Review

Haemogregarines and Criteria for Identification

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Simple Summary: Taxonomic classification of haemogregarines belonging to Apicomplexa can become difficult when the information about the life cycle stages is not available. Using a self-reporting, we record different haemogregarine species infecting various animal categories and exploring the most systematic features for each life cycle stage. The keystone in the classification of any species of haemogregarines is related to the sporogonic cycle more than other stages of schizogony and gamogony. Molecular approaches are excellent tools that enabled the identification of apicomplexan parasites by clarifying their evolutionary relationships.

Abstract: Apicomplexa is a phylum that includes all parasitic protozoa sharing unique ultrastructural features. Haemogregarines are sophisticated apicomplexan blood parasites with an obligatory heteroxenous life cycle and haplohomophagic alternation of generations. Haemogregarines are common blood parasites of fish, amphibians, lizards, snakes, turtles, tortoises, birds, and mammals. Haemogregarine ultrastructure has been so far examined only for stages from the vertebrate host. PCR-based assays and the sequencing of the 18S rRNA gene are helpful methods to further characterize this parasite group. The proper classification for the haemogregarine complex is available with the criteria of generic and unique diagnosis of these parasites.

Keywords: haemogregarines; gamogony; sporogony; schizogony; molecular analysis

1. Introduction

Phylum Apicomplexa was described by Levine [1] to include parasitic protozoa sharing unique ultrastructural features known as the “apical complex” (Figure 1). Haemogregarines (Figure 2) are ubiquitous adeleorine apicomplexan protists inhabiting the blood cells of a variety of ectothermic and some endothermic vertebrates [2–4]. They have also an obligatory heteroxenous life cycle (Figure 3), where asexual multiplication occurs in the vertebrate host; while sexual reproduction occurs in the hematophagous invertebrate vector [5]. This family contains four genera, according to Levine [6]: Haemogregarina Danilewsky [7], Karyolysus Labbé [8], Hepatozoon Miller [9], and Cyriella Lainson [10]. Barta [11] conducted a phylogenetic analysis of representative genera in phylum Apicomplexa using biological and morphological features to infer evolutionary relationships in this phylum among the widely recognized groups. The data showed that the biologically diverse Haemogregarinidae family should be divided into at least three families (as suggested by Mohammed and Mansour [12]), were family Haemogregarinidae, containing the genera Haemogregarina and Cyriella; family Karyolysidae Wennyon [13], of the genus Karyolysus; and family Hepatozooidae Wenyon [13], of the genus Hepatozoon, since the four genera currently in the family do not constitute a monophyletic group. The picture is further complicated by evidence from a study by Petit et al. [14] of a new Brazilian toad haemogregarine parasite Haemolivia stellata.
Figure 1. The general structure for the apical complex for Apicomplexa.

Figure 2. Haemogregarines as a part of phylum Apicomplexa.
Figure 3. The life cycle of the apicomplexan parasites.

It undergoes sporogonic development in its tick host’s gut wall and has a complex life cycle that resembles *Karyolysus* species much more than *Hepatozoon, Haemogregarina,* and *Cyrilia* species. Haemogregarines can be morphologically classified based on the developmental details of sporogonic phases of the parasite in the vector, which provide the main characters for classification, the morphology of gametocytes in the red blood cells, and an evaluation of the stages of development [15,16]. Although useful, this methodology is not sufficient for a taxonomic diagnosis [17,18], also the classical systematics has been problematic because of the variability to which morphological details are subjected [19]. Therefore, the use of molecular methods from blood or tissue samples [20–22], with appropriate molecular phylogeny study, became an essential adjunct to existing morphological and biological characters for use in the inference of evolutionary history relationships among haemoprotozoan parasites [23–25]. Molecular data has been carried out based using PCR assays targeting the nuclear 18s ribosomal RNA gene, which have been extensively applied to characterize hemoparasites DNA more fully in the absence of complete life cycles [26–32].

In the present critical review of the haemogregarines complex, the proper classification, the criteria of generic and unique diagnosis, and the cosmopolitan distribution of haemogregarines among the vertebrate and invertebrate hosts are examined because of their relevant characteristic and taxonomic revisions.

2. Materials and Methods

This review included all related published scientific articles from January 1901 to December 2020. This article was conducted by searching the electronic databases NCBI, ScienceDirect, Saudi digital library, and GenBank database, to check scientific articles and
M.Sc./Ph.D. Thesis related to the research topic of this review. Studies published in the English language were only included and otherwise are excluded.

Relevant studies were reviewed through numerous steps. In the first step, target published articles were identified by using general related terms related to the morphological features, such as “Haemogregarines” and “Apicomplex”. The second step involved screening the resulting articles by using highly specific keywords of the generic features for stages in the life cycle of haemogregarines species, including “Merogony”, “Gamogony”, “Sporogony”, “Infective stages”, “Motile stage”, “Infection sites”, and “sporozoites”. The last step of the review focused on selected studies involving the use of molecular analysis for accurate taxonomic identification by using highly specific keywords, including “PCR”, “Genetic markers”, “Variable regions”, “18S rRNA”, and “Phylogenetic analysis”.

The obtained data were presented in tables and figures and were: Table 1 representing the characteristic features for the haemogregarines genera, Tables 2–6 showing haemogregarines species, the vertebrate host, site of the merogonic stage, the invertebrate vectors, site of gamogony and sporogonic stages, geographical locality for hosts, and the authors for publishing data, Table 7 with the primer sets used for the amplification and sequencing for the appropriate gene of 18S rRNA for haemogregarines, and Table 8 representing all the sequenced and deposited haemogregarines in the GenBank database until now.

3. Results and Discussion

In this review, the different stages of the apicomplexan life cycle were used to identify haemogregarines. However, in most cases, their assignment to one or another genus cannot be considered more than provisional. Accordingly, about 82 haemogregarines in 155 research articles were identified previously. Osimani [33] stated that the differences between the haemogregarines relied more on the host’s identity than the parasite’s characteristics. Mohammed and Mansour [12] reported that haemogregarines gamonts morphology does not provide generic identification with a reliable key. However, Telford et al. [34], and Herbert et al. [35] stated that the determination of generic haemogregarines should not be based exclusively on the gamonts’ form, the type of parasitized host cells, and their effect on the host and site merogony in host cells. While the most characteristic feature for the basic identification via the sporogonic stage.

