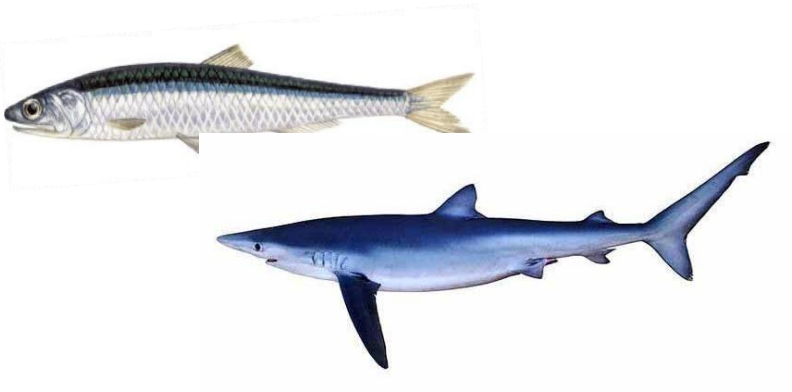

Taxonomic revision of fish coccidians, with an evaluation of microparasite infection in the European anchovy (*Engraulis encrasicolus*) and phylogenetic analysis of coccidians infecting the blue shark (*Prionace glauca*)

Sílvia Simões Rodrigues

Master's degree in Biological Aquatic Resources

Biology Department

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Supervisor

Aurélia Saraiva, Teacher, Faculty of Sciences of the University of Porto (FCUP)

Co-Supervisor

Raquel Xavier, Auxiliar Investigator, Research Center in Biodiversity and Genetic Resources (CIBIO)

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FACULDADE DE CIÊNCIAS
UNIVERSIDADE DO PORTO

Todas as correções determinadas pelo júri, e só essas, foram efetuadas.

O Presidente do Júri,

Porto, _____/_____/_____

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RESUMO

A pesca de captura marinha tem aumentado nos últimos anos, já que a produção global de pesca de captura atingiu um recorde de 96,4 milhões de toneladas em 2018, e pequenos peixes pelágicos como a anchova europeia são fortemente comercializados (FAO, 2020). As pressões antropogénicas, incluindo as mudanças climáticas e a sobrepesca, têm ameaçado todas as populações de peixes, incluindo grandes predadores como o tubarão azul, diminuindo a produtividade e a distribuição dos stocks de peixes marinhos (FAO, 2020). As alterações climáticas também têm sido associadas a mudanças nos sistemas parasita-hospedeiro, incluindo aqueles em ambientes aquáticos. Atualmente, o número de espécies de parasitas pode estar altamente subestimado, incluindo Apicomplexa e Myxozoan. Parasitas marinhos têm-se mostrado socialmente relevantes para a saúde pública, pesca e aquacultura, além de serem importantes indicadores biológicos e ambientais (Morris & Costello, 2020). Com este estudo, pretendeu-se contribuir para esforço científico cada vez maior em parasitologia de peixes.

O primeiro objetivo desta tese foi realizar uma revisão da literatura de espécies dos três principais géneros de parasitas Apicomplexa (*Calyptospora*, *Eimeria* e *Goussia*) reportados até o momento em peixes. Os outros dois objetivos eram examinar e caracterizar infeções por cocídios e mixozoários na anchova europeia, *Engraulis encrasicolus*, e examinar as afinidades filogenéticas dos coccídeos que infetam o tubarão azul, *Prionace glauca*.

Para construir a tabela-resumo (Anexo I) e atingir o primeiro objetivo, foi realizada uma busca exaustiva de artigos identificando parasitas de peixes Coccidia e uma coleta detalhada de informações sobre cada um deles. Para abordar os restantes objetivos, anchovas europeias recém-capturadas do norte de Portugal no outono foram examinadas e uma caracterização das afinidades filogenéticas de coccídeos em material preservado do tubarão azul, capturado em duas áreas de *nursery* relatadas no Oceano Atlântico (ao largo da Península Ibérica, e do oeste da África do Sul; e também do Brasil) foi realizada.

A Tabela 11 lista um total de 244 espécies de coccídeos. Vinte e seis dessas espécies passaram por uma mudança taxonómica de género e trinta e oito dessas linhagens foram caracterizadas molecularmente nos últimos treze anos, período em que menos peixes Coccidia foram descobertos, mas que demonstra o crescente esforço no uso de ferramentas moleculares. Na Anexo I também é evidente a confusão taxonómica dos coccídeos de peixe, pois algumas sinonímias não são consensuais entre os

taxonomistas e há espécies antigas insuficientemente descritas. No entanto, os resultados de diversos estudos, como o presente, reiteram a importância de complementar as ferramentas moleculares com a análise morfológica de tecidos e vice-versa.

Oocistes de parasitas coccídeos foram encontrados no fígado, rim e músculo de apenas três das quarenta e oito anchovas europeias e as características morfológicas gerais encaixam na morfologia geral descrita para as espécies de *Goussia*. Além disso, esporos de *Kudoa* sp. foram encontrados no rim, fígado e músculo de dezanove amostras de anchova e encaixam na morfologia geral descrita para *K. thyrsites*. Sequências do 18S rRNA dos coccídeos de anchova europeia foram agrupadas dentro de um clado que englobava a espécie *Calyptospora* e um grupo não monofilético/ parafilético de *Goussia* spp. que foi recentemente proposto como o "grupo *Clupearum*" (sensu Xavier et al. 2020). A reconstrução filogenética do "grupo *Clupearum*" mostrou ainda que as linhagens sequenciadas de cada espécie de hospedeiro eram geralmente monofiléticas, reconhecendo um certo grau de especificidade do hospedeiro. Parasitas de hospedeiros Engraulidae foram agrupados com hospedeiros Clupeidae, contradizendo a hipótese de Xavier et al. (2021) a respeito de algum grau de coevolução do grupo *Clupearum* com os seus hospedeiros, pelo menos a nível intrafamiliar. No entanto, confirma-se o que já foi verificado em estudos anteriores a respeito da especificidade das linhagens do grupo "*Clupearum*" a cada espécie de hospedeiro.

As sequências das oocistes do tubarão azul foram agrupadas com outras sequências de cocídios obtidas do músculo de tubarões azuis capturados ao largo dos Açores, Portugal (Xavier et al., 2018b), sem que houvesse uma estruturação geográfica.

Assim as afinidades filogenéticas entre as linhagens de Cocidia que parasitam o tubarão azul nas principais áreas de berçário do norte do Oceano Atlântico, refletem a panmixia verificada anteriormente do hospedeiro. No entanto, a falta de dados dos outras áreas de *nursery* – nomeadamente da África do Sul e Brasil – não nos permite retirar estas conclusões para os parasitas de tubarão azul do sul do Oceano Atlântico. Finalmente, de acorde com a análise filogenética, as relações genéticas dos cocídios de elasmobrânquios são mais basais do que aquelas que parasitam repteis, pássaros e mamíferos, corroborando a hipótese de que a coevolução entre essas linhagens de Cocidia e peixes cartilaginosos hospedeiros é ancestral a todos os outros grupos de vertebrados.

Idealmente, no futuro, um maior número de estudos parasitológicos em peixes permitirá identificar se uma determinada parasitose num certo hospedeiro se trata de uma nova

ocorrência. Será possível uma melhor gestão das doenças de peixes em peixes selvagens e de cultura, contribuindo, em última análise, para a conservação da biodiversidade marinha e para um atendimento mais satisfatório da demanda por produtos pesqueiros, beneficiando também o setor económico. Estudos que combinem uma abordagem morfológica e genética, que abranjam mais hospedeiros e baseados em múltiplos marcadores moleculares, serão fundamentais para percebemos melhor a evolução dos cocídios de peixes.

Palavras-chave: peixes; Apicomplexa; Cocidia; *Goussia*; *Eimeria*; *Calyptospora*; Myxosporidia; *Kudoa*; Oceano Atlântico Norte.

ABSTRACT

Marine capture fisheries have increased in recent years, as global capture fisheries production reached a record 96.4 million tons in 2018, and small pelagic fish such as the European anchovy are heavily traded (FAO, 2020). Anthropogenic pressures, including climate change and overfishing, have threatened all fish populations, including large predators like the blue shark, decreasing the productivity and distribution of marine fish stocks (FAO, 2020). Climate change has also been linked to changes in host-parasite systems, including those in aquatic environments. Currently, the number of parasite species may be highly underestimated, including Apicomplexa and Myxozoan. Marine parasites have been shown to be socially relevant to public health, fisheries and aquaculture, in addition to important biological and environmental indicators (Morris & Costello, 2020). This study intended to contribute to the increasing scientific effort in fish parasitology.

The first objective of this thesis was to carry out a literature review of species of the three main genera of Apicomplexa parasites (*Calyptospora*, *Eimeria* and *Goussia*) reported to date in fish. The other two objectives were to examine and characterize coccidia and myxozoan infections in the European anchovy, *Engraulis encrasicolus*, and to examine the phylogenetic affinities of the coccidia that infect the blue shark, *Prionace glauca*.

To build the summary table (Annex I - Table 11) and achieve the first objective, an exhaustive search of articles identifying Coccidia fish parasites and a detailed collection of information about each of them was carried out. To address the remaining objectives, European anchovies freshly caught from northern Portugal in the autumn season were examined and a genetic characterization of the phylogenetic affinities of coccidia in preserved blue shark material, captured in two reported nursery areas in the Atlantic Ocean (offshore from the Iberian Peninsula, and from the west of South Africa; and also from Brazil) was carried out.

Annex I lists a total of 244 species of coccidia. Twenty-six of these species have undergone a taxonomic genus change, and thirty-eight of these lineages have been molecularly characterized, a period when fewer Coccidia fish have been discovered, but demonstrates the growing effort in the use of molecular tools. In Anex I the taxonomic confusion of fish Coccidia is also evident, as some synonyms are not consensual among taxonomists and there are old species insufficiently described. However, the results of several studies, such as the present one, reiterate the importance of complementing the molecular tools with the morphological analysis of tissues and vice versa.

Coccidian oocysts were found in the liver, kidney and muscle of only three of the forty-eight European anchovies, and the general morphological characteristics fit the general morphology described for the *Goussia* species. Furthermore, *Kudoa* sp. spores were found in the kidney, liver and muscle of nineteen anchovy samples and fit the general morphology described for *K. thyrsites*. 18S rRNA sequences from European anchovy Coccidia were grouped within a clade that encompassed the species *Calyptospora* and a non-monophyletic/paraphyletic group of *Goussia* spp. which was recently proposed as the "*Clupearum* group" (sensu Xavier et al. 2020). The phylogenetic reconstruction of the "Clupearum group" also showed that the sequenced lineages of each host species were generally monophyletic, recognizing a certain degree of host specificity. Parasites of Engraulidae hosts were grouped with Clupeidae hosts, contradicting the hypothesis of Xavier et al. (2021) about some degree of co-evolution of the clupearum group with its hosts, at least at the intrafamilial level. However, it confirms what has already been verified in previous studies regarding the specificity of the "*Clupearum*" group strains to each host species.

