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SELECTED ADAPTATIONS TO THE PARASITIC MODE OF LIFE IN SPOROZOANS (*APICOMPLEXA)*, WITH PARTICULAR EMPHASIS ON THE GENUS *EIMERIA*

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Abstract

This study critically examines the key adaptations underlying the parasitic success of sporozoans (Apicomplexa), with a particular focus on the genus Eimeria. By synthesizing current literature, the paper identifies how specific morphological, biological, and physiological traits enable Eimeria spp. to infect a diverse array of hosts and thrive in various environments. Understanding these core adaptations provides essential insights into the mechanisms underlying Eimeria's impact, including the pathogenesis of coccidiosis – a disease characterized by diarrhea, dehydration, and potentially death. This paper distinguishes and discusses two main categories of adaptations: (1) biological adaptations, which include features related to reproduction, development, and life cycle strategies; and (2) morphological adaptations, which encompass structures such as the apical complex, cytoskeletal elements, and the forms of developmental stages. The integration of these categories of adaptations enables the parasites to efficiently locate, colonize, and persist within their hosts. Understanding these adaptations and factors influencing infection is crucial for revealing Eimeria pathogenesis and spread. Moreover, this knowledge also helps to disrupt their life cycles and prevent infection.

Keywords: Apicomplexa, Eimeria spp., adaptations, parasitism

Introduction

Protozoa comprise more than 200,000 species, of which about 10,000 are parasitic organisms (Cox, 2010). The genus *Eimeria* belongs to the phylum *Apicomplexa*, which includes exclusively intracellular parasitic species (Pojmańska, 2005; Weng et al., 2024). The disease caused by *Eimeria spp.* infection, i.e. *coccidiosis/eimeriosis*, is diagnosed primarily in young animals, in which infection parameters are generally higher than in older animals (López-Osorio et al., 2020; Ali et al., 2025; Disfani et al., 2025). The most common symptoms of coccidiosis are diarrhoea and loss of appetite. These lead to weakness and dehydration and, in

young animals, may result in death (von Samson-Himmelstjerna et al., 2006; López-Osorio et al., 2020; Ayana et al., 2022). The disease causes major economic losses to breeders, resulting not only from increased mortality but also from reduced body weight and productivity (Gilbert et al., 2020; Zhou et al., 2023; Rahmani et al., 2024). Costs associated with treatment of affected animals and prevention of infection also reduce the profitability of production. It is estimated that annual global losses associated with coccidiosis in poultry alone amount to as much as GBP 10.4 billion (approximately PLN 50 billion) (Blake et al., 2020).

Infection is often caused by multiple *Eimeria* species (Xu et al., 2022), which differ in pathogenicity. For example, *Eimeria tenella* is one of the most pathogenic species occurring in poultry, and infections in young birds result in high flock mortality (Matsubayashi et al., 2019). In cattle, *E. bovis* and *E. zuernii* are of greatest clinical importance (Chen et al., 2024).

The spread of coccidiosis is favoured by neglected, damp environments that provide suitable conditions for the development and survival of the parasite's dispersal stages (Ola-Fadunsin et al., 2019; Li et al., 2021; Badri et al., 2024). Older animals also play an important role in the epidemiology of coccidiosis because they may shed oocysts asymptomatically and thus serve as a source of infection for juveniles, which are more susceptible (Matos et al., 2018; de Macedo et al., 2020). Following recovery from an intense infection, the host develops short-lived immunity (Smith and Hayday, 2000; Wattrang et al., 2016; Matos et al., 2018).

Coccidiosis occurs in many animal species; however, species of the genus *Eimeria* show high specificity both with regard to host selection and their site of development within the host (Weng et al., 2024). In Poland, *Eimeria spp.* infections have been reported in various animal species, including wildlife—roe deer, red deer, European bison, moose, wild boar and hares (Pilarczyk et al., 2004; Demiaszkiewicz and Pyziel, 2009; Kuligowska et al., 2014; Balińska and Demiaszkiewicz, 2022)—as well as farm animals, including alpacas, cattle, sheep, goats, horses and poultry (Klockiewicz et al., 2007; Studzińska et al., 2008; Antoszek and Balicka-Ramisz, 2009; Balicka-Ramisz et al., 2012; Gaweł et al., 2015; Tomczuk et al., 2015; Balicka-Ramisz et al., 2020; Nosal et al., 2023).