The reviewed species belonged to the four genera within Hemogregarinidae (Table 1). Following the parsimony analysis in the phylogenetic study of the representative genera in phylum Apicomplexa performed by Siddall and Desser [36] primarily based on ultrastructural observations, it was concluded that the variations between the different haemogregarines genera are mainly reflected by the sporogony features. Besides, Dvořáková et al. [37] added that the host specificity, together with the haemogregarine’s careful morphological and biological analysis, is a sound criterion for accurate identification. These species are common in different animals as fish (Table 2), amphibians (Table 3), reptiles (Tables 4–7), birds (Table 8), and mammals (Table 9).
Table 1. Characters of different groups of haemogregarines used in the parsimony analysis carried out by Barta [19] and Siddall and Desser [36].

| Comparable Features          | Karyolysis | Haemogregarina | Cryilia | Hepatozoon | Haemolivia |
|------------------------------|------------|----------------|---------|------------|------------|
| Conoid present               | ?          | In all non-gametes | In all non-gametes | In all non-gametes | In all non-gametes |
| Crystalloid bodies +/-       | +/−        | +/−            | +       | +/−        | +/−        |
| Merogony +/-                 | + Intra-cellular | + Intra-cellular | + Intra-cellular | + Intra-cellular | + Intra-cellular |
| Micropores +/-               | +          | +/−            | +       | +/−        | +/−        |
| Mitochondria                 | Cristate   | Cristate       | Cristate | Cristate   | Cristate   |
| Mitosis                      | Centriolar | Centriolar     | ?       | Centriolar | Centriolar |
| Amylopectin granules +/-    | +          | −/−            | +       | +/−        | +/−        |
| Polar ring complex +/-      | +          | +/−            | +       | +/−        | +/−        |
| Gametogenesis                | Extra-cellular | Extra-cellular | Extra-cellular | Extra-cellular | Intra-cellular |
| No. of microgametes/each     | 2          | 4              | 4       | 4          | 2–4        |
| microgamont                  |            |                |         |            |            |
| Gamonts                      | Anisogamous | Anisogamous    | Anisogamous | Anisogamous | Anisogamous |
| Syzygy                       | +          | +/−            | +       | +/−        | +/−        |
| Zygote                       | Non-motile | Non-motile     | Non-motile | Non-motile | Non-motile |
| Sporogony                    | Extra-cellular | Extra-cellular | Extra-cellular | Extra-cellular | Intra-cellular |
| Persistent cysts +/-        | −          | −/−            | −       | +/−        | +/−        |
| No. of flagella/microgametes | 1          | 1              | Absent  | 1          | ?          |
| Arrangement of flagella in   | Terminal   | Terminal       | ?       | Terminal   | Terminal   |
| microgametes                 |            |                |         |            |            |
| No. of sporozoites/oocyst    | 20–30      | 8              | >20     | 4–16       | 10–25      |

Note: (+) presence, (-) absence, (?) not detected.
Table 2. Haemogregarines of fish.

| Species of Haemogregarines | The Vertebrate Host | Site of Merogony | Invertebrate Vector | Site of Gamogony and Sporogony | Locality | Authors |
|----------------------------|---------------------|------------------|--------------------|--------------------------------|----------|---------|
| Cyrilia gomesi             | Synbranchus marmoratus | Leucocytes      | Haementeria latzi  | Stomach                        | Sao Paulo, Brazil | Nakamoto et al. [38] |
| Haemogregarina bigemina    | Lipophrys folis and Coryphoblennius galerita | Blood cells | Gnathia maxillaris | Hindgut                        | Portugal Atlantic west coast | Davies et al. [39] |
|                            |                     | Intra-erythrocytic gamonts are only described |                     |                                 |                      |                     |
| Haemogregarina vltavensis  | Perca fluviatilis   |                  |                    | Czechoslovakia                 |          | Lom et al. [40] |
| Haemogregarina leptocotti  | Leptocottus armatus | Blood cells      |                  | California USA                 |          | Hill and Hendrickson [41] |
| Haemogregarina rolofsi     | Sebastes melanops   | Blood cells      |                  | California USA                 |          | Hill and Hendrickson [41] |
| Haemogregarina bigemina    | Clinus superciliosus and Clinus cottoides | Intra-erythrocytic | Gnathia africana | South Africa                   | Davies and Smit [42] |
| Haemogregarine sp.         | Scomber scombrus L. | Leucocytes       |                  | Northwest and Northeast Atlantic ocean |         | Maclean and Davies [43] |
| Haemogregarina curtata     | Clinus cottoides, Parablemmius cornutus | Intra-erythrocytic | Zeylanicobdella arugamensis | Host gut tissue | South Africa | Hayes et al. [44] |
| Haemogregarina balistapi   | Rhinecanthus aculeatus | Intra-erythrocytic | Gnathia aureamaculosa | Host gut tissue | Great Barrier Reef, Australia | Curtis et al. [45] |
| Cyrilia sp.                | Potamotrygon wallacei | Intra-erythrocytic |                  | Rio Negri                      | Oliveira et al. [46] |
| Haemogregarina daviesensis | Lepidosiren paradoxa | Intra-erythrocytic |                  | Eastern Amazon region          | Esteves-Silva et al. [47] |
Table 3. Haemogregarines of amphibians.

| Species of Haemogregarines | The Vertebrate Host | Site of Merogony | Invertebrate Vector | Site of Gamogony and Sporogony | Locality | Authors |
|-----------------------------|---------------------|------------------|---------------------|-------------------------------|----------|---------|
| Pseudohaemogregarina nutti | *Rana nutti*        | Erythrocytes and liver | –                   | –                             | Germany  | Awerenzew [48] |
| Haemogregarina theileri    | *Rana angloensis*   | Erythrocytes and liver | Ticks              | Gut wall                      | Njoro, Kenya | Ball [49] |
| Haemolivia stellate        | Brazilian toads     | Liver             | –                   | –                             | Brazil    | Petit et al. [14] |
| Haemogregarina nucleobisecans | *Bufo himalayanus*  | Erythrocytes and liver | –                   | –                             | India     | Ray [50] |
| Hepatozoon sipedon         | *Nerodia sipedon*   | Various internal organs | *Culex pipiens*     | Hemocoel                       | Ontario, Canada | Smith et al. [51] |
| Hepatozoon catesbianae     | *Rana catesbeiana*  | Erythrocytes and liver | *Culex territans*   | Malpighian tubules            | Ontario, Canada | Desser et al. [52] |
| Hepatozoon cainani         | *Rana catesbeiana*  | Intra-erythrocytic | *Culex fatigans*    | Extra-erythrocyctic gametocytes | State of Mato Grosso | Lainson et al. [53] |
| Hepatozoon theileri        | *Amietia quecketti* | Intra-erythrocytic gamonts are only described | –                   | –                             | South Africa | Conradie et al. [54] |
| Hepatozoon involucrum      | *Hyperolius marmoratus* | Intra-erythrocytic | –                   | –                             | KwaZulu-Natal, South Africa | Netherlands et al. [55] |
| Hepatozoon tenais          | *Afrixalus fornasinii* | Intra-erythrocytic | –                   | –                             | KwaZulu-Natal, South Africa | Netherlands et al. [55] |
| Hepatozoon thori           | *Hyperolius marmoratus* | Intra-erythrocytic | –                   | –                             | KwaZulu-Natal, South Africa | Netherlands et al. [55] |
Table 4. Haemogregarines of lizards.