The blue shark oocysts sequences were grouped with other Coccidia sequences obtained from the muscle of blue sharks captured off the Azores, Portugal (Xavier et al., 2018b), without any geographic structure.

Thus, the phylogenetic affinities between the Cocidia strains that parasitize the blue shark in the main nursery areas of the northern Atlantic Ocean, reflect the previously verified panmixy of the host. However, the lack of data from other nursery areas – namely from South Africa and Brazil – does not allow us to draw these conclusions for blue shark parasites from the southern Atlantic Ocean. Finally, according to phylogenetic analysis, the genetic relationships of coccidian elasmobranch are more basal than those that parasitize reptiles, birds and mammals, supporting the hypothesis that the coevolution between these Cocidia lineages and cartilaginous host fish is ancestral to all other vertebrate groups.

Ideally, in the future, a greater number of parasitological studies in fish will allow to identify whether a certain parasitosis in a certain host is a new occurrence. Better management of fish diseases in wild and farmed fish will be possible, ultimately contributing to the conservation of marine biodiversity and a more satisfactory response to the demand for fish products, also benefiting the economic sector. Studies that combine a morphological and genetic approach, covering more hosts and based on multiple molecular markers, will also be essential for a better understanding of the evolution of fish coccidia.

Keywords: fish; Apicomplexa; Cocidia; *Goussia*; *Eimeria*; *Calyptospora*; Myxosporidia; *Kudoa*; North Atlantic Ocean.

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INTRODUCTION

Marine capture fisheries have been increasing over the past few years, as the global capture fisheries production reached a record of 96.4 million tonnes in 2018 (FAO, 2020). Small pelagic fish like sardines, anchovy, mackerel and herring are heavily traded (FAO, 2020). Large predators like pelagic sharks are also frequently captured for consumption or by accident in pelagic longline fisheries for tunas and sword fish (Midinoudéwa et al., 2020).

Small pelagic fish are essential for the balance of marine ecosystems, as they transfer the energy from lower (plankton) to upper trophic (large predators) levels in food webs (Peck et al., 2021; Qendouci et al., 2018). They are crucial to suppress the human demand of fish food, but are also critical for fishmeal and fish oil production required by the growing agri- and aquaculture industries (Peck et al., 2021).

On the other hand, large predators balance the other fish stocks through prey-predator interactions, maintaining the existence and balance of food webs and ensuring the species diversity within the ecosystem (Midinoudéwa et al., 2020; Motivarash et al., 2020). Apex pelagic predators, like pelagic sharks, have the potential to shape the entire ecological structure of oceanic communities at large geographical scales, through their vast distribution and large-scale movements (Boerder et al., 2019).

Anthropogenic pressures like climate change and overfishing have been threatening all fish populations, decreasing both the productivity and distribution of marine fish stocks (FAO, 2020). The proportion of biologically sustainable marine fish stocks decreased 90% from 1974 to 2017 (FAO, 2020). The demand for shark products, including fins, has been growing over time (Liu et al., 2021), and without jurisdictional management strategies sharks are still too vulnerable to overexploitation and by-catch by pelagic longline fisheries (Midinoudéwa et al., 2020; Motivarash et al., 2020). A study by Peck et al. (2021) predict that the increase of water temperature, oxygen depletion and ocean acidification will drastically affect the productivity and distribution of small pelagic fish in Humboldt, California, Benguela and Canary Islands. Factors associated with ocean deoxygenation have also been shown to decrease shark maximum dive depths, contributing to the constriction of the blue shark habitat (Vedor et al., 2021).

Climate change has also been linked to changes in host-parasite systems, including those in aquatic environments (Atehmengo & Nnagbo, 2014; Karvonen et al., 2010; Lõhmus & Björklund, 2015; Lymbery et al., 2020; Marcogliese, 2008, 2016; Palm, 2011; Short et al., 2017). Rising water temperatures have been linked to an increase in the

incidence of parasitic diseases and their associated vectors (Karvonen et al., 2010; Short et al., 2017), and this may have cascading consequences to fish immune response, parasite avoiding-strategies, and parasite life cycles, among others (Palm, 2011). Public health issues and economic losses may be magnified by the interferences caused by the potential rising parasitic incidence in aquatic ecosystems (Short et al., 2017).

Currently, the number of parasite species may be highly underestimated, as it is believed that there may be at least as many parasite as host species (Costello, 2016). Along with the influence of climate change, the insufficient knowledge on many speciose parasitic taxa makes it even more difficult to estimate the abundance and distribution of marine parasites (Tedesco et al., 2020). Palm (2011) estimated the existence of up to 120,000 fish parasite species, including both Protista and Metazoa. It is estimated that there are about one million unnamed Apicomplexan species, adding to the more than 6000 already discovered (Adl et al., 2007; Seeber & Steinfelder, 2016). A molecular characterization of marine Apicomplexa parasites tracked the potential existence of a larger and highly diverse group of parasites, yet to be recognized (Del Campo et al., 2019). Myxozoan parasites are also greatly underestimated, as an increasing number of new species reports continue to be described, including in marine environments (Okamura et al., 2018; Rocha, 2019).

Marine parasites have proven to be relevant for public health, fisheries and aquaculture, as well as important biological and environmental indicators as they may provide information on trophic and host population structure of ecosystems and may also reflect the impact of pollution (Morris & Costello, 2020).

Therefore, it is crucial to continue the efforts in parasitic description for a better understanding of their biology and ecology and all of the information implied in that.

The hosts

European anchovy (Engraulis encrasicolus Linnaeus, 1758)

The European anchovy (*Engraulis encrasicolus* L., 1758) is a small pelagic fish species distributed by the Mediterranean Sea (including the Black and the Azov Seas), and also along the eastern Atlantic coast from Norway to the South Africa (Akalin et al., 2018). Presently, this species is found mostly in the Mediterranean and off the Atlantic coast of Portugal, Spain and France (*FAO Fisheries & Aquaculture - Species Fact Sheets - Engraulis encrasicolus (Linnaeus, 1758)*, 2021) (Figure 1).

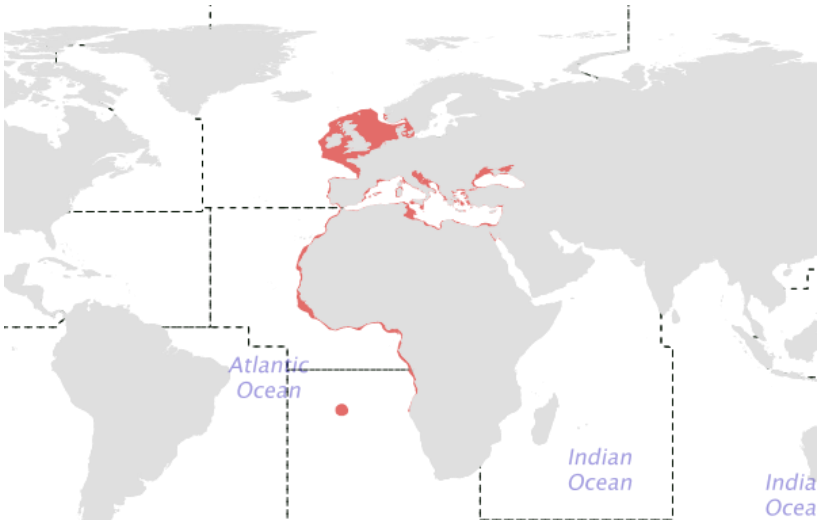

Figure 1: Geographical distribution of *Engraulis encrasicolus*. Red – areas where the occurrence of *Engraulis encrasicolus* is certain. Source: FAO fishing areas. www.fao.org (accessed on 12/2020).

The European anchovy is a short-lived fish, commonly living a maximum of 5 years (Froese & Pauly, 2021). Average length at maturity is 13.5 cm, and maximum length 20 cm, but those in tropical waters are usually smaller than those in northern waters (Froese & Pauly, 2021). The European anchovy is a pelagic spawner - gametogenesis is continuous and the spawning is multiple being temperature the main factor that determines the spawning season, mainly from April to November – with peaks usually in the warmest months, which makes the species a spring-summer spawner (Frimodt & Dore, 1995; Koranteng, 1993).

Being mainly a coastal marine species, it tolerates salinities from 5 to 41 ppt. The European anchovy migrates to shallower coastal waters in large shoals, entering lagoons and estuaries during warm months to reproduce, and moving to deeper coastal waters from September to January (Froese & Pauly, 2021). Planktonic organisms are the main food source of this species (Frimodt & Dore, 1995).

According to Qendouci et al. (2018), whatever the season or the fish size, European anchovies are exclusively zooplanktivorous, preying mostly on copepods. This species' position in the trophic chain is essential for the dynamic balance of the ecosystem because it plays an important role in the energy transfer from plankton to large predators of upper trophic levels (Qendouci et al., 2018). Anchovy is also the main food resource for some highly valuable commercial pelagic and/or demersal fishes such as *Scomber scombrus* L., *Thunnus thynnus* L., *Thunnus alalunga* Bonnaterre, *Xiphias gladius* L., and *Merluccius merluccius* L. (Karachle & Stergiou, 2017).

This fish species has a clear interest to fisheries, being mainly caught in the Mediterranean and Black Seas but also in Eastern Central Africa and Northeast Atlantic (FAO, 2018). The global capture of European anchovy has grown over the years until the late 80s, where it peaked. Since then, these numbers have been lowering, but still represent a valuable economic source in fisheries (Figure 2).

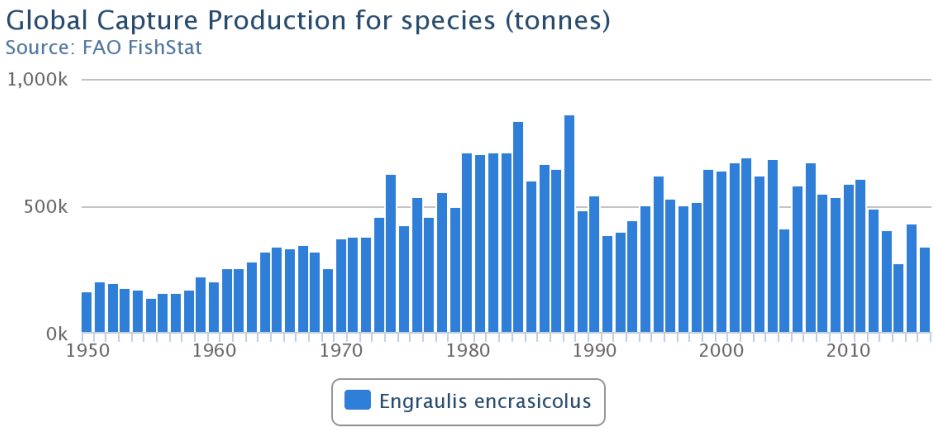

Figure 2: Global capture (tonnes) of *Engraulis encrasicolus*. Source: FAO Fisheries & Aquaculture - Species Fact Sheets - *Engraulis encrasicolus* (Linnaeus, 1758). www.fao.org/ (accessed on 12/2020).

