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New species of avian *Hepatozoon* (Apicomplexa: Haemogregarinidae) and a re-description of *Hepatozoon neophrontis* (Todd & Wohlbach, 1912) Wenyon, 1926

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Abstract

Seven new species of avian *Hepatozoon*, *H. lanis*, *H. malacotinus*, *H. numidis*, *H. pittae*, *H. estrildus*, *H. sylvae* and *H. zosteropis*, respectively, are described from the Laniinae, Malaconotinae, Numidinae, Pittidae, Poephilinae, Sylviinae and Zosteropidae. *Hepatozoon adiei* Hoare, 1924 is synonymised with *Hepatozoon neophrontis* (Todd & Wolbach, 1912) Wenyon, 1926 from the Accipitridae and *H. neophrontis* re-described. Four species of *Hepatozoon* described by de Beaurepaire Aragão from Brazil are reviewed and *Hepatozoon tanagrae* (de Beaurepaire Aragão, 1911) Hoare, 1924 is synonymised with *H. rhamphocoeli* (de Beaurepaire Aragão, 1911) Hoare 1924 and *H. brachyspizae* (de Beaurepaire Aragão) Hoare, 1924 with *H. paroariae* (de Beaurepaire Aragão, 1911) Hoare, 1924. Illustrations and measurements for *Hepatozoon albatrossi* Peirce & Prince, 1980, *H. atticorae* (de Beaurepaire Aragão, 1911) Hoare, 1924 and *H. parus* Bennett & Peirce, 1989 are also presented to complete the review of the known avian species. The value of some potential morphological characteristics for distinguishing species of *Hepatozoon* is discussed.

Introduction

The genus *Hepatozoon* Miller, 1908 has been classified by Levine (1988) as a genus of the Haemogregarinidae, and we accept this classification. Members of the genus *Hepatozoon* in avian hosts are represented by seven poorly known species (Bennett & Peirce, 1989). The distribution of two species, *H. atticorae* (de Beaurepaire Aragão, 1911) Hoare, 1924 and *H. parus* Bennett & Perice, 1989, seem to be widespread, whereas *H. adiei* Hoare, 1924 and *H. albatrossi* Peirce & Prince, 1980 are so far only known from the type-localities. Additionally, the full life-cycle is unknown for any of the avian species although several life-cycles are known for both mammalian and reptilian forms. Recently, Bennett *et al.* (1992) showed that an argasid tick and a flea are the probable intermediate hosts of *H. atticorae* of swallows. This paucity of knowledge arises from the fact that most infections with *Hepatozoon* are extremely light and readily overlooked, as there may be no more than one to two parasites on a blood film. Even when infections are heavy, there

has been little attempt to develop useful morphological criteria for separation of species. In addition, because of the absence of life-cycle studies, the degree of host specificity is unknown. As a result, if *Hepatozoon* infections are detected at all, they are usually dismissed as "*Hepatozoon* sp." at best or termed "*Haemogregarina* sp." or even "*Atoxoplasma*" and then subsequently ignored.

Over the past few years, the blood smear collection of the International Reference Centre for Avian Haematozoa has assembled numerous blood films containing *Hepatozoon* spp. Most of these contain only one or two parasites and are not suitable for taxonomic study. However, several blood films have moderate to heavy infections with enough parasites per smear to provide a statistically adequate base for analysis of various morphometric parameters. It must also be assumed until proved to the contrary that as with species of both *Haemoproteus* Kruse, 1890 and *Leucocytozoon* Sambon, 1908, species of *Hepatozoon* are host-specific at the familial or sub-familial rather than at the species level. Based on this assumption, seven new species of *Hepatozoon* are described herein from the avian groups Laniidae (both Laniinae and Malaconotinae), Numidinae, Pittidae, Poephilinae, Sylviinae and Zosteropidae. *Hepatozoon adiei* is synonomised with *H. neophrontis* from the Accipitridae and re-described. To provide a complete review of all the described avian species of *Hepatozoon*, measurements of *Hepatozoon atticorae*, *H. albatrossi* and *H. parus* are also repeated while the status of *Hepatozoon brachyspizae*, *H. paroariae*, *H. rhamphocoeli* and *H. tanagrae* (all described by Beaurepaire Aragão, 1911) is reviewed. Descriptive material and illustrations for 13 avian species of the genus is now available.

