

Diego Santiago-Alarcon
Alfonso Marzal *Editors*

Avian Malaria and Related Parasites in the Tropics

Ecology, Evolution and Systematics

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To my lovely wife Ana Marina who has taught me empathy and that living is enjoying the small everyday gifts that nature gives us for free. To my parents, Francisco Javier and María del Carmen, who taught me the value of education, hard work, and dedication. To Tuza, Oso, Chispa, and Goddi.

Diego Santiago-Alarcon

To my dear wife Rocío, for being my unconditional partner. You are and always will be my support and happiness. You are my little gift every day. To our children Rosario and Alfonso, for filling us with love and joyfulness. To my parents, Alfonso and María del Carmen, for teaching me the value of education and hard work.

Alfonso Marzal

Foreword

The tropics and temperate climates differ considerably in the mean and the variance in temperature, precipitation, and wind. While certain areas vary considerably in climate over the years, others show clear patterns of consistency with effects on life history of the numerous organisms that inhabit these areas. In particular, richness and abundance of parasites are predominantly high in the tropics, especially the haemosporida (Price 1980; Combes 2001; Valkiūnas 2005). In fact, ecological theory predicts a strong positive relationship between the abundance and diversity of parasites and their hosts (Morand and Krasnov 2010). The crucial difference between the temperate zones and the tropics is the dissimilarity in prevalence and parasitemia or intensity of infection (Morand and Krasnov 2010). Already Darwin's contemporary Alfred R. Wallace emphasized the greatly exaggerated difference in interspecific interactions between hosts and parasites in tropical regions and the fitness consequences for the hosts (reviews in Coley and Aide 1991; Schemske et al. 2009). Does biodiversity differences between temperate and tropical regions result in a higher tropical diversity due to a richer set of ecological interactions, or are they simply due to random sampling at different levels? Are haemosporidians different from all other parasites, or do they just constitute part of the combined coevolutionary interactions between hosts and parasites like any other kind of host–parasite interaction, with parasites in the tropics having more severe fitness consequences for their hosts?

Haemosporidians are an important cause of parasite virulence and are also the ancestors of malaria parasites including human malaria. Hence, they are at the origin of one of the most significant and debilitating human diseases. These effects also apply to the consequences of climate change on host–parasite interactions with different impacts on haemosporidians and other parasites (Møller et al. 2013). Because vector-borne parasite interactions involve hosts, parasites, and the important vectors that transmit them, a full understanding of all parties requires in-depth studies of each of these. Encounter rate probability and an array of anti-parasite defenses such as physical removal of parasites (e.g., preening intensity), chemical defenses (e.g., uropygial secretions), immune function, and micro-habitat choice by vectors all contribute to differences in host–parasite interactions. Furthermore,

different interspecific interactions (e.g., brood parasitism, predation, and competition) appear to be particularly susceptible to haemosporidian infections. Brood parasites are rarely infected with blood parasites because it is common for cuckoos *Cuculus canorus*, great spotted cuckoos *Clamator glandarius*, cowbirds, or any other species. This surprising finding either suggests that brood parasites are particularly resistant to haemosporidians and they rarely encounter vectors or their peculiar lack of or reduction in parental care reduces the prevalence and intensity of infection by haemosporidians. In contrast, predators suffer frequently from blood parasite infections, especially by the debilitating parasite genus *Plasmodium*. The fitness costs of haemosporidian infections have so far only been studied in a handful of cases. For example, blood parasites have been shown to affect the laying date (Marzal et al. 2005), reproductive success (Merino et al. 2000) and survival of their hosts (Martínez-de la Puente et al. 2010). So far, the number of experimental studies of haemosporidians that has been performed in the tropics is scarce (see Chap. 17 of this volume). Studies of temperate zone birds indicate that viability, predation, and future fitness prospects are all linked to blood parasitism.

Tropical species are commonly less abundant than their temperate counterparts, but with clear latitudinal trends in prevalence and parasitemia. Such latitudinal patterns of biodiversity show evidence of latitudinal maxima in both hosts and parasites (Morand and Krasnov 2010), but also in diseases caused by these parasites (Guernier et al. 2004), though there are exceptions to this general pattern (e.g., genera *Leucocytozoon*; Fecchio et al. 2019). Differences in life history of hosts and parasites are typically linked to differences in latitude and abundance. Indeed, Møller et al. (2009) showed that virulence in the tropics is much higher than in the temperate zone even when controlling for differences in host size, general ecology, and differences in similarity among taxa due to common phylogenetic descent. A number of different potential mechanisms have been suggested to account for such effects. If there are more parasite taxa in the tropics, this implies a higher diversity of infection being correlated with a higher diversity of potential food. In other words, multiple parasites select for more intense competition for limiting resources. Is competition more common and more intense in the tropics than elsewhere? We can make the prediction that experimental manipulation of the level of parasitism at different latitudes should result in higher virulence in the tropics.

Birds commonly migrate between tropics and temperate climates with hundreds of millions of migrants moving twice annually between the northern and the southern hemisphere. Several studies have shown that migration affects host–parasite interactions (see Chap. 16 of this volume). For example, barn swallows in the tropics have body condition depending on environmental conditions, but also on host–parasite interactions. Molt in the tropics affects timing of migration and subsequent timing of reproduction as shown by barn swallows (Møller et al. 1995).

Invasions may contribute to the history of host–parasite interactions, particularly for the evolution of novel interactions, immune adaptations, and native biodiversity losses (see Chap. 15). These interactions may be of recent origin partly due to invasions of parasites, vectors, and hosts as in Hawaii, Galapagos, and other tropical regions that may all contribute to the dynamics of haemosporidians in the tropics.

For instance, house sparrows (*Passer domesticus*) constitute a model system for the study of invasion biology, with the widespread occurrence of haemosporidians being determined by enemy release resulting in blood parasites doing better in areas where open niches are abundant. Moreover, blood parasites may do better in areas where novel weapons are particularly suitable for invasion of alien environments, where diversity and prevalence are low (Marzal et al. 2018). The first cases of interactions between haemosporidians and tropical birds derive from reports of the 1900s, but the link between hosts life history and parasite infection risk dates back to the mid-1950s (see Chap. 1).