| Species of Haemogregarines | The Vertebrate Host | Site of Merogony | Invertebrate Vector | Site of Gamogony and Sporogony | Locality | Authors |
|----------------------------|---------------------|------------------|---------------------|--------------------------------|----------|---------|
| *Hepatozoon mesnili*      | Gecko verticillatus | Endothelial cells of all host organs | Culex fatigans and Aedes albopictus | Stomach | Saigon | Robin [36] |
| *Haemogregarina triatomae* | Tupinambis teguixin | Liver and lung | Triatoma s布鲁维亚里亚 | Intestine | South America | Osimani [33] |
| *Hepatozoon argantis*     | Agama mossambica   | Liver            | Argas brumphi       | Gut and homocoelomic cavity | East Africa, Mossambic | Garnham [57] |
| *Hepatozoon sauromalii*   | Sauromalus sp.     | Liver            | Ophionyssus sp.     | Hemocoel | – | Lewis and Wagner [58] |
| *Haemogregarina sp.*      | Tarentola annularis| Lung             | –                   | – | Sudan | Elvasila [59] |
| *Hepatozoon lygosomarum*  | Leiolopisma nigriplantare | Liver and spleen | Ophionyssus saurarum | Wall of the gut caeca | Canterbury, New Zealand | Allison and Desser [60] |
| *Haemogregarina wallatrensis* | Calotes versicolor | Peripheral blood, liver, lung, and bone marrow | – | – | India | Saratchandra [61] |
| *Hepatozoon gracilis*     | Mabuya quinquetaeniata | Liver | Culex pipiens molesus | Hemocoel | – | Giza, Egypt | Bashtar et al. [62] |
| *Haemogregarina sp.*      | Podarcis bocagei and Podarcis carbonelli | Intra-erythrocytic | – | – | NW Portugal | Roca and Galdón [63] |
| *Haemogregarina ramadani* | Acanthodactylus boskianus | Intra-erythrocytic | – | – | – | Giza, Egypt | Abdel-Baki and Al-Quraishy [64] |
| *Hepatozoon sp.*          | Podarcis vaucheri   | Intra-erythrocytic | – | – | Qena, Egypt | Moreira et al. [65] |
| *Haemogregarina sp.*      | Tarentola annularis | Intra-erythrocytic | – | – | – | Rabie and Hussein [66] |
| *Karyolysus lacazei*      | Lacerta agilis      | Intra-erythrocytic | Ophionyssus saurarum and Ixodes ricinus | – | Poland, Slovakia | Haklová-Kočičková et al. [18] |
| *Karyolysus lacazei*      | Varanus niloticus   | Intra-erythrocytic | – | – | – | Ndumo Game Reserve, South Africa | Cook et al. [31] |
| *Karyolysus paradoxa*     | Varanus albigularis, | Intra-erythrocytic | – | – | – | Eastern Amazon region | Esteves-Silva et al. [47] |
| *Haemogregarina daviesensis* | Lepidosiren paradoxa| Intra-erythrocytic | – | – | South Sinai, Egypt | Abou Shafeey et al. [67] |
| *Haemogregarina sp.*      | Scincus scincus     | Intra-erythrocytic | – | – | – | Czech Republic | Zechmeisterová et al. [68] |
Table 5. Haemogregarines of snakes.

| Species of Haemogregarines | The Vertebrate Host | Site of Merogony | Invertebrate Vector | Site of Gamogony and Sporogony | Locality | Authors |
|---------------------------|---------------------|------------------|---------------------|-------------------------------|----------|---------|
| Hepatozoon rarefaciens    | Drymachon corais    | Lung             | Culex tarsalis, Anopheles albintarus, Aedes sierrensis | Hemocoel | California, USA | Ball and Oda [69] |
| Haemogregarnia matrihensis| Psammophis schokari | Intra-erythrocytic| –                   | –                             | Egypt    | Ramadan [70] |
| Hepatozoon fusifex        | Boa constrictor     | Lung             | Culex tarsalis       | Hemocoel                      | USA      | Ball et al. [71] |
| Hepatozoon aegypti        | Spalerosophis diadema| Lung            | Culex pipiens molestus| Hemocoel                      | Egypt    | Bashtar et al. [72] |
| Hepatozoon mocassini      | Agkistrodon piscivorus leucostoma | Liver parenchyma cells | Aedes aegypti | Hemocoel | Louisiana, USA | Lowichik et al. [73] |
| Hepatozoon seurati        | Cerastes cerastes   | Liver, lung, and spleen | Culex pipiens molestus | Hemocoel                      | Aswan, Egypt | Abdel-Ghaffar et al. [74] |
| Hepatozoon mohlhorni      | Echis carinatus     | Liver, lung, and spleen | Culex pipiens molestus | Hemocoel                      | Siwash and Baharia Oasis, Egypt | Bashtar et al. [75] |
| Hepatozoon matrihensis    | Psammophis schokari | Liver and lung   | Culex pipiens molestus | Hemocoel                      | Faiyum, Ismailia, Egypt | Bashtar et al. [76] |
| Hepatozoon ghaffari       | Cerastes vipera     | Liver, lung, and spleen | Culex pipiens molestus | Hemocoel                      | Aswan, Egypt | Shazly et al. [77] |
| Hepatozoon sipedon        | Nerodia sipedon and Rana pipiens | Liver and internal organs | Culex pipiens, and Culex territans | Hemocoel | Ontario, Canada | Smith et al. [81] |
| Haemogregarnia garnhamii  | Psammophis schokari | Intra-erythrocytic | –                   | –                             | Egypt    | Saoud et al. [78] |
| Hepatozoon aqorgbor       | Python regius       | Intra-erythrocytic | –                   | –                             | Ghana    | Sloboda et al. [79] |
| Haemogregarnia sp.        | Cerastes cerastes gasperetti | Intra-erythrocytic | –                   | –                             | Jizan, Saudi Arabia | Al-Farraj [80] |
| Hepatozoon garnhamii      | Psammophis schokari | Intra-erythrocytic | –                   | –                             | Riyadh, Saudi Arabia | Abdel-Baki et al. [29] |
| Hepatozoon sp.            | Zamenis longissimus | Intra-erythrocytic | –                   | –                             | Iran     | Sajjadi and Javanbakht [81] |
| Hepatozoon aegypti        | Spalerosophis diadema | Intra-erythrocytic | –                   | –                             | Riyadh, Saudi Arabia | Abdel-Haleem et al. [82] |
Table 6. Haemogregarines of turtles and tortoises.

