

Checklist of the avian species of *Plasmodium* Marchiafava & Celli, 1885 (Apicomplexa) and their distribution by avian family and Wallacean life zones

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Abstract

The 34 valid species of avian *Plasmodium* are listed with their authorities and type-hosts. *Plasmodium* species are also listed by the avian family in which they occur and by the number of avian families and species which they parasitise. A key to the subgenera of *Plasmodium* occurring in birds is presented. The distribution of the parasites by the Wallacean life zones is discussed; *Plasmodium* records in birds from the Australian zone is sharply lower than for any other life zone.

Introduction

Avian species of the genus *Plasmodium* Marchiafava & Celli, 1885 have long been of interest to parasitologists and malariologists as models for study of various aspects of human malaria. Their ease of maintenance through blood passage and/or storage in liquid nitrogen has enabled the elucidation of many aspects of the schizogonic stages of their life cycles in the vertebrate host, including the presence or absence of host specificity under purely experimental conditions. This ease of maintenance has, however, resulted in less attention being paid to the sporogonic cycles in the culicine vectors and, as a consequence, the vectors of many species of avian *Plasmodium* are still unknown.

Species of the closely-related apicomplexan genera *Haemoproteus* Kruse, 1890 and *Leucocytozoon* Sambon, 1908 are considered to be host specific at the host familial or subfamilial levels

(Bennett & Peirce, 1988; Bennett, Earlé, Peirce, Huchzermeyer & Squires-Parsons, 1991). However, avian species of *Plasmodium* have, apparently, a much broader host spectrum in many cases, although there are a number of species of *Plasmodium* that are known from only a single family, suggesting that there may be a degree of host familial specificity in this genus as well. The distribution of the avian species of *Plasmodium* by host family has never been thoroughly documented to determine whether the various species show specificity or preferences for specific avian groups, although Garnham (1966) listed the then known hosts of a number of species of avian *Plasmodium*. Since Garnham's (1966) classic treatise on *Plasmodium*, there have been numerous surveys of avian populations around the world for their haematozoan parasites. This has inevitably led to an increase in both the number of described species as well as the number of hosts and host families parasitised by specific *Plasmodium* taxa.

Table 1. Valid species of the avian *Plasmodium* together with their type-host and family. Letters in parentheses refer to the subgenera of *Plasmodium* in which the species occur: H. = *Haemamoeba*; G = *Giovannolaia*; N. = *Novyella*; Hu. = *Huffia*.

<i>Plasmodium</i> species	Type-host and family
<i>P. (G.) anasum</i> Manwell & Kuntz, 1965	<i>Anas clypeata</i> , Anatidae
<i>P. (N.) bertii</i> Gabaldon & Ulloa, 1981	<i>Aramides cajanea</i> , Rallidae
<i>P. (H.) cathemerium</i> Hartmann, 1927	<i>Passer domesticus</i> , Passeridae
<i>P. (G.) circumflexum</i> Kikuth, 1931	<i>Turdus pilaris</i> , Turdinae
<i>P. (H.) coturnixi</i> Bano & Abbasi, 1983	<i>Coturnix coturnix</i> , Phasianinae
<i>P. (N.) dissanaikei</i> de Jong, 1971	<i>Psittacula krameri</i> , Psittacidae
<i>P. (G.) durae</i> Herman, 1941	<i>Meleagris gallopavo</i> , Meleagrinae
<i>P. (Hu.) elongatum</i> Huff, 1930	<i>Passer domesticus</i> , Passeridae
<i>P. (G.) fallax</i> Schwetz, 1930	<i>Ciccaba woodfordii</i> , Strigidae
<i>P. (G.) formosanum</i> Manwell, 1962	<i>Arborophila crudigularis</i> , Phasianinae
<i>P. (G.) gabaldoni</i> Garnham, 1977	<i>Columba livia</i> , Columbidae
<i>P. (H.) gallinaceum</i> Brumpt, 1935	<i>Gallus gallus</i> , Phasianinae
<i>P. (G.) garnhami</i> Guindy, Hoogstraal & Helmy Mohammed, 1965	<i>Upupa epops</i> , Upupidae
<i>P. (H.) giovannolai</i> Corradetti, Verolini & Neri, 1963	<i>Turdus merula</i> , Turdinae
<i>P. (H.) griffithsi</i> Garnham, 1966	<i>Meleagris gallopavo</i> , Meleagrinae
<i>P. (G.) gundersi</i> Bray, 1962	<i>Ciccaba woodfordii</i> , Strigidae
<i>P. (G.) hegneri</i> Manwell & Kuntz, 1966	<i>Anas crecca</i> , Anatidae
<i>P. (Hu.) hermani</i> Telford & Forrester, 1975	<i>Meleagris gallopavo</i> , Meleagrinae
<i>P. (Hu.) huffi</i> Muniz, Soares & Batista, 1951	<i>Ramphastos toco</i> , Ramphastidae
<i>P. (N.) juxtannucleare</i> Versiani & Gomes, 1941	<i>Gallus gallus</i> , Phasianinae
<i>P. (N.) kempii</i> Christensen, Barnes & Rowley, 1983	<i>Meleagris gallopavo</i> , Meleagrinae
<i>P. (N.) leanucleus</i> Huang, 1988	<i>Passer domesticus</i> , Passeridae
<i>P. (G.) lophurae</i> Coggeshall, 1938	<i>Lophura ignita</i> , Phasianinae
<i>P. (H.) matutinum</i> Huff, 1937	<i>Turdus migratorius</i> , Turdinae
<i>P. (N.) nucleophilum</i> Manwell, 1935	<i>Dumetella carolinensis</i> , Mimidae
<i>P. (N.) paranucleophilum</i> Manwell & Sessler, 1971	<i>Tachyphonus</i> sp., Thraupinae
<i>P. (G.) pediocetti</i> (Shillinger, 1942) emend. Stabler, Kitzmiller & Braun (1973)	<i>Tympanuchus phasianellus</i> , Tetraoninae
<i>P. (G.) pinotti</i> Muniz & Soares, 1954	<i>Ramphastos toco</i> , Ramphastidae
<i>P. (G.) polare</i> Manwell, 1935	<i>Hirundo pyrrhonota</i> , Hirundinidae
<i>P. (H.) relictum</i> Celli & Sanfelice, 1891	<i>Passer hispanoliensis</i> , Passeridae
<i>P. (N.) rouxi</i> Sergent, Sergent & Catanei, 1928	<i>Passer hispanoliensis</i> , Passeridae
<i>P. (H.) subpraecox</i> Grassi & Feletti, 1892	<i>Athene noctua</i> , Strigidae
<i>P. (H.) tejerai</i> Gabaldon & Ulloa, 1977	<i>Meleagris gallopavo</i> , Meleagrinae
<i>P. (N.) vaughani</i> Novy & MacNeal, 1904	<i>Turdus migratorius</i> , Turdinae

For a detailed listing of the avian hosts parasitised by the different species of *Plasmodium*, consult Bennett *et al.* (1982) and Bishop & Bennett (1992).

These surveys have been summarised by Bennett, Whiteway & Woodworth-Lynas (1982) and Bishop & Bennett (1992).

This present study was undertaken to present both the valid avian species of the genus and to show their distribution and occurrence in the various avian families and subfamilies as they are currently systematically arranged. In addition, the distribution of the avian species of the genus by Wallacean life zone is also considered to determine whether specific taxa have marked geographical boundaries.

Materials and methods

The 34 valid species of avian *Plasmodium* (Table I) are taken as those treated by Garnham (1966) and considered valid by Greiner, Bennett, Laird & Herman (1975). Species described since that time are considered valid only if their description is accompanied by both life-cycle and host specificity studies as well as detailed comparisons with similar species. The host family distribution (Table II) is derived from the Host-Parasite Catalogue of Avian Haematozoa by Bennett *et al.*

Table II. Distribution of species of *Plasmodium* in avian families and subfamilies. Numbers in parentheses following each *Plasmodium* species indicates number of host species of that family recorded with the specific *Plasmodium* species. Certain families are listed as being infected with *Plasmodium* sp. only; no further specific diagnosis was made. Families not appearing in the table have not been recorded with *Plasmodium* at this time.