The interaction between haemosporidians and their hosts constitutes an important model system for the study of host–parasite–vector interactions. There is an extensive development of research, in particular on malaria in humans, but also on malaria in domesticated animals and wild animals more recently as demonstrated in the present volume. A search on Web of Science resulted in 326,231 hits with most being for blood parasite*. Surprisingly, there has been very little experimental research on this system. Why are there only a couple of experimental studies that have attempted to use medication as a tool for understanding the consequences of prevalence and parasitemia of blood parasite infections? Likewise, there have only been few studies attempting to link haemosporidians infections with the ecological and evolutionary consequences of such infections. High prevalence and parasitemia, particularly in tropical host species, suggests that parasitologists and ecologists should increase their research effort to study such effects in the tropical zones and compare them with the same type of studies in the temperate areas. Why such studies are virtually absent is difficult to understand. This book constitutes an excellent basis for the development of such research agenda.

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Chapter 1

Research on Avian Haemosporidian Parasites in the Tropics Before the Year 2000



Diego Santiago-Alarcon and Alfonso Marzal

Abstract In 1884, only 5 years after A. Laveran discovered agents of human malaria, Vassily Danilewsky reported the first description of the pathological effects of avian malaria on their bird hosts. Shortly after, Sir Ronald Ross carried out the first investigation on the life cycle of avian *Plasmodium* parasites, being the first to show that the malaria parasite is transmitted by the bite of infected mosquitoes. Since its discovery until now, bird malaria parasites have played a major role as model organisms in human malaria research. Experiments with avian malaria have significantly contributed to the description of the life cycle of *Plasmodium* parasites and for early antimalaria drug screening. Avian malaria and related haemosporidian parasites are globally distributed; host diversity and environmental factors in the tropical regions favor the prevalence and diversity of this group of parasites. Thus, a large number of studies on bird haemosporidians during the last century, particularly taxonomic descriptions, were conducted in a wide range of tropical birds, mainly in African countries. Although the number of publications on this topic was not big during the first half of the last century, it significantly increased from late 1970s, reaching a maximum on early 1990s. During these periods, internationally recognized researchers such as G.F. Bennett, M.A. Peirce, and R.A. Earlé, among others, published a number of studies reporting data of avian haemosporidian infections in many host taxa covering many tropical regions, as well as the descriptions of 134 novel species. During the last three decades, important contributions by G. Valkiūnas have organized and enriched the knowledge on the taxonomy of this group of protozoans. Here, we have conducted an extensive search for avian haemosporidians publications in the Web of Science Core Collection and a bibliometric analysis of the found documents during the period of 1909–2000. In this

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chapter, we present an extensive synthesis of research conducted on avian malaria and related haemosporidian parasites across the different tropical regions (America, Africa, Asia, Australia, and Oceania).

Keywords Avian malaria · *Haemoproteus* · *Leucocytozoon* · Parasite taxonomy · *Plasmodium* · Tropical parasitology

1.1 Introduction

Avian haemosporidians are vector-borne parasites belonging to the genera *Plasmodium*, *Haemoproteus*, *Leucocytozoon*, and *Fallisia* (Valkiūnas 2005; Santiago-Alarcon et al. 2012a; see Chaps. 2 and 5). This group of parasites is globally distributed with the exception of polar regions (Clark et al. 2014), and a large genetic diversity (>3500 lineages) has been discovered during the past decade (Bensch et al. 2009). Such genetic diversity has allowed the experimental study of different lineages' virulence belonging to the same or different *Plasmodium* morphospecies (e.g., Palinauskas et al. 2011, 2018; Ilgūnas et al. 2019a, b). Additionally, a new simple centrifugation method to obtain high-quality DNA from haemosporidian parasites (Palinauskas et al. 2013) has allowed more in-depth genomics and transcriptomic studies, leading to the recovery of the first avian haemosporidian genome (*Haemoproteus tartakovskyi*, Bensch et al. 2016) and some transcriptomes as well (Videvall et al. 2017; see also Chap. 4). However, the history of avian haemosporidian research starts more than 100 years earlier, when in 1880 Charles Louis Alphonse Laveran discovered gametocytes circulating in the peripheral blood of infected human patients. Some years later, in 1884 Vassily Danilewsky (Danilewsky 1884) working in Ukraine discovered the broad distribution of intracellular malaria-like parasites infecting birds. These organisms were classified later in the genera *Plasmodium*, *Haemoproteus*, and *Leucocytozoon*. Importantly, he developed the first investigations showing the pathological effects of these blood parasites on avian hosts and demonstrated similarities to pathologies caused by malaria parasites in humans (Danilewsky 1889; Valkiūnas 1985) and the initial seasonality patterns of the infections on wild birds (Marzal 2012). Later, in 1897 William MacCallum discovered sexual processes (e.g., exflagellation) in haemosporidians using *Haemoproteus columbae* infecting pigeons as model organisms (Cox 2010). Also, during 1897, Sir Ronald Ross, a British officer in the Indian Medical Service, who knew of V. Danilewsky's studies on bird malaria, discovered the involvement of mosquitoes (Diptera: Culicidae) in the transmission of *Plasmodium* sp. (probably *Plasmodium relictum*) in birds (Ross 1898). In 1902, Ross was awarded the Nobel Prize in Physiology and Medicine for these contributions, which were essential in understanding malaria epidemiology and transmission. After the discovery of the involvement of mosquitoes of several genera, mainly *Culex* and *Aedes* in the transmission of avian *Plasmodium* (Huff 1927), bird malaria parasites became an experimental model for human malaria research in many

laboratories. But with the discovery of rodent haemosporidians by 1948 (Killick-Kendrick 1974), and later primate malaria (Cox 2010; Santiago-Alarcon et al. 2012a), the avian haemosporidians decreased in popularity as a model system for the study of human malaria. However, studies on avian malaria parasites still have played an essential role in advances of medicine, parasitology, ecology, and evolution, among others fields. For example, the test of synthetic compounds (e.g., plasmodochin and atebirin) in birds allowed the discovery of effective antimalarial drugs in humans and methods to study exo- and erythrocytic parasite stages in vitro (Coatney et al. 1953; Ball and Chao 1961; Ball 1964; McGhee et al. 1977). Furthermore, during the last 15 years, avian haemosporidians have become a model system to study the ecology and evolution of this antagonistic interaction (e.g., Bensch et al. 2000; Ricklefs and Fallon 2002; Marzal et al. 2008; Knowles et al. 2011; Santiago-Alarcon et al. 2014; Renner et al. 2016; Pacheco et al. 2018), which is paving the road to develop novel pathogen control and prevention strategies aiding both medical and animal health (e.g., Asghar et al. 2015, 2016).