| Species of Haemogregarines | The Vertebrate Host | Site of Merogony | Invertebrate Vector | Site of Gamogony and Sporogony | Locality | Authors |
|-----------------------------|---------------------|------------------|--------------------|-------------------------------|----------|---------|
| Hemogregarina nicoriae     | Nicoria trijuga     | Circulating blood and lung | Ozobranchus shipleyi | Intestinal epithelium         | Ceylon   | Robertson [83] |
| Haemogregarina balli       | Chelydra serpentine | Lacunar endothelial cells, liver, lung, and spleen | Placobdella ornata | Gastric and intestinal caeca | Ontario, Canada | Siddall and Desser [84] |
| Hepatozoon mauritanicum    | Testudo graeca      | Endothelial cells of all host organs as liver, lung, spleen . . . etc | Hyalomma aegyptium | The intestinal epithelium of the tick | –        | Michel [85] |
| Haemogregarina pseudomydis | Pseudemys scripta elegans | Leucocytes and Erythrocytes | Placobdella parasitica | – | Louisiana, USA | Acholonu [86] |
| Haemogregarina gangetica   | Trionyx gangeticus | Erythrocytes and lung | – | – | India | Misra [87] |
| Haemogregarina ganapatii   | Lissemys punctata granosa | Peripheral blood and Liver and lung Erythrocytes and Kupffer’s cells of the liver | Mooreotorix cotylifer | Gastric and intestinal caeca of the leech | China | Chai and Chen [88] |
| Haemogregarina sinensis    | Trionyx sinensis    | Intra-erythrocytic | Placobdella costata | Gut cells | Romania | Mihalca et al. [89] |
| Haemolivia mauritanica     | Emys orbicularis    | Intra-erythrocytic | Hyalomma aegyptium | – | Israel | Paperna [90] |
| Haemolivia mauritanica     | Testudo graeca      | Intra-erythrocytic | – | – | Western Palaearctic realm | Široký et al. [91] |
| Haemolivia stepanowi       | Emys orbicularis, Mauremys caspica, M. rivulata, M. leprosa | Intra-erythrocytic | – | – | Western Palaearctic | Dvořáková et al. [23] |
| Haemolivia mauritanica     | Lissemys punctata and Geoclemys hamiltonii | Intra-erythrocytic | – | – | West Bengal, India | Hossen et al. [4] |
| Haemolivia mauritanica     | Testudo graeca and Testudo marginata | Intra-erythrocytic | – | – | North African | Harris et al. [93] |
Table 6. Cont.

| Species of Haemogregarines | The Vertebrate Host | Site of Merogony | Invertebrate Vector | Site of Gamogony and Sporogony | Locality | Authors |
|-----------------------------|---------------------|------------------|---------------------|--------------------------------|----------|---------|
| Haemogregarina sp.          | Rhinoclemmys funera and Kinosternon leucostomum | Intra-erythrocytic | –                   | –                              | Costa Rica | Rossow et al. [94] |
| Haemogregarina sp. Podocnemis unifilis | Intra-erythrocytic | – | – | Brazilian Amazonia | Soares et al. [95] |
| Haemogregarina sundarbanensis Lissemys punctata | Intra-erythrocytic | – | – | West Bengal, India | Molla et al. [96] |
| Haemogregarina stepanowi Emys orbicularis | Intra-erythrocytic | – | – | Belgrade Zoo Araguaia River Basin, Brazil | József et al. [24] |
| Haemogregarina sp. Podocnemis expansa | Cuora galbinifrons, Leucocephalon yavonai, Lissemys punctata | Intra-erythrocytic | – | – | Southeast Asia | Dvořáková et al. [37] |
| Haemogregarina sacaliae Cuora galbinifrons, Leucocephalon yavonai, Lissemys punctata | Intra-erythrocytic | – | – | South African | Cook et al. [31] |
| Haemogregarina pellegrini Land tortorise, Stigmochelys pardalis | Intra-erythrocytic | – | – | Sicily | Arizza et al. [98] |
| Haemogregarina sp. Mauremys caspica | Intra-erythrocytic | – | – | Iran | Rakhshandehroo et al. [99] |
| Haemogregarina sp. Macrocelys temminckii Mesoclemmys vanderhaegi | Intra-erythrocytic | – | – | Caldwell Zoo, Texas | Alhaboubi et al. [100] |
| Haemogregarina sp. Podocnemis Unifilis | Intra-erythrocytic | – | – | Brazil | Goes et al. [101] |
| Haemogregarina podocnemis | PODOCNEMIS UNIFILIS | Intra-erythrocytic | – | – | Brazil | Úngari et al. [102] |
### Table 7. Haemogregarines of crocodilians.

| Species of Haemogregarines | The Vertebrate Host | Site of Merogony | Invertebrate Vector | Site of Gamogony and Sporogony | Locality | Authors |
|----------------------------|---------------------|-----------------|---------------------|-------------------------------|----------|---------|
| Haemogregarina crocodilinorum | *Alligator mississippiensis* | Intra-erythrocytic | *Placobdella multilineata* | Intestinal epithelial cells of the leech | Southern USA includes Arkansas, Carolina, and Florida | Börner [103] |
| Haemogregarina caimani (= Hepatozoon caimani) | *Caiman latirostris* | Intra-erythrocytic | *Culex dolosus* | Hemocoel | Brazil | Pessôa and de Biasi [104] |
| Haemogregarina pettiti (=Hepatozoon pettiti Hoare 1932) | *Crocodilus niloticus* | Erythrocytes and liver | *Glossina palpalis* | Intestine | Uganda, Senegal, West Africa | Hoare [105] |
| Hepatozoon sp. | *Caiman c. yacare* | Intra-erythrocytic | *Phaeotabanus fervens* | Intestine | Pantanal, Brazil | Viana and Marques [106] |
| Hepatozoon caimani | *Caiman yacare* | Intra-erythrocytic | – | – | Pantanal region, Brazil | Viana et al. [107] |

### Table 8. Haemogregarines of birds.

| Species of Haemogregarines | The Vertebrate Host | Site of Merogony | Invertebrate Vector | Site of Gamogony and Sporogony | Locality | Authors |
|----------------------------|---------------------|-----------------|---------------------|-------------------------------|----------|---------|
| Hepatozoon atticorae | *Hirundo spilodera* | Intra-erythrocytic | *Ornithodoros peringueyi* and *Xenopsylla trispinis* | Hemolymph | South Africa, South America, Jamaica, Europea | Bennett et al. [108] |
| Hepatozoon prionopis | *Prionops plumatus* | Intra-erythrocytic | – | – | Transvaal, South Africa | Bennett and Earle [109] |
| Hepatozoon lanis | *Lanius collaris* | Intra-erythrocytic | – | – | South Africa | Bennett et al. [108] |
| Hepatozoon malacotinus | *Dryoscopus cubla* | Intra-erythrocytic | – | – | South Africa | Bennett et al. [108] |
| Hepatozoon numidis | *Numida meleagris* | Intra-erythrocytic | – | – | South Africa | Bennett et al. [108] |
| Hepatozoon pittae | *Pitta arcurae* | Intra-erythrocytic | – | – | Sabah | Bennett et al. [108] |
| Hepatozoon estrildus | *Lonchura cucullata* | Intra-erythrocytic | – | – | Zambia | Bennett et al. [108] |
| Hepatozoon squacrum | *Parisoma subcaeruleum* | Intra-erythrocytic | – | – | South Africa | Bennett et al. [108] |
| Hepatozoon passeris | *Zosterops pallida* | Intra-erythrocytic | – | – | South Africa | Bennett et al. [108] |
| Hepatozoon squamifrons | *Sporopipes squamifrons* | Intra-erythrocytic | – | – | Botswana, South Africa | Bennett et al. [108] |
Table 9. Haemogregarines of mammals.