In Portugal, the catches of European anchovy have been growing in the last few years, almost tripling their numbers from 2015 to 2019 (Table 1).

Table 1: European anchovy catches in Portugal, in tonnes in live weight, throughout the years. Source: Eurostat – Catches in North-east Atlantic (from 2000 onwards). www.fao.org/ (accessed on 12/2020).

Year	Catches (tonnes in live weight)
2010	130
2011	2,920
2012	786
2013	386
2014	827
2015	2,617
2016	7,107
2017	9,144
2018	8,347
2019	9,272

The European anchovy is typically consumed canned, salted or processed, but also marketed fresh or frozen in African countries (*FAO Fisheries & Aquaculture - Species Fact Sheets - Engraulis encrasicolus (Linnaeus, 1758)*, 2021). A recent study showed that European Anchovy is a very nutritious species due to their significant values of vitamin A, iodine, zinc, calcium, and iron (Aakre et al., 2020). In Portugal, the production of anchovies in the canning factories continues to be relevant.

Blue shark (Prionace glauca Linnaeus, 1758)

The blue shark (*Prionace glauca* Linnaeus, 1758) is an oceanic-pelagic and fringe littoral species distributed worldwide in temperate and tropical oceans, preferring relatively cool water from 7 to 16°C but tolerating water at 21°C or even more (*FAO Fisheries & Aquaculture - Species Fact Sheets – Prionace glauca (Linnaeus, 1758)*, 2021).

P. glauca is a physically distinctive shark due to a slender body and long pectoral fins, with indigo blue dorsal coloration, metallic blue flanks, and abruptly white under sides (Nakano & Stevens, 2008).

This shark is among the most wide-ranging of large-open ocean predators, and very likely the most abundant of all pelagic sharks in the global oceans (Aires-da-Silva et al., 2014). The blue shark has a circumglobal distribution, occurring in the Atlantic basin, Indo-west Pacific and eastern Pacific (Figure 3). As an offshore species it occurs from the surface to 600 m depth (Nakano & Stevens, 2008), but it can also occur inshore in areas with a narrow continental shelf or off oceanic islands (*FAO Fisheries & Aquaculture - Species Fact Sheets – Prionace glauca (Linnaeus, 1758)*, 2021).

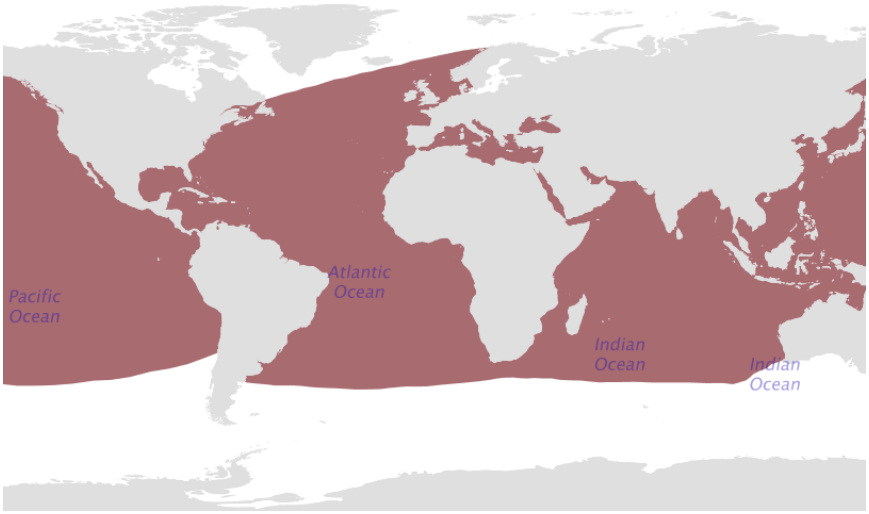

Figure 3: Geographical distribution of *Prionace glauca*. Red - areas where the occurrence of *Prionace glauca* is certain. Source: FAO fishing areas. www.fao.org (accessed on 06/2021).

Blue shark is a long-lived chondritic whose maximum lifespan is still unknown but it is believed that it can live up to 20 years. Size at birth is about 35 to 44 cm and can reach up to 400 cm in length (*FAO Fisheries & Aquaculture - Species Fact Sheets – Prionace glauca (Linnaeus, 1758)*, 2021), with males and females growing to similar sizes (Nakano & Stevens, 2008). Females are sexually mature at 220 cm length (5-6 years old) and males at 180 cm length (4-5 years old) (Biton-Porsmoguera et al., 2018).

Blue sharks are viviparous, with gestation lasting almost a year and producing from 4 to 135 young a litter. Even though the annual fecundity is uncertain, females may breed every year (Nakano & Stevens, 2008). The thicker skin of maturing and adult females evidences sexual dimorphism (Froese & Pauly, 2021). Diet composition is based on small pelagic prey, especially bony fishes and, a very important one, squid. However, it also ingests other invertebrates, small sharks, and mammals, as well as seabirds caught at the surface of the water. Non-pelagic bottom fishes and invertebrates also incorporate this diet (Froese & Pauly, 2021).

This species is often found in large aggregations, determined according to size, sex and reproductive stage, and often close to or at the water surface in temperate waters (Nakano & Stevens, 2008). The blue shark has highly complex migratory behavior, defied by feeding, ontogeny and reproduction, and can cover distances ~1,000–10,000s km including east–west and north–south trans-oceanic movements and cross multiple national borders during its life cycle (Veríssimo et al., 2017).

The high mobility of pelagic sharks, even when young, along with the lack of understanding of what exactly constitutes a shark nursery, makes it difficult to define nursery areas (Hareide et al., 2007). Even so, on the blue shark, multiple nursery areas have been proposed for the North and South Atlantic: in the Bay of Biscay (Coelho et al., 2018), off Iberian Peninsula (Stevens, 1990), off the Azores (Aires da Silva et al., 2008; Aires da Silva et al., 2014; Vandeperre et al., 2014) in the Gulf of Guinea (Castro & Mejuto, 1995), off Namibia (Coelho et al., 2018), off South Africa (da Silva et al., 2010; Jolly et al., 2013; Midinoudéwa et al., 2020; Petersen et al., 2009), and off Brazil and Uruguay (Coelho et al., 2018).

Blue shark is frequent by-catch of swordfish and tuna longline pelagic fisheries, or as recreational fisheries worldwide (Aires-da-Silva et al., 2008) (Figure 4).

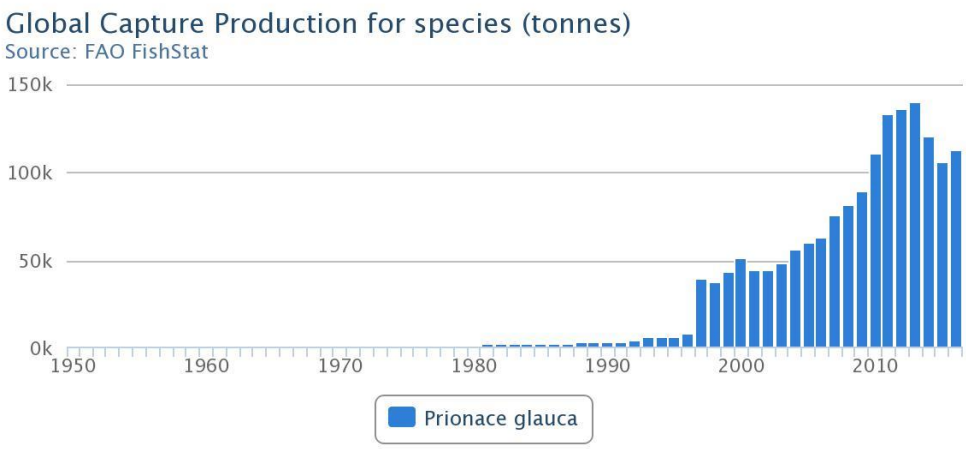

Figure 4: Global capture (tonnes) of *Prionace glauca*. Source: FAO Fisheries & Aquaculture - Species Fact Sheets – *Prionace glauca* (Linnaeus, 1758). www.fao.org/ (accessed on 05/2021).

However, blue sharks themselves are an important fishery resource in Northeast Atlantic waters where the fishing effort of high-seas longline fisheries and reported catches of *P. glauca* are high (Compagno, 1984). Although their stock structure remains uncertain, there is evidence to support a single North Atlantic stock and they are treated as such for assessment purposes (de Bruyn & Cortés, 2015). Nevertheless, multiple genetic markers suggest a scenario of panmixia across the entire Atlantic (Veríssimo et al., 2017).

In Azores, the traditional Portuguese longline fishery for swordfish captured increasing numbers of blue sharks in the mid-1990s (Aires-da-Silva et al., 2006).

According to FAO reports the blue shark was the most captured of Atlantic shark catched by European Union member states. A total of 23372 tonnes were captured: 15604 in Spain, 7115 in Portugal, 518 in the UK, and 134 in France (FAO, 2020). In England and Ireland, small target fisheries operated off the southwest coasts (Fordham, 2006). Spanish and Portuguese long-liners catch mostly small individuals and juveniles represent the major part of shark landings at Vigo fish market, being 73% of blue sharks (Biton-Porsmoguera et al., 2018).

Sharks are marketed as fresh, frozen, dried or salted, for human consumption and also fish meal. Hides for leather, fins for soup, and liver to produce oil (Biton-Porsmoguera et al., 2018; Froese & Pauly, 2021).

The parasites

Apicomplexa

Apicomplexa are an important group of parasitic Alveolata protists, characterized for having an apical complex - a set of organelles, only visible with the transmission electron microscope (TEM) - that assist in the process of invasion of the host cell. These organelles allow the invasive stage of apicomplexans to penetrate the host cells (Lom & Dyková, 1992; Steinhagen & Davies, 2008).

Piscine apicomplexan parasites can be divided in two major groups, the Coccidia Leuckart 1897, which are able infect several organs, and the Hematozoa Vivier 1982, which occur in host blood cells (Steinhagen & Davies, 2008).

Coccidia comprises a ubiquitous group of oocysts forming apicomplexan parasites of vertebrates (Lom & Dyková, 1992). The most frequently coccidian parasites detected in fishes belong to genera *Goussia* Labbé, 1896, *Eimeria* Schneider, 1875, and to the more recently described genus *Calyptospora* Hawkings and Fournie, 1984 (Molnár et al., 2012).