The malaria disease generated by parasites of the genus *Plasmodium* has been recognized in ancient cultures around the globe, from Chinese documents by 2700 B.C. to Egyptian papyri by 1500 B.C. But more solid evidence comes from ancient Greeks 800–400 B.C., who provided the natural history of the disease, with its characteristic fevers and enlarged parenchymal internal organs such as livers and spleens (Cox 2010). The history of avian haemosporidian parasite studies in the tropics started at the beginning of the twentieth century, for example, with the discovery of louse flies (Diptera: Hippoboscidae) as vectors of *H. columbae* in Brazil (Aragão 1908), and expeditions from the Liverpool School of Tropical Medicine to West Africa (e.g., Gambia, Congo), where haemosporidian infections in humans, domestic and wild animals were reported (Todd and Wolbach 1912). Nonetheless, the first work conducted in tropical areas was the one leading to the discovery of the involvement of mosquitoes transmitting avian malaria (probably *P. relictum*) in India (Ross 1898). Thus, there is already a long history of avian haemosporidian research in tropical regions, but most of it was focused on reporting infections in bird species by parasites of different haemosporidian genera (e.g., Todd and Wolbach 1912; Greiner et al. 1975; Bennett and Herman 1976; McClure et al. 1978; White et al. 1978), as well as on taxonomic descriptions of new parasites, where 62 novel species were described from Asia (mainly in India), 48 from Africa (mainly in South Africa), 24 from America (mainly in Brazil), and 8 from Oceania (Table 1.1; summaries of taxonomic and nomenclature work and keys for haemosporidian parasite species are available in Valkiūnas 2005; Valkiūnas and Iezhova 2018).

In this chapter, we searched for publications in the Web of Science Core Collection (www.webofknowledge.com) from the year 1909–2000, including all languages and document types. We used the following Boolean search keywords:

TS = ((Haemosporid* OR avian malaria OR Plasmodium OR Haemoproteus OR Leucocytozoon) AND (Tropic* OR Neotropic* OR Afrotropic* OR Ethiopia* OR IndoMalay* OR Oriental OR Austral* OR Oceania*)).

Table 1.1 Avian haemosporidian species initially described in tropical regions and their current taxonomic status

Species	Taxonomic status ^a	Type host	Region	Country/locality	Reference
Africa (n = 48)					
<i>Haemoproteus africanus</i>	Valid	Green-backed twainpot (<i>Mandingoa nitidula</i>)	Africa	Tanzania/Amani	Bennett and Peirce (1991)
<i>Haemoproteus balearicae</i>	Valid	Black crowned crane (<i>Balearica pavonina</i>)	Africa	United Kingdom/Surrey ^b	Peirce (1973)
<i>Haemoproteus balmorali</i>	Valid	Spotted flycatcher (<i>Muscicapa striata</i>)	Africa	Zambia/Balmoral	Peirce (1984b)
<i>Haemoproteus borgesi</i>	Valid	Fine-spotted woodpecker (<i>Campethera punctuligera</i>)	Africa	Guinea	Tendeiro (1947)
<i>Haemoproteus bubalornis</i>	Valid	White-billed buffalo weaver (<i>Bubalornis albirostris</i>)	Africa	Kenya/Ngulia	Bennett and Peirce (1991)
<i>Haemoproteus bucerotis</i>	Valid	Northern red-billed hornbill (<i>Tockus erythrorhynchus</i>)	Africa	Botswana/Gaborone	Bennett et al. (1995)
<i>Haemoproteus burhini</i>	Valid	Spotted thick-knee (<i>Barhinus capensis</i>)	Africa	South Africa/Satara, Kruger National Park	Bennett et al. (1995)
<i>Haemoproteus chelidonis</i>	<i>Incertae sedis</i>	Northern house-martin (<i>Delichon urbicum</i>)	Africa		Franchini (1922), White and Bennett (1978)
<i>Haemoproteus crumenium</i>	Valid	Marabou stork (<i>Leptoptilos crumenifer</i>)	Africa	Kenya/Nairobi	Peirce and Cooper (1977)
<i>Haemoproteus cublae</i>	Valid	Black-backed puffback (<i>Dryoscopus cubla</i>)	Africa	Zambia/Balmoral	Peirce (1984c)
<i>Haemoproteus enucleator</i>	Valid	African pygmy kingfisher (<i>Ispidina picta</i>)	Africa	Uganda/Entebbe	Bennett et al. (1972)
<i>Haemoproteus hirundinis</i>	Valid	Hirundinidae (<i>Pseudhirundo</i> sp.)	Africa	Algeria	White and Bennett (1978)
<i>Haemoproteus indicator</i>	Valid	Greater honeyguide (<i>Indicator indicator</i>)	Africa	Uganda/Zika Forest	Bennett et al. (1986a)

<i>Haemoproteus janovyi</i>	Valid	White-backed vulture (<i>Gyps africanus</i>)	Africa	South Africa/Sengwa wildlife research area, Zimbabwe	Greiner and Mundy (1979)
<i>Haemoproteus killangoi</i>	Valid	African yellow white-eye (<i>Zosterops senegalensis</i>)	Africa	Uganda/Zika Forest	Bennett and Peirce (1981)
<i>Haemoproteus lairdi</i>	Valid	Blue-breasted bee-eater (<i>Merops variegatus</i>)	Africa	Uganda/Entebbe	Bennett et al. (1978)
<i>Haemoproteus mcleani</i>	<i>Species inquirenda</i>	Southern fiscal (<i>Lanius collaris</i>)	Africa	South Africa/Pretoria	Bennett et al. (1995)
<i>Haemoproteus montezi</i>	Valid	Purple-crested turaco (<i>Gallinix porphyreolophus</i>)	Africa	Mozambique	Bennett and Peirce (1990)
<i>Haemoproteus motacillae</i>	Valid	Western Yellow Wagtail (<i>Motacilla flava</i>)	Africa	Uganda/Entebbe	Bennett and Peirce (1990)
<i>Haemoproteus neseri</i>	Valid	Chorister robin-chat (<i>Cossypha dichroa</i>)	Africa	South Africa/Louis Trichardt, Transvaal	Bennett and Earlé (1992)
<i>Haemoproteus pelouroi</i>	Valid	Hadada ibis (<i>Bostrychia hagedash</i>)	Africa	Guinea	Tendeiro (1947)
<i>Haemoproteus porzanae</i>	Valid	Baillon's crane (<i>Zapornia pusilla</i>)	Africa	Tunisia/Kairouan	Coatney (1936)
<i>Haemoproteus pratasi</i>	Valid	Helmeted guineafowl (<i>Numida meleagris</i>)	Africa	Guinea	Tendeiro (1947)
<i>Haemoproteus psittaci</i>	Valid	Grey parrot (<i>Psittacus erithacus</i>)	Africa	United Kingdom/Wickford, Essex ^b	Bennett and Peirce (1992)
<i>Haemoproteus queleae</i>	Valid	Red-headed quelea (<i>Quelea erythrops</i>)	Africa	Equatorial Guinea/San Thomé	Bennett and Peirce (1991)
<i>Haemoproteus sequeirae</i>	Valid	Splendid sunbird (<i>Cinnyris coccinigastrus</i>)	Africa	Guinea	Tendeiro (1947)