| Species of Haemogregarines | The Vertebrate Host | Site of Merogony | Invertebrate Vector | Site of Gamogony and Sporogony | Locality | Authors |
|-----------------------------|---------------------|------------------|---------------------|--------------------------------|----------|---------|
| Hepatozoon perniciosum      | Laboratory white rats | The liver        | Echinolaelaps echinoidis | Stomach                         | Washington, USA | Miller [9] |
| Hepatozoon griseisciei     | Sciurus carolinensis | Bone marrow, liver, lung, and spleen (with intra-leucocytic gametocytes) | Euhagaemogamasus ambulans, Echinolaelaps echinoidis and Haemogamasus reidi | Stomach                         | Washington, Marland, Georgia, USA | Desser [110] |
| Hepatozoon erhardovae      | Clethrionomys glareolus | Lung             | Xenopsylla cheopis, Ctenophthalmus agyrtes, C. assimilis and Nosopsyllus fasciatus | Stomach and fat-body cells      | Munich, Germany | Göbel and Krampitz [111] |
| Hepatozoon sylvatici       | Apodemus sylvaticus and Apodemus flavicollis | Bone marrow and liver | Laelaps agilis | Stomach                         | Austria | Frank [112] |
| Hepatozoon sp.             | Dogs                | Intra-erythrocytic | –                   | –                              | Brazil   | Forlano et al. [113] |
| Hepatozoon canis           | Dogs                | Intra-erythrocytic | –                   | –                              | Italy    | Otranto et al. [114] |
| Hepatozoon felis           | Cats                | Intra-erythrocytic | –                   | –                              | India    | Baneth et al. [115] |
| Hepatozoon canis           | Dogs                | Intra-erythrocytic | Rhipicephalus sanguineus | –                             | Mato Grosso do Sul, Brazil | Ramos et al. [116] |
| Hepatozoon canis           | Dogs                | Intra-erythrocytic | –                   | –                              | Central-western Brazil | Paiz et al. [117] |
| Hepatozoon sp.             | Cerdocyon thous, Nasua nasua, Leopards pardalis, Canis familiaris, Thrichomys fosieri, Oecomys namaroc, Clyomys laticeps, Thylamys macrurus, Monodelphis domestics | Intra-erythrocytic | Amblyomma sculptum, A. pareum, A. tigrinum, Rhipicephalus microplus, R. sanguineus, A. auricularium | –                             | Brazil   | De Sousa et al. [118] |
| Hepatozoon felis           | Panthera leo        | –                | Rhipicephalus sanguineus | –                             | Thailand | Bhusri et al. [119] |
| Hepatozoon canis           | Dogs                | Intra-erythrocytic | –                   | –                              | Czech Republic | Mitkova et al. [120] |
| Hepatozoon felis           | Dogs                | Intra-erythrocytic | –                   | –                              | Northeastern Iran | Barati and Razmi [121] |
| Hepatozoon canis           | Cats                | Intra-erythrocytic | –                   | –                              | Turkey    | Tuna et al. [122] |
| Hepatozoon canis           | Dogs                | Intra-erythrocytic | –                   | –                              | United Kingdom | Attipa et al. [123] |
| Hepatozoon felis           | Felis silvestris, Caracal caracal, Panthera pardus, P. leo, Leptailurus serval | Muscle and Liver | –                   | –                              | Limpopo and Mpumalanga | Harris et al. [124] |
| Hepatozoon luiperdjie      | Panthera pardus     | Leukocytes       | –                   | –                              | Limpopo Province, South Africa | Van As et al. [125] |
| Hepatozoon canis           | Dogs                | Intra-erythrocytic | –                   | –                              | Manila, Philippines | Baticados et al. [126] |
In the schizogony (merogony) stage, haemogregarines are characterized by their considerable ability to invade and develop within different organs and cell types inside the vertebrate host (Tables 2–9). Bray [127] proposed that haemogregarines with schizonts in the liver should be placed in the genus *Hepatozoon*. In contrast, those species that precede schizogony in other organs should belong to another genus as *Haemogregarina* or *Karyolysus*. However, only in the lung of the river turtle, *Trionyx gangeticus* infected with *Haemogregarina gangetica*, was described by Misra [87]. In addition to the usual location of merogonic development in the liver, lung, and spleen, Ball et al. [71] have found certain merogonic stages in the highly infected snakes’ brain and heart. Siddall and Desser [84] described merogonic stages in the lacunar endothelial cells of the circulatory system of the leech and its proboscis, besides the liver, lung, and spleen in the turtle. Yanai et al. [128] also described nodular lesions containing schizonts and merozoites of *Hepatozoon* sp. of the heart’s martens, perisplenic, and perirenal adipose tissues, the diaphragm, mesentery, and tongue. Ungari et al. [102] reported that the genus *Haemogregarina* underwent schizogony in the circulating blood cells as in turtles and fish, and the genus *Hepatozoon* underwent schizogony in the liver. Additionally, there are two morphologically different meronts were the micro- and macromeronts. The presence of these two forms of meronts was mentioned to be a fundamental feature of the whole haemogregarine [74,129,130].

Gametocytes are usually the only stages of the parasite detected by scientists. Their morphology, unfortunately, does not provide a reliable clue to the generic differentiation. Together with other relevant data, their morphological characteristics offer a reliable basis for specific identification [35,67]. The haemogregarines gametocytes appeared as sausage-shaped and generally lie singly within erythrocytes (Tables 2–9), but sometimes free in extracellular space, which is consistent with Telford et al. [34], Sloboda et al. [79] as the presence of free extracellular gametocytes. They are also observed in the leucocytes of fish (Table 2), birds (Table 8), and mammals (Table 9).

The shape, size, and structure of infected blood-corpuscles often undergo considerable changes. Hypertrophy may result directly from the gametocyte’s added intraerythrocytic volume or represent an erythrocyte adaptation to the gametocyte’s presence [53,82,131,132]. An entirely different cell response occurred when the gametocytes of *Hemogregarina* sp. invaded erythrocytes of *Rana berlandieri*. The erythrocytes undergo hypertrophy, and the plasmalemma of the infected erythrocyte demonstrated numerous microvilli-like outgrowings. Hussein [133] also described the hypertrophy of *Karyolysus*-infected erythrocytes. Most haemogregarine gametocytes do not invade the host cell’s nucleus but instead move it to the opposite side or the other host cell’s other pole. This is contrary to the effect of the genus *Karyolysus* on the infected erythrocytes. *Karyolysus* has a karyolytic impact on the host cell’s nucleus and is therefore identified *Karyolysus* Reichenow [134].

Little work had been done to identify the actual arthropod vectors of haemogregarines, as the transmission by inoculation of blood was rarely successful. In general, the invertebrate vectors of haemogregarines were the most challenging problem facing this group’s research progress [49]. The haemogregarines displayed a wide distribution of vertebrate host infections, and a large number of invertebrate vectors (Tables 2–9). In all haemogregarines, fertilization is of Adelea type; both micro- and macrogamonts lie in syzygy within the same parasitophorous vacuole. Syzygy can stimulate the production of the associated gamonts in haemogregarines, since only the parasites found in pairs were mostly differentiated, which is consistent with Davies and Smit [42]. Regarding the number of microgametes produced by each microgamont, the members of the suborder Adeleidea were characterized by the production of only a few (four or less) microgametes [135]. Simultaneously, the formation of multiple microgametes has been identified in most haemogregarines species [52]. However, there are some suggestions that multiple microgamete formation does not occur in the entire genus *Hepatozoon* [111]. Regarding the number of flagella in microgametes in haemogregarines, contradictions were recorded. While monoflagellated microgametes have been described for haemogregarines species [74], biflagellated microga-
metes were also recorded for other haemogregarines [52]. On the other hand, Michel [85] reported non-flagellated microgametes in *Hepatozoon mauritanicum*.