Materials and methods

This study was based on blood smears collected by either collaborators around the world or by the authors. All specimens are deposited in the International Reference Centre for Avian Haematozoa (IRCAH), Memorial University of Newfoundland. The bulk of the material was derived from eastern and southern Africa. Smears were air-dried and fixed in either 100% methanol or ethanol or in May-Grünwald-Giemsa and then stained with Giemsa's stain, either in the country of origin or at IRCAH. Representative parasites were drawn with the aid of a camera lucida and the length and area measurements obtained with a Zeiss MOP-3 Digital Analyzer.

Hepatozoon Miller, 1908

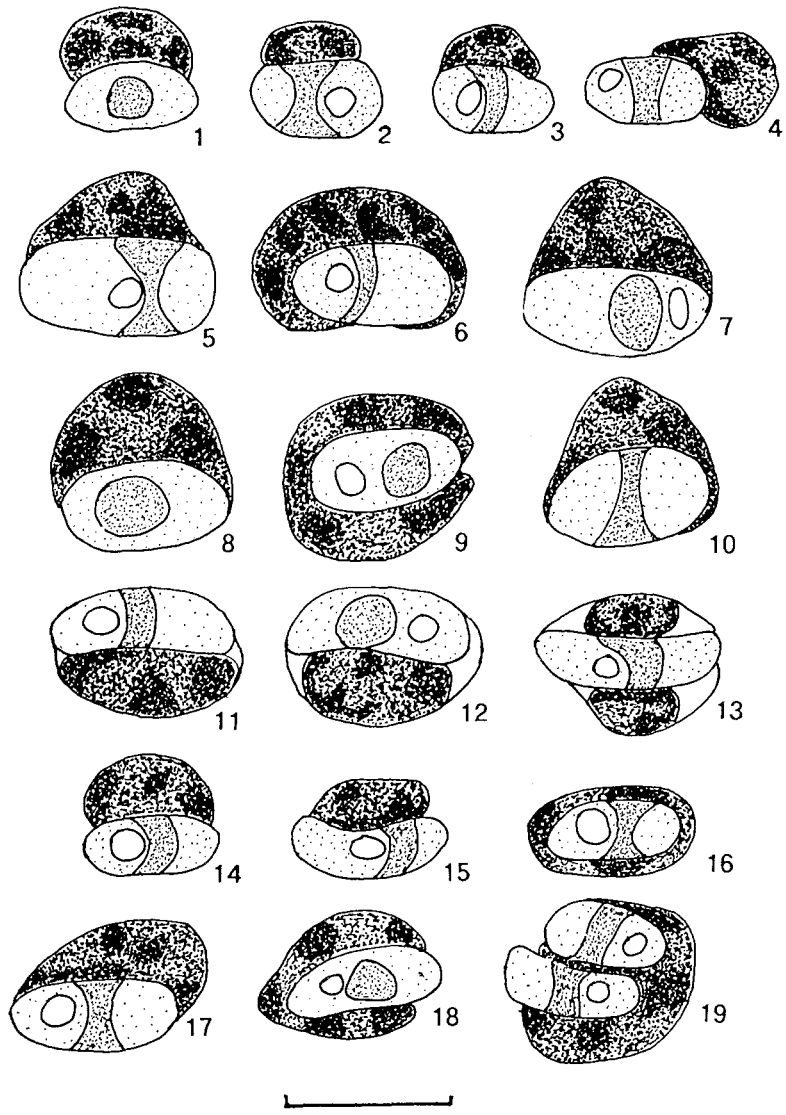
Examination of 18 blood films from 14 avian species representing seven families or subfamilies revealed the presence of seven new species of *Hepatozoon* and one previously described species. These species are described below, and are presented in the alphabetic order of the host family. Two other species of the genus are also discussed.

Hepatozoon lanis n. sp.

Type-host: Common fiscal *Lanius collaris* L. (Laniidae: Laniinae).
Type-locality: Bloemfontein, Republic of South Africa.

Description

Gametocyte (Figs. 1–4, Table I). Gametocytes associated exclusively with small monocytes which are not hypertrophied; host cell cytoplasm rarely seen; parasite lying along side host cell nucleus, occasionally attached to one end (Fig. 4); parasite occupies 57% of area of host cell-parasite complex; gametocytes small, rod-shaped, with rounded ends, broadly ovoid to more slender and slightly crescentic; nucleus relatively large, occupying 25% of area of parasite, usually band or ribbon-like and closely appressed to wall, sometimes appearing as round mass centrally in parasite (Fig. 1); parasite vacuole, when present, usually round to broadly ovoid, staining grey-green.