Little is known regarding the life cycle of these parasites, encompassed in the Eimeriidae family. However, it seems they could have a monoxenous or heteroxenous life cycle (Dyková & Lom, 2006).

Generally, Eimeriorines have a monoxenous life cycle. They usually complete their life cycle in the gastrointestinal tract of a single host, which ingests the infectious stage (sporozoites free or inside oocysts), supports parasite asexual and sexual reproduction, and then excretes oocysts to begin the cycle anew (Rosenthal et al., 2016). Initially, the sporozoite enters a host cell, growing and transforming into a large meront. The meront divides through multiple asexual fissions and produces several merozoites, which are elongated cells that can replicate again by multiple asexual replications (merogony). The merozoites enter other host cells and may do one or two repeats of merogony. Gamogony is initiated by the last generation of merozoites, that enter another host cell to differentiate either into a male or female gamont - microgamont or macrogamont, respectively. This gamont divides to produce microgametes. On the other hand, macrogamonts grow and become macrogametes, which are fertilized by the microgametes, forming the zygote. The zygote initiates sporogony by dividing and secreting a protective envelope, becoming an oocyst. This structure contains the sporozoites, which may be free or enclosed in sporocysts (Lom & Dyková, 1992) (Figure 5).

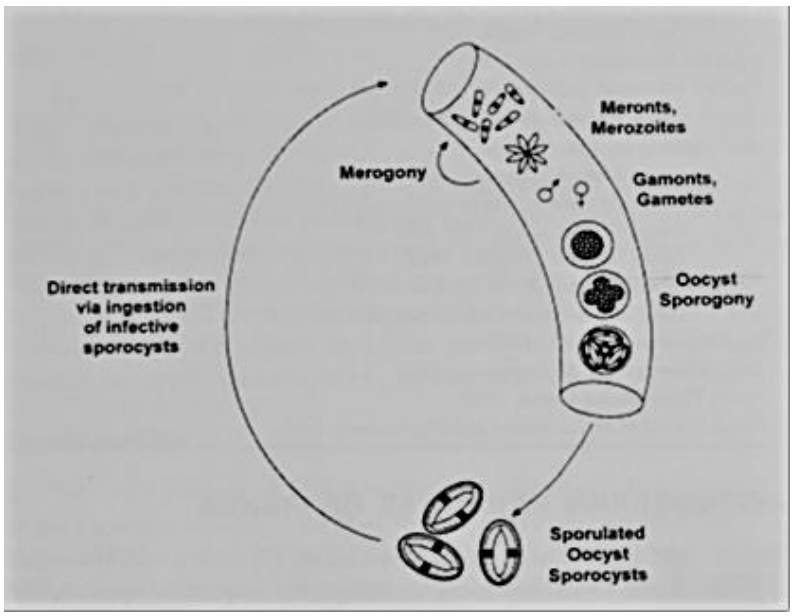

Figure 5: Monoxenous development of *Goussia iroquina* from the intestine of *Pimephales promelas*. Merogonic, gamonic and sporogonic development takes place in intestinal ephitelial cells of a cyprinid host. Oocyst are liberated in the feces. Source: Steinhagen & Davies, 2008.

Except for the zygote, a diploid structure until its first meiotic division, all other stages are haploid. The morphometric characterization of the oocyst, sporocysts, and sporozoites, as well as the way the sporocysts open – through Stieda body or valves – are the main features that determine the genera and species of parasites. The mode of the life cycle is also important for this matter (Steinhagen & Davies, 2008).

The vast majority of fish coccidia develops tetrasporocystic oocysts with a thin oocyst envelope. Species that develop a Stieda body, a sporocyst shell plugged by a stopper-like structure, are traditionally assigned to the genus *Eimeria;* the genus *Goussia* is characterized by tetrasporocystic oocysts with a sporocyst wall composed of two adherent valves separated by a suture longitudinal line (Dykova & Lom, 1981); and the genus *Calyptospora* is distinguished by bivalved sporocysts, sporopodia, supporting a membranous veil surrounding the, and an anterior apical open (Overstreet et al., 1984; Rosenthal et al., 2016).

The use of these characters to identify fish coccidia to genus and species, based solely on morphometric features has been highly questioned for many years and by many authors. Therefore, nowadays a molecular phylogenetic analysis is much needed and recommended to achieve and accurate diagnosis. To this effect, the 18S rRNA has been widely used to characterize *Eimeria*, *Goussia*, and *Calyptospora* lineages (e.g. (Rosenthal et al., 2016; Whipps et al., 2012), among many others). This molecular

marker has also been used to shed light on the evolutionary history of fish coccidian. For example, phylogenetic analyses have revealed which morphological and development characteristics arose independently in the different groups (e.g. (Bartosova-Sojkova et al., 2015; Rosenthal et al., 2016), among others), and have also shed light on the degrees of co-evolution with hosts (e.g. (Molnár et al., 2012; Xavier et al., 2018a)).

Reported pathogenicity associated with coccidia infection varies from negligible to serious effects that impact fish fitness, both in aquaculture and wild fish (e.g. (Abollo et al., 2001; Alvarez-Pellitero et al., 1993; Costa & Mackenzie, 1994; Lovy & Friend, 2015; Pinto, 1956; Xavier et al., 2020)).

Morrison and Hawkins (1984) reported 85% of mature fish infected by *Goussia clupearum* from liver and 90-100% of mature fish infected by *Eimeria sardinae* from testis of herring (*Clupea harengus* Linnaeus, 1758) caught in waters near Nova Scotia. Infection of liver and testicular tissue and their replacement could stress fish and reduce sperm production, respectively. Lovy and Friend (2015) detected *Goussia ameliae* in the pyloric caeca of alewife (*Alosa pseudoharengus* A. Wilson, 1811) captured in the Maurice River, New Jersey (USA), with a prevalence of 92% and 34% in young-of-the-year and adult fish, respectively, causing intestinal epithelial necrosis and sloughing associated with the release of oocysts. Pasnik et al. (2005) reported a coccidiosis among stocked young-of-year bluegill (*Lepomis macrochirus* Rafinesque, 1810) from an impoundment lake in Norfolk County, Virginia (USA), and the infected fish were described as anorexic and lethargic, with little to no abdominal fat and no food in their stomach and intestines. Xavier et al. (2020) reported a high prevalence coccidiosis (>82%) in blue whiting (*Micromesistius poutassou* Risso, 1827) in all organs analyzed (liver, stomach, intestine, gonads), being the liver heavier infected. A significant negative correlation was found between the abundance of the parasites in the liver and host condition index, indicating a negative effect on the fitness of this host.

All the above mentioned symptoms caused by high prevalence coccidiosis could eventually lead to a decrease of the affected fish stock populations. Therefore, it's crucial to properly identify coccidian species and to know its diversity (Atehmengo & Nnagbo, 2014; Del Campo et al., 2019), geographical distribution, infection levels and their pathogenicity.

Myxozoa

Myxozoa Grassé, 1970 is a highly diverse cosmopolitan group of microscopic obligate cnidarians endoparasites (Ben-David et al., 2016). Presently, there are a total of 2425 species described and inserted in the clades Malacosporea Canning, Curry, Feist, Longshaw et Okamura, 2000, and Myxosporea Bütschli, 1881 (Alama-Bermejo & Holzer, 2021).

Through evolution, myxozoans lost numerous genetic and phenotype features, such as true gametes, embryogenesis, epithelial structures, nervous system, gut, and cilia (Atkinsona et al., 2018). However, they are characterized for exhibiting complex life cycles as well as pluricellular spores used as transmission (Alama-Bermejo & Holzer, 2021; Ben-David et al., 2016; Fiala et al., 2015).

The Malacosporea is characterized by proliferative stages that occur in freshwater bryozoans, both as vermiform organisms (genus *Buddenbrockia*), or as closed sacs (genus *Tetracapsuloides*) (Fiala et al., 2015; Lom & Dykova, 2006). The proliferative stages are latter released as malacosporean spores to the water (Yokoyama et al., 2012). Sporoplasms of these spores penetrate the skin or gills' epithelium of vertebrate host and are transported to the target organ/tissue through the blood. After a complex reproductive process spores are formed and released to the water, where they are infective for bryozoans (Figure 6). These spores are characterized by soft valves that aren't able to protect against potential environmental damages, making them very short-lived (Yokoyama et al., 2012).

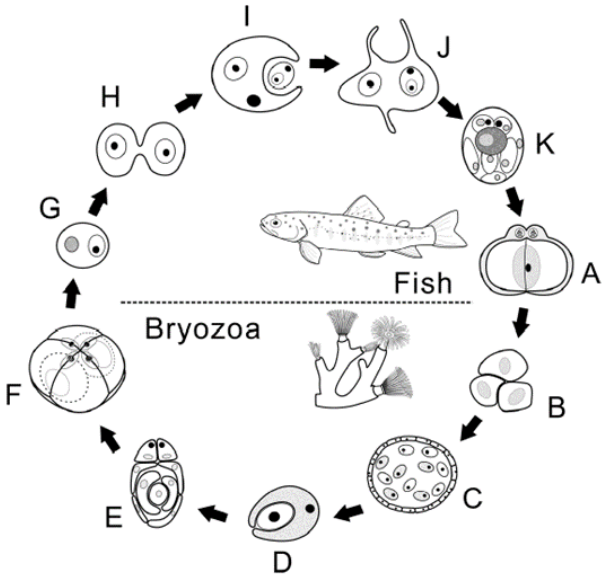

Figure 6: Diagram of the life cycle of *Tetracapsuloides bryosalmonae* (Malacosporea), alternating between fish and bryozan host. A: Fishmalacospore infects freshwater bryozoans. B: Presaccular cell aggregates in coelomic cavity of bryzoans. C: Early spore sac floating in bryozoan coelomic fluid. It contains stellate and sporogenic cells. D: Sporogenic cell becomes enclosed by stellate cells. E: Maturing spore with capsulogenic cells, valve cell and forming sporoplasms. F: Mature bryozoa-spore infects fish. G: Proliferative stage (cell doublet with primary cell and secondary cell inside) in kidney interstitium. These stages are in close contact to host phagocytes (not shown). H: Division of cell doublet resulting in 2 cell doublets. I: Engulfment of one cell doublet by another resulting in a S-T-doublet (primary cell enclosing one secondary and one secondary with tertiary cell). J: S-T-doublet in kidney tubule. Source: Yokoyama et al. (2012).

The Myxosporea spores can possess 2 to 15 shell valves, 1 to 2 sporoplasms and 1 to 15 polar capsules (Lom & Dykova, 2006).