Fertilization follows, leading to the formation of a zygote that becomes an oocyst. The oocyst is surrounded by a flexible membrane rather than a wall, and it produces sporozoites that may undergo further merogony. Sporogony is elucidated for just a few known haemogregarines species, the vast majority of which is supposed to investigate this aspect of their life-cycle, as reported by Forlano et al. [113]. There is also another potential criterion for distinguishing between *Hepatozoon* and *Haemogregarina* based on the presence or absence of oocysts containing sporocysts in the invertebrate vector, which is consistent with Levine [6]. When the developing mite reaches the nymphal stage, the sporozoites attain their maturity. The sporozoites eventually get the nymph’s stomach and pass out with their faeces, which are considered infection sources of the vertebrate host (lizard). The morphological characteristics of the gamonts and meronts found in the blood cells sometimes provide inadequate information for differential diagnoses [37], meaning that assigning species of haemogregarines to one of these genera must be based on the characteristics of its sporogony in the invertebrate vectors [6,64]. However, data on invertebrate vectors and sporogony are missing for the majority of species [23].

Until now, the current taxonomy of haemogregarines is facing a great challenge due to the high variation in gamont morphology, low host specificity, unknown invertebrate hosts in many cases, and fewer details of sporogony. Therefore, molecular approaches are now available to distinguish populations of morphologically identical but genetically different parasites, including DNA and polymerase chain reaction (PCR) based approaches [22,136–141]. Some studies based on PCR-based assays as the reference diagnostic test for epidemiological studies, which given their greater sensitivity, particularly for testing different hosts with intermittent levels of parasitemia via a low infection rate by gamonts, as Otranto et al. [114], Haklová-Kočková et al. [18], Jőzsef et al. [24], Ramos et al. [116], and Mitkova et al. [120]. Notably, all the molecular evidence comes from the complete and partial sequences of the small subunit (SSU) ribosomal DNA (rDNA) 18S gene is a sufficient phylogenetic marker to approximate ordinal level relationships and those within orders [68,98,119,142–145]. Previous molecular studies of Harris et al. [22] and Barta et al. [19] demonstrated that the haemogregarine species are clustered in sister clades with interspecies linked more with the host geographic distribution, rather than host species. There are universal primer sets that were able to molecularly characterize haemogregarines, as mentioned in Table 10. However, many species with sequences deposited in the GenBank database are not identified correctly at the generic level. Table 11 expressed only haemogregarines identified at the species level and others identified at the generic level are excluded.

### Table 10. Primer sets used in the phylogenetic analysis of haemogregarines by 18S rRNA gene.

| Primer Set | Primer Sequence | Reference |
|------------|-----------------|-----------|
| 4558F     | 5′- GCT AAT ACA TGA GCA AAA TCTCAA -3′ | Mathew et al. [146] |
| 2733R     | 5′- CGG AAT TAA CCA GAC AAA T -3′ | Mathew et al. [146] |
| 2867F     | 5′- ACCGTTGAT CCT GCT GCC AG -3′ | Mathew et al. [146] |
| 2868R     | 5′- TGA TCC TTC TGC AGG TTC ACC TAC -3′ | Mathew et al. [146] |
| HEMO1     | 5′- TAT TGG TTT TAA GAA CTA ATT TTA TGA TG -3′ | Perkins and Keller [147] |
| HEMO2     | 5′- CTT CTC TTT CCT TTA AGT GAT AAG GTT CAC -3′ | Perkins and Keller [147] |
| HepF      | 5′- ATA CAT GAG CAA AAT CTC AAC -3′ | Inokuma et al. [148] |
| HepR      | 5′- CCT ATT CCA TGC AGG AG -3′ | Inokuma et al. [148] |
| HepF300   | 5′- GATCTGACCTATCAGCATTGAC -3′ | Ujvari et al. [20] |
| HepR900   | 5′- CAAAATCAAGATTTACACCTGAC -3′ | Ujvari et al. [20] |
Table 10. Cont.

| Primer Set | Primer Sequence | Reference |
|------------|-----------------|-----------|
| HEP-1      | 5′- CGC GAA ATT ACC CAA TT -3′ | Criado-Fornelio et al. [149] |
| HEP-2      | 5′- CAG ACC GAT GTC TTT YAG CAG -3′ | Tabar et al. [150] |
| Piroplasmid-F | 5′- CCA GCA GGC GGC GTA ATT -3′ | Kvičerová et al. [26] |
| Piroplasmid-R | 5′- CTT GGC CCA TCT AGG CAT CTC -3′ | Kledmanee et al. [151] |
| EF         | 5′- GAA ACT GGC AAT GGC TCA TT -3′ | Zintl et al. [152] |
| Hep-001F   | 5′- CCT GGC TAT ACA TGA AAA TCT -3′ | Hodžič et al. [153] |
| Hep-737R   | 5′- CCA ACT GTC CCT ATC AAT CAT TAA AGC -3′ | Rakhshandehroo et al. [99] |
| BTH-1F     | 5′- CGC GGA CCA CAA TCA CTA CCA CAT CT -3′ | Alhaboubi et al. [100] |
| BTH-1R     | 5′- TCG CAG TAG TAG TTT CAG CAG -3′ | Kvičerová et al. [26] |
| GF2        | 5′- AGG ACT TTG ATT TCG TGG -3′ | Kledmanee et al. [151] |
| GR2        | 5′- CCA GAA ACT TGC ATT CTC CTC -3′ | Zintl et al. [152] |
| Haemog11_F | 5′- ATT GTA GGA GGA GGT CCA TGG -3′ | Kvičerová et al. [26] |
| Haemog11_R | 5′- GCG TTA GAC ACG CAA AGT CTG -3′ | Kvičerová et al. [26] |
| HemoFN     | 5′- CCY TGG TAA TTC TAG AGC TAT -3′ | Kvičerová et al. [26] |
| HemoRN     | 5′- GAT AGG GCT TAC GGA GATTT TAC ATG AGC -3′ | Kvičerová et al. [26] |

Table 11. List of sequences for haemogregarines from GenBank database based on the 18S rRNA gene.