Figs 1–19. Composite line drawings of various species of avian *Hepatozoon*. 1–4. *H. lanis* from *Lanius collaris* (1,2) and *L. ludovicianus* (3,4). 5–7. *H. malacotinus* from *Dryoscopus cubla*. 8–10. *H. numidis* from *Numida meleagris*. 11–13. *H. pittae* from *Pitta arcuata*. 14–16. *H. estrildus* from *Lonchura cucullata*. 17–19. *H. sylvae* from *Parisoma subcaeruleum* (17,18) and *Phylloscopus trochilis* (19). *Scale-bar*: 10 μm.

Type-material

Hapantotype: Blood film no. 104670 from *Lanius collaris*, coll. D.H. de Swardt, Bloemfontein, Republic of South Africa, June 6, 1989.

Parahapantotype: Blood film no. 27157 from *Lanius ludovicianus*, coll. C.M. Herman, Kern Co., California, September 2, 1949.

Distribution: Western North America to South Africa; presumably throughout the range of the Laniinae.

Comments

Hepatozoon lanis n. sp. is the smallest of the described avian species of *Hepatozoon* and the curious side-by-side arrangement of parasite and host cell nucleus is quite unique. Both characters serve

Table I. Morphometric parameters of seven species of *Hepatozoon* from the Laniinae, Malaconotinae, Numidinae, Pittidae, Poephilinae, Sylviinae and Zosteropidae. All measurements are the mean in micrometres with the standard deviations in parentheses. N = number measured.

	H. lanis	*H. malacotinus*	*H. numidis*	*H. pittae*	*H. estrildus*	*H. sylvae*	*H. zosteropis*
N	45	36	12	20	16	24	20
Maximum length parasite	7.8 (0.8)	10.8 (0.9)	9.5 (0.8)	10.6 (0.8)	8.8 (0.8)	9.2 (1.0)	8.3 (0.7)
Maximum width parasite	3.6 (0.5)	5.1 (0.5)	5.3 (0.5)	3.7 (0.5)	3.7 (0.3)	3.5 (0.5)	3.3 (0.5)
Area of parasite	23.9 (4.2)	44.4 (6.4)	40.9 (5.3)	32.1 (4.3)	27.0 (3.6)	26.2 (4.8)	22.7 (4.0)
Length parasite nucleus	3.6 (0.8)	4.4 (1.0)	4.7 (0.9)	3.6 (0.4)	3.5 (0.5)	3.5 (0.7)	3.5 (0.8)
Width parasite nucleus	1.4 (0.4)	2.3 (0.7)	2.9 (0.8)	3.0 (0.6)	2.2 (1.1)	2.2 (0.6)	1.8 (0.7)
Area parasite nucleus	5.4 (2.0)	9.1 (2.8)	9.6 (2.1)	8.2 (2.0)	5.3 (1.5)	5.9 (2.3)	5.3 (1.9)
Diam. parasite vacuole	1.8 (0.4)	2.4 (0.4)	1.9 (0.1)	1.7 (0.4)	2.1 (0.2)	1.5 (0.4)	1.9 (0.3)
Area parasite vacuole	2.2 (0.8)	3.1 (0.9)	1.9 (0.2)	1.7 (0.6)	2.6 (0.6)	1.2 (0.6)	2.0 (0.6)
Area host-parasite complex	42.1 (7.3)	89.1 (10.3)	85.9 (12.8)	68.8 (9.6)	52.0 (7.8)	64.3 (8.8)	50.8 (10.3)

to readily distinguish this species. The measurements of material from the two shrikes from opposite sides of the globe and equator were remarkably close, with most measurements being identical and the remainder lying within ± 0.2 μm of each other. This remarkable similarity suggests a rather uniform genetic population.

***Hepatozoon malacotinus* n. sp.**

Type-host: Puff-backed shrike *Dryoscopus cubla* (Shaw) (Laniidae: Malaconotinae).
Type-locality: Pretoria, Republic of South Africa.

Description

Gametocyte (Figs. 5–7, Table I). Gametocytes associated exclusively with large monocytes; host cell cytoplasm and nuclear material normally surrounds at least part of parasite, and frequently appears as a cap (Fig. 5); parasite occupies 50% of area of host cell-parasite complex; gametocytes large, cylindrical to broadly ovoid (but not crescentic) with rounded ends; nucleus central to subcentral, relatively small, occupying 20% of area of parasite, either band-like and closely appressed to inside of cell wall (Fig. 6) or round and more centrally located in parasite (Fig. 7); parasite vacuole prominent and large, staining grey-green and centrally located in close association with nucleus, vacuole usually round.