Acanthizidae – thornbills, scrubwrens	<i>Plasmodium</i> sp. (1)
Accipitridae – hawks. (6 species of <i>Plasmodium</i> recorded)	<i>P. circumflexum</i> (4); <i>P. elongatum</i> (3); <i>P. fallax</i> (3); <i>P. lophurae</i> (3); <i>P. relictum</i> (5); <i>P. vaughani</i> (1).
Alaudidae – larks (6 species of <i>Plasmodium</i> recorded)	<i>P. cathemerium</i> (2); <i>P. circumflexum</i> (2); <i>P. elongatum</i> (2); <i>P. relictum</i> (7); <i>P. subpraecox</i> (1); <i>P. vaughani</i> (3).
Alcedinidae – kingfishers (1 species of <i>Plasmodium</i> recorded)	<i>P. vaughani</i> (1).
Anatidae – ducks and geese (11 species of <i>Plasmodium</i> recorded)	<i>P. anasum</i> (1); <i>P. cathemerium</i> (1); <i>P. circumflexum</i> (14); <i>P. elongatum</i> (3); <i>P. gabaldoni</i> (2); <i>P. hegneri</i> (2); <i>P. nucleophilum</i> (2); <i>P. polare</i> (3); <i>P. relictum</i> (14); <i>P. subpraecox</i> (1); <i>P. vaughani</i> (10).
Apodidae – swifts (3 species of <i>Plasmodium</i> recorded)	<i>P. cathemerium</i> (1); <i>P. relictum</i> (1); <i>P. rouxi</i> (1).
Ardeidae – herons and bitterns (2 species of <i>Plasmodium</i> recorded)	<i>P. elongatum</i> (2); <i>P. relictum</i> (4).
Bubalornithidae – buffalo weavers (1 species of <i>Plasmodium</i> recorded)	<i>P. relictum</i> (1).
Bucconidae – puffbirds (1 species of <i>Plasmodium</i> recorded)	<i>P. relictum</i> (1).
Bucerotidae – hornbills	<i>Plasmodium</i> sp. (2).
Campephagidae – cuckoo-shrikes (1 species of <i>Plasmodium</i> recorded)	<i>P. relictum</i> (2).
Caprimulgidae – nightjars (3 species of <i>Plasmodium</i> recorded)	<i>P. cathemerium</i> (1); <i>P. nucleophilum</i> (1); <i>P. polare</i> (1).
Charadriidae – plovers (1 species of <i>Plasmodium</i> recorded)	<i>P. relictum</i> (1).
Ciconiidae – storks (2 species of <i>Plasmodium</i> recorded)	<i>P. relictum</i> (1); <i>P. vaughani</i> (1).
Cochlearidae – boat-billed stork	<i>Plasmodium</i> sp. (1).
Conopophagidae – South American gnateaters (1 species of <i>Plasmodium</i> recorded)	<i>P. vaughani</i> (1).
Columbidae – pigeons and doves (10 species of <i>Plasmodium</i> recorded)	<i>P. cathemerium</i> (5); <i>P. circumflexum</i> (6); <i>P. dissanaikai</i> (1); <i>P. elongatum</i> (3); <i>P. gabaldoni</i> (1); <i>P. lophurae</i> (3); <i>P. nucleophilum</i> (2); <i>P. polare</i> (2); <i>P. relictum</i> (11); <i>P. vaughani</i> (9).
Coraciidae – rollers (4 species of <i>Plasmodium</i> recorded)	<i>P. circumflexum</i> (1); <i>P. garnhami</i> (1); <i>P. lophurae</i> (1); <i>P. relictum</i> (1).
Corvidae – crows and jays (9 species of <i>Plasmodium</i> recorded)	<i>P. cathemerium</i> (4); <i>P. circumflexum</i> (6); <i>P. elongatum</i> (2); <i>P. gallinaceum</i> (1); <i>P. juxtannucleare</i> (1); <i>P. lophurae</i> (2); <i>P. polare</i> (1); <i>P. relictum</i> (11); <i>P. vaughani</i> (6).
Cotingidae – cotingas (1 species of <i>Plasmodium</i> recorded)	<i>P. nucleophilum</i> (1).
Cracidae – currasows	<i>Plasmodium</i> sp. (6).
Cuculidae – cuckoos (3 species of <i>Plasmodium</i> recorded)	<i>P. lophurae</i> (1); <i>P. relictum</i> (3); <i>P. vaughani</i> (3).
Dendrocolaptidae – woodcreepers (2 species of <i>Plasmodium</i> recorded)	<i>P. nucleophilum</i> (1); <i>P. vaughani</i> (1).
Dicruridae – drongos (4 species of <i>Plasmodium</i> recorded)	<i>P. dissanaikai</i> (2); <i>P. polare</i> (1); <i>P. relictum</i> (1); <i>P. vaughani</i> (1).
Drepaniidae – Hawaiian honeycreepers (1 species of <i>Plasmodium</i> recorded)	<i>P. relictum</i> (3).
Emberizidae – emberizids	
Cardinalinae – cardinals and grosbeaks (6 species of <i>Plasmodium</i> recorded)	<i>P. cathemerium</i> (1); <i>P. circumflexum</i> (1); <i>P. elongatum</i> (1); <i>P. relictum</i> (3); <i>P. rouxi</i> (1); <i>P. vaughani</i> (4).