(continued)

Table 1.1 (continued)

Species	Taxonomic status ^a	Type host	Region	Country/locality	Reference
<i>Haemoproteus stellaris</i>	Valid	Grey-rumped swallow (<i>Pseudhirundo griseopyga</i>)	Africa	Uganda/Kasenyei	White and Bennett (1978)
<i>Haemoproteus telfordi</i>	Valid	Black-bellied bustard (<i>Lissotis melanogaster</i>)	Africa	Zaire/Kundelungu, Katanga	Bennett et al. (1975)
<i>Haemoproteus timalus</i>	Valid	Rufous chatterer (<i>Argya rubiginosa</i>)	Africa	Kenya/South Horr	Bennett et al. (1991c)
<i>Haemoproteus undulatus</i>	Valid	Red-faced mousebird (<i>Urocolius indicus</i>)	Africa	South Africa/Kruger National Park	Bennett and Earlé (1992)
<i>Haemoproteus uraeginthus</i>	Valid	Red-cheeked cordon-bleu (<i>Uraeginthus bengalus</i>)	Africa	Chad/N'Djamena	Bennett and Peirce (1991)
<i>Plasmodium durae</i>	Valid	Wild turkey (<i>Meleagris gallopavo</i>)	Africa	Kenya/Langata, Nairobi	Herman (1941); see also Laird (1978)
<i>Plasmodium fallax</i>	Valid	African wood owl (<i>Strix woodfordii</i>)	Africa	Congo	Schwetz (1930)
<i>Plasmodium garnhami</i>	Valid	Eurasian hoopoe (<i>Upupa epops</i>)	Africa	Egypt/Imbaba District, Giza	Guindy et al. (1965)
<i>Plasmodium gundersi</i>	Valid	African wood owl (<i>Strix woodfordii</i>)	Africa	Liberia/Harbel, Marshall Territory	Garnham (1966)
<i>Plasmodium rouxi</i>	Valid	Spanish sparrow (<i>Passer hispaniolensis</i>)	Africa	Algeria/Mitidja plains, Algiers	Sergent et al. (1928)
<i>Leucocytozoon balmorali</i>	Valid	Black-backed puffback (<i>Dryocopus cubla</i>)	Africa	Zambia/Balmoral	Peirce (1984d)
<i>Leucocytozoon caprimulgi</i>	Valid	Square-tailed nightjar (<i>Caprimulgus fossii</i>)	Africa	Congo/Haute-Sangha	Bennett et al. (1992b)
<i>Leucocytozoon centropi</i>	Valid	White-browed coucal (<i>Centropus superciliosus</i>)	Africa	South Africa/Pietermaritzburg	Bennett et al. (1993a)
<i>Leucocytozoon colius</i>	Valid	Speckled mousebird (<i>Colius striatus</i>)	Africa	South Africa/Lydenburg, Transvaal	Bennett et al. (1993b)

<i>Leucocytozoon dizini</i>	Valid	Western grey plantain-eater (<i>Crinifer piscator</i>)	Africa	Guinea Bisáu	Tendeiro (1947)
<i>Leucocytozoon eurystomi</i>	Valid	Blue-throated roller (<i>Eurystomus gularis</i>)	Africa	Congo/Haute-Sangha	Bennett et al. (1993b)
<i>Leucocytozoon neavei</i>	Valid	Helmeted guineafowl (<i>Nimida meleagris</i>)	Africa	Sudan/Khartoum	Sambon (1909)
<i>Leucocytozoon schoutedeni</i>	Valid	Red junglefowl (<i>Gallus gallus</i>)	Africa	Congo/Bukama, Lake Upemba, Katanga	Rodhain et al. (1913)
<i>Leucocytozoon sousadiasi</i>	Valid	Black-headed lapwing (<i>Vanellus tectus</i>)	Africa	Guinea Bisáu	Tendeiro (1947)
<i>Leucocytozoon struthionis</i>	Valid	African ostrich (<i>Struthio camelus</i>)	Africa	South Africa/Cape Province, Middelburg District	Walker (1912)
<i>Leucocytozoon toddi</i>	Valid	Lizard buzzard (<i>Kaupifalco monogrammicus</i>)	Africa	Congo	Sambon (1908)
<i>Leucocytozoon vandenbrandeni</i>	Valid	African darter (<i>Anhinga rufa</i>)	Africa	Congo/Leopoldville	Rodhain (1931)
Asia and Oceania (n = 66)					
<i>Haemoproteus aegithinae</i>	Valid	Common iora (<i>Aegithina tiphia</i>)	Asia	India/Nagao	de Mello (1935b)
<i>Haemoproteus anhi</i>	Valid	Paddyfield pipit (<i>Anthus novaeseelandiae</i>)	Asia	India/Goa	de Mello (1935b)
<i>Haemoproteus anigonis</i>	Valid	Demoiselle crane (<i>Grus virgo</i>)	Asia	India/Junagad	de Mello (1935b)
<i>Haemoproteus bennetti</i>	Valid	Greater yellow-nape (<i>Chrysophlegma flavinucha</i>)	Asia	India/Darjeeling W.B.	Greiner et al. (1977)
<i>Haemoproteus bilobata</i>	Valid	Fire-tufted barbet (<i>Psittopogon pyrolophus</i>)	Asia	India/Mt. Brinchang, Malaya	Bennett and Nandi (1981)

(continued)

Table 1.1 (continued)

Species	Taxonomic status ^a	Type host	Region	Country/locality	Reference
<i>Haemoproteus centropi</i>	Valid	Greater coucal (<i>Centropus sinensis</i>)	Asia	India/Diu	de Mello (1935b)
<i>Haemoproteus contortus</i>	Valid	Eurasian whimbrel (<i>Niemenius phaeopus</i>)	Southeast Asia	Philippine Islands/Batangas	Bennett (1979)
<i>Haemoproteus coraciae</i>	Valid	Indian roller (<i>Coracias benghalensis</i>)	Asia	India/Goa	Bishop and Bennett (1986)
<i>Haemoproteus cornuata</i>	Valid	Blue-throated barbet (<i>Psilopogon asiaticus</i>)	Asia	Bhutan/West Bhutan	Bennett and Nandi (1981)
<i>Haemoproteus dicaeus</i>	Valid	Crimson-breasted flowerpecker (<i>Prionochilus percussus</i>)	Southeast Asia	Malaysia/Subang	Bennett and Bishop (1990)
<i>Haemoproteus dicruri</i>	Valid	Black drongo (<i>Dicrurus macrocerus</i>)	Asia	India/Pragana	Peirce (1984e)
<i>Haemoproteus elani</i>	Valid	Black-winged kite (<i>Elanus caeruleus</i>)	Asia	India/Daman	de Mello (1935b)
<i>Haemoproteus eurylaimus</i>	Valid	Silver-breasted broadbill (<i>Serilophus lunatus</i>)	Southeast Asia	Thailand/Chieng-mai	Bennett et al. (1991d)
<i>Haemoproteus eurystomae</i>	Valid	Oriental dollarbird (<i>Eurystomus orientalis</i>)	Southeast Asia	Malaysia/Rantau Panjang	Bishop and Bennett (1986)
<i>Haemoproteus fuscae</i>	Valid	White-throated kingfisher (<i>Halcyon smyrnensis</i>)	Asia	India/Santo Estevam	de Mello and da Fonseca (1937)
<i>Haemoproteus gallinulae</i>	Valid	Common moorhen (<i>Gallinula chloropus</i>)	Asia	India/Carambolim Lake, Ilhas, Goa	de Mello (1935b)
<i>Haemoproteus halcyonis</i>	Valid	White-throated kingfisher (<i>Halcyon smyrnensis</i>)	Asia	India/Canacona	de Mello (1935b)
<i>Haemoproteus handai</i>	Valid	Plum-headed parakeet (<i>Pittacula cyanocephala</i>)	Asia	Pakistan/Lahore	Bennett and Peirce (1986)

<i>Haemoproteus herodiadis</i>	Valid	Intermediate egret (<i>Ardea intermedia</i>)	Asia	India/Lake Carambolim, Ilhas Goa	de Mello (1935a)
<i>Haemoproteus iwa</i>	Valid (Levin et al. 2011)	Great frigatebird (<i>Fregata minor</i>)	Oceania	USA/Hawaii, Laysan Island	Work and Rameyer (1996)
<i>Haemoproteus lanii</i>	Valid	Long-tailed shrike (<i>Lanius schach</i>)	Asia	India/Pondá	de Mello (1936)
<i>Haemoproteus manwelli</i>	Valid	Little green bee-eater (<i>Merops orientalis</i>)	Asia	India/Maharashtra	Bennett et al. (1978)
<i>Haemoproteus megapodius</i>	Valid	Dusky scrubfowl (<i>Megapodius freycinet</i>)	Asia	India/Campbell Bay, Great Nicobar Island	Nandi and Mandal (1980)
<i>Haemoproteus meropis</i>	Valid	Little green bee-eater (<i>Merops orientalis</i>)	Asia	India/Nagpur	Bennett (1978)
<i>Haemoproteus monarchus</i>	Valid	Island monarch (<i>Monarcha cinerascens</i>)	Oceania	New Guinea	Bennett et al. (1991c)
<i>Haemoproteus nettionis</i>	Valid	Chestnut teal (<i>Anas castanea</i>)	Oceania	Australia/New South Wales	Coatney (1936)
<i>Haemoproteus nucleophilus</i>	Valid	Black berrypecker (<i>Melanocharis nigra</i>)	Oceania	Papua New Guinea/L. Kopiago, Southern highlands	Bennett and Bishop (1990)
<i>Haemoproteus orientalis</i>	Valid	Little green bee-eater (<i>Merops orientalis</i>)	Asia	India/Maharashtra	Bennett et al. (1978)
<i>Haemoproteus orioli</i>	Valid	Eurasian golden-oriole (<i>Oriolus oriolus</i>)	Asia	India/Nova Goa	Peirce (1984f)
<i>Haemoproteus orizivora</i>	Valid	Java sparrow (<i>Lonchura oryzivora</i>)	Southeast Asia	Indonesia/West Java	Peirce (1984h)
<i>Haemoproteus otocompsae</i>	Valid	Red-whiskered bulbul (<i>Pycnonotus jocosus</i>)	Asia	India/Malim (Baedez)	Peirce (1984i), Rahal et al. (1987)

(continued)

Table 1.1 (continued)

Species	Taxonomic status ^a	Type host	Region	Country/locality	Reference
<i>Haemoproteus pachycephalus</i>	Valid	Golden whistler (<i>Pachycephala pectoralis</i>)	Southeast Asia	Philippine Islands/Mindanao	Bennett et al. (1991c)
<i>Haemoproteus pastoris</i>	Valid	Rosy starling (<i>Pastor roseus</i>)	Asia	India/Pragana	de Mello (1935b)
<i>Haemoproteus philippinensis</i>	Valid	Cinereous bulbul (<i>Hemixos flavala</i>)	Southeast Asia	Malaysia/Mount Brinchang, Pahang	Rahal et al. (1987)
<i>Haemoproteus pittae</i>	Valid	Blue-banded pitta (<i>Pitta arquata</i>)	Southeast Asia	Borneo	Bennett et al. (1991d)
<i>Haemoproteus plataleae</i>	Valid	Eurasian spoonbill (<i>Platalea leucorodia</i>)	Asia	India/Diu	de Mello (1935b)
<i>Haemoproteus pitlotis</i>	Valid	Yellow-faced honeyeater (<i>Caligavis chrysops</i>)	Oceania	Australia/Milson Island, New South Wales	Coatney (1936), Bennett et al. (1994)
<i>Haemoproteus rileyi</i>	Valid	Indian peafowl (<i>Pavo cristatus</i>)	Asia	India/Patna	Malkani (1936)
<i>Haemoproteus rotator</i>	Valid	Pin-tailed snipe (<i>Gallinago stenura</i>)	Southeast Asia	Philippine Islands/Palawan	Bennett (1979)
<i>Haemoproteus sanguinis</i>	Valid	Red-whiskered bulbul (<i>Pycnonotus jocosus</i>)	Asia	India/Calcutta, Bengal	Rahal et al. (1987)
<i>Haemoproteus thereicerycis</i>	Valid	Brown-headed barbet (<i>Psilopogon zeylanicus</i>)	Asia	India/Cortim, Nova Goa	de Mello (1935b), Bennett and Nandi (1981)
<i>Haemoproteus trogonis</i>	Valid	Scarlet-rumped trogon (<i>Harpactes dauvaucelii</i>)	Southeast Asia	Malaysia/Subang	Bennett and Peirce (1990)
<i>Haemoproteus upuae</i>	Valid	Eurasian hoopoe (<i>Upupa epops</i>)	Asia	India/Daman	de Mello (1935b)
<i>Haemoproteus wenyoni</i>	Valid	Common tailorbird (<i>Orthotomus sutorius</i>)	Asia	India/Nova Goa	Peirce (1984g)
<i>Haemoproteus xantholaemae</i>	Valid	Coppersmith barbet (<i>Psilopogon haemacephalus</i>)	Asia	India/Telinkhery, Nagpur	Bennett and Nandi (1981)

<i>Haemoproteus zosteropsis</i>	Valid	Oriental white-eye (<i>Zosterops palpebrosus</i>)	Asia	India/Calcutta	Bennett and Peirce (1981)
<i>Plasmodium anasum</i>	Valid	Northern Shoveler (<i>Spatula clypeata</i>)	Asia	China/Lin-pien Ping-tung Hsien, Taiwan	Manwell and Kuntz (1965)
<i>Plasmodium coturnixi</i>	Valid	Common quail (<i>Coturnix coturnix</i>)	Asia	Pakistán/Kohat	Bano and Abbasi (1983)
<i>Plasmodium dissanaikai</i>	Valid	Rose-ringed parakeet (<i>Psittacula krameri</i>)	Asia	Sri Lanka/Ja-ela	de Jong (1971)
<i>Plasmodium formosanum</i>	Valid	Taiwan partridge (<i>Arborophila crudigularis</i>)	Asia	China/Nan Tou Hsien, Taiwan	Manwell (1962)
<i>Plasmodium gallinaceum</i>	Valid	Red junglefowl (<i>Gallus gallus</i>)	Asia	Sri Lanka	Brumpt (1935)
<i>Plasmodium gallinulae</i>	Valid	Common moorhen (<i>Gallinula chloropus</i>)	Asia	India/Lake Carambolim, Ilhas Goa	de Mello (1935b)
<i>Plasmodium griffithsi</i>	Valid	Wild turkey (<i>Meleagris gallopavo</i>)	Asia	Burma/Rangoon	Garnham (1966)
<i>Plasmodium hegeneri</i>	Valid	Common teal (<i>Anas crecca</i>)	Asia	China/Lo-tung, I-lan Hsien, Taiwan	Manwell and Kuntz (1966)
<i>Plasmodium herodiadis</i>	Valid	Intermediate egret (<i>Ardea intermedia</i>)	Asia	India/Lake Carambolim, Ilhas Goa	de Mello (1935a)
<i>Plasmodium lophurae</i>	Valid	Bornean fireback (<i>Lophura ignita</i>)	Asia	Borneo	Coggeshall (1938)
<i>Leucocytozoon anellobiae</i>	Valid	Little wattlebird (<i>Anthochaera chrysoptera</i>)	Oceania	Australia/Brisbane, Queensland	Bennett et al. (1994)
<i>Leucocytozoon caulleryi</i>	Valid	Red junglefowl (<i>Gallus gallus</i>)	Southeast Asia	Vietnam/Tonkin, Hanoi	Mathis and Léger (1909)

(continued)

Table 1.1 (continued)

Species	Taxonomic status ^a	Type host	Region	Country/locality	Reference
<i>Leucocytozoon dubreuilii</i>	Valid	Redwing (<i>Turdus iliacus</i>) ^c	Southeast Asia	Vietnam/Tonkin, Hanoi	Bennett et al. (1993c)
<i>Leucocytozoon leboeufi</i>	Valid	Yellow bittern (<i>Ixobrychus sinensis</i>)	Southeast Asia	Vietnam/Tonkin, Hanoi	Mathis and Léger (1911)
<i>Leucocytozoon macclurii</i>	Valid	Dark-sided thrush (<i>Zoothera marginata</i>) ^c	Southeast Asia	Thailand/Chiengmai	Bennett et al. (1993c), Valkūnas 2005
<i>Leucocytozoon marchouxii</i>	Valid	Red-collared dove (<i>Streptopelia tranquebarica</i>)	Southeast Asia	Vietnam/Tonkin, Hanoi	Bennett et al. (1992b)
<i>Leucocytozoon nyctyornis</i>	Valid	Blue-bearded bee-eater (<i>Nyctyornis albertoni</i>)	Asia	India/Rani, Kamrup District, Assam	Nandi (1986a)
<i>Leucocytozoon simondi</i>	Valid	Common teal (<i>Anas crecca</i>)	Southeast Asia	Vietnam/Tonkin, Hanoi	Mathis and Léger (1910)
<i>Leucocytozoon squamatus</i>	Valid	Scaly-bellied woodpecker (<i>Picus squamatus</i>)	Asia	India/Pnritop, Uddampur, Jammu, Kashmir	Nandi (1986b)
<i>Leucocytozoon tawaki</i>	Valid	Fiordland penguin (<i>Eudyptes pachyrynchus</i>)	Oceania	New Zealand/Kaikoura, Jackson's Head, South Island	Bennett et al. (1992b)
America (n = 24)					
<i>Fallisia (Plasmodioides) neotropicalis</i> ^d	Valid	Rock pigeon (<i>Columba livia</i>)	South America	Venezuela/El Saman, Villa Bruzual, Portuguesa	Gabaldon et al. (1985)
<i>Haemoproteus apodus</i>	Valid	Ashy-tailed swift (<i>Chaetura andrei</i>)	South America	Brazil/Sao Paulo, Guaratuba	Bennett et al. (1986a)
<i>Haemoproteus bucconis</i>	Valid	White-eared puffbird (<i>Nyctalus chacuru</i>)	South America	Brazil/Sao Paulo, Itapetinga	Bennett et al. (1986a)
<i>Haemoproteus circumnuclearis</i>	Valid	Olive-striped flycatcher (<i>Mionectes olivaceus</i>)	South America	Colombia/Río Verde, Valle	Bennett et al. (1986b)
<i>Haemoproteus cracidarum</i>	Valid	Rufous-vented chachalaca (<i>Orientalis ruficauda</i>)	South America	Venezuela/San Juan de los Morros, Guarico	Bennett et al. (1982)

<i>Haemoproteus formicarius</i>	Valid	Plain antvireo (<i>Dysithamus mentalis</i>)	South America	Brazil/Itapetininga	Bennett et al. (1987)
<i>Haemoproteus furnarius</i>	Valid	White-eyed foliage-gleaner (<i>Automolus leucophthalmus</i>)	South America	Brazil/Itapetininga	Bennett et al. (1987)
<i>Haemoproteus ortalidum</i>	Valid	Rufous-vented chachalaca (<i>Ortalis ruficauda</i>)	South America	Venezuela/Jácara, Falcón	Bennett et al. (1982)
<i>Haemoproteus souzalopesi</i>	Valid	Fuscous flycatcher (<i>Cnemotriccus fuscatus</i>)	South America	Brazil/ Sao Paulo, Guaratuba	Bennett et al. (1986b)
<i>Haemoproteus trochili</i>	Valid	White-tipped sicklebill (<i>Eutoxeres aquila</i>)	South America	Colombia/Río Zabaletas	White et al. (1979)
<i>Haemoproteus vireonis</i>	Valid	Red-eyed vireo (<i>Vireo olivaceus</i>)	South America	Brazil/Itapetininga	Bennett et al. (1987)
<i>Haemoproteus witti</i>	Valid	Red-billed streamertail (<i>Trochilus polytmus</i>)	South America	Jamaica/Greenhills	White et al. (1979)
<i>Plasmodium bertii</i>	Valid	Grey-necked wood rail (<i>Aramides cajaneus</i>)	South America	Venezuela/Guaquitas, Barinas	Gabaldon and Ulloa (1981)
<i>Plasmodium columbae</i>	Valid	Rock pigeon (<i>Columba livia</i>)	South America	Brazil/Sao Paulo	Carini (1912)
<i>Plasmodium forresteri</i>	Valid	Northern barred owl (<i>Strix varia</i>)	North America	USA/Trenton, Gilchrist County, Florida	Telford et al. (1997)
<i>Plasmodium gabaldoni</i>	Valid	Rock pigeon (<i>Columba livia</i>)	South America	Venezuela/Villa Brunzal, Portuguesa State	Garnham (1977)
<i>Plasmodium hermani</i>	Valid	Wild turkey (<i>Meleagris gallopavo</i>)	North America	USA/Palmdale, Glade's County, Florida	Telford and Forrester (1975)
<i>Plasmodium huffi</i>	Valid	Toco toucan (<i>Ramphastos toco</i>)	South America	Brazil	Muniz et al. (1951)

(continued)

Table 1.1 (continued)

Species	Taxonomic status ^a	Type host	Region	Country/locality	Reference
<i>Plasmodium juxtamuclae</i>	Valid	Red junglefowl (<i>Gallus gallus</i>)	South America	Brazil/Minas Gerais	Versiani and Gomes (1941)
<i>Plasmodium lutzi</i>	Valid	Grey-necked wood rail (<i>Aramides cajaneus</i>)	South America	Brazil/Sao Paulo	Lucena (1939)
<i>Plasmodium paramucrophilum</i>	Valid	Tanager (<i>Tachyphonus sp.</i> ; Thraupidae)	South America	Northeast Brazil ^b	Manwell and Sessler (1971)
<i>Plasmodium pinotii</i>	Valid	Toco toucan (<i>Ramphastos toco</i>)	South America	Brazil	Muniz and Soares de (1954)
<i>Plasmodium tejerai</i>	Valid	Wild turkey (<i>Meleagris gallopavo</i>)	South America	Venezuela/Santa Inés, Miranda, Trujillo	Gabaldon and Ulloa (1977)
<i>Leucocytozoon grisi</i>	Valid	Sandhill crane (<i>Antigone canadensis</i>)	North America	USA/Payne's Prairie, Florida	Bennett et al. (1992b)

Synonyms are not listed in the table, only those species that are currently valid or species where not enough information exists yet to firmly establish their taxonomic identity

^aTaxonomic status is given according to Valkiūnas (2005) review, in which it was specified and grounded. Many parasites described from tropical regions turned out to be synonyms of currently valid species names because the bird host family was used as the main taxonomic trait during their description, which is now well established that using bird families is not a valid taxonomic practice (Valkiūnas and Ashford 2002); using information about bird families is recommended only as an initial guide toward species identifications. Some of the synonyms might be validated in the future; however, additional research is needed to prove each case

^bThe type hosts were imported from Africa into Surrey and Essex; some were captive at a zoological garden and from a veterinary practice clinic in Essex; host species is endemic to West Africa or equatorial Africa (from Guinea to Tanzania)

^cThe work by Gabaldon et al. (1985) also included the description of a new subgenus, *Plasmodioides*

^dThe type host species was not provided in the original description, but it is suspected to be the one listed in the table based on the common name

^eIt is a likely location given that the parasite was described from an imported bird to the USA from South America

In total, we retrieved 671 articles, and after a thorough review, we eliminated papers that were not related to the field or that were outside of the tropics; at the end 176 research papers remained. Subsequently, we conducted a bibliometric analysis using the R package bibliometrix v. 2.0.0 (Aria and Cuccurullo 2017), with the objective of determining productivity across years, country, and author contributions. From the 176 research papers of the period 1912–2000, we found an average of 13.1 citations per manuscript. The beginning of last century was a slow start for the field of avian haemosporidian research in the tropics (an average of <1 article per year from 1912 to 1962); the field started in earnest approximately by the year 1976 with nine publications (the years with the most number of articles published were 1978 [11], 1984 [16], 1991 [14], 1992 [11], 1993 [13]) and had an annual percentage growth rate of 5.75 for the analyzed period. The top five journals where most tropical avian haemosporidian research was published during last century were *Canadian Journal of Zoology* (15), *Journal of Natural History* (12), *Journal of Parasitology* (11), *Journal of Wildlife Diseases* (8), and *South African Journal of Wildlife Research* (8). The most productive authors (i.e., >5 papers) were, in decreasing order, G.F. Bennett (45), M.A. Peirce (26), R.A. Earlé (16), N.C. Nandi (13), A. Gabaldon (12), G. Ulloa (12), M.A. Bishop (7), E.C. Greiner (6), F.W. Huchzermeyer (6), and A.K. Mandal (6) (Fig. 1.1). More recently, G. Valkiūnas has been the leading haemosporidian taxonomist; he and his colleagues have been the researchers in charge of organizing and enriching the taxonomy of avian haemosporidians during the past three decades around the world (e.g., Valkiūnas 2005; Valkiūnas and Iezhova 2018; Fig. 1.2). In terms of productivity by country, the most publications during the last century came from India with 60 publications, followed by South Africa and Brazil with 25 papers each, and then by Mexico, Venezuela, Argentina, Australia, and Malaysia with between 12 and 15 papers each (Fig. 1.3).



Fig. 1.1 Word cloud showing the most frequent words ($n = 250$) used in the titles, author lists, and abstracts from the 176 publications analyzed for tropical research on avian haemosporidian parasites. For the word clouds, we used the outlines of a rock pigeon (*Columba livia*) (a) and a red junglefowl (*Gallus gallus*) (b). We intend this as homage to these two widespread and charismatic species that have given so much in many different aspects (e.g., food, sport, service in war) to humans throughout the centuries. For the avian haemosporidian research, pigeons and chickens have provided material for the description of new species and have been model hosts for experimental infections, among other benefits



Fig. 1.2 Pictures of some important scientists for the field of tropical avian haemosporidian research during the last century (1900–2000): Gordon F. Bennett (a), Mike A. Peirce (b), Ellis C. Greiner (c), Gediminas Valkiūnas (d)

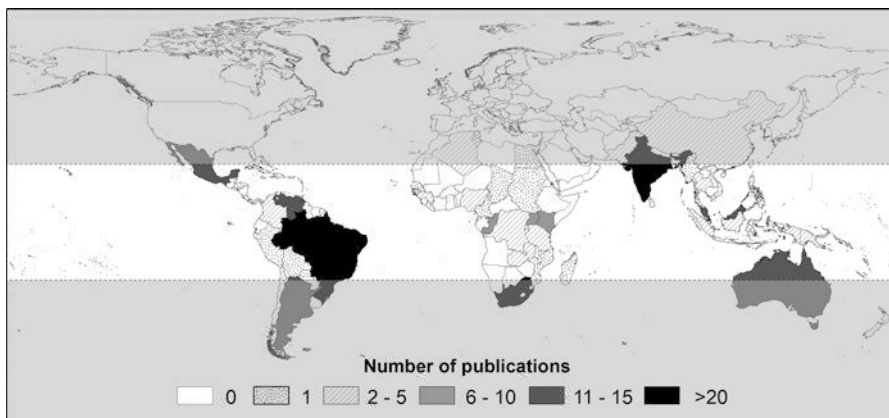


Fig. 1.3 Number of publications by country in tropical and some subtropical regions around the world. The light grey shaded region on the map delimits the tropical areas across the world

Below, we provide an exhaustive synthesis of the research conducted on avian haemosporidians in the different tropical regions (i.e., America, Africa, Asia, and Oceania; for practical purposes, we are combining Australia and Oceania into the same region). It is important to remember that all studies discussed here are based on microscopic examination of blood films. Thus, prevalence for different countries may not be precise because of researchers' experience, and also when combined with molecular methods (polymerase chain reaction, PCR) researchers can detect low intensity infections missed by microscopic examination; however, PCR methods can also miss infections due to probes' high specificity, therefore making the use of both desirable (Valkiūnas et al. 2008a; see Chap. 2 for an introduction to haemosporidian life cycles and study methods).

1.2 Studies in the Tropics

1.2.1 Africa

A large expedition conducted at the beginning of the last century (1911) in Gambia by the Liverpool School of Tropical Medicine had the objective to study human trypanosomiasis, but researchers also collected samples from nonhuman mammals ($n = 39$), birds ($n = 108$), and reptiles ($n = 28$) (Todd and Wolbach 1912). *Leucocytozoon* was detected in vultures and bush fowl (francolins), and pigments producing Haemosporida parasites (i.e., *Haemoproteus*, *Plasmodium*) were detected in several bird species, but high parasitemia infections were recorded only in pigeons, bush fowl, and vultures (Todd and Wolbach 1912).

A parasite survey conducted in Senegal included a total of 809 birds from 43 species, where blood parasite prevalence was low (11.5%) compared to other parts of Africa (e.g., Ghana 32%, $n = 135$; Uganda 31%, $n = 1998$; Kenya 25%, $n = 377$; Tchad 23%, $n = 389$; Abyssinia 23%, $n = 5046$); most infections (80%) were of *Haemoproteus* parasites (Bennett et al. 1978; see Bennett et al. 1992a for sub-Saharan birds, where *Haemoproteus* parasites were also the most common [19%], followed by *Leucocytozoon* [8.3%] and *Plasmodium* species [3.5%]). There was similar avian haemosporidians prevalence across Africa considering an east-west comparison, with the exception of Tanzania and Zaire, where prevalence was higher (47% and 72.2%, respectively) compared to most other countries, particularly for the genera *Plasmodium* and *Leucocytozoon* (Bennett and Herman 1976; Bennett et al. 1978). Moreover, prevalence seasonality in Senegal was clearly defined, with highest infection rate from December to May (10–17%) and lowest from June to November (0–9%). This result was unexpected given that the rainy season is from July to September (higher prevalence was recorded during the rainy season in Uganda; Bennett et al. 1974, 1977) and those are favorable conditions for the development of insect vectors (Bennett et al. 1978). A study conducted in eastern Africa (Kenya, Tanzania, Zaire) surveyed 647 birds from 146 species, showing a 37.2% of