Type-material
Hapantotype: Blood film no. 96955 from *Dryoscopus cubla* coll. T. Cassidy, Pretoria, Republic of South Africa, February 23, 1986.
Parahapantotypes: Blood film no. 92443 from *Dryoscopus cubla*, coll. M.A. Peirce, Balmoral, Zambia, April 11, 1980; blood film no. 106808 from *Laniarius atrococcineus*, coll. Herholdt, Nossob Camp, Cape Province, Republic of South Africa, April 26, 1989.

Other hosts and distribution: *Laniarius ferrugineus*, Transvaal. This *Hepatozoon* is known only from Malaconotinae from Kenya east and south to the Republic of South Africa, and presumably throughout the distributional range of the Malaconotinae in Africa. The apparent absence of this species from the western portion of the continent is probably due to paucity of examinations of shrikes from this area.

Comments

An *Hepatozoon* from *Dryoscopus cubla* was first described and illustrated by Peirce (1984) who refrained from naming a new species due to insufficient numbers of parasites in his material; this is probably the same species as *Hepatozoon malacotinus* n. sp. *H. malacotinus* is the largest of the described avian *Hepatozoon*. Its size and type of host cell readily distinguishes this species from *H. lanis* of the Laniinae, with which it has little similarity. In fact, the two species are so dissimilar, although the host species occupy the same

geographical range, that one might question whether the host birds are really members of the same avian family or whether they belong in quite diverse groups. In addition, this evidence suggests that the two species of *Hepatozoon* are host specific. The puff-backed shrikes are endemic to the Ethiopian region and presumably *H. malacotinus* is restricted to this region also.

***Hepatozoon numidis* n. sp**

Type-host: Helmeted guineafowl *Numida meleagris* (L.) (Phasianidae: Numidinae).
Type-locality: Onderstepoort, Republic of South Africa.

Description

Gametocyte (Figs. 8–10, Table I). Gametocytes associated exclusively with large monocytes; parasites normally aligned along one side of monocyte which forms cap-like structure (Figs. 8,10); on occasion, parasite lies within body of monocyte (Fig. 9); parasite occupies 48% of area of host cell-parasite complex; gametocytes bluntly cylindrical or broadly ovoid (but not crescentic), with rounded ends; nucleus central to sub-central, large (largest of described avian *Hepatozoon*), occupying 24% of area of parasite, usually as round mass more central in parasite but occasionally as band appressed closely to inner wall of parasite (Fig. 10); parasite vacuole, when present (in only 2 of 12 specimens seen), lightly stained grey and not associated with nucleus.

Type-material
Hapantotype: Blood film no. 116603 from *Numida meleagris*, coll. Huchzermeyer, Onderstepoort, Republic of South Africa, October, 1989.

Distribution: Presumably in sub-Saharan Africa throughout range of guineafowl. As these birds have been widely introduced around the world, *Hepatozoon numidis* may well have a wide distribution much beyond that of the endemic range of its hosts.

Comments

Hepatozoon numidis n. sp. is a large parasite, almost the size of *H. malacotinus* and rather similar in all respects. Separation of the two into distinct species is primarily based on the fact the *H. numidis* occurs in a member of the evolutionarily more primitive Phasianidae, while *H. malacotinus* occurs in a family of the evolutionarily advanced Passeriformes.

***Hepatozoon pittae* n. sp.**

Type-host: Blue-banded pitta *Pitta arcuata* (Gould) (Pittidae).
Type-locality: Sabah (North Borneo).

Description

Gametocyte (Figs. 11–13, Table I). Gametocytes associated with both large and small monocytes, parasite lying alongside host cell nucleus (Fig. 13), more rarely surrounded by host cell nucleus; parasite occupies 47% of area of host cell-parasite complex; gametocytes rod-shaped, broadly to narrowly cylindrical, usually crescentic and with rounded ends; nucleus central, large, occupying 25% of area of parasite, either as band appressed closely to inner surface of parasite wall (Fig. 11) or as round mass more deeply centred in parasite (Fig. 12); parasite vacuole small, round to ovoid, staining pale green.

Type-material
Hapantotype: Blood film no. 9449 from *Pitta arcuata*, coll. Kuntz, Sabah (North Borneo), March 23, 1965.

Other records and distribution: *Pitta sordida* from Fraser's Hill, Malaysia. The only records for *Hepatozoon pittae* are from pittas in southeastern Asia. Lack of records from India and Africa may be the result of insufficient sampling of this avian family.

Comments

Hepatozoon pittae n. sp. is one of the larger of the avian *Hepatozoon*, but the area of the host cell-parasite is not large, a reflection of the small size of the monocyte invaded; the nucleus of the parasite is also relatively large. The parasite is best recognised by being a large *Hepatozoon* that lies alongside the host cell nucleus, in a fashion similar to that shown by *H. lanis*, but this parasite is considerably larger.