Table II. Continued

Coerebinae – bananaquits (2 species of <i>Plasmodium</i> recorded)
<i>P. pinotti</i> (1); <i>P. vaughani</i> (1).
Emberizinae – emberizines (11 species of <i>Plasmodium</i> recorded)
<i>P. cathemerium</i> (10); <i>P. circumflexum</i> (9); <i>P. elongatum</i> (7); <i>P. fallax</i> (1); <i>P. lophurae</i> (2); <i>P. nucleophilum</i> (4); <i>P. pinotti</i> (1); <i>P. polare</i> (4); <i>P. relictum</i> (26); <i>P. rouxi</i> (2); <i>P. vaughani</i> (17).
Icterinae – grackles, troupials (9 species of <i>Plasmodium</i> recorded)
<i>P. cathemerium</i> (6); <i>P. circumflexum</i> (6); <i>P. elongatum</i> (3); <i>P. matutinum</i> (1); <i>P. nucleophilum</i> (4); <i>P. polare</i> (3); <i>P. relictum</i> (15); <i>P. rouxi</i> (1); <i>P. vaughani</i> (15).
Parulinae – wood warblers (5 species of <i>Plasmodium</i> recorded)
<i>P. cathemerium</i> (2); <i>P. circumflexum</i> (5); <i>P. polare</i> (3); <i>P. relictum</i> (4); <i>P. vaughani</i> (15).
Thraupinae – tanagers (7 species of <i>Plasmodium</i> recorded)
<i>P. cathemerium</i> (2); <i>P. circumflexum</i> (4); <i>P. nucleophilum</i> (6); <i>P. paranucleophilum</i> (1); <i>P. pinotti</i> (1); <i>P. polare</i> (1); <i>P. relictum</i> (12); <i>P. vaughani</i> (7).
Estrildidae – waxbills, munias and whydahs
Estrildinae – twinspots, firefinches (5 species of <i>Plasmodium</i> recorded)
<i>P. circumflexum</i> (1); <i>P. nucleophilum</i> (1); <i>P. relictum</i> (6); <i>P. rouxi</i> (1); <i>P. vaughani</i> (5).
Poephilinae – munias (3 species of <i>Plasmodium</i> recorded)
<i>P. circumflexum</i> (3); <i>P. relictum</i> (7); <i>P. rouxi</i> (1).
Viduiinae – whydahs (1 species of <i>Plasmodium</i> recorded)
<i>P. vaughani</i> (1).
Falconidae – falcons (3 species of <i>Plasmodium</i> recorded)
<i>P. circumflexum</i> (2); <i>P. polare</i> (1); <i>P. relictum</i> (7).
Formicariidae – antbirds (4 species of <i>Plasmodium</i> recorded)
<i>P. pinotti</i> (1); <i>P. polare</i> (1); <i>P. relictum</i> (2); <i>P. vaughani</i> (6).
Fregatidae – frigate birds (1 species of <i>Plasmodium</i> recorded)
<i>P. circumflexum</i> (1).
Fringillidae – bramblings, chaffinches, canaries
Carduelinae – canaries, siskins (7 species of <i>Plasmodium</i> recorded)
<i>P. cathemerium</i> (3); <i>P. circumflexum</i> (3); <i>P. elongatum</i> (8); <i>P. nucleophilum</i> (2); <i>P. relictum</i> (15); <i>P. rouxi</i> (3); <i>P. vaughani</i> (5).
Fringillinae – bramblings (5 species of <i>Plasmodium</i> recorded)
<i>P. cathemerium</i> (1); <i>P. circumflexum</i> (1); <i>P. lophurae</i> (1); <i>P. relictum</i> (2); <i>P. vaughani</i> (1).
Furnariidae – ovenbirds
<i>Plasmodium</i> sp. (6).
Gruidae – cranes (1 species of <i>Plasmodium</i> recorded)
<i>P. relictum</i> (1).
Hirundinidae – swallows (6 species of <i>Plasmodium</i> recorded)
<i>P. circumflexum</i> (1); <i>P. lophurae</i> (1); <i>P. nucleophilum</i> (2); <i>P. polare</i> (2); <i>P. relictum</i> (9); <i>P. vaughani</i> (4).
Jacaniidae – jacanas
<i>Plasmodium</i> sp. (2).
Laniidae – shrikes
Laniinae – true shrikes (5 species of <i>Plasmodium</i> recorded).
<i>P. cathemerium</i> (3); <i>P. garnhami</i> (1); <i>P. polare</i> (1); <i>P. relictum</i> (7); <i>P. vaughani</i> (2).
Malaconotinae – puff-back shrikes (4 species of <i>Plasmodium</i> recorded)
<i>P. circumflexum</i> (1); <i>P. relictum</i> (4); <i>P. rouxi</i> (2); <i>P. vaughani</i> (4).
Laridae – gulls and terns (2 species of <i>Plasmodium</i> recorded)
<i>P. cathemerium</i> (1); <i>P. relictum</i> (2).
Meropidae – bee-eaters (5 species of <i>Plasmodium</i> recorded)
<i>P. circumflexum</i> (2); <i>P. lophurae</i> (1); <i>P. polare</i> (1); <i>P. relictum</i> (2); <i>P. vaughani</i> (3).
Mimidae – mockingbirds, thrashers (6 species of <i>Plasmodium</i> recorded)
<i>P. cathemerium</i> (3); <i>P. circumflexum</i> (3); <i>P. elongatum</i> (3); <i>P. nucleophilum</i> (2); <i>P. relictum</i> (4); <i>P. vaughani</i> (4).
Motacillidae – wagtails, pipits (6 species of <i>Plasmodium</i> recorded)
<i>P. cathemerium</i> (3); <i>P. circumflexum</i> (5); <i>P. elongatum</i> (1); <i>P. polare</i> (2); <i>P. relictum</i> (10); <i>P. vaughani</i> (7).
Momotidae – motmots
<i>Plasmodium</i> sp. (1).
Muscicapidae – muscicapids
Monarchinae – fantails (3 species of <i>Plasmodium</i> recorded)
<i>P. nucleophilum</i> (1); <i>P. relictum</i> (2); <i>P. vaughani</i> (1).
Muscicapinae – Old World flycatchers (6 species of <i>Plasmodium</i> recorded)

Table II. Continued

	<i>P. cathemerium</i> (1); <i>P. circumflexum</i> (2); <i>P. nucleophilum</i> (2); <i>P. polare</i> (1); <i>P. rouxi</i> (1); <i>P. vaughani</i> (5).
Sylviinae. Old World warblers (9 species of <i>Plasmodium</i> recorded)	<i>P. cathemerium</i> (2); <i>P. circumflexum</i> (7); <i>P. fallax</i> (1); <i>P. giovannolai</i> (1); <i>P. nucleophilum</i> (2); <i>P. polare</i> (3); <i>P. relictum</i> (20); <i>P. rouxi</i> (5); <i>P. vaughani</i> (9).
Timaliinae – babblers (5 species of <i>Plasmodium</i> recorded)	<i>P. circumflexum</i> (1); <i>P. dissanaikiei</i> (1); <i>P. relictum</i> (5); <i>P. rouxi</i> (6); <i>P. vaughani</i> (7)
Turdinae – thrushes (11 species of <i>Plasmodium</i> recorded)	<i>P. cathemerium</i> (6); <i>P. circumflexum</i> (8); <i>P. elongatum</i> (5); <i>P. giovannolai</i> (1); <i>P. matutinum</i> (5); <i>P. nucleophilum</i> (2); <i>P. pinotti</i> (1); <i>P. polare</i> (1); <i>P. relictum</i> (30); <i>P. rouxi</i> (9); <i>P. vaughani</i> (32).
Musophagidae – turacos (2 species of <i>Plasmodium</i> recorded)	<i>P. relictum</i> (1); <i>P. vaughani</i> (1).
Nectariniidae – sunbirds (5 species of <i>Plasmodium</i> recorded)	<i>P. elongatum</i> (1); <i>P. polare</i> (1); <i>P. relictum</i> (1); <i>P. rouxi</i> (1); <i>P. vaughani</i> (7).
Oriolidae – orioles (3 species of <i>Plasmodium</i> recorded)	<i>P. relictum</i> (1); <i>P. rouxi</i> (1); <i>P. vaughani</i> (1).
Otididae – bustards (1 species of <i>Plasmodium</i> recorded)	<i>P. relictum</i> (1).
Paradisaeidae – birds of paradise	<i>Plasmodium</i> sp. (1).
Paradoxornithidae – parrot-bills	<i>Plasmodium</i> sp. (2).
Paridae – chickadees and tits (5 species of <i>Plasmodium</i> recorded)	<i>P. cathemerium</i> (1); <i>P. circumflexum</i> (4); <i>P. polare</i> (4); <i>P. relictum</i> (4); <i>P. vaughani</i> (6).
Passeridae – sparrows (9 species of <i>Plasmodium</i> recorded)	<i>P. cathemerium</i> (3); <i>P. circumflexum</i> (3); <i>P. elongatum</i> (3); <i>P. leanucleus</i> (1); <i>P. nucleophilum</i> (2); <i>P. polare</i> (3); <i>P. relictum</i> (8); <i>P. rouxi</i> (2); <i>P. vaughani</i> (6).
Phasianidae – galliforms	
Meleagrinae – turkeys (8 species of <i>Plasmodium</i> recorded)	<i>P. durae</i> (1); <i>P. griffithsi</i> (1); <i>P. hermani</i> (1); <i>P. juxtannucleare</i> (1); <i>P. kempi</i> (1); <i>P. lophurae</i> (1); <i>P. pinotti</i> (1); <i>P. tejerae</i> (1).
Numidinae – guineafowl (5 species of <i>Plasmodium</i> recorded)	<i>P. circumflexum</i> (1); <i>P. durae</i> (1); <i>P. fallax</i> (1); <i>P. relictum</i> (2); <i>P. rouxi</i> (1).
Odontophorinae – quail (2 species of <i>Plasmodium</i> recorded)	<i>P. hermani</i> (1); <i>P. pediocettii</i> (1).
Phasianinae – fowl, francolins (11 species of <i>Plasmodium</i> recorded)	<i>P. circumflexum</i> (1); <i>P. coturnixi</i> (1); <i>P. durae</i> (2); <i>P. formosanum</i> (2); <i>P. gallinaceum</i> (3); <i>P. juxtannucleare</i> (5); <i>P. lophurae</i> (2); <i>P. pediocettii</i> (4); <i>P. polare</i> (1); <i>P. relictum</i> (10); <i>P. rouxi</i> (3).
Tetraoninae – grouse (3 species of <i>Plasmodium</i> recorded)	<i>P. circumflexum</i> (2); <i>P. pediocettii</i> (5); <i>P. relictum</i> (3).
Picidae – woodpeckers (2 species of <i>Plasmodium</i> recorded)	<i>P. circumflexum</i> (1); <i>P. relictum</i> (2).
Pipridae – manakins (3 species of <i>Plasmodium</i> recorded)	<i>P. nucleophilum</i> (2); <i>P. relictum</i> (1); <i>P. vaughani</i> (1).
Pittidae – pittas (3 species of <i>Plasmodium</i> recorded)	<i>P. relictum</i> (1); <i>P. rouxi</i> (1); <i>P. vaughani</i> (1).
Platysteiridae – puffbacks, wattle-eyes (2 species of <i>Plasmodium</i> recorded)	<i>P. relictum</i> (1); <i>P. rouxi</i> (1).
Ploceidae – weaver finches (8 species of <i>Plasmodium</i> recorded)	<i>P. cathemerium</i> (2); <i>P. circumflexum</i> (3); <i>P. elongatum</i> (1); <i>P. nucleophilum</i> (6); <i>P. polare</i> (1); <i>P. relictum</i> (11); <i>P. rouxi</i> (8); <i>P. vaughani</i> (12).
Procellariidae – shearwaters	<i>Plasmodium</i> sp. (1).
Prunellidae – hedge sparrows (1 species of <i>Plasmodium</i> recorded)	<i>P. relictum</i> (1).
Psittacidae – parrots (5 species of <i>Plasmodium</i> recorded)	<i>P. circumflexum</i> (3); <i>P. dissanaikiei</i> (1); <i>P. nucleophilum</i> (2); <i>P. relictum</i> (2); <i>P. vaughani</i> (2).
Ptilonorhynchidae – bower birds (1 species of <i>Plasmodium</i> recorded)	<i>P. relictum</i> (1).

Table II. Continued

Pycnonotidae – bulbuls (7 species of <i>Plasmodium</i> recorded)	<i>P. circumflexum</i> (5); <i>P. dissanaikai</i> (1); <i>P. leanucleus</i> (1); <i>P. polare</i> (3); <i>P. relictum</i> (4); <i>P. rouxi</i> (11); <i>P. vaughani</i> (15).
Rallidae – rails (10 species of <i>Plasmodium</i> recorded)	<i>P. berti</i> (1); <i>P. cathemerium</i> (1); <i>P. circumflexum</i> (1); <i>P. dissanaikai</i> (1); <i>P. elongatum</i> (1); <i>P. formosanum</i> (1); <i>P. polare</i> (1); <i>P. relictum</i> (4); <i>P. rouxi</i> (1); <i>P. vaughani</i> (3).
Ramphastidae – toucans (6 species of <i>Plasmodium</i> recorded)	<i>P. cathemerium</i> (1); <i>P. huffi</i> (1); <i>P. nucleophilum</i> (2); <i>P. pinotti</i> (1); <i>P. rouxi</i> (1); <i>P. vaughani</i> (1).
Scolopacidae – sandpipers (4 species of <i>Plasmodium</i> recorded)	<i>P. circumflexum</i> (3); <i>P. elongatum</i> (1); <i>P. relictum</i> (4); <i>P. vaughani</i> (1).
Sittidae – nuthatches (1 species of <i>Plasmodium</i> recorded)	<i>P. relictum</i> (1).
Spheniscidae – penguins (3 species of <i>Plasmodium</i> recorded – many are zoo records although natural infections of <i>P. relictum</i> have been recorded in South African penguins)	<i>P. cathemerium</i> (1); <i>P. elongatum</i> (4); <i>P. relictum</i> (8).
Strigidae – owls (9 species of <i>Plasmodium</i> recorded)	<i>P. cathemerium</i> (1); <i>P. circumflexum</i> (1); <i>P. elongatum</i> (4); <i>P. fallax</i> (3); <i>P. gundersi</i> (1); <i>P. polare</i> (3); <i>P. relictum</i> (3); <i>P. subpraecox</i> (3); <i>P. vaughani</i> (1).
Sturnidae – starlings (8 species of <i>Plasmodium</i> recorded)	<i>P. cathemerium</i> (1); <i>P. circumflexum</i> (6); <i>P. elongatum</i> (1); <i>P. lophurae</i> (1); <i>P. nucleophilum</i> (9); <i>P. relictum</i> (7); <i>P. rouxi</i> (1); <i>P. vaughani</i> (6).
Threskiornithidae – ibises and spoonbills (1 species of <i>Plasmodium</i> recorded)	<i>P. nucleophilum</i> (1).
Tinamidae – tinamous (3 species of <i>Plasmodium</i> recorded)	<i>P. pediocettii</i> (2); <i>P. polare</i> (1); <i>P. relictum</i> (1).
Trochilidae – hummingbirds	<i>Plasmodium</i> sp. (5).
Troglodytidae – wrens (4 species of <i>Plasmodium</i> recorded)	<i>P. cathemerium</i> (1); <i>P. circumflexum</i> (1); <i>P. relictum</i> (1); <i>P. vaughani</i> (2).
Trogonidae – trogons	<i>Plasmodium</i> sp. (2).
Turnicidae – button quail (1 species of <i>Plasmodium</i> recorded)	<i>P. vaughani</i> (1).
Tyrannidae – New World flycatchers (5 species of <i>Plasmodium</i> recorded)	<i>P. circumflexum</i> (1); <i>P. nucleophilum</i> (6); <i>P. polare</i> (1); <i>P. relictum</i> (6); <i>P. vaughani</i> (2).
Tytonidae – barn owls	<i>Plasmodium</i> sp. (3).
Upupidae – hoopoes (2 species of <i>Plasmodium</i> recorded)	<i>P. garnhami</i> (1); <i>P. relictum</i> (1).
Vireonidae – vireos and pepper-shrikes	Cyclarhinae – pepper shrikes (1 species of <i>Plasmodium</i> recorded)
	<i>P. relictum</i> (1).
	Vireoninae – vireos (4 species of <i>Plasmodium</i> recorded)
	<i>P. circumflexum</i> (2); <i>P. nucleophilum</i> (3); <i>P. relictum</i> (1); <i>P. vaughani</i> (1).
Zosteropidae – white-eyes (4 species of <i>Plasmodium</i> recorded)	<i>P. circumflexum</i> (1); <i>P. relictum</i> (4); <i>P. subpraecox</i> (1); <i>P. vaughani</i> (3).

(1982) and Bishop & Bennett (1992). The classification of the avian families and subfamilies follows Edwards (1982, 1986) in the main, as well as Maclean (1986) and the American Ornithologists' Union Checklist of the Birds of North America (1983). In Table II, the occurrence of each species of avian *Plasmodium* is listed, followed in parentheses by the number of host species in that family

in which the particular parasite species was recorded. It is hoped that this will give some indication of the frequency that a given *Plasmodium* species can be expected to be encountered in a given host family. In Table III, the frequency of occurrence of a *Plasmodium* species in avian families and species (natural infections only) is listed to provide an indication of those parasite taxons

Table III. Frequency of occurrence of *Plasmodium* species in avian families and species (natural infections only).

Parasite species	Number of host	
	families	species
<i>P. anasum</i>	1	1
<i>P. bertii</i>	1	1
<i>P. cathemerium</i>	29	70
<i>P. circumflexum</i>	43	138
<i>P. coturnixi</i>	1	1
<i>P. dissanaikiei</i>	6	7
<i>P. durae</i>	3	4
<i>P. elongatum</i>	21	59
<i>P. fallax</i>	5	9
<i>P. formosanum</i>	2	3
<i>P. gabaldoni</i>	2	3
<i>P. gallinaceum</i>	2	4
<i>P. garnhami</i>	3	3
<i>P. giovannolai</i>	2	2
<i>P. griffithsi</i>	1	1
<i>P. gundersi</i>	1	1
<i>P. hegneri</i>	1	2
<i>P. hermani</i>	2	2
<i>P. huffi</i>	1	1
<i>P. juxtannucleare</i>	3	7
<i>P. kempi</i>	1	1
<i>P. leanucleus</i>	2	2
<i>P. lophurae</i>	11	18
<i>P. matutinum</i>	2	6
<i>P. nucleophilum</i>	25	68
<i>P. paranucleophilum</i>	1	1
<i>P. pediocettii</i>	4	12
<i>P. pinotti</i>	6	6
<i>P. polare</i>	28	51
<i>P. relictum</i>	70	359
<i>P. rouxi</i>	24	65
<i>P. subpraecox</i>	4	6
<i>P. tejerai</i>	1	1
<i>P. vaughani</i>	53	265

NB. 9 of 34 (26.5%) species of *Plasmodium* known from only a single host.

4 of 34 (11.8%) species of *Plasmodium* known from only two hosts.

23 of 34 (67.7%) species of *Plasmodium* known from eight hosts or less.

that can be expected to be encountered most frequently. In Table IV, the distribution of the avian *Plasmodium* species in the six Wallacean life zones are recorded. The figures indicate the number of host species parasitised for that *Plasmodium* species for each life zone. For example, *Plasmodium cathemerium* occurred in 36 avian species in the Nearctic, 37 species in the Palearctic, 7 in the Oriental, 4 in the Ethiopian and 10

in the Neotropical region for a total of 94 species infected with this parasite around the world. The percentage of the total host species for each life zone is given in parentheses for those *Plasmodium* species in which there were more than 10 host species recorded. Following on the previous example, 36 species of birds were infected with *P. cathemerium*, i.e. 36 species in the Nearctic is 38.3% of the total of 94 species infected by this parasite. The total host species numbers are not the same in Tables III and IV, as some avian species have distributional ranges embracing more than one life zone and they are counted for each life zone in which they were found infected. Thus, in Table IV, there were 94 avian hosts recorded for *Plasmodium cathemerium* although only 70 different host species have been recorded for this parasite (Table III).

Results and discussion

Avian species of *Plasmodium* are distributed in the four subgenera *Haemamoeba*, *Huffia*, *Giovannolaia* and *Novyella* (all described by Corradetti, Garnham & Laird, 1963). The four subgenera are distinctive and species can be assigned to their appropriate subgenus by using the following key to the subgenera developed by Greiner *et al.* (1975), which was adapted from Garnham (1966).

Key to the avian subgenera of Plasmodium

- 1 Gametocytes round or nearly so; mature parasites typically displace host cell nucleus towards pole *Haemamoeba*
- Gametocytes elongated; mature forms do not displace host cell nucleus towards pole ... 2
- 2 Schizonts present in circulating erythrocyte precursors, not in mature erythrocytes ... *Huffia*
- Schizonts in mature erythrocytes, not in erythrocyte precursors 3
- 3 Erythrocytic schizonts generally larger than erythrocyte nucleus and contains noticeable amount of cytoplasm *Giovannolaia*
- Erythrocytic schizonts smaller than erythrocyte

Table IV. Distribution of species *Plasmodium* in their avian species hosts by Wallacean life zone. Percentage of species in each zone in parentheses

<i>Plasmodium</i> species	Nearctic	Palaearctic	Oriental	Ethiopian	Neotropical	Australian	Total
<i>P. anasum</i>			1				1
<i>P. bertii</i>					1		1
<i>P. cathemerium</i>	36 (38.3)	37 (39.4)	7 (7.5)	4 (4.3)	10 (10.6)		94
<i>P. circumflexum</i>	62 (38.8)	44 (27.5)	21 (13.1)	22 (13.8)	10 (6.3)	1 (0.6)	160
<i>P. coturnixi</i>			2				2
<i>P. dissanaikai</i>			7				7
<i>P. durae</i>			1	3			4
<i>P. elongatum</i>	41 (61.2)	20 (29.9)		4 (6.0)	2 (3.0)		67
<i>P. fallax</i>		2 (18.2)	3 (27.3)	6 (54.6)			11
<i>P. formanosum</i>			2				2
<i>P. gabaldoni</i>				3			3
<i>P. galinaceum</i>			3				3
<i>P. garnhami</i>		4					4
<i>P. giovannolai</i>		1	1				2
<i>P. griffithsi</i>				1			1
<i>P. gundersi</i>				1			1
<i>P. hegneri</i>		1	1				2
<i>P. hermani</i>	3	1					4
<i>P. huffi</i>					1		1
<i>P. juxtannucleare</i>		1 (10)	4 (40)	2 (20)	3 (30)		10
<i>P. kempfi</i>	1						1
<i>P. leanucleus</i>			2				2
<i>P. lophurae</i>	1 (5.2)	15 (79.0)	3 (15.8)				19
<i>P. matutinum</i>	2	4	1				7
<i>P. nucleophilum</i>	13 (17.3)	4 (5.3)	11 (14.7)	14 (18.7)	33 (44.0)		75
<i>P. paranucleophilum</i>					1		1
<i>P. pediocetti</i>	12 (100)						12
<i>P. pinotti</i>	1	1			5		7
<i>P. polare</i>	18 (32.0)	14 (25.0)	10 (18.0)	7 (12.5)	7 (12.5)		56
<i>P. relictum</i>	75 (17.9)	141 (33.6)	64 (15.3)	77 (18.4)	55 (13.1)	7 (1.7)	419
<i>P. rouxi</i>	3 (4.1)	6 (8.1)	25 (33.8)	37 (50.0)	3 (4.0)		74
<i>P. subpraecox</i>	2	2	3				7
<i>P. tejerai</i>					1		1
<i>P. vaughani</i>	92 (28.6)	48 (15.0)	51 (15.9)	69 (21.5)	61 (19.0)		321
Total number bird species infected	362 (26.2)	346 (24.8)	223 (16.1)	250 (18.2)	193 (14.1)	8 (0.01)	1382
Total species of <i>Plasmodium</i>	15	18	21	14	14	2	
Percent of total <i>Plasmodium</i>	44.2	52.9	61.8	41.2	41.2	5.9	

nucleus; without noticeable cytoplasm
 *Novyella*

Garnham (1966) recognised several valid subspecies of avian *Plasmodium*, particularly of the cosmopolitan *P. relictum*. Most of such subspecies were recognised on the basis of variations in the schizogonic cycle and periodicity or their ability to infect canaries or other hosts, but not on the basis of morphology. The validity of these subspecies by current criteria places them in question and as a consequence, they have not been identi-

fied in the tables. Garnham further described in some detail and stressed the morphological variance which could occur when strains of specific species of *Plasmodium* were experimentally transmitted to different hosts from divergent families. If such morphological variability also occurs in natural infections in the wild, then it is quite likely that many records of species of *Plasmodium* from surveys of natural infections are in error. It is difficult to identify *Plasmodium* to the species level from blood stages alone, even when all developmental stages are present in quantity in a

single smear. It is, therefore, probable that some of the host records cited in Table II are in error, but they must be accepted until the material on which they are based can be reviewed.

The 34 valid species of *Plasmodium* represent an assemblage of species of which 9 (26.5%) are known only from a single host, 4 (11.8%) from two hosts and a total of 23 (67.7%) from three to eight hosts (Table III). Little can be said about the distribution of these species. On the other hand, the most commonly encountered species is *P. relictum* (Table III), which has been recorded in 359 species from 70 avian families; the second most frequently encountered species is *P. vaughani* (265 hosts) followed by *P. circumflexum* (138 avian hosts). The remaining eight species occur in 9–70 host species. Distributionally, the avian species of *Plasmodium* fall into two discrete groups. The first contains those which appear to have a narrow host range, possibly verging on host specificity (or possibly restricted by specific vector culicines), and the second group, which apparently has no host restriction, is found widely throughout the avian orders (Tables II, III).

The Wallacean life zones, with the exception of the Australian which has virtually no records of *Plasmodium*, are remarkably similar in terms of their number of *Plasmodium* species (Table IV). Each of the five main zones have a number of species with only one or two recorded hosts and the total number of species per zone ranges from 14–19. The Oriental and Palaearctic regions have the most species of *Plasmodium*, while the Nearctic has the most host species. All three zones are similar and this may reflect the collecting effort put into these zones. Generally, the three zones that represent the former supercontinent of Laurasia have a greater number of recorded avian hosts and *Plasmodium* species than the three zones that formed the former supercontinent of Gondwanaland. The long geological isolation of both the Neotropical and Australian zones may have contributed to a lack of evolution of suitable vector mosquitoes of parasites within their particular avifauna. The almost total lack of *Plasmod-*

ium in the Australian region is surprising. This lack may be an artifact produced by little sampling effort, although several surveys have shown that New Zealand lacks, to all intents and purposes, an avian blood parasite fauna of any description. However, one might expect a far greater occurrence of *Plasmodium* in New Guinea, which has a rich and diverse avifauna. Lack of records here is undoubtedly due to lack of sampling effort. With time, it may be shown that the Australian region has an avian *Plasmodium* diversity similar to the other life zones.

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