Myxosporean can be coelozoic (located in body cavities or cavities of body organs) or histozoic (located in tissues) (Lom & Dykova, 1992, 2006). Their life cycle has been studied over the years, and alternates between a vertebrate host (usually a fish), where the myxosporean phase occurs, and an invertebrate host (typically annelids), where the actinospore phase occurs (Ben-David et al., 2016) (figure 7).

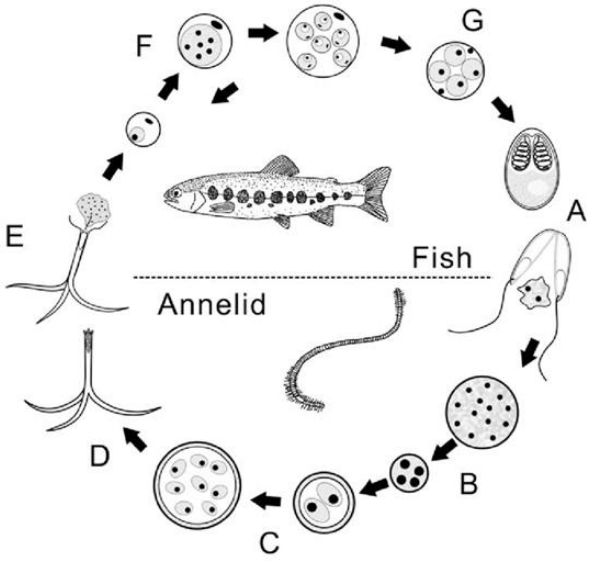

Figure 7: Diagram of the life cycle of myxosporean alternating fish and annelid hosts. A: The polar filaments are extruded to anchor the spore to the gut epithelium, followed by opening of shell valves of myxospore. B: Gametogony. C: Sporogony of actinosporean phase. D: Mature actinospore stages develop in a pansporocyst, and actinospores are released into the water. E: Upon contact of actinospores with the skin or gills of the fish host, polar filaments extrude to anchor the spore to the skin or gills, facilitating invasion of the sporoplasms into the fish. F: Presporogonic multiplication in a cell-in-cell state. G: Sporogony of myxosporean phase. Source: Yokoyama et al. (2012).

Some mixosporideans are threatening pathogens for economically important wild and cultured fish (Atkinsona et al., 2018; Lom & Dykova, 2006), from both marine and freshwater habitats (Alama-Bermejo & Holzer, 2021; dos Santos et al., 2019; Mackenzie & Kalavati, 2014). In addition, there are some zoonotic species. For example, Kawai et al. (2012) identified *Kudoa septempunctata* infecting the muscle of olive flounder (*Paralichthys olivaceus),* as the causative agent of novel food poisoning outbreaks in Japan by consumption of raw olive flounder.

OBJECTIVES

Although the veterinary importance of Apicomplexa and Myxozoan parasites is widely recognized, knowledge regarding species infecting piscine hosts is still scarce, particularly in the case of marine species (Del Campo et al., 2019; Sakai et al., 2019; Xavier et al., 2020; Xavier et al., 2018a).

The first goal of this thesis was to conduct a **1)** literature review of species of the three main genera of Apicomplexa parasites (*Calyptospora*, *Eimeria* and *Goussia*) reported to date in fish. To this end a summary table that references all of these species, their characteristics and geographical distribution is presented in Annex I. This was to be helpful to the scientific community, but also to everyone who is interested in the subject, to find such specific information compiled.

The other two objectives were to **2)** examine and characterize coccidian and myxozoan infections in the European anchovy, *Engraulis encrasicolus*, and **3)** examine the phylogenetic affinities of coccidian infecting the blue shark, *Prionace glauca*. Specifically, the following questions were addressed:

Q1) *Which coccidia and myxosporidia parasites infect the European anchovy? What are their phylogenetic affinities?*

Q2) *Which genetic lineages of coccidians infect the panmictic populations of blue shark captured in different nursery areas? Could they be used as biological tags to distinguish between capture localities?*

To accomplish objective **1)** a summary table was built, based on an exhaustive search of articles reporting fish Apicomplexa parasites. A detailed collection of information regarding each species was carried out and all the information was organized in the table, which includes the bibliographical references related to each species of parasites.

To address the objective **2)** and the first set of questions (**Q1**) freshly captured European anchovies from the north of Portugal were examined. Initially, the intent was to examine material from two different seasons (autumn 2020 and spring 2021); however, the restrictions imposed to control the pandemic situation caused by Covid-19 included the prohibition of commercial fisheries for an extended period thus precluding the second (spring) sampling.

To address objective **3)** (and **Q2**) a genetic characterization of coccidian infections on preserved material of the blue shark, *Prionace glauca*, captured in two reported nursery areas in the Atlantic Ocean: off western Iberia, and off western South Africa; and also off

Brazil was performed. These data were put in a phylogenetic context along with sequences obtained by Xavier et al. (2018b) where genetic characterization of Coccidians infecting the blue shark off the Azores (a third nursery area) was made.

MATERIAL AND METHODS

Summary table from literature review (Annex I – Table 11)

For the construction of Table 11, the first step was to gather all possible articles regarding fish Coccidia. Articles were only accessible from the year 1944 up to 2021.

In alphabetical order, all the Coccidia species known and accepted to date and their respective synonyms were listed. Some synonyms are not consensually accepted, being valid only to certain authors. In those cases, the synonyms, according to some authors, are mentioned, but the species involved are also singly displayed in the table.

Species or synonymy only referenced by Duszynski, Couch and Upton (2003) in online website(s) “Coccidia of the world” are marked with an asterisk (*****), as this information has not been peer reviewed.

For each species, information from different articles was merged and recorded as a whole. Morphological features described correspond to the set of information registered about the species so far; measurements of oocysts, sporocysts, sporozoites, oocyst and/or sporocyst residuum, and sporopodium/sporopodia indicate the minimum and maximum (in µm) recorded in all different reports till the present moment. Host(s) species recorded parasitizing the parasite are designated in the respective column, as well as the geographical area where they were documented. Bibliographical references are listed in the last column, englobing all the articles used for the listing and characterization of each Coccidia species.

European anchovy

1. Host sample collection

A total of forty-eight European anchovy specimens were obtained dead from a local market in Matosinhos in October of 2020. Fish were weighted (BW in grams), total length (TL in centimeters), and standard length (SL in centimeters) were determined. The samples were frozen until further examination.

2. Parasite sample collection

After thawing, fish were dissected (Figure 8). The liver, gonads, stomach, intestine, kidney, and muscle were placed in a lip of the petri dish with phosphate-buffered saline (PBS). Similar portions of the liver, gonads, muscle, and kidney were macerated with a scalpel and squashed with the base of the petri dish. The intestine and stomach were open and similar portions of mucosa were scrapped with a scalpel blade and blended with a similar volume of PBS. The blend of each organ was squeezed out into a centrifuge tube, with the suspension being allowed to rest for at least 30 minutes.

Figure 8: Dissection of the European anchovy. 1-First cut; 2- Second cut. Source: European commission website https://fish-commercial-names.ec.europa.eu/fish-names/species_en?sn=15302 (accessed on 09/2021). Posterior edition by Sílvia Rodrigues, 2021.

3. Observation under the optical microscope

Three drops of the sediments were pipetted to a microscope slide and covered with a coverslip. Slides were observed under the optical microscope. Some oocysts and sporocysts were measured according to Lom and Dyková (1992), and photographed with a camera integrated into the microscope. When detected, *Kudoa* sp. spores were also measured according to Burger and Adlard (2010) (Figure 9), and photographed.

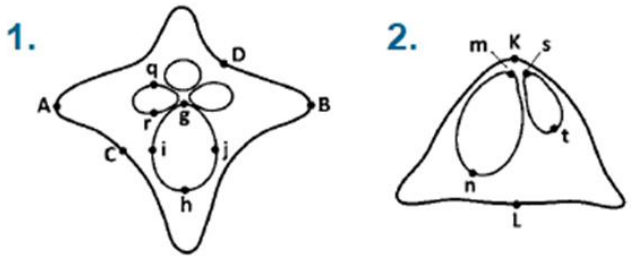

Figure 9: Schematics for morphological characterization of kudoid spores in apical (1) and side (2) views, for stellate spores with 1 polar capsule much larger than the others. A–B=Width, C–D=Thickness, g–h=Apical large polar capsule length, i–j=Apical large polar capsule width, q–r=Apical small polar capsule width, m–n=Side large polar capsule length, and s–t=Side small polar capsule length. Source: Burger and Adlard (2010).

4. Infection levels

Abundance in each organ was detected and punctuated according to a semi-quantitative scale, as shown in Table 2. Prevalence of infection (%) in the set of analyzed individuals was calculated.

Table 2: Semi-quantitative scale used to punctuate the abundance of infection.

Scale	Level of infection	Number of parasites
0	No infection	0
1	Low	1-19
2	Medium	20-49
3	High	≥ 50

The solutions of the infected tissues from different organs were preserved in 90% graded ethanol, for posterior molecular analysis.

5. Molecular analysis

5.1. DNA extraction and PCR amplification

Coccidia

The European anchovy samples were analyzed according to the methodology proposed by Xavier et al. (2020). DNA extraction was performed using PureLink® Genomic DNA Mini Kit (Invitrogen, UK), following the manufacturer's instructions.

All extractions were frozen until PCR (Polymerase Chain Reaction) amplification of a portion of the 18S rRNA gene using primer pairs HEP300/HEP900 (~600bp) (Ujvari et al., 2004). Invitrogen Platinum Taq DNA Polymerase was used, with a final concentration of magnesium of 1.5mM and 2 µL of DNA. A positive control and a negative control were used in all reactions. The strips of PCR were marked according to the sample name.

PCR cycles consisted of: 7 min of initial denaturation at 94ºC, followed by 36 cycles of 30s at 94ºC (denaturation); 45s at 60ºC (annealing); and 45 mins at 72ºC (elongation). A final elongation step was performed at 72ºC for 7 mins.

PCR products were viewed in a 2% agarose gel using GelRed on an Ultra-violet transilluminator. Positive PCRs were sent for sequencing in GENEWIZ (Genewiz, Leipzig, Germany).

Kudoa sp.

European anchovies samples infected with *Kudoa* sp. were analyzed according to the methodology proposed by Cavaleiro et al. (2021). All extractions were frozen until PCR amplification of a portion of the 18S rRNA gene. Nested PCR was performed with initial

primer pair 18e + 18g (Hillis & Dixon, 1991) followed by PCR with specific *Kudoa* primer pair KUD1f + KUD2r (Hervio et al., 1997). Invitrogen Platinum Taq DNA Polymerase was used, with a final concentration of magnesium of 1.5mM and 2 µL of DNA. A positive control and a negative control were used in all reactions. The strips of PCR were marked according to the sample name.