Coccidia are cosmopolitan organisms, and their wide distribution is attributable to their ability to adapt to the host and to the high resistance of oocysts to changing geoclimatic conditions (Balicka-Ramisz, 2000). Parasites of the genus *Eimeria* have evolved numerous morphological, physiological and biological adaptations specific to intracellular parasitism (Combes, 1999). Adaptations to a parasitic mode of life facilitate locating, colonizing and persisting in a host and obtaining energy from the food available within it, ultimately enabling reproduction and colonization of new hosts (Niewiadomska et al., 2001; Kolářová and Valigurová, 2021).

Biological adaptations

Biological adaptations include traits associated with completion of the parasite **life cycle** (Niewiadomska et al., 2001). The first element of biological adaptation is the **mode of reproduction**. Asexual reproduction is common among protozoa, but representatives of the *Apicomplexa* also undergo a sexual process leading to the formation of gametes (Gibson, 2021). Apicomplexan protozoa therefore exhibit an alternation-of-generations type of **development**, with asexual divisions (schizogony/merogony, sporogony/sporulation) and a sexual process (gametogony) (Bowman, 2012). The **life cycle** of *Eimeria spp.* is direct and proceeds through these three phases: sporogony occurs in the external environment, whereas schizogony and gametogony take place in the host (López-Osorio et al., 2020).

Host infection occurs through ingestion of infective (sporulated) oocysts. Sporozoites are released from the oocysts in the intestine, enter epithelial cells—usually intestinal cells—and transform into trophozoites. Trophozoites grow and develop into a stage known as a

schizont (meront) (Gundłach and Sadzikowski, 2004; Bowman, 2012). Schizonts feed intensively and increase in size. Their nuclei divide repeatedly, producing first-generation merozoites, which are released into the intestinal lumen after rupture of the host cell and then invade new cells. According to Daugschies and Najdrowski (2005), schizogonic divisions of each schizont produce more than 10^5 merozoites.

Schizogony, the number of rounds of which is characteristic of the *Eimeria* species (Zhu et al., 2025), is repeated several times, producing successive generations of merozoites. After entering new epithelial cells, the final programmed generation of merozoites differentiates into immature female and male sex cells—gametocytes—and gametogony begins. A female gametocyte develops into one mature macrogamete, whereas a male gametocyte divides into numerous flagellated microgametes. Each macrogamete is fertilized by one microgamete, producing a zygote that, after forming a resistant wall, develops into an oocyst (Mesa-Pineda et al., 2021). Oocysts are shed with faeces into the external environment, where sporogony takes place. During sporogony, divisions of the sporont produce four sporoblasts within the oocyst; these acquire new walls and form four sporocysts. The sporocyst nuclei divide again, producing two sporozoites in each sporocyst. Thus, one oocyst contains eight sporozoites in total (Mares et al., 2023). Appropriate oxygen availability, temperature and humidity are required for this process (Mesa-Pineda et al., 2021). Owing to their thick walls, oocysts are resistant to adverse environmental factors such as drought, sunlight and unfavourable temperatures, and they may remain infective for long periods (Peek and Landman, 2011).

Both sexual and asexual reproduction in *Eimeria spp.* are of major, although different, biological significance. The purpose of schizogony is multiplication of the parasite within the host, i.e. a substantial increase in the number of developmental forms derived from a single sporozoite (Mesa-Pineda et al., 2021). Gametogony results in the formation of dispersal stages, which become infective through sporogony; this enables infection of new hosts and plays an important role in parasite spread (Yaeger, 1996; Zhao et al., 2024). Sexual reproduction also generates genetic variation, which may facilitate adaptation of populations to new environments or to changing environmental factors (Ashu and Xu, 2015). In addition, the high fecundity of parasites is an important biological adaptation that greatly increases the probability of completing the life cycle by compensating for losses caused by adverse external environmental conditions (Combes, 1999; Doherty et al., 2022).

Morphological adaptations

Morphological adaptations of parasites concern, among other features, body structure and shape, modifications of internal systems, and locomotory, attachment and sensory apparatuses (Niewiadomska et al., 2001). As unicellular organisms, protozoa of the genus *Eimeria* possess all basic cellular organelles. Morphologically, a protozoan cell corresponds to a single metazoan cell, but physiologically and biologically it constitutes an independent organism (Gavelis et al., 2021).

Coccidia possess a number of adaptations that specialize them for intracellular parasitism. One such adaptation is the reduction of locomotory organelles; however, some developmental stages (zoites) are motile and can move by bending, gliding or undulation. In *Eimeria spp.*, gliding is most commonly reported as the mode of locomotion (Russell and Sinden, 1981; Gubbels and Duraisingh, 2012; Harding and Frischknecht, 2020).

One of the most important adaptations is the **apical complex** located at the anterior end of zoite cells. It consists of the apical ring, conoid, rhoptries and micronemes. It stiffens the cell and facilitates parasite entry into host cells. The cone-shaped coccidian conoid, attached to the apical ring, is composed of spirally arranged tubulin fibres, two intraconoidal microtubules and preconoidal rings (Haase et al., 2022). Cortical (subpellicular) microtubules are also anchored

in the apical ring (Padilla et al., 2024); they form part of the cytoskeleton, determine parasite shape and also provide rigidity to the cell (Guizetti and Frischknecht, 2021). In the avian parasite *Eimeria tenella*, there are exactly 24 such microtubules (Burrell et al., 2022). The conoid can retract into and protrude from the zoite cell during secretion of substances involved in motility or invasion (Gui et al., 2023). Club-shaped rhoptries and micronemes are secretory organelles containing products essential for adhesion to and invasion of host cells (Burrell et al., 2022). They are located near the intraconoidal microtubules and, together with *microtubule-associated vesicles*, form an organized secretory system within the conoid (Burrell et al., 2022). Rhoptries secrete proteins that form connections between parasite and host membranes, inhibit host defence proteins and modify signalling pathways; they also determine parasite survival and pathogenicity within the host cell (Oakes et al., 2013; Ben Chaabene et al., 2021). Micronemes, which are the first organelles to discharge their contents, likewise contribute to parasite motility, adhesion and entry into host cells (Gubbels and Duraisingh, 2012; Valleau et al., 2023).

All parasites belonging to the *Apicomplexa* undergo substantial morphological changes during their life cycle (Harding and Frischknecht, 2020). **Sporozoites** are crescent-, worm- or cylindrical-shaped forms that move rapidly by alternating elongation and contraction (Czapik, 1992). A **schizont** (agamont) is a structure derived from a sporozoite and preparing for division. First-generation **schizont**s are the largest (Bafundo and McCullough, 2025) and may be visible to the naked eye as white dots on the intestinal epithelium (Preena, 2019). **Merozoites** are crescent-shaped cells produced from **schizont**s and are capable of active movement. They enter new cells, where they grow and once again assume a spherical shape. Asexual divisions produce several new parasite generations, some of which migrate to subsequent epithelial cells and become spherical (López-Osorio et al., 2020). **Macro- and microgametes** develop independently from macro- and microgametocytes. Macrogametes are large, uninucleate, spherical cells. Microgametes are smaller and spindle-shaped and are capable of efficient movement owing to the presence of two flagella (López-Osorio et al., 2020).

Summary

A parasitic mode of life is associated with the development of effective morphological, physiological and biological adaptations that determine parasite survival in the host and the survival of its dispersal stages in the environment (Aleuy and Kutz, 2020). Knowledge of parasite adaptations, especially biological ones, makes it possible to control the parasite effectively at an appropriate stage of its cycle and to prevent completion of the life cycle and infection of further individuals (Blasco-Costa and Poulin, 2017; Cable et al., 2017). Dispersal stages (oocysts) are shed with faeces into the environment, where their survival depends on numerous external factors. Despite their thick, resistance-enhancing walls, many oocysts die as a result of unfavourable temperature or humidity, or because they enter an unsuitable host (Svensson et al., 1995; Lassen et al., 2013; López-Osorio et al., 2020). Appropriate management measures can therefore effectively control the level of *Eimeria* infection in animals and help prevent infection (Ahmad et al., 2024).

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SELECTED ADAPTATIONS TO THE PARASITIC MODE OF LIFE IN SPOROZOANS (*APICOMPLEXA),* WITH PARTICULAR EMPHASIS ON THE GENUS *EIMERIA*

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SUMMARY

This study critically examines the key adaptations underlying the parasitic success of sporozoans (Apicomplexa), with a particular focus on the genus *Eimeria*. By synthesizing current literature, the paper identifies how specific morphological, biological, and physiological traits

enable *Eimeria* spp. to infect a diverse array of hosts and thrive in various environments. Understanding these core adaptations provides essential insights into the mechanisms underlying *Eimeria*'s impact, including the pathogenesis of coccidiosis – a disease characterized by diarrhea, dehydration, and potentially death. This paper distinguishes and discusses two main categories of adaptations: (1) biological adaptations, which include features related to reproduction, development, and life cycle strategies; and (2) morphological adaptations, which encompass structures such as the apical complex, cytoskeletal elements, and the forms of developmental stages. The integration of these categories of adaptations enables the parasites to efficiently locate, colonize, and persist within their hosts. Understanding these adaptations and factors influencing infection is crucial for revealing *Eimeria* pathogenesis and spread. Moreover, this knowledge also helps to disrupt their life cycles and prevent infection.

Keywords: Apicomplexa, *Eimeria* spp., adaptations, parasitism