [11.6 ± 0.74]
Width	2.46 ± 0.55	2.15 ± 0.39	2.01 ± 0.47
Nucleus length	2.86 ± 0.47	2.37 ± 0.29	2.4 ± 0.47
Nucleus width	2.13 ± 0.61	1.8 ± 0.33	1.2 ± 0.49
Microgametocytes	n = 4	none	n = 4
Length [cross]	14.5 ± 1.41 [10.8 ± 0.75]		12.97±1.29 [12.15 ± 0.9]
Width	3.62 ± 0.29		2.01 ± 0.32
Nucleus length	4.78 ± 0.92		8.6 ± 2.86
Nucleus width	2.84 ± 0.36		1.7 ± 0.14

approximately 0.7. Pigment granules, numbering 15 to 26 are conspicuous and scattered; in some smooth surfaced gametocytes, they tend to aggregate into one or several masses. Early gametocytes located in the erythrocyte are detached from both the erythrocyte wall and nucleus and grow into elongated plasmodia, sometimes undulating and remain detached from both the cell wall and nucleus. Only with advanced differentiation do the gametocytes associate intimately with the erythrocyte nuclei.

Infections have been reported from numerous parrots of many species from Southeast Asia (Bennett & Peirce, 1986). Miltgen et al. (1981) described *Hae. handai* schizogony in muscle fibres of *Psittacula roseata* from Thailand.

Pycnonotidae

Haemoproteus sanguinis Chakravarty & Kar, 1945 (Table 12)

Alophoixus bres Lesson [syn. ***Criniger bres*** (Lesson)]

Locality. – Malaysia: Johor, 2003; Indonesia: Java, Lingo mountain secondary forest, Jul.2001.

Criniger ochraceus Moore

Locality. – Malaysia: Fraser's Hill, Nov.2002 and May 2003.

Pycnonotus cyaniventris Blyth

Locality. – Malaysia: Johor, 2003.

Pycnonotus erythrophthalmos (Hume)

Locality. – Malaysia: Johor, 2003.

Pycnonotus goiavier (Scopoli)

Locality. – Malaysia: Cameron Highlands, Jun.2003 and Nov.2003.

Pycnonotus plumosus Blyth

Locality. – Malaysia: Sarawak.

Pycnonotus simplex Lesson

Locality. – Indonesia: Java, Lingo lowland secondary forest, Apr.2001 and 2002.

Tricholestes criniger (Blyth)

Locality. – Malaysia: Johor, 2003.

Type host. – ***Pycnonotus jocosus*** , Calcutta, India.

Haemoproteus otocompsae de Mello 1935
(Table 12)

Alophoixus bres

***Locality.* –** Indonesia: Java, Lingo mountain secondary forest, Jul.2001.

Criniger ochraceus

***Locality.* –** Malaysia: Fraser's Hill, Nov.2002.

Pycnonotus cyaniventris

***Locality.* –** Malaysia: Johor, 2003.

Pycnonotus erythrophthalmos

***Locality.* –** Malaysia: Johor, 2003.

Pycnonotus goiavier

***Locality.* –** Malaysia:Cameron Highlands, Jun.2003.

Pycnonotus plumosus

***Locality.* –** Malaysia: Sarawak.

Pycnonotus simplex

***Locality.* –** Indonesia: Java, Lingo lowland secondary forest, Apr.2001 and 2002.

***Type host.* –** *Pycnonotus jocosus* (Malim, India).

***Remarks on* Haemoproteus *spp. of Pycnonotidae.* –** We are certain of the identity of *H. sanguinis* in all the examined Pycnonotidae, but we are not certain about the identity of *Hae. otocompsae*. Both occur in the same individual host, but *Hae. sanguinis* outnumbers the presumed *Hae. otocompsae* in all examined hosts. At times, differentiation between *Hae. otocompsae* and *Hae. sanguinis* is difficult. The few microgametocytes presumably of *Hae. otocompsae* seen in the Javan material occupy three-quarters or more of the erythrocyte (robust) while grossly displacing the erythrocyte nucleus (NDR 0.47; in Rahal et al. (1987) description NDR = 0.55). In the Malaysian material, they cause swelling of the erythrocyte without displacing its nuclei. The microgametocytes of many *Haemoproteus* spp., however, with aging, turn robust, and displace the host-cell nucleus. Differentiation between macrogametocytes of both species (both relatively slender) based on the degree of erythrocyte nuclear displacement (0.72 ± 0.09 vs. 0.82 ± 0.17 for *Hae. otocompsae* and *Hae. sanguinis*, respectively) is even more ambiguous. In conclusion, we have doubts as to the validity of the differences and may justify the synonymy proposed by Peirce (1984).

Leucocytozoon pycnonoti Bennett, Earle & Peirce 1992
(Fig. 17)

Alophoixus bres

***Locality.* –** Malaysia: Johor, 2003.

***Type host.* –** *Pycnonotus barbatus* (Desfontaine) (South Africa).

***Description.* –** Gametocytes are all of the round type. The macrogametocytes size is 10.6 ± 1.2 × 9.4 ± 0.64 (n = 5), with a 3.8 ± 1.1 × 2.4 ± 0.2 nuclei and conspicuous nucleolus. Their blue-staining cytoplasm contains vacuoles and black corpuscles. The 22.7 ± 1.3 host cell nucleus invests 72 ± 5.6% of the 32.6 ± 2.3 circumference in two macrogametes; however, the host-cell nucleus is residual (30 and 50 long, respectively), occupying only 21% and 30% of the macrogametocyte perimeter, respectively. The microgametocytes sizes are 8.8 ± 1.3 × 4.0 ± 1.0 (n = 3), the 20.5 ± 3.9 host cell nuclei enclose 80 ± 5.6% of the microgametocyte 25.5 ± 3.17 circumference.