| Parasites                  | Hosts                        | Accession Number in GenBank |
|----------------------------|------------------------------|-----------------------------|
| Haemogregarina podocnemis  | Podocnemis unifilis          | MF476203.1 - MF476205.1     |
| Haemogregarina pellegrini  | Platysternon megacephalum     | KM887509.1                  |
| Haemogregarina sacalae     | Sacalia quadriocellata        | KM887507.1                  |
| Haemogregarina stepanovi   | Mauremys leprosa             | MT345287.1                  |
|                           | Emys orbicularis             |                             |
|                           | Mauremys leprosa             |                             |
|                           | Mauremys riolata             |                             |
|                           | Mauremys caspica             |                             |
| Haemogregarina bigemina    | Lipophrys pholis             |                             |
| Haemogregarina balli       | Chelydra serpentine          |                             |
| Hepatozoon fitzsimonsi     | Kinixys zombensis            |                             |
| Hepatozoon ursi            | Chersina angulate            |                             |
|                           | Ursus thibetanus japonicus   | EU041718.1, AB586028.1, LC431855.1 - LC431853.1 |
|                           | Melursus urisinus            | HQ892437.1 - HQ892429.1     |
| Hepatozoon sechellensis    | Gradisilia alternans         |                             |
|                           | Apodemus sylcaticus           |                             |
| Hepatozoon ajorbor         | Ctenophthalmus agypti        |                             |
|                           | Python regius                |                             |
|                           | Rhombomys opimus             |                             |
| Hepatozoon musa            | Crotalus durissus            |                             |
|                           | Philodryas natterei          |                             |
|                           | Hyperotus marmoratus         |                             |
| Hepatozoon involucrum      | Ursus arctos                 |                             |
| Hepatozoon clamatae        | Rana pipiens                 |                             |
| Hepatozoon catesbianae     | Rana clamitans               |                             |
| Hepatozoon aegypti         | Spalerosophis diadema        |                             |
| Hepatozoon martis          | Martes foina                 |                             |
| Hepatozoon procyonis       | Nasua nasua                  |                             |
| Hepatozoon griseisciuri    | Scinurus carolinensis        |                             |
| Parasites | Hosts | Accession Number in GenBank |
|-----------|-------|-----------------------------|
| *Hepatozoon sciuri* | *Scinus vulgaris* | MN104636.1 - MN104640.1, AF206668.1, KU729739.1 |
| *Hepatozoon americanum* | *Canis familiaris* | MN793001.1, MN793000.1, KP119773.1, KX512804.1, KJ999676.1, MG041605.1 |
| *Hepatozoon theleri* | *Amietia queckettii* | Caiman crocodilus | MF322538.1, MF322539.1, MG435046.1 - MG435049.1 |
| *Hepatozoon caimani* | *Caiman crocodilus* | Felis silvestris silvestris | KX757032.1, MH078194.1, KY649445.1, MG041595.1 - MG041599.1 |
| *Hepatozoon silvestris* | *Felis catus* | MG041600.1 - MG041603.1 |
| *Hepatozoon tenius* | *Afrixalus fornasini* | AF206668.1, KU729739.1 |
| *Hepatozoon torri* | *Hyperolius argus* | KJ608372.1 |
| *Hepatozoon luiperdjie* | *Panthera pardus pardus* | KF119772.1 |
| *Hepatozoon eharodoviae* | *Snakes* | MN793002.1 - MN793004.1, KP119772.1 |
| *Hepatozoon domerguei* | *Eurycercus retractus* | MG041601.1, MG041603.1 |
| *Hepatozoon tuatarae* | *Sphenodon punctatus* | HG972969.1, HG97770.1 |
| *Hepatozoon cf. ophisauri* | *Rhombomys opimus* | KP119772.1 |
| *Hepatozoon colubri* | *Amblyomma cajennense* | MG061503.1, EU289922.1, DQ701888.1, MK910141.1 - MK910144.1, MK757993.1 - MK757995.1, MN791089.1, MN791088.1, MN393913.1, MN393910.1, MK649571.1 - MK649576.1, MK214285.1 - MK214288.1, MG254622.1 - MG254625.1, MC091084.1 - MC091092.1, HC092070.1, HC092071.1 - HC092073.1, HC092074.1, HC092075.1 |
| *Haemaphysalis longicornis* | *Lycalopex vetulus* | MT107092.1 - MT107097.1, MT107087.1 - MT107091.1, LC169075.1 |
| *Haemaphysalis concinna* | *Lycalopex gymnocercus* | MH595911.1 - MH595921.1, MG087347.1, KY056823.1, MG241129.1, KT587790.1, KT587789.1, KY196999.1, KY197000.1 - KY197002.1, QX867389.1, MN207197.1 |
| *Rhipicephalus sanguineus* | *Canis aureus* | KF322145.1, KC886721.1, KC886729.1 - KC886733.1, KJ572975.1, KJ643545.1, JX466886.1 - JX466880.1 |
| *Rhipicephalus microplus* | *Lycalopex vetulus* | KJ868814.1, KJ572977.1 - KJ572975.1, KJ643545.1, JX466886.1 - JX466880.1 |
| *Rhipicephalus decoloratus* | *Kinixys species* | KX816958.1 |
| *Canis lupus familiaris* | *Didelphis albiventris* | KJ392884.1, KJ392885.1, KF322145.1, KC886721.1, KC886729.1 - KC886733.1 |
| *Lycalopex vetulus* | *Didelphis albiventris* | KJ868814.1, KJ572977.1 - KJ572975.1, KJ643545.1, JX466886.1 - JX466880.1 |
| *Lycalopex gmynecerus* | *Lycalopex vetulus* | KX816958.1 |
| *Didelphis albiventris* | *Lycalopex gmynecerus* | KJ392884.1, KJ392885.1, KF322145.1, KC886721.1, KC886729.1 - KC886733.1 |
| *Canis aureus* | *Lycalopex gmynecerus* | KJ392884.1, KJ392885.1, KF322145.1, KC886721.1, KC886729.1 - KC886733.1, KJ392884.1, KJ392885.1, KF322145.1, KC886721.1, KC886729.1 - KC886733.1 |
| *Lycalopex gmynecerus* | *Lycalopex gmynecerus* | KX816958.1 |
| *Didelphis albiventris* | *Lycalopex gmynecerus* | KJ392884.1, KJ392885.1, KF322145.1, KC886721.1, KC886729.1 - KC886733.1, KJ392884.1, KJ392885.1, KF322145.1, KC886721.1, KC886729.1 - KC886733.1 |
| *Canis aureus* | *Lycalopex gmynecerus* | KJ392884.1, KJ392885.1, KF322145.1, KC886721.1, KC886729.1 - KC886733.1, KJ392884.1, KJ392885.1, KF322145.1, KC886721.1, KC886729.1 - KC886733.1 |
| *Lycalopex gmynecerus* | *Lycalopex gmynecerus* | KX816958.1 |
| *Didelphis albiventris* | *Lycalopex gmynecerus* | KJ392884.1, KJ392885.1, KF322145.1, KC886721.1, KC886729.1 - KC886733.1, KJ392884.1, KJ392885.1, KF322145.1, KC886721.1, KC886729.1 - KC886733.1, KJ392884.1, KJ392885.1, KF322145.1, KC886721.1, KC886729.1 - KC886733.1 |
| *Canis aureus* | *Lycalopex gmynecerus* | KJ392884.1, KJ392885.1, KF322145.1, KC886721.1, KC886729.1 - KC886733.1, KJ392884.1, KJ392885.1, KF322145.1, KC886721.1, KC886729.1 - KC886733.1, KJ392884.1, KJ392885.1, KF322145.1, KC886721.1, KC886729.1 - KC886733.1, KJ392884.1, KJ392885.1, KF322145.1, KC886721.1, KC886729.1 - KC886733.1 |
Table 11. Cont.

| Parasites | Hosts | Accession Number in GenBank |
|-----------|-------|-----------------------------|
| **Felis catus** | | KY469446.1, MN689671.1 - MN689661.1 |
| | | KY322141.1-KY322144.1, KC886720.1 - KC886728.1, MK757741.1 - MK757792.1, MN103520.1, MN103519.1, MH699884.1 - MH699892.1, MG077048.1 - MG077087.1, KY693670.1, KJ868819.1 - KJ868815.1, KU893118.1 - KU893127.1, KM096414.1 - KM096411.1, KJ572979.1, KJ572978.1, EU165370.1, GU376458.1 - GU376446.1, DQ869909.1, AY731062.1, MW295531.1, MN463026.1 - MN463021.1 |
| **Vulpes vulpes** | | KF322141.1-KF322144.1, KC886720.1 - KC886728.1, MK757741.1 - MK757792.1, MN103520.1, MN103519.1, MH699884.1 - MH699892.1, MG077048.1 - MG077087.1, KY693670.1, KJ868819.1 - KJ868815.1, KU893118.1 - KU893127.1, KM096414.1 - KM096411.1, KJ572979.1, KJ572978.1, EU165370.1, GU376458.1 - GU376446.1, DQ869909.1, AY731062.1, MW295531.1, MN463026.1 - MN463021.1 |
| **Ixodes ricinus** | | KF322141.1-KF322144.1, KC886720.1 - KC886728.1, MK757741.1 - MK757792.1, MN103520.1, MN103519.1, MH699884.1 - MH699892.1, MG077048.1 - MG077087.1, KY693670.1, KJ868819.1 - KJ868815.1, KU893118.1 - KU893127.1, KM096414.1 - KM096411.1, KJ572979.1, KJ572978.1, EU165370.1, GU376458.1 - GU376446.1, DQ869909.1, AY731062.1, MW295531.1, MN463026.1 - MN463021.1 |
| **Hydrochoerus hydrochaeris** | | KU597235.1 - KU597242.1, KCS84780.1 |
| **Cuon alpinus** | | KU597235.1 - KU597242.1, KCS84780.1 |
| **Dermacentor reticulatus** | | KU597235.1 - KU597242.1, KCS84780.1 |
| **Pseudolopex gymnocercus** | | KU597235.1 - KU597242.1, KCS84780.1 |
| **Panthera leo** | | KU597235.1 - KU597242.1, KCS84780.1 |
| **Panthera tigris** | | KU597235.1 - KU597242.1, KCS84780.1 |
| **Camelus dromedarius** | | KU597235.1 - KU597242.1, KCS84780.1 |
| **Hepatozoon apri** | | KU597235.1 - KU597242.1, KCS84780.1 |
| **Sus scrofa leucomystax** | | KU597235.1 - KU597242.1, KCS84780.1 |
| **Amietophrynus gutturalis** | | KU597235.1 - KU597242.1, KCS84780.1 |
| **Amietophrynus garmani** | | KU597235.1 - KU597242.1, KCS84780.1 |
| **Sclerophrys maculata** | | KU597235.1 - KU597242.1, KCS84780.1 |
| **Sclerophrys pusilla** | | KU597235.1 - KU597242.1, KCS84780.1 |
| **Hepatozoon cf. felis** | | KU597235.1 - KU597242.1, KCS84780.1 |
| **Felis silvestris silvestris** | | KU597235.1 - KU597242.1, KCS84780.1 |
| **Puma concolor** | | KU597235.1 - KU597242.1, KCS84780.1 |
| **Eira barbara** | | KU597235.1 - KU597242.1, KCS84780.1 |
| **Lycalopex gymnoucercus** | | KU597235.1 - KU597242.1, KCS84780.1 |
| **Leopardus pardalis** | | KU597235.1 - KU597242.1, KCS84780.1 |
| **Asian lion** | | KU597235.1 - KU597242.1, KCS84780.1 |
| **Prionailurus bengalensis** | | KU597235.1 - KU597242.1, KCS84780.1 |
| **Prionailurus trionemotis** | | KU597235.1 - KU597242.1, KCS84780.1 |
| **Panthera onca** | | KU597235.1 - KU597242.1, KCS84780.1 |
| **Panthera tigris** | | KU597235.1 - KU597242.1, KCS84780.1 |
| **Rhipicephalus sanguineus** | | KU597235.1 - KU597242.1, KCS84780.1 |
| **Eurasin lynx** | | KU597235.1 - KU597242.1, KCS84780.1 |
| **Haemolivia parvula** | | KU597235.1 - KU597242.1, KCS84780.1 |
| **Kinyxs zambensis** | | KU597235.1 - KU597242.1, KCS84780.1 |
| **Haemolivia stellata** | | KU597235.1 - KU597242.1, KCS84780.1 |
| **Amblyomma dissimile** | | KU597235.1 - KU597242.1, KCS84780.1 |
| **Amblyomma rotundatum** | | KU597235.1 - KU597242.1, KCS84780.1 |
| **Haemolivia mariae** | | KU597235.1 - KU597242.1, KCS84780.1 |
| **Egerinia stokesii** | | KU597235.1 - KU597242.1, KCS84780.1 |
| **Tiliqua rugosa** | | KU597235.1 - KU597242.1, KCS84780.1 |
| **Haemolivia mauritanica** | | KU597235.1 - KU597242.1, KCS84780.1 |
| **Hyalomma aegyptium** | | KU597235.1 - KU597242.1, KCS84780.1 |
| **Haemolivia mauritanica** | | KU597235.1 - KU597242.1, KCS84780.1 |
| **Hyalomma sp.** | | KU597235.1 - KU597242.1, KCS84780.1 |
| **Canis lupus familiaris** | | KU597235.1 - KU597242.1, KCS84780.1 |
| **Testudo marginata** | | KU597235.1 - KU597242.1, KCS84780.1 |
| **Kangaroo mouse cricetulus** | | KU597235.1 - KU597242.1, KCS84780.1 |
| **Ixodes ricinus** | | KU597235.1 - KU597242.1, KCS84780.1 |

**Note:** Accession numbers are for GenBank except where otherwise specified.
4. Conclusions

Few haemogregarine characteristics provide a reliable basis for the related parasite to recognized genera. Details of the sporogonic cycle seem to be the only reliable criterion as they are the “Key-stone” in the classification system. Morphological characteristics of the gametocytes do not help in this respect. Features of the schizogonic stages, when these are known, are not much better as criteria of generic value. Molecular phylogenetic studies using the appropriate genetic markers are helpful tools for the accurate taxonomic identification for haemogregarines. Further studies are recommended to include other nuclear and mitochondrial genes to provide more information about the genetic variability among haemogregarines.

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