***Hepatozoon estrildus* n. sp.**

Type-host: Bronze manakin *Lonchura cucullata* (Swainson)(Estrildidae: Poephilinae).
Type-locality: Copper Chalice, Zambia.

Description

Gametocyte (Figs. 14–16, Table I). Gametocytes associated exclusively with small monocytes, parasite lying within or alongside host cell nucleus; little host cytoplasm visible; parasite occupies 53% of area of host cell-parasite complex; gametocytes small, broadly ovoid to crescentic; nucleus proportionately large, occupying 24% of area of parasite, usually band or ribbon-like and closely appressed to inside wall of parasite; nuclear position variable, central to terminal; parasite vacuole prominent, usually centrally located, staining grey-green.

Type-material
Hapantotype: Blood film no. 92360 from *Lonchura cucullata*, coll. Peirce, Copper Chalice, Zambia, March 30, 1980.

Comments

Hepatozoon estrildus n. sp. is highly reminiscent of *H. lanis* of shrikes. *Hepatozoon estrildus* is a little larger in most dimensions, but it would be difficult to separate the species on purely morphological grounds. The basic reason for separation, until experimental cross-transmission proves otherwise, is that the two species occur in rather widely differing families of the Passeriformes.

***Hepatozoon sylvae* n. sp.**

Type-host: Cape tit-warbler *Parisoma subcaeruleum* (Vieil.) (Muscicapidae: Sylviinae).
Type-locality: Roodewal, Republic of South Africa.

Description

Gametocyte (Figs. 17–19, Table I). Gametocytes usually associated with small monocytes, parasites usually lying alongside host cell nucleus (Fig. 17), but sometimes surrounded by it (Fig. 18); parasite occupies only 40% of host cell-parasite complex; gametocytes small, slender, crescentic but occasionally more stubby (Fig. 17); nucleus relatively small but occupying 23% of area of parasite; nucleus usually as band appressed closely to inner surface of parasite wall, but also can be round and more deeply centred in parasite (Fig. 18); nucleus usually central in location; parasite vacuole small (Smallest of described avian *Hepatozoon*) but distinct, staining grey-green.

Type-material
Hapantotype: Blood film no. 104787 from *Parisoma subcaeruleum*, coll. D.H. de Swardt, Roodewal, Republic of South Africa, May 9, 1989.
Parahapantotype: Blood film no. 116023 from *Parisoma layardi*, coll. du Toit, Bloemfontein, May 15, 1990; blood film nos. 80390, 80396, 92114, from *Phylloscopus trochilis* coll. C.J. Mead, Tring, Herts., UK on May 13, 1979, July 1, 1978 and April 29, 1976, respectively.

Distribution: Present records indicate *Hepatozoon sylvae* occurs in members of the Sylviinae ranging from the United Kingdom to South Africa. Presumably the species occurs through the distributional range of the Sylviinae.

Comments

Hepatozoon sylvae n. sp. is one of the longer but more slender of the described species. The associated monocyte seems to undergo considerable distortion and the shape of the host cell-parasite complex is highly variable. In one monocyte from a *Phylloscopus trochilis*, two parasites were seen in a single host cell (Fig. 19), the only such occurrence noted among all the *Hepatozoon* spp. observed in this study, although de Beaurepaire Aragão (1911, Plate 3, Fig. 79) illustrated a similar condition for *H. brachyspizae* (now *H. paroariae*).

***Hepatozoon zosteropis* n. sp.**

Type-host: Pale white-eye *Zosterops pallida* Swainson (Zosteropidae).
Type-locality: Bloemfontein, Republic of South Africa.

Description

Gametocyte (Figs. 20–23, Table I). Gametocytes associated mainly with small monocytes but occasionally with larger ones; little host cell cytoplasm seen; parasite usually lies alongside host cell nucleus (small monocytes – Figs. 20,21) but within the larger ones (Fig. 22) parasite occupies 45% of area of host cell-parasite complex; gametocytes as slender rods with rounded ends, sometimes crescentic; nucleus relatively small, occupying 23% of area of parasite; nucleus as ribbon or band, closely appressed to inside wall of gametocyte but round forms not seen; nucleus located centrally; parasite vacuole, when present, a small and poorly staining organelle, usually round but sometimes ovoid, staining pale grey.

Type-specimen
Hapantotype: Blood film no. 104184 from *Zosterops pallida*, coll. Earlé, Bloemfontein, Republic of South Africa, February 25, 1989.

Comments

Hepatozoon zosteropis n. sp. is a relatively small *Hepatozoon* with little to characterise it. It is similar in appearance and morphology to both *H. lanis* and *H. estrildus*, and is considered to be separate as it occurs in a distinctive and unique family of the Passeriformes. Cross-transmission studies are required to confirm its species status.

***Hepatozoon neophrontis* (Todd & Wolbach, 1912) Wenyon, 1926**
Synonym: *Hepatozoon adiei* Hoare, 1924.

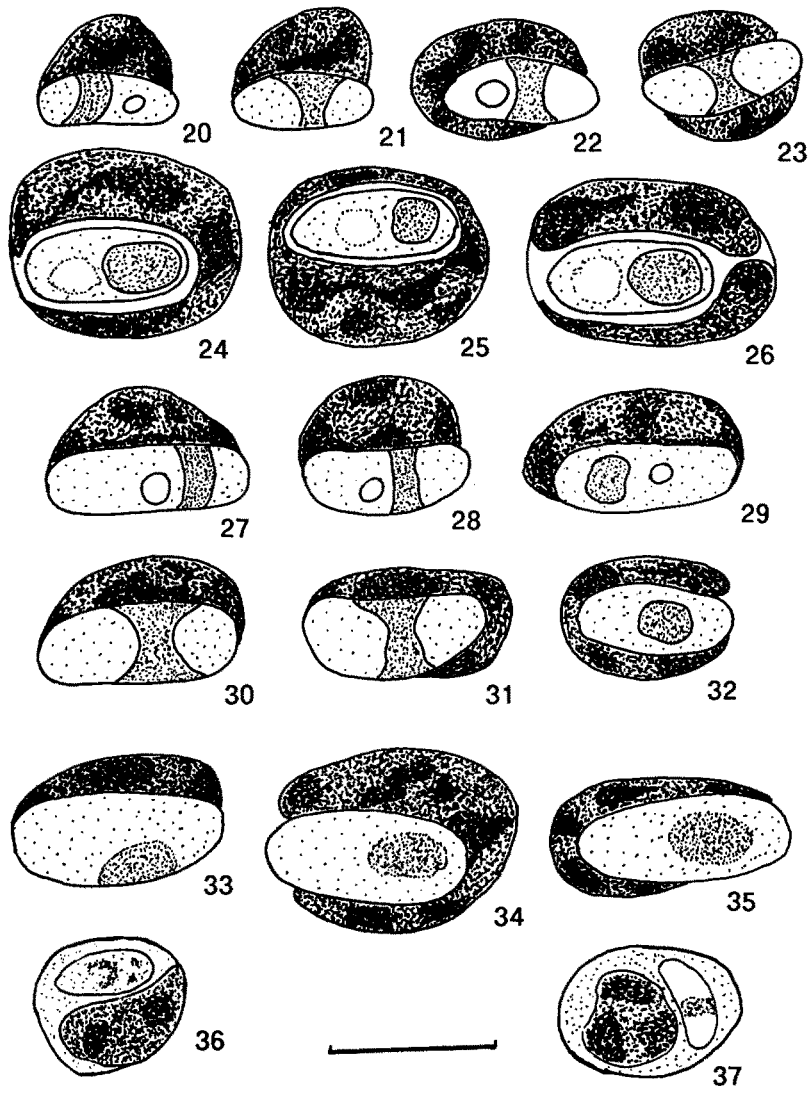
Type-host: *Necrosyrtes* (= *Neophron*) *monachus* (Temminck) (Accipitridae).

Type-locality: Sokuta, Gambia.

Description

Gametocyte (Figs. 24–26, Table I). Gametocytes associated exclusively with large monocytes which are variously distorted, sometimes lying beside host cell nucleus but usually enclosed, either partially or completely, within host cell, leaving clear almost "cyst-like wall" surrounding parasite; parasite occupies only 32% of host cell-parasite complex; gametocytes of medium size, rod-shaped (but not crescentic), with rounded ends; nucleus relatively large and prominent, occupying 25% of area of parasite, usually as round or ovoid mass, but not band or ribbon-like, terminal in position; parasite vacuole not prominent, staining very pale pink, frequently without distinct boundaries.

Type-material
Neohapantotype: Blood film no. 59344 from the lappet-faced vulture *Torgos tracheliotus*, coll. P. Mundy, Gonarezhou Game Reserve, Zimbabwe, June 20, 1975.
Paraneohapantotypes: Blood film no. 59356 from white-backed vulture *Gyps africanus*, coll. P. Mundy, Gonarezhou Game Reserve, Zimbabwe, June 20, 1975; blood film no. 59071 from *Gyps africanus*, coll. P. Mundy, Sengwa Wildlife Re-



Figs 20–37. Composite line drawings of gametocytes of various species of avian *Hepatozoon*. 20–23. *H. zosteropis* from *Zosterops pallida*. 24–26. *H. neophrontis* from *Torgos tracheliotus* (24,25) and *Aquila rapax* (26). 27–29. *H. atticorae* from *Hirundo spilodera*. Re-drawn from neohapantotype material. 30–32. *H. parus* from *Parus atricapilla*. Re-drawn from hapantotype material. 33–35. *H. albatrossi* from *Diomedea* sp. Re-drawn from parahapantotype material. 36. *H. rhamphocoeli*. Re-drawn from de Beaurepaire Aragão (1911). 37. *H. paroariae*. Re-drawn from de Beaurepaire Aragão (1911). *Scale-bar*: 10 μm.

serve, Zimbabwe, July 10, 1974; blood film no. 77561 from tawny eagle *Aquila rapax*, coll. F.W. Huchzermeyer, Onderstepoort, Republic of South Africa, July 28, 1980.

Additional hosts and distribution: *Buteo jamaicensis*, Colorado, USA; *Milvus migrans*, Kenya; *Neophron percnopterus*, Tadzikhistan; *Pandion haliaeetus*, unknown. The parasite appears to be widespread in accipitrids around the world and presumably most "haemogregarines" and "atoxoplasms" of the Accipitridae can be referred to this species.

Comments

Hepatozoon neophrontis is a parasite that is exclusively associated with large monocytes which are distorted considerably in some cases. The host

cell-parasite complex is the largest of the described avian species, but it is probable that *H. albatrossi* (for which this figure is not available), is larger. The parasite is unique in that it normally lies within the monocyte and appears to be surrounded by a clear "wall" which separates the parasite from the monocyte. This phenomenon was reported by Hoare with the parasite in an Indian "eagle", and illustrated by Zmeev (1936) for the parasite, which he termed *H. adiei* from *Neophron percnopterus*, and by Peirce & Cooper (1977) for a young parasite seen in *Milvus migrans* in Kenya. This characteristic is unique among the avian species of this genus.

Todd & Wolbach (1912) described and illustrated *Leucocytogregarina neophrontis* from a vulture, *Necrosyrtes* (= *Neophron*) *monachus*, emphasizing the clear area between the parasite and the cytoplasm of the host cell; their illustrations could have been any as illustrated herein. However, they presented no measurements. Wenyon (1926) considered that all members of *Leucocytogregarina* were, in reality, members of the genus *Hepatozoon* Miller, 1908, a move supported by Bray (1964) and Levine (1973), and Levine (1988) lists both *Hepatozoon adiei* Hoare, 1924 and *H. neophrontis* as members of the genus. Critical comparison of the illustrations and descriptions of *H. neophrontis* by Todd & Wolbach (1912) with those of *H. adiei* given by Hoare (1924) indicate that the parasites are the same. Zmeev's (1936) illustrations of *H. adiei* from the Asian vulture are also clearly *H. neophrontis* and are identical to the parasites studied herein from both African vultures and tawny eagle. Therefore, *Hepatozoon adiei* Hoare, 1924 is declared a synonym of *Hepatozoon neophrontis* (Todd & Wolbach, 1912) and all the hepatozoid parasites of the Accipitridae should be referred to this species.

Discussion

The species of *Hepatozoon* differ from other apicomplexan blood parasites in that: (1) they apparently occur only in leucocytes (usually monocytes) in birds and mammals; (2) micro- and macrogametocytes cannot be separated on the basis of parasite staining characteristics or by nuclear size; and (3) many have a round to ovoid, grey to greenish vacuole lying adjacent to the nucleus (the presence of this vacuole can be variable in some species). The nucleus of the parasites, as pointed out by Bennett & Peirce (1989) is highly variable, ranging from a disc to a ribbon or band-like organelle lying closely appressed to the inner side of the parasite wall. It is probable that the variability of these highly pleomorphic organelles makes length and width measurements of little value in species characterisation, although the area measurements may have some value.