***Remarks.* –** *Leucocytozoon pycnonoti* Bennett, Earle & Peirce, 1992 was described from *Pyc. barbatus* from South Africa, *Leucocytozoon* found in many Asian as well as African species including *Alo. bres* and *P. xanthopygos* were regarded by Bennett et al. (1992) as conspecific with *Leu. pycnonoti.* Valkiunas [1997 (2005)] also synonymised this species with *Leu. majoris*. The majority of the gametocytes are *Leu. majoris*-like, with over 70% of their perimeter enclosed by the host-cell, however some follow the *Leu. fringillinarum* pattern with < 40% enclosed perimeter. Such mixed character has been observed also in *Leucocytozoon* infections of *P. xanthopygos* in Israel (Paperna & Josef, unpublished data). The ambiguity of the host-cell investment as markers for differentiating species, has been already mentioned elsewhere,

Plasmodium **sp.**

Pycnonotus simplex

***Locality.* –** Indonesia: Java, Lingo lowland secondary forest,

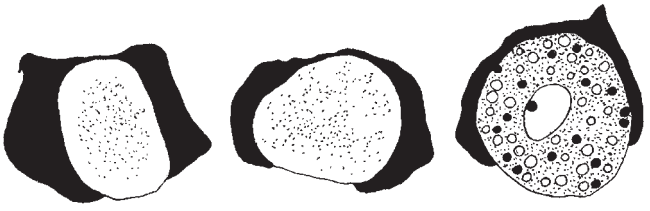

Fig. 17. *Leucocytozoon pycnonoti* from *Alophoixius bres*, Malaysia (from left: two microgametes and a macrogametocyte).

Table 13. Measurements of *Haemoproteus rhiphiduris* from *Rhipidura albicolis.*

Parameter	Data
Uninfected erythrocytes	n = 10
Length	10.8 ± 0.59
Width	6.4 ± 0.33
Nucleus length	5.2 ± 0.54
Nucleus width	2.7 ± 0.23
Erythrocytes with macrogametocytes	n = 9
Length	12.2 ± 0.86
Width	6.2 ± 0.63
Nucleus length	5.3 ± 0.33
Nucleus width	2.3 ± 0.25
NDR	0.82 ± 0.14
Macrogametocytes	n = 10
Length [cross]	13.1 ± 0.91 [11.2 ± 0.99]
Width	2.0 ± 0.23
Nucleus length	3.0 ± 0.56
Nucleus width	1.8 ± 0.28
Erythrocytes with microgametocyte	n = 10
Length	12.7 ± 0.51
Width	6.2 ± 0.35
Nucleus length	5.3 ± 0.31
Nucleus width	3.6 ± 2.87
NDR	0.72 ± 0.16
Microgametocytes	n = 10
Length [cross]	14.0 ± 1.38 [11.9 ± 0.48]
Width	2.05 ± 0.30
Nucleus length	4.6
Nucleus width	1.8

2002. Trophozoites and schizonts with three and four nuclei were observed.

Rhipidura albicollis (Vieil.) (Rhipiduridae)

Haemoproteus rhipiduri Bennett, Bishop, Peirce 1991
(Fig. 18) (Table 13)

***Locality.* –** Malaysia: Fraser's Hill, Aug. and Nov.2002, Feb. and Jul.2003.

***Type host.* –** *Rhipidura javanica*, Thailand.

***Description.* –** The gametocytes extend the entire length of the erythrocyte, filling the entire space between the nucleus and the erythrocyte pellicle and lightly adheres to the nucleus. The macrogametocyte nucleus is median, occasionally submedian, and in gravid specimens, becomes conspicuously large (up to 4.4 × 2.2). The pigment granules, usually numbering approximately 12, are typically round or sometimes spiky. The degree of nuclear displacement varies, usually slight (NDR > 0.7) to moderate (< 0.7). The early gametocyte adheres to the erythrocyte nucleus. The young gametocyte, while retaining adherence to the nucleus, extends throughout the length of the erythrocyte.

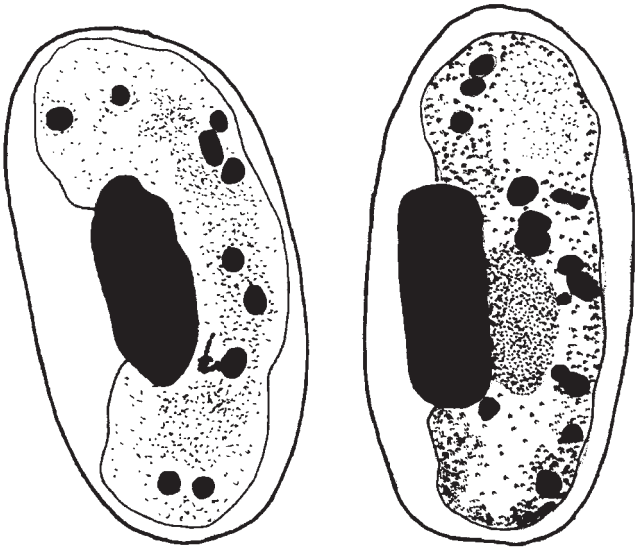

Fig. 18. *Haemoproteus rhipiduris* from *Rhipidura albicollis*, Malaysia (from left: microgametocyte and macrogametocyte).

***Remarks.* –** The recovered gametocytes closely match those of Bennett et al.'s (1991) description in shape and size. Valkiunas [1997 (2005)] synonymied *Hae. rhipiduri* with *Hae. fallisi*. However, there are many differences between the two, most conspicuously *Hae. fallisi* being stout and the macrogametocyte nuclei being distally positioned. Even the young gametocytes have an extended rather than stout shape.

***Stachyris* (Timaliidae)**

Haemoproteus tenuis, new species
(Fig. 19)

Stachyris nigricollis (Temm.)

***Locality.* –** Malaysia: Fraser's Hil, Aug. and Nov.2002.

***Description.* –** The observed gametocytes are slender, extend throughout the length of the erythrocyte with the side facing the host nucleus being curled (undulated) and only the tips touching the nucleus. Uninfected erythrocytes are 10.5 ± 0.65 × 6.4 ± 0.21 in size, with 5.4 ± 0.36 × 2.4 ± 0.27 nuclear size. The macrogametocyte-infected erythrocytes are 10.5–12.8 × 5.3– 5.9 in size, their nuclei 4.9–5.7 × 2.0–3.5 in size, and not or only lightly displaced: NDR = 0.71–0.94. Macrogametocytes (n = 3) are 13.2–15.4 (cross 11.6–12.8) long, 1.8–2.4 wide (n = 3), the nuclei 2.2–3.2 × 1.5–1.7 in size, are submedian. The microgametocyte-infected erythrocytes are 12.1 ± 0.91 × 6.1 ± 0.57 in size; their nuclei 5.5 ± 0.20 × 2.0 ± 0.16 in size and only in some cases is lightly displaced: NDR 0.64–1.0 (0.82 ± 0.12). The microgametocytes (n = 5) are 14.5 ± 1.18 (cross 11.7 ± 0.67) long and 2 ± 0.14 wide.

***Etymology.* –** Named for the slender shape of the gametocytes.

***Remarks.* –** There are only a few known species of *Haemoproteus* which retain slender gametocytes at maturity. None of such species of *Hae. balearicae* Peirce, 1973, of cranes, *Hae. contortus* Bennett, 1979, of waders and *Hae. nisi* Peirce & Marquiss, 1983, of hawks and buzzards, might be affiliated with the presently described species. It is however not beyond a doubt that these gametocytes are not fully mature.

Leucocytozoon sp. 13
(Fig. 20)

Stachyris chrysaea Blyth

***Locality.* –** Malaysia: Fraser's Hill, May 2003.

***Remarks.* –** Two macrogametocytes found: 9.4, 10.5 × 8.4, 8.5 in size with 30.1, 27.4 circumference and 2.4, 4.3 × 3.2, 2.8 nuclei. The cytoplasm contains some vacuoles and dark debris. The 23.8 and 22.4 host-cell nucleus covers 79% and 76% of the gametocyte, respectively.

Plasmodium **sp.**

***Stachyris gramniceps* (Temminck)**

***Locality.* –** Lingo lowland secondary forest, Java, Jun.2002. One erythrocyte is infected with binucleate schizont.

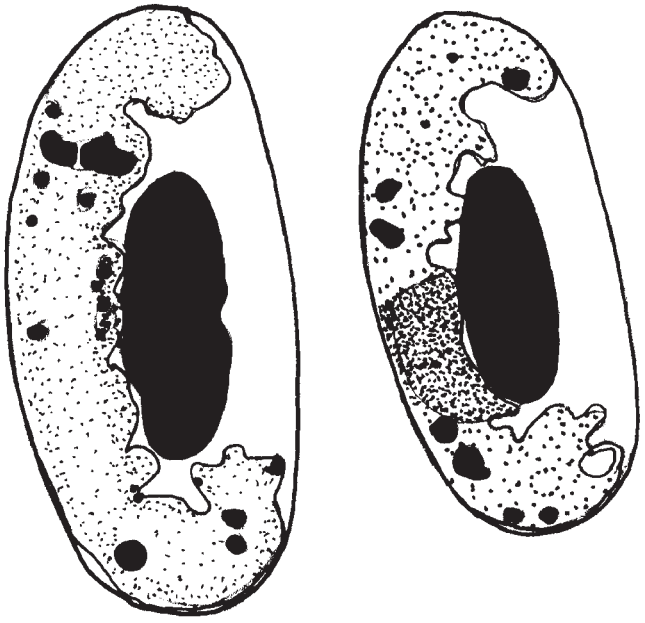

Fig. 19. *Haemoproteus tenuis* from *Stachyris nigricollis*, Malaysia (from left: microgametocyte and macrogametocyte).

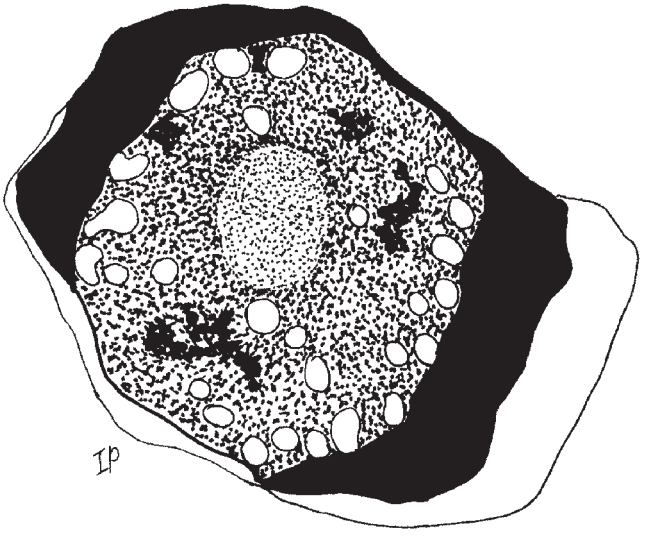

Fig. 20. *Leucocytozoon* sp.13 from *Stachyris chrysaea*, Malaysia (macrogametocyte).

Strigidae

Haemoproteus noctuae Celli & Sanfelice, 1891
(Figs. 21, 22) (Table 14)

Ninox scutulata (Raffles)

***Locality.* –** Singapore: 2001 (Owl 2),

***Type host.* –** *Athene noctua* (Rome, Italy).

***Description.* –** The gametocytes, after developing along one side of the erythrocyte cell nucleus ("halteridial" sensu Bishop & Bennett, 1989), continue to grow around the nucleus and finally their distal ends merge to form a ring around the nucleus ("circumnuclear" sensu Bishop & Bennett, 1989). The gametocytes do not adjoin tightly to the nucleus and leave spaces notably around both tips of the host-cell nucleus. The extended gametocytes do not occupy all the extra-nuclear volume of the erythrocyte and do not displace the nucleus even when they are still halteridial. The macrogametocytes form the complete ring stage more frequently than microgametocytes, but none of the gametocytes form amoeboid or projecting body outlines

***Remarks.* –** Bishop & Bennettt (1989) and later Valkuinas, [1997(2005)] regarded all the haemoproteids described from various strigid birds of diverse geographical regions which develop into circumnuclear gametocytes, to belong to the same species *Hae. noctuae* described by Celli & Sanfelice (1891) from *Athene noctua*. None of the later descriptions were made from a material from the type host. Bishop & Bennettt (1989) illustrated halterid and circumnuclear specimens with amoeboid outlines, while illustrations presented by Valkiunas [1997 (2005)] included specimens with both smooth and projecting margins. Valkiunas noted differences in the abundance of smooth and amoeboid gametocytes among host populations of different geographical locations. Gametocytes from *Athene noctua* from France (Brumpt collection, Museum National d'Histoire Naturelle, Paris) were smooth and closely resemble our observed gametocytes (Paperna, unpub. data).

Fig. 21. *Haemoproteus noctuae* from *Ninox scutulata*, Singapore (macrogametocytes).

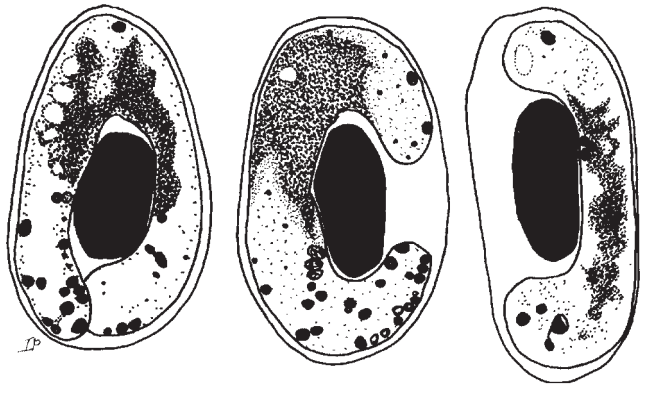

Fig. 22. *Haemoproteus noctuae* from *Ninox scutulata*, Singapore (microgametocytes).

Haemoproteus cf. *noctuae* Celli & Sanfelice 1891
(Figs. 23, 24) (Table 14)

Glaucidium brodiei (Burton)

***Locality.* –** Malaysia: Fraser's Hill, Oct.2002.

***Description.* –** The gametocytes observed are robust with either amoeboid surface and/or with numerous projections. The gametocytes embrace the erythrocyte nucleus, in few cases the tips meeting on the other end of the nucleus, or even forming a circum-nuclear body. Nuclear displacement occurs in some macrogametocyte-infected cells. The gametocytes contain variable amounts of dense-red staining granules of volutin (volutin granules according to Bishop & Bennett, 1989, stain blue to violet), the granule aggregating more usually at the gametocytes extremities, or inside their projections, if present. Sometimes, the volutin material merges into a solid eosinophilic mass. Although macrogametocyte's mean nuclear size is close to that measured in *H. noctuae*, described above, in some cases the nucleus is remarkedly larger (5.7–6.6 × 2.0 –2.4). The pigment granules are as numerous and similarly dispersed as in *H. noctuae* described above. The trophozoites are first detached of both the nucleus and erythrocyte border, but further develop attached to the nucleus; double and triple trophozoite infections were observed.

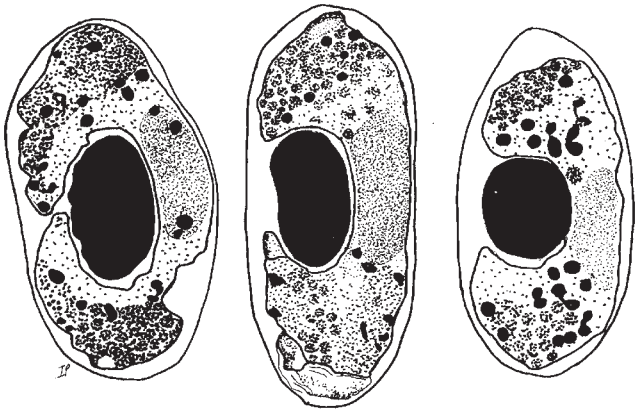

Fig. 23. *Haemoproteus* cf. *noctuae* from *Glaucidium brodiei*, Malaysia (macrogametocytes).

Table 14. Measurements of *Haemoproteus noctuae* from *Ninox scutulata* and *H.* cf. *noctuae* from *Glaucidium brodiei* (Strigidae). H = halteridial; C = circumnuclear.

Parameter	*Hae. noctuae*	*Hae.* cf. *noctuae*
Uninfected erythrocytes	n = 12	n = 12
Length	13.2 ± 0.73	13.3 ± 1.18
Width	6.4 ± 0.37	7.1 ± 0.58
Nucleus length	6.3 ± 0.55	6.3 ± 0.28
Nucleus width	2.4 ± 0.22	3.5 ± 0.36
Erythrocytes with macrogametocytes	n = 8 (H), 7 (C)	n = 9
Length	14.4 ± 0.87 (H)	15.3 ± 0.90
	14.1 ± 0.56 (C)	
Width	7.3 ± 0.80 (H)	7.2 ± 0.96
	6.7 ± 0.91 (C)	
Nucleus length	6 ± 4.3 (H + C)	5.3 ± 0.60
Nucleus width	2.4 ± 0.27 (H + C)	3.4 ± 0.41
NDR	0.87 ± 0.06(H + C)	0.63 ± 0.19
Range	0.78–0.97	0.40–0.92
Macrogametocytes	n = 9 (H), 6 (C)	n = 5 (H), 4(C)
Length [cross]	18.8 ± 2.37 (H) [12.4 ± 1.11 (H)]	18.7 ± 1.23 (H) [13.2 ± 0.90 (H)]
	25.1 ± 1.28 (C) [13.2 ± 0.33 (C)]	24.9 ± 0.84 (C) [13.1 ± 2.90 (C)]
Width	2.4 ± 0.33 (H)	3.1 ± 0.65 (H)
	2.4 ± 0.48 (C)	2.6 ± 0.40 (C)
Nucleus length	4.1 ± 0.81 (H)	4.5 ± 0.56 (H)
	3.5 ± 0.70 (C)	5.4 ± 1.08 (C)
Nucleus width	1.9 ± 0.37 (H)	2.3 ± 0.55 (H)
	1.7 ± 0.51 (C)	2.2 ± 0.19 (C)
Erythrocytes with microgametocyte	n = 7 (H), 2 (C)	n = 9
Length	13.7 ± 0.69 (H)	15.7 ± 0.43
	13.3, 14.7 (C)	
Width	7.1 ± 1.51 (H)	8.0 ± 0.82
	7.6, 6.7 (C)	
Nucleus length	5.9 ± 0.42 (H)	5.10 ± 0.57
	4.9, 6.3 (C)	
Nucleus width	2.4 ± 0.29 (H)	3.2 ± 0.28
	2.5, 2.5 (C)	
NDR	0.85 ± 0.08 (H)	0.80 ± 0.18
	0.97, 0.7 (C)	
Microgametocytes	n =7 (H), 2 (C)	n = 4 (H), 5 (C)
Length [cross]	15.7 ± 1.67 (H) [12.3 ± 0.77 (H)]	18.4 ± 1.65 (H) [13.4 ± 1.34 (H)]
	24.2, 24.5 (C) [12.5 (C)]	23.0 ± 0.84 (C) [14.7 ± 0.78 (C)]
Width	2.4 ± 0.38 (H)	2.2 ± 0.38 (H)
	2.1, 2.9 (C)	2.7 ± 0.91 (C)
Nucleus length	8.3 ± 0.49 (H)	
	7.9 (C)	
Nucleus width	1.7 ± 0.42 (H)	
	2.4 (C)	

***Remarks.* –** The *Haemoproteus* from *Gla. brodiei* is readily distinguished from the *Haemoproteus* from *Nin. scutulata*. The amoeboid surface and the projections are very conspicuous in the gametocytes from *Gla. brodiei*, but are lacking in the gametocytes from *Nin. scutulata*. The parasites of both hosts, nonetheless, largely demonstrate common features with *Hae. noctuae* as described earlier. Bishop and Bennett (1989) write that the occurrence of volutin is not consistent; in some host birds they occur repeatedly on subsequent checks, in others only occasionally. None of the gametocytes from *Nin. scutulata* contain volutin. However, volutin was present in *Hae. syrnii* from another *Nin. scutulata* (see vide). McClure et al. (1978) reported from same host from Thailand and Malaysia, three species of *Haemoproteus*, *Hae. noctuae*, *H. syrnii* and *H. cellii*, but none were described.

Although infections from wide range of strigid hosts are regarded as *H. noctuae*, the structural diversity among populations from diverse hosts and geographical locations cannot be ignored (note the considerable list of synonymised species in Bishop & Bennett (1989) and Valkiunas [1997(2005)]. Re-appreciation of the interspecific diversity among *Haemoproteus* of owls, possibly on a genetic level, may provide a different outlook on the divergence of the haemoproteids associated with strigid birds.

Haemoproteus syrnii (Mayer, 1910)
(Table 15)

Ninox scutulata (Raffles)

***Locality.* –** Singapore: Jun.2001 (Owl 1).

Strix seloputo Horsefield

***Locality.* –** Singapore: 2003 (Owl 3).

***Type host.* –** *Strix aluco* (Germany).

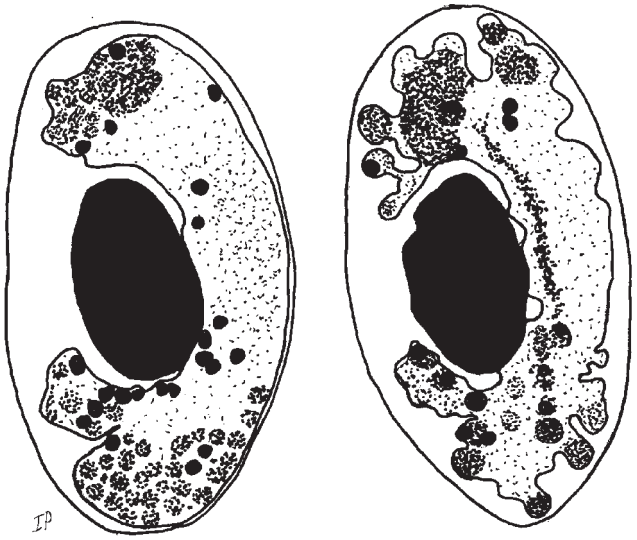

Fig. 24. *Haemoproteus* cf. *noctuae* from *Glaucidium brodiei*, Malaysia (microgametocyte).

***Remarks.* –** Descriptions of Bishop & Bennett (1989) and Valkiunas [1997 (2005)] were made from neotypes, not from conspecific hosts and from different geographical locations. Although infections in *S. seloputo* and in part in *N. scutulata* were comprised of premature gametocytes, they conformed in shape with the past descriptions. The one gravid microgametocyte found, embraces the nucleus and is loaded with volutin.

The parasites vary in their displacement impact on the host-cell nucleus (NDR ranging from 0.34 to 0.91), but the computed means conform earlier reported (NDR 0.6 vs. 0.6). A striking difference between *H. syrnii* and *H. noctuae* recovered in our material, and not emphasized earlier, is the greater concentration of pigment granules in the former. Granules (numbering 20-30) are of variable sizes but some look coarser than those from *H. noctuae*, and many gametocytes also contained variable amounts of aggregated volutin. This difference is also evident from material in our collection from other species of owls from Europe (Brumpt collection, Museum National d'Histoire Naturelle, Paris, Paperna, unpub. data).

Plasmodium ninoxi, new species
(Fig. 25)

Ninox scutulata (Raffles)

***Locality.* –** Singapore: Jun.2001 (Owl 1). Parasitaemia was predominant by gametocytes (64%). The trophozoites (35%) could be either of *Plasmodium* or of coexisting *Haemoproteus* infection, only one erythrocyte with two binucleate round schizonts was detected.

***Etymology.* –** Named by its host generic name.

***Description.* –** The erythrocyte infected with two schizonts (16.5 × 6.2, with 4.8 × 3.4 nucleus) is elongated (see table 19) with the nucleus (4.8 × 3.4) retained in median position. The schizonts were in polar positions (approximately

Fig. 25. *Plasmodium* (*Giovannolaia*) *ninoxi*, from *Ninox scutulata*, Singapore (from left: two meronts, microgametocyte, macrogametocyte).

Table 15. Measurements for *Haemoproteus syrnii* from *Ninox scutulata* and *Strix seloputo.*

Parameter	*Ninox scutulata*	*Strix seloputo*
Uninfected erythrocytes	n = 9	n = 11
Length	13.3 ± 0.80	13.6 ± 0.97
Width	7.0 ± 0.47	8.6 ± 1.12
Nucleus length	6.1 ± 0.30	6.3 ± 0.67
Nucleus width	2.8 ± 0.34	2.8 ± 0.74
Erythrocytes with macrogametocytes	n = 4	n = 10
Length	15.0 ± 2.05	14.1 ± 1.10
Width	7.1 ± 0.71	8.6 ± 0.83
Nucleus length	6.6 ± 0.64	6.3 ± 0.48
Nucleus width	2.7 ± 0.17	3.0 ± 0.34
NDR (range)	0.67 ± 0.17 (0.45–0.84)	0.63 ± 0.16 (0.34–0.91)
Macrogametocytes	n = 4 {2 mature}	n = 7
Length [cross]	{22, 22 #} [12, 13 {11, 13}]	8.2 ± 0.62
Width	2.5, 2.9 {2.7, 2.7}	3.5 ± 1.12
Nucleus length	2.4, 2.8 {2.5, 2.8}	2.4 ± 0.34
Nucleus width	1.1, 2 {2.0, 2.2}	2.8 ± 0.74
Erythrocytes with microgametocyte	n = 4	n = 7
Length	13.9 ± 0.53	14.9 ± 0.97
Width	7.4 ± 0.55	8.4 ± 0.90
Nucleus length	6.1 ± 0.48	6.4 ± 0.30
Nucleus width	2.8 ± 0.19	2.8 ± 0.35
NDR (range)	0.52 ± 0.21 (0.36–0.78)	0.68 ± 1.33 (0.50–0.86)
Microgametocytes	n =3 «1 gravid»	n =6
Length [cross]	[«22.4»]	
Width	10.7 ± 0.56 «14.1»	9.4 ± 0.85
Nucleus length	3.2 ± 0.25 «2.8»	3.4 ± 0.59
Nucleus width		

3.2–3.5 in diameter) each with two nuclei. The rounded gametocytes develop at the polar end of the erythrocyte, the macrogametocytes are 9.8–11.2 × 2.7–4.2 with 2.4–3.1 × 2.0–2.2 nucleus; the microgametocytes are 8.4–11.2 × 4.2–6.3 in size. The infected erythrocyte may become elongated or swallen, but its nucleus retains a median position: NDR in macrogametocytes 0.71–0.72, in microgametocytes 0.67–0.94. The erythrocytes infected with macrogametocytes are 14.7–16.1 × 6.2–7.7, with 5.5–6.2 × 2.9–3.1 nucleus and infected with microgametocytes are 14.0–17.9 × 4.2–7.4 with 6.7–8.0 × 2.7–2.8 nucleus (non- infected 14.5 ± 0.18 × 6.6 ± 0.27, with 6.5 ± 0.46 × 3.0 ± 0.62 nucleus, n = 5). The pigment granules, together with volutin, are aggregated in the schizonts and scattered in the gametocytes.

***Remarks.* –** No displacement of the erythrocyte nucleus, inpite of the round shape of the gametocyte excludes a possible relationship with the subgenus *Haemamoeba,* as well as with *Pla.* (*H.*) *subpraecox* (Grassi & Felletti, 1892) reported from owls. Rounded gametocytes without, or with moderate displacement of the erythrocyte nucleus are found in *Pla. juxtanucleare* Versiani & Gomes 1941, of galliform birds. Schizonts are reminiscent of the presently described, but *Pla. juxtanucleare* gametocytes are considerably smaller. Neither the schizonts, nor the gametocytes found in *N. scutulata* bear resemblance to *Pla.* (*Giovannolaia*) *fallax* Schwetz 1930, described from the strigiid *Ciccaba woodfordi.* Laird (1997) demonstrates, however, gametocytes he names *Pla. fallax* from Thai and the Philippine owls (*Otus lempiji* and *Ninox philippensis*) located "hooked around the distal end of the erythrocyte nucleus"; which might be reminiscent of the gametocytes of the presently described species.

The gametocytes sometimes cannot be readily distinguished from juvenile *Hae. syrnii* gametocytes. There are a few species with round or polar-positioned gametocytes identified as *Haemoproteus* on the argument that schizogonic stages could not be found {see Valkiunas, [1997 (2005): *Hae. ortalidum*, *Hae. parus*, *Hae. souzalopesi*}. The finding of binucleate schizonts, however, favoured the affiliation of this infection to *Plasmodium.* A PCR test of a blood samples from this host was positive for *Plasmodium*: genebank accession no. AY099035.1 (Perkins & Schall, 2002).

Plasmodium cf. *gundersi* (Bray, 1962)

Strix seloputo (Horsfield)

***Locality.* –** Singapore: 2003.
Type species: *Ciccaba woodfordi* (Smith) (Strigidae), from Liberia, Africa.

***Remarks.* –** Only two infected erythrocytes were found, each with elongate binucleated plasmodium 7.6 × 2.4 and 11.6 × 2.7. The infected erythrocytes retain their shape, with only slight displacement of the nucleus (NDR = 0.73, 0.74). These were most reminiscent of *Pla. gundersi*.

Tadorna radja (Lesson) (Radja duck) (Anatidae)

Haemoproteus nettionis **Johnson & Cleland,1909.**

***Locality.* –** Singapore: Jurong BirdPark, 1998.

***Type host.* –** *Anas castanea* (Eyton) (New South Wales, Australia). Found in one duck. The level of parasitaemia was approximately 6%, with counts containing 20% trophozoites, 20% juvenile macrogametocytes, 15% microgametocytes and 50% macrogametocytes (the micro-macrogametocyte ratio is 1:3–23% microgametocytes).

***Remarks.* –** A cosmopolitan species of ducks; another 13 ducks of diverse exotic species in the park, were negative to any blood parasites.

Trichastoma tickelli Blyth (Timaliidae)

Haemoproteus cf. *rhipiduris*
Bennett, Bishop, Peirce, 1991

***Locality.* –** Malaysia: Fraser's Hill, Feb.2003.

***Description.* –** The gravid gametocytes extend throughout the erythrocyte length, grip the nucleus and fill the space between the nucleus and the erythrocyte margins. The macrogametocyte-infected erythrocytes (n = 3) are 12.8–14.3 × 5.9–6.6 in size with a 4.8–5.5 × 2.2–2.9 nucleus, and are lightly displaced (NDR = 0.60–0.77). The uninfected erythrocytes are 12.4 ± 0.57 × 7.3 ± 0.29 in size with a 5.7 ± 0.21 × 2.6 ± 0.14 nucleus. The macrogametocytes are 12.1–15.4 long (cross 11.4–12.5), 1.1–1.8 wide. The nucleus is median, large, 2.4–3.5 × 1.3–1.8 in size, while the pigment granules are round, number 13–20, and are medium-sized. The microgametocyte-infected erythrocytes (n = 3) are 11.9–14.4 × 5.1–6.6 in size, while the 5.1–5.5 × 2.2–2.6 nucleus is very lightly displaced (NDR = 0.74–0.86). The microgametocytes are 15.4–16.5 (cross: 11.9–14.5) × 2.2–2.4 in size, with either numerous small or fewer (numbering 10–15) large pigment granules.

***Remarks.* –** The gravid gametocytes are reminiscent of *Hae. rhipiduris.*

***Turdus obscurus* Gmelin (Turdidae)**

Haemoproteus fallisi Bennett & Campbell, 1972
(Fig. 26)

***Locality.* –** Malaysia: Fraser's Hill, Nov.2002; Cameron Highlands, Mar.2003.

***Type host.* –** *Turdus migratorius* (Canada).

***Description.* –** The macrogametocyte-infected erythrocytes 13.2–14.5 × 6.6–9.9 in size, with 6.6–6.8 × 2.4–3.1 nucleus and NDR of 0.59–0.97 (n = 4). The microgametocyte-infected erythrocytes 13.2–13.3 × 6.4–7.1 in size with 5.7–6.2 × 2.4–2.9 nucleus and NDR of 0.5, 1.0 (n = 2); the uninfected erythrocytes were 13.2 ± 0.96 × 6.8 ± 0.48 in size with 6.5 ± 0.74 × 2.7 ± 0.39 nucleus (n = 9). The macrogametocytes, 9.7 ± 0.76 × 2.5 ± 0.44 in size (n = 10) only lightly, if at all, grip the host nucleus. Their 2.3 ± 0.57 × 1.4 ± 0.39 nucleus is located close to or at the distal end of the macrogametocyte. The microgametocytes are 11.4–11.9 × 2.1–3.1 in size; some are longer (14 μm) and grip the host-cell nucleus more firmly. The pigment granules, numbering 10-14, are fine or coarse, in the longer microgametocytes aggregating either on one or both distal ends. The young gametocytes develop attached to the nucleus.

***Remarks.* –** The stout gametocytes are characteristic of *Hae. fallisi*.

Leucocytozoon dubreuilli Mathis & Leger 1911
(Fig. 27)

***Locality.* –** Malaysia: Fraser's Hill, Nov.2002.

***Type host.* –** *Turdus* sp. [North Vietnam (Tonkin)].

***Description.* –** Three macrogametocytes were found, 10.5–13.3 long, 10.8–10.9 wide, with a perimeter of 33.6–36.4; the nucleus 3.4–4.2 × 2.4–3.4 in size and the cytoplasm is foamy, vacuolated. The host-cell nucleus is 21.0–21.7, covering 60 –62% of the gametocyte perimeter.

Fig. 26. *Haemoproteus fallisi* from *Turdus obscurus*, Malaysia (from left: microgametocyte and two macrogametocytes).

***Remarks.* –** Identified as *Leu. dubreuilli* by the characteristic lateral thickenings of the host-cell nucleus. Found in both Old World and New World species of *Turdus*.

Zoothera sibirica (Pallas) (Turdidae)

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

***Locality.* –** Malaysia: Cameron Highlands, Mar.2003.

***Remarks.* –** One macrogametocyte was found, no measurements were taken.

Leucocytozoon sp. 14
(Fig. 28).

***Locality.* –** Malaysia: Cameron Highlands, Mar.2003. Found in two birds, one macrogametocyte in each bird.

***Description.* –** Macrogametocyte (one measured) size 10.4 × 9.1; nucleus 4.9 × 2.8; perimeter 32.2, host cell nucleus covers 24.5, 76% of the gametocyte. The cytoplasm contains many vacuoles.

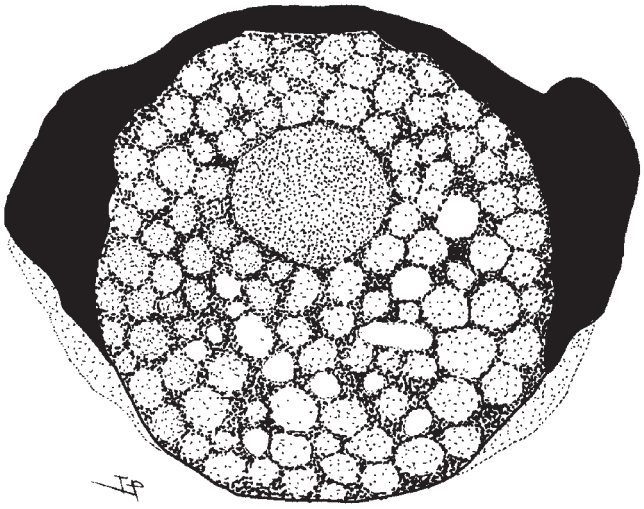

Fig. 27. *Leucocytozoon dubreuili* from *Turdus obscurus*, Malaysia (macrogametocyte).

Fig. 28. *Leucocytozoon* sp. 14. from *Zoothera sibirica*, Malaysia (macrogametocyte).

***Remarks.* –** Possibly conspecific to the above described is *Leu. maccluri*, Greiner, 1976 described from *Zoo. marginata*, Thailand (Chiang Mai), it contains both elongated and round forms. Round forms approximate in size the ones presently described and the host nucleus encloses over 50% of the gametocyte.

DISCUSSION

Haemoproteus are the most commonly found haemosproridians in avian hosts. Far less abundant are species of *Leucoytozoon* and *Plasmodium*. This is true not only for Southeast Asia but anywhere similar studies have been performed (Ashford et al., 1976; Peirce & Mead, 1976; Paperna & Josef, unpub. data). Besides the actual predominant abundance of *Haemoproteus* over the other haemosporidians, parasitaemia of *Haemoproteus* gametocytes usually persists for long durations in the peripheral blood. Some species of *Leucocytozoon* apparently aggregate in the visceral blood (liver, kidney, spleen) while being rare or absent in the peripheral blood; this has been demonstrated in the case of *Leu. gentili* infecting sparrows (*Passer domesticus biblicus*, Gill & Paperna, 2005). Since most studies of birds' blood parasites are done on the peripheral blood, such species with preferences for visceral circulation likely to escape our attention. *Plasmodium* parasitaemia duration in the peripheral blood in comparison to *Haemoproteus* is restricted: the schizogonic cycle in the erythrocytes may last less than a few weeks, and gametocytes, even if they persist, become very scarce [Valkiunas, 1997(2005), Paperna & Josef, unpub. data]. Findings from experimental infection may not necessarily yield similar results. Many natural infections of *Plasmodium* in birds may therefore escape detection.

The prospects for adequate specific taxonomic identification by morphological criteria are fairly good for *Haemoproteus*, while in the case of *Leucocytozoon* and *Plasmodium*, ambiguously defined limits for species bias our concept of the actual host-parasite relationships. In the case of *Haemoproteus*, we find a clearly defined morphotype associated with a particular bird host, or few closely related hosts. Matters become less decisive when we examine affiliations between parasite morphotypes and hosts among species of *Leucocytozoon* and *Plasmodium*. The morphological markers available for differential diagnosis are not clear-cut, and their interpretation may become ambiguous. Most found and described species of *Leucocytozoon* remained unnamed. The applied taxonomic distinctive character in *Leucocytozoon*: how much of the parasite perimeter is enclosed by the host-cell nucleus, has its limitations and ambiguities and cannot provide us with a sound, inclusive species differentiation system. On the other hand, the validity of an "all inclusive" species of *Leu. major* and *Leu. fringillinarum* as proposed by Valkiunas [1997 (2005)] is questionable. In the case of *Plasmodium*, both schizogonic stages and gametocytes are essential for diagnosis. Moreover, much of the definitions of species

also include traits obtained through experimental infections of canaries and other non-related bird hosts (Laird, 1997). Obviously such procedures cannot be implemented in the study of wild populations. The ultimate solution might be to introduce molecular methodology. Studies done so far (Bensch et al., 2000; 2004; Fallon et al., 2003; Waldenstorm, 2002), did not attempted, however, to link their so-called lineages (haplotypes) with the conventional (by morphology) specific identity of the parasites they studied. By failing to do this, they compromised any possibility for a critical comparison of the two methodologies.

Reported species of haemosporidians include species with apparently restricted range of distribution to one or a few closely related avian species over restricted geographical ranges and species widely distributed through their association to widely distributed hosts, which may be of the same species, genus or family. Species with restricted ranges should be expected to occur among the specialized inhabitants of the tropical rain forest. Likely examples are the following: *Hae. aegithinae* of *Aegithina tipha* and other Irenidae; *Haemoproteus* spp. found in *Alcippe peracensis* and *Heterophasia picadoides* and probably also *Hae. rhipiduri* from *Rhipidura albicolis* and *Hae. tenuis* from *Stachyris nigricollis*.

Example for a cosmopolitan range of distribution is *Hae. columbae*, host-specific to the feral and wild pigeon *Columbia livia* (Paperna & Smallridge, 2000). Species of *Haemoproteus* and apparently also a species of *Leucocytozoon* accompany Pycnonotidae also beyond the tropics. Other examples of a widely distributed species are *H. handai* found on diverse species of parrots (Bennett & Peirce, 1986); *Hae. noctuae* and *Hae. syrnii* in owls (Strigiformes, Bishop & Bennett, 1989) and *Hae. nettonis* in ducks (Williams & Bennett, 1980). A wide distribution in numerous hosts is also attained in *Hae. timalus* by its association with the bird family Timaliidae, which is represented by numerous species (bablers and others) in tropical Asia and Africa. *H. wenyoni* also occurs in numerous host species {over 20, mainly Sylviidae, Vakiunas [1997 (2005)]}. It has been nonetheless also identified from a timaliid and muscicapiid bird hosts in this study.

Migratory birds carry their associated parasites throughout their migration ranges. Not many migrants, breeding in the palaearctic zone, were included in our collection, but the best example are the thrushes. For example *Turdus obscurus*, which was found infected by two haemosporidians, which are associated with Turdidae in the holarctic zone: *Hae. fallisi* and *Leu. dubereulli* (the second was first described from a thrush in Indochina). *H. fallisi* has been found in our study in the Siberian thrush *Zoothera sibirica* [*Leu. maccluri* found on the same host is presently known only from Indochina, Greiner (1976)]. Another migrant is *Ficedula solitaria* carrying *Hae. pallidus* with it apparently from the north [Valkiunas, 1997 (2005)].

Singapore is attractive to invasive bird species, such birds, notably the Indian (house) crow (*Corvus splendens*) and the common mynah (*Acridotheres tristis)* predictably, or surprisingly, depending on the interpreter (Clay, 2003; Torchin et al., 2003), were only rarely found infected. The parasites found constituted either a fraction of the parasites they are associated with in their native country [in case of *Cor. splendens* in India: Nandi and Mandal (1978) and Bishop & Bennett (1992)], or carried newly acquired parasites (in the case of the common mynah: see Valkiunas & Iezhova, 1993 and this communication).

McClure et al.'s (1978) study, in spite of its important contribution, remains incomplete because of numerous unidentified species and thus has limited value in subsequent faunistic and biodiversity evaluation studies. Our study, in spite of its limited extent, may contribute to the understanding of the Southeast Asian biodiversity that is in constant transition (Brooks et al., 2003). It will be worthwhile to get adequate documentation on "coextinctions" of hosts and their co-evolved parasites (see Koh et al., 2004) to further evaluate the biodiversity crisis imposed on the Southeast Asian environment by anthropogenic transitions.

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