Cycling parameters had the following set up: initial PCR run: denaturation 95 °C for 3 min, followed by 30 cycles of 94 °C for 1 min, 58 °C for 1 min s, 72 °C for 2 min and after cycles a terminal extension at 72 °C for 10 min; II run: denaturation 95 °C for 3 min, followed by 35 cycles of 94 °C for 40 s, 55 °C for 50 s, 72 °C for 1 min 40 s with terminal extension at 72 °C for 10 min. PCR products were purified using a Gel/PCR DNA Fragments Extraction Kit (Geneaid Biotech Ltd., New Taipei City, Taiwan), submitted to a new PCR with the same conditions mentioned above for *Kudoa*, and then sequenced.

Blue shark

1. Host sample collection

Blue shark DNA extractions were obtained from CIBIO's collections, and corresponded to a subset of samples used in the work of Verissimo et al. (2017) (Figure 10). Sampling was described in detail in that work. Briefly, young-year-old and 1-year and 2-year-old blue shark samples were collected at three reported nursery areas in the Atlantic Ocean: 1) off the Azores, 2) off western Iberia, and 3) off western South Africa. Two groups of cohorts were captured in two time intervals: (a) between 2003 and 2008, and (b) between 2012 and 2015. Additional samples were obtained from observers on board commercial fishing vessels operating in Brazilian waters prior to 2012. Although these samples are not considered to be from juvenile blue sharks, given the lack of information from specimens from that region, they were analyzed. Tissue samples were obtained from dorsal fins or muscle tissue (~1 cm^3), preserved in 96% ethanol and stored at room temperature.

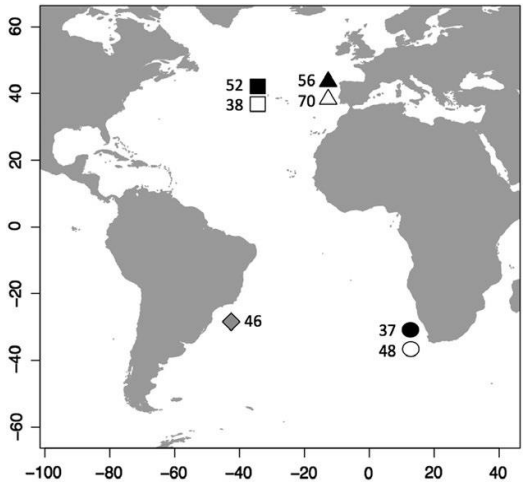

Figure 10: Sampling locations of blue sharks in Atlantic waters made by Veríssimo et al. (2017). Triangles - Iberian Peninsula, squares - Azores, circles - western South Africa, diamond - western Brazil. Black symbols - individuals from cohorts between 2003 and 2008 (2000s), white symbols - individuals from cohorts between 2012 and 2015 (2010s). Source: Veríssimo et al. (2017).

2. Molecular analysis

2.1. DNA extraction and PCR amplification

Due to the impossibility to perform a morphological analysis of the coccidians infecting the blue shark, these were characterized solely using a molecular approach.

Polymerase Chain Reaction (PCR) was performed on a subset of the samples used in that study: 109 individuals from western Iberia; 40 individuals from South Africa; and 10 individuals from Brazil (Figure 11).

Figure 11: Locations of the subset of samples of blue shark on which was performed PCR. Squares – western Iberia, Circles – South Africa, and Triangles – Brazil.

Invitrogen Platinum Taq DNA Polymerase was used, with a final concentration of magnesium of 1.5mM and 2 µL of DNA. A positive control and a negative control were used in all reactions. The strips of PCR were marked according to the sample name.

PCR cycles consisted of: 7 min of initial denaturation at 94ºC, followed by 36 cycles of 30s at 94ºC (denaturation); 45s at 60ºC (annealing); and 45 mins at 72ºC (elongation). A final elongation step was performed at 72ºC for 7 mins.

PCR products were viewed in a 2% agarose gel using GelRed on an Ultra-violet transilluminator. Positive PCRs were sent for sequencing in GENEWIZ (Genewiz, Leipzig, Germany).

Molecular analysis - sequence analysis

Sequences were manually checked and edited using Codon Code Aligner vs 9.0.2 (Codon Code Corporation, Centerville, Massachusetts). Blast algorithm was used for taxonomic assignment and to select closely related sequences deposited in GenBank, as well as outgroups to include in phylogenetic analysis. BIOEDIT was used to perform final alignment trimming. Sequences were aligned with MAFFT software using default parameters (Katoh et al., 2019). The best model of evolution was chosen using the software jModeltest2 (Darriba et al., 2012) and the Akaike Information Criterium. Phylogenetic reconstruction was performed using both Maximum Likelihood (ML), implemented in the software PhyML using 1000 bootstrap (Guindon et al., 2010) and Bayesian inference (BI), implemented in the software Mr. Bayes (Ronquist et al., 2012). For the BI analysis, two independent runs (each with four chains for 5×10^7 generations) were performed for the European anchovy dataset. For the blue shark dataset one run

with 3×10^7 generations was performed. Trees and parameters were sampled every 1000 generations, with the heating parameter set to 0.25. Convergence of parameters was checked using the software Tracer vs 1.6. (Rambaut et al., 2014). A majority-rule consensus tree was estimated combining results from both analyses, after discarding 25% of the total samples as burn-in.

RESULTS

Summary table from literature review (Annex I - Table 11)

After an exhaustive review of fish Coccidia reports from 1944 to 2021, a total of 244 species were listed in Annex I. Twenty-six of those species have gone through a taxonomic genus change (Table 3). The majority of these (twenty-three) were reassigned from *Eimeria* to *Goussia*, mainly due to the ancient insufficient morphological descriptions and the lack of directions for a clear taxonomic classification. Deficient observation of sporocysts features are the most common reason. For example, when in lack of the Stieda body, which currently accepted taxonomy determines is only present in *Eimeria* species, authors still assumed those species belonged to the genus *Eimeria*. Further studies eventually reported the absence of a Stieda body or Stieda body-like structures and officially reassigned them to *Goussia*.

Only three of the listed species were reassigned from *Goussia* to *Eimeria* for the opposite reason, i.e. the observation of a sporocyst shell plugged by a stopper-like structure, the Stieda body.

The genus *Calyptospora* was erected in 1984 by Overstreet et al. to encompass species with sporocysts, without Stieda or sub-Stieda bodies, with a veil supported by sporopodia, and with an anterior apical opening (Overstreet et al., 1984).

Table 3: All of the latest taxonomic changes suffered by species listed in Annex I – Table 11.

Old species name	New assigned name
Eimeria funduli Hawkins, Fournie & Overstreet, 1984	***Calyptospora funduli*** (Hawkins, Fournie & Overstreet, 1984) Duszynski, Solangi & Overstreet, 1979
Goussia truttae Léger & Hesse, 1919	***Eimeria truttae*** (Léger & Hesse, 1919) Stankovitch, 1921
Goussia variabilis (Thélohan, 1893) Labbé, 1896	***Eimeria variabilis*** (Thélohan, 1893) Reichenow, 1921
Eimeria alburni Stankovitch, 1920	***Goussia alburni*** (Stankovitch, 1920) Yakimoff, 1929
Eimeria auxidis Dogiel, 1948	***Goussia auxidis*** (Dogiel, 1948) Dykova & Lom, 1983
Eimeria bigemina Labbe, 1896	***Goussia bigemina*** (Labbe, 1896) Yakimoff, 1929
Eimeria carpelli Léger & Stankovitch, 1921	***Goussia carpelli*** (Léger & Stankovitch, 1921) Dykova & Lom 1983
Eimeria clupearum (Thelohan, 1894) Doflein, 1909	***Goussia clupearum*** (Thelohan, 1894) Labbe, 1896

Eimeria cruciata (Thélohan, 1892) Yakimoff, 1929	***Goussia cruciata*** (Thelohan, 1892) Labbe, 1896
Eimeria cylindrospora Stankovitch, 1921	**Goussia cylindrospora** Stankovitch, 1921 (Rosenthal, Dunams-Morel, Ostoros & Molnar, 2016)
Eimeria cyprinorum Stankovitch, 1921	***Goussia cyprinorum*** Stankovitch, 1921
Eimeria degiustii Molnar & Fernando, 1974	***Goussia degiustii*** (Molnar & Fernando, 1974) Dyková & Lom, 1983
Eimeria gadi Fiebiger, 1913	***Goussia gadi*** Fiebiger, 1913 (Dyková & Lom, 1981)
Eimeria hupehensis Chen & Hsieh, 1964	***Goussia hupehensis*** (Chen & Hsieh, 1964) Rosenthal, Dunams-Morel, Ostoros & Molnar, 2016
Eimeria laureleus Molnar & Fernando, 1974	***Goussia laureleus*** (Molnar & Fernando, 1974) Li & Desser, 1985
Eimeria legeri (Simond, 1901) Reichenow, 1921	***Goussia legeri*** Stankovitch, 1920
Eimeria leucisci Schulman & Zaika, 1964	***Goussia leucisci*** (Schulman & Zaika, 1964) Lom, Desser, & Dykova, 1989
Eimeria lucida (Labbé, 1893) Reichenow, 1921	***Goussia lucida*** (Labbé, 1893) Labbé, 1896
Eimeria metchnikovi (Laveran, 1897) Reichenow, 1921	***Goussia metchnikovi*** (Laveran, 1897) Dykova & Lom, 1983
Eimeria minuta (Thélohan, 1892) Doflein, 1909	***Goussia minuta*** (Thélohan, 1892) Labbé, 1896
Eimeria motellae (Labbé, 1893) Yakimoff, 1929	***Goussia motellae*** (Labbé, 1893) Labbé, 1896
Eimeria siliculiformis Schulman & Zaika, 1962	***Goussia siliculiformis*** (Schulman & Zaika, 1962) Dykova & Lom, 1981
Eimeria sinensis Chen, 1956	***Goussia sinensis*** (Chen, 1956) Rosenthal, Dunams-Morel, Ostoros & Molnar, 2016)
Eimeria subepithelialis Moroff & Fiebiger, 1905	***Goussia subepithelialis*** (Moroff & Fiebiger, 1905) Dykova & Lom, 1983
Eimeria thelohani (Labbé, 1896) Yakimoff, 1929	***Goussia thelohani*** Labbé, 1896
Eimeria vanasi Landsberg & Paperna, 1987	***Goussia vanasi*** (Landsberg & Paperna, 1987) Lom & Dyková, 1992

A description of the number of species described throughout the years was made (Graphic 1).

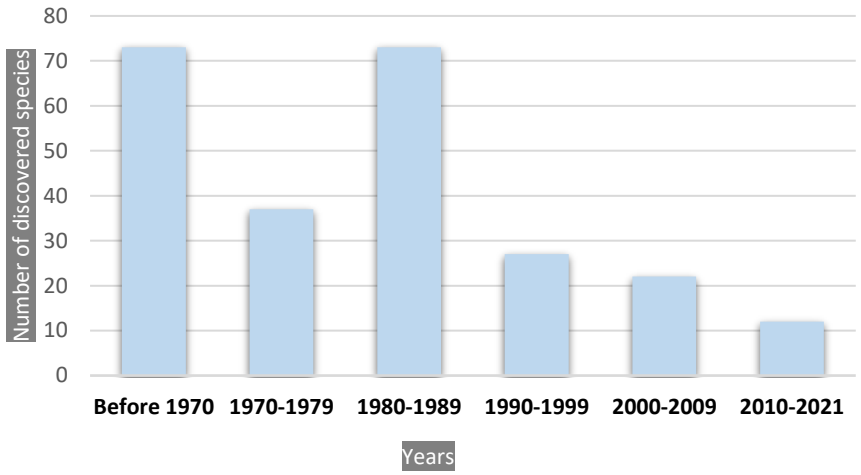

Figure 12: Graphic 1 - Estimative of the number of Coccidian parasites species described throughout the years.

The majority of species listed in Annex I were discovered before 1970 and during the 80s. Thirty-five to forty species were discovered from 1970 to 1979, twenty-five to thirty from 1990 to 1999 and about twenty of them in the 2000s. Despite the relatively new technological resources that are currently available, the number of new reported species has decreased in the last decades and mainly in the last eleven years.

Finally, a total of thirty-eight Coccidia lineages, corresponding to only 16% of the 244 listed species, were molecularly characterized so far (Table 4).

Table 4: Coccidia lineages listed in Annex I – Table 11 molecularly sequenced so far.

Sequenced lineage	GenBank accession number	Bibliographical reference(s)
Goussia neglecta	FJ009242	Jirků et al. (2009), Rosenthal et al. (2016)
G. noelleri	FJ009241	
G. kuehae	JF261140	Gibson-Kueh et al. (2011), Rosenthal et al. (2016)
Calyptospora spinosa	FJ904637	Whipps et al. (2012), Rosenthal et al. (2016)
Eimeria anguillae	GU479633	Molnar et al. (2012), Rosenthal et al. (2016)
E. daviesae	GU479675	
E. percae	GU479663	
E. variabilis	GU479674	
E. nemethi	GU479634	
Goussia ameliae	KP411007	Lovy and Friend (2015), Rosenthal et al. (2016)
G. clupearum	KT252255 KT252256	Rosenthal et al. (2016)

G. zarnowskii	GU479643	
G. subepithelialis	GU479655	
G. vargai	GU479637	
G. balatonica	GU479659 GU479638 GU479650 GU479671	
G. desseri	GU479666 GU479665 GU479641 GU479664	
G. koertingi	GU479647	
G. hupehensis	GU479672 GU479658	
G. carpelli	GU479640	
G. chalupskyi	GU479653	
G. cyprinorum	GU479464	
G. cylindrospora	GU479669 GU479668	
G. bohemica	GU479654	
G. acerinae	GU479536	
G. sinensis	GU479635	
G. kessleri	GU479645	
G. bayae	MH758783	
G. Janae	MF468318 GU479642 GU479651	
G. pannonica	GU479642 GU479651	
G. szekely	GU479656	
G. zarnowskii	GU479643	
G. leucisci	GU479649	
G. siliculiformis	GU479657	
Calyptospora funduli	GU479670	
C. spinosa	FJ 904637	
Eimeria rutili	GU479667	Molnar et al. (2012), Rosenthal et al. (2016)
Calyptospora paranaidji	MH480605	da Silva et al. (2019)
C. serrasalmi	MH167351 MH167352 FJ904642	Rosenthal et al. (2016), Negrao et al. (2019)

Microparasites in the European anchovy

Characterization of host samples

Table 5 provides a characterization of the host samples indicating their biometric data, length (cm) and weight (g), and Fulton's Condition Factor ($K=BW/TL^3$).

Table 5: Biometric data - minimum and maximum values (mean ± standard deviation) - of the forty-eight European anchovy (*Engraulis encrasicolus*) samples and Fulton's condition factor values (K).

Length (cm)	14.9 - 17.3 (15.9 ± 0.581)
Weight (g)	22.2 - 41.3 (30.1 ± 4.040)
K value	0.606 - 0.837 (0.74 ± 0.055)

Morphological analysis

Coccidia oocysts

Oocysts of coccidian parasites were found in the liver, kidney and muscle of only three of the 48 European anchovies, resulting in a prevalence of 1.4%. Specifically, one sample was infected in both the kidney and muscle, one was infected in the liver and the in the other only the muscle was infected (Table 6).

Table 6: European anchovy samples infected with Coccidian oocysts and the respective infected organs. EEx – *Engraulis encrasicolus* sample number; 0 – no infection (0 parasites); 1 – low infection (1-19 parasites).

European anchovy sample	**Infected organ**		
	Liver	Kidney	Muscle
EE4	0	1	1
EE8	1	0	0
EE36	0	0	1

Overall morphological features fit the general morphology described for *Goussia* species. Oocysts were spherical or irregularly shaped, each containing 4 ellipsoidal sporocysts in random positions. No Stieda or sub-Stieda body/bodies were observed (Figures 13 and 14).

Figure 14: Coccidian oocyst infecting the muscle of European anchovy.

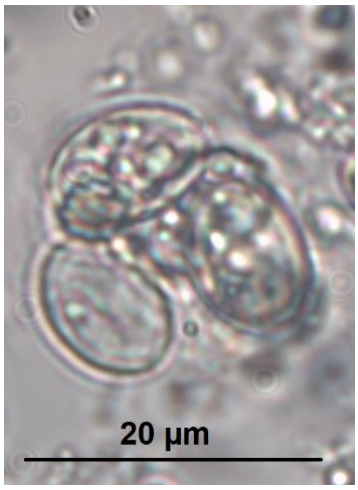

Figure 13: Coccidian oocyst infecting the liver of European anchovy. Notice that oocyst wall is almost imperceptible.

Measurements, in µm, of two detected oocysts are displayed in Table 7.

Table 7: Measurements of two Coccidia oocysts, in µm – minimum and maximum (mean ± standard deviation).

	Minimum – maximum (mean ± standard deviation)
Oocyst diameter	17.9 – 21.2 (19.6 ± 2.31)
Sporocyst length	9.8 (9.8 ± 0)
Sporocyst width	5.7 – 6.5 (6.11 ± 0.58)

Kudoa sp. spores

Kudoa sp. spores were found in the liver kidney, and muscle of nineteen anchovy samples, resulting in a prevalence of 39,6%. Concretely, thirteen samples had low levels of infection, four samples had medium levels of infection and two samples had high levels of infection (Table 8).

Table 8: European anchovy samples infected with *Kudoa* sp. spores and the respective infected organs. EEx – *Engraulis encrasicolus* sample number; 0 – no infection (0 parasites); 1 – low infection (1-19 parasites); 2 – medium infection (20-49 parasites); 3 – high infection (≥ 50 parasites).

European anchovy sample	**Infected organ**		
	Liver	Kidney	Muscle
EE1	0	0	1
EE6	0	0	2
EE9	0	0	1
EE11	0	0	3
EE14	0	0	1
EE15	0	0	1
EE20	0	0	1
EE21	0	0	1
EE24	0	0	1
EE26	0	0	1
EE27	0	1	1
EE28	0	0	2
EE29	1	0	1
EE30	0	1	3
EE31	0	0	2
EE32	0	0	1
EE33	0	0	1
EE34	0	0	2
EE35	0	0	1

Spores were quadrate in apical view, with broad and flattened base and clearly defined edges and rounded or dome-shaped in side view. Each spore contained four polar ovoidal capsules, unequal in size, one larger, with pointed end, fitting the general morphology described for *K. thyrsites* (Figures 15 and 16).

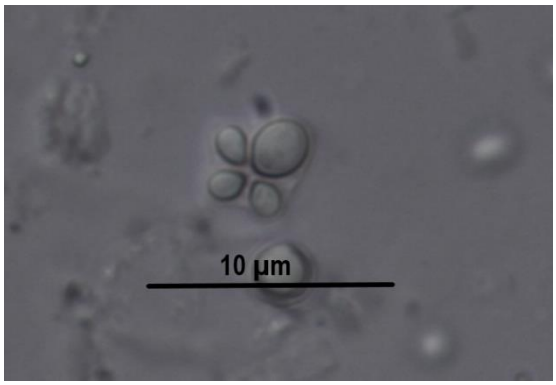

Figure 16: Apical view of *Kudoa* sp. spores infecting the muscle of European anchovy.

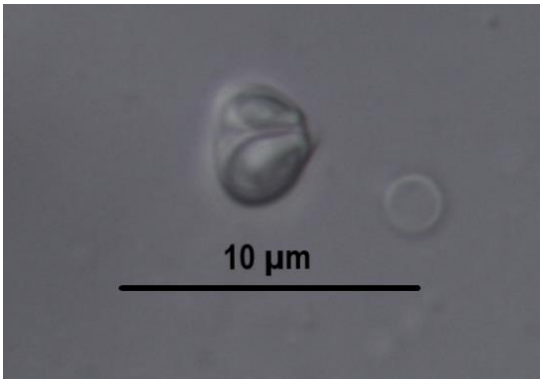

Figure 15: Side view of *Kudoa* sp. spores infecting the muscle of European anchovy.

Measurements, in µm, of eighteen spores, according to Figure 9, are displayed in Table 9.

Table 9: Measurements, in µm, of eighteen *Kudoa* sp. spores– minimum and maximum (mean ± standard deviation).

	Minimum – maximum (mean ± standard deviation)
Spore width	10.4 – 12.4 (11.4 ± 1.00)
Spore thickness	6.2 – 10.1 (7.6 ± 1.11)
Apical small polar capsule width	2.1 – 2.5 (2.1 ± 0.12)
Apical large polar capsule length	4.1 – 7.3 (5.4 ± 0.71)
Apical large polar capsule width	3.1 – 5.2 (4.1 ± 0.36)

None of the European samples were simultaneously infected with Coccidia oocysts and *Kudoa* sp. spores.

Molecular analysis

European anchovy

Coccidia

Molecular characterization was attempted for both Coccidia and *Kudoa* samples, but only Coccidia samples were successfully amplified in Polymerase Chain Reaction.

DNA extraction was performed on four tissue samples infected with Coccidia: one from the liver, one from the kidney and two of them from the muscle. All of the four samples were successfully amplified, but only two of them – the one from the liver and one from the muscle - produced good quality Coccidia sequences. The other retrieved sequences were too noisy probably due to co-amplification of other organisms (e.g. bacteria).

The outgroup used for the phylogenetic reconstruction (Figure 16) was *Eimeria tropidura* (Aquino-Shuster, Duszynski & Snell, 1990; GenBank accession number AF324217) parasitizing a reptile (Megía Palma et al., 2015). Final sequence alignment had 655 bp and the GTR+I+G model of sequence evolution (AIC=10800, -lnL= 5296) was implemented in BI and ML analysis.