Hoare (1924) referred five of de Beaurepaire Aragão's (1911) seven species of intra-leucocytic parasites (originally described as *Haemogregarina*) to the genus *Hepatozoon*. One of these, *Hepatozoon atticorae*, has subsequently been redescribed (Bennett & Peirce, 1989) and its potential intermediate hosts identified (Bennett *et al.*, 1992). The remaining four species were *Hepatozoon rhamphocoeli* from *Ramphocelus bresilius*, *H. paroariae* from *Paroaria dominicana* (= *P. larvata*), *H. tanagrae* from *Thraupis* (= *Tanagra*) *palmarum* and *H. brachyspizae* from *Zonotrichia* (= *Brachyspiza*) *capensis*. These four species were beautifully illustrated in full colour but were accompanied by a minimum of descriptive material. Two of the avian hosts, *Ramphocelus bresilius* and *Thraupis palmarum*, are members of the subfamily Thraupinae of the Emberizidae. The other two, *Paroaria dominicana* and *Zonotrichia capensis*, are both members of the subfamily Emberizinae of the Emberizidae and thus all four hosts belong to the same avian family. However, de Beaurepaire Aragão operated on the one host-one parasite philosophy prevalent at the time and described a new parasite for every host species.

Hepatozoon rhamphocoeli (Fig 36) was described as 8.2 μm in length and 3.3 μm in breadth, while *H. tanagrae* was 6.3 μm in length and 3.0 μm in breadth. Both species lacked the parasite vacuole (which de Beaurepaire Aragão (1911) carefully illustrated for *H. atticorae* in which it is prominent), both were crescentic and both were in large monocytes. The illustrations show virtually

Table II. Morphometric parameters of *Hepatozoon neophrontis* from the Accipitridae, *H. albatrossi* from the Diomedidae, *H. atticorae* from the Hirundinidae and *H. parus* from the Paridae. All measurements are the mean in micrometres with the standard deviations in parentheses. N = number measured.

	H. neophrontis	*H. albatrossi**	*H. atticorae**	*H. parus**
N	30	10	130	215
Maximum length parasite	9.6 (0.9)	13.0 (0.9)	9.5 (1.1)	10.4 (1.2)
Maximum width parasite	4.6 (1.1)	6.1 (0.5)	3.7 (0.5)	4.0 (0.6)
Area of parasite	36.0 (5.6)	64.2 (11.7)	29.6 (6.5)	34.0 (7.0)
Length parasite nucleus	3.9 (0.7)	4.8 (0.9)	3.0 (0.8)	4.0 (0.8)
Width parasite nucleus	3.1 (0.5)	3.3 (0.5)	1.7 (0.5)	2.2 (0.9)
Area parasite nucleus	8.8 (2.2)	12.9 (3.3)	4.1 (1.7)	8.0 (2.8)
Diameter parasite vacuole	2.5 (0.7)	–	1.2 (0.2)	2.1 (0.4)
Area parasite vacuole	3.9 (1.6)	–	1.1 (0.4)	3.1 (1.1)
Area host-parasite complex	114.7 (17.3)	not available	not available	not available

*Data from Bennett & Peirce (1989).

identical parasites, although *H. tanagrae* is somewhat smaller. Assuming that these two species show the same degree of variability as shown by other *Hepatozoon* species (Tables I,II), then the length measurements overlap. Clearly both parasites, from host species in the same subfamily, are the same species and as the first revisers (since neither of the names has any special appropriateness) *H. rhamphocoeli* is chosen as the valid name as it has precedence of position and *H. tanagrae* falls as a synonym of it (Article 24, Recommendation 24A, ICZN, 1985).

Hepatozoon paroariae (Fig. 37) is described as 6 μm in length and 3 μm in breadth, the identical measurements cited for *H. brachyspizae*. Both species are slender and crescentic in shape, lack the parasite vacuole and occur in large monocytes. On the basis of the illustrations, these two species are identical and could not be separated without knowledge of the host identify; furthermore, they occur in hosts of the same subfamily. Therefore, by designation of the first revisers (see above) *H. brachyspizae* falls as a synonym of *Hepatozoon paroariae*.

All four of de Beaurepaire Aragão's parasites occur in hosts of the same avian family, albeit in two subfamilies of the Emberizidae. All four are remarkably similar morphologically, including the two dimensions cited, occur in large monocytes and all lack a parasite vacuole. A strong case could be made to consider all four to belong to a single species. However, until experimental evidence is available to prove that species of *Hepatozoon* do cross subfamilial boundaries, it is probably unwise to make this final set of synonymies at this time, however much they maybe justified on the base of morphology.

To provide a complete review of the avian species of *Hepatozoon*, measurements (Table II) and illustrations (Figs. 27–35) of *Hepatozoon albatrossi*, *H. atticorae* and *H. parus* are also presented. The measurements (Table II) are derived from Bennett & Peirce (1989), while the illustrations (Figs. 27–35) are re-drawn from hapantotype, parahapantotype, etc., blood films. Therefore, at this time, we suggest that there are 13 valid species of avian *Hepatozoon* with descriptions, illustrations and/or measurements.

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