The results from Blast search in Gen-Bank showed that all the sequences generated in the present study shared the highest percent identity (97%) with the sequence from *Goussia* sp. from the European pilchard (*Sardina pilchardus*) (GenBank accession number: MW006822) (Xavier et al. 2021).

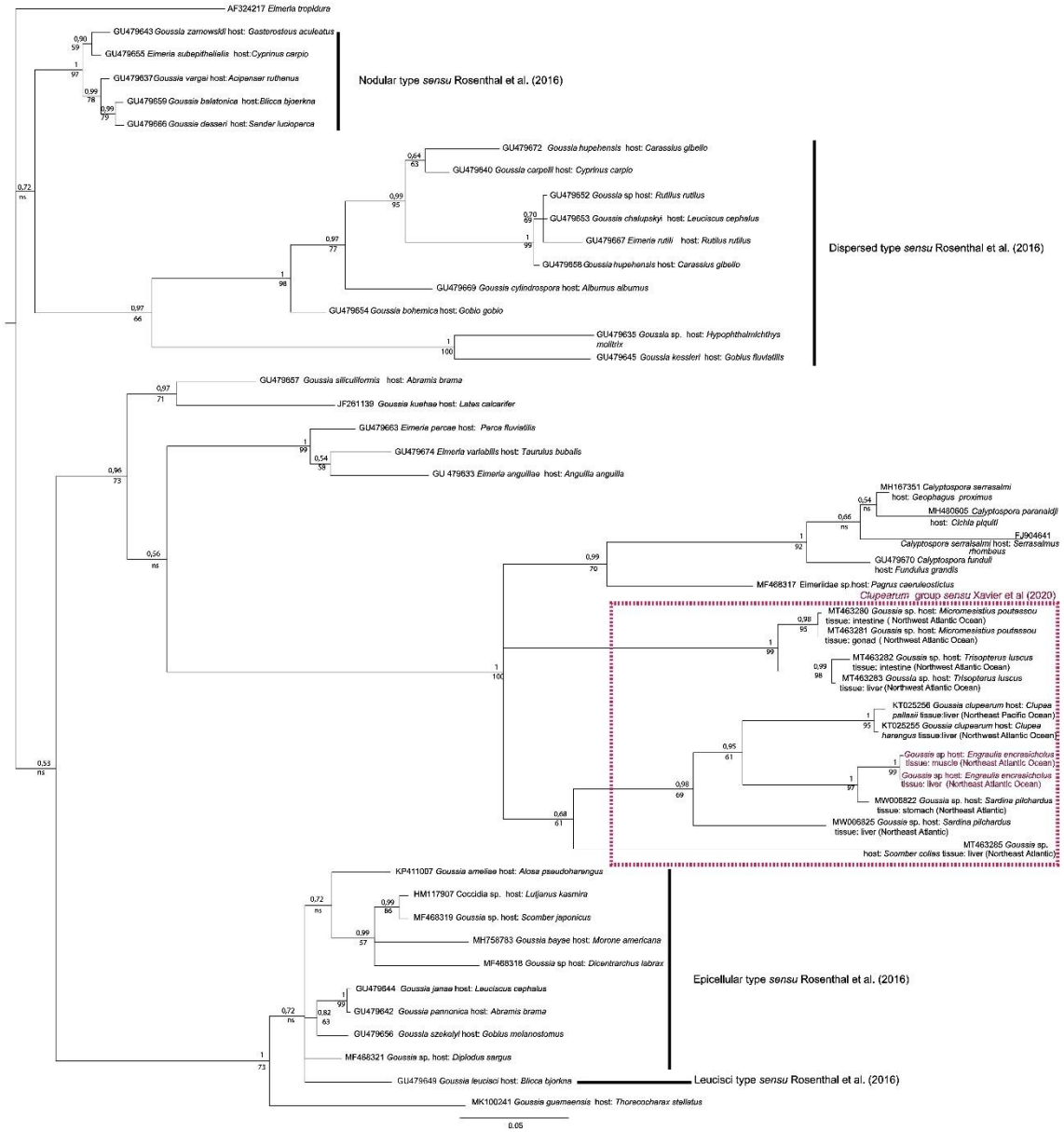

Figure 17: Phylogenetic reconstruction based on partial 18S rRNA gene sequences generated in the present study and those of their closest relatives. The best Bayesian Inference tree is depicted posterior probabilities (BI) and bootstrap values (ML) and are presented above and below each node, respectively. Sequences generated in the present study are highlighted in purple. ns- non significant - ML bootstrap supports were lower than 50%.

All the sequences generated in the present work clustered within a clade that encompassed *Calyptospora* species, and a non-monophyletic/paraphyletic group of *Goussia* spp. that was recently proposed as the "*Clupearum* group" (sensu Xavier et al. 2020). Lineages within this group include *Goussia* parasites sequenced from *Micromesistius poutassou* (GenBank accession numbers: MT463280 and MT463281), *Trisopterus luscus* (GenBank accession numbers: MT463282 and MT463283), *Scomber*

colias (GenBank accession number: MT463285), *Sardina pilchardus* (GenBank accession numbers: MW006822 and MW006825) and *Goussia clupearum* from *Clupea harengus* (GenBank accession number: KT025255) and *C. pallasi* (GenBank accession number: KT025256)..

Representatives of other four different *Goussia* groups erected by Rosenthal et al. (2016) were also included in this analysis (Figure 16) and are displayed in Table 10.

Table 10: Representation of the *Goussia* groups defined by Rosenthal et al. (2016) and the "*Clupearum* group" (sensu Xavier et al., 2020). Species reassigned from *Eimeria* to *Goussia* by Rosenthal et al. (2016) are already updated in this table, reflecting information given in Annex I – Table 11.

Group	Characteristics	***G. clupearum* and phylogenetic related lineages published in Rosenthal et al. (2016), Xavier et al. (2020) and Xavier et al. (2021)**	**GenBank accession number**
***Nodular* type**	Large oocysts that develop in particular portions of the intestinal epithelium over an annual cycle. Oocyst size varies from 21.0 to 30.0 µm diameter.	*Goussia zarnowskii* (Jastrzębski, 1982)	GU479643
		G. subepithelialis (Moroff and Fiebiger, 1905) Dykova and Lom, 1983	GU479655
		G. vargai (Molnar, 1986)	GU479637
		G. balatonica (Molnar, 1989)	GU479659
		G. desseri (Molnar, 1996)	GU479666
***Dispersed* type**	Small oocysts developing throughout the gut and throughout the year. Oocyst size varies from 8.0 to 13.0 µm diameter.	*G. hupehensis* (Chen and Hsieh, 1964)	GU479672 GU479658
		G. carpelli (Léger and Stankovitch, 1921) Dykova and Lom 1983	GU479640
		Goussia sp.	GU479652
		G. chalupskyi (Lukes, 1995)	GU479653
		Eimeria rutili (Dogel and Bychovski, 1938)	GU479667
		Goussia cylindrospora (Stankovitch, 1921)	GU479669
		G. bohemica (Lukes, 1994)	GU479654
		G. sinensis (Chen, 1956)	GU479635
		G. kessleri (Molnar, 2000)	GU479645
***Epicellular* type**	Intermediately sized oocysts developing epicellularly in enterocytes over a large area of the intestine via an annual cycle. Oocyst size varies from 14.0 to 19.0 µm diameter.	*G. ameliae* (Lovy and Friend, 2015)	KP411007
		Coccidia sp.	HM117907
		Goussia sp.	MF468319
		G. bayae (Matsche, Adams and Blazer, 2019)	MH758783
		Goussia sp.	MF468318
		G. janae (Lukes and Dyková, 1990)	GU479644
		G. pannonica (Molnar, 1989)	GU479642
		G. szekely (Molnar, 2006)	GU479656
		Goussia sp.	GU4698321

***Leucisci* type**	Large oocysts in the renal tubules, requiring an annual cycle of development. Oocyst size varies from 30.0 to 35.0 µm diameter.	*G. leucisci* (Schulman and Zaika, 1964) Lom, Desser, and Dykova, 1989	GU479649
***Clupearum* group**	Species which are able to infect multiple fish organs, including the intestine, and are also phylogenetically related and morphologically similar to *G. clupearum*. Oocyst size variable from 8.0 to 31.3 µm (large diameter type) or from 4. To 10.0 µm (small diameter type).	*Goussia* sp.	MT463280
		Goussia sp.	MT463281
		Goussia sp.	MT463282
		Goussia sp.	MT463283
		Goussia clupearum (Thelohan, 1894) Labbe, 1896	KT025256 KT025255
		Goussia sp.	MW006822
		Goussia sp.	MW006825
		Goussia sp.	MT463285

In the present study, *Goussia leucisci*, the representative of the "Leucisci group", clustered with the "Epicellular type" clade, which was also found in many previous studies (e.g. Xavier et al., 2020).

The BI and ML phylogenetic analyses were generally congruent with only four exceptions which question the monophyly of a) nodular and dispersed *Goussia*; b) epicellular and leuscici type *Goussia*; c) *Calyptospora* + *Goussia clupearum* group + a monophyletic group that included *Eimeria variabilis*, *E. anguillae* and *E. percae*; and finally d) some relations between *Calyptospora* species (Figure 16). In all previous cases ML bootstrap supports were lower than 50% (and therefore coded in the tree as ns- non significant) and BI posterior probabilities ranged from 54-72%.

Kudoa sp.

A total of seven PCR products were purified using the Gel/PCR DNA Fragments Extraction Kit (Geneaid Biotech Ltd., New Taipei City, Taiwan) and submitted to a new PCR with the same conditions mentioned above for Kudoa. Three samples amplified in the reaction, but none of them produced good quality sequences. Therefore, no phylogenetic reconstruction was carried out.

Blue shark

Out of the 159 DNA samples used in this study and available from the study by Verissimo et al. (2017) at CIBIO's DNA collections, only 38 (Northeast Atlantic) + 21 (South Africa) + 3 (Brazil) were successfully amplified. From these only 2 positives from samples collected from the Northeast Atlantic rendered high quality Apicomplexa sequences. The other sequences obtained from positive PCRs from the samples collected in this region either amplified non-target taxa (bacteria, ciliates, fungi and algae) or were too noisy probably due to co-amplification of several of these taxa. The sequences from South Africa and Brazil were too noisy probably due to a combination of co-amplification of other taxon (e.g. bacteria; fungi; algae) combined with the high degradation of the DNA, which did not allow to conclude whether they were Apicomplexa sequences or not.

For phylogenetic reconstructions, *Goussia noelleri* (Jirků, Jirků, Oborník, Lukes and Modrý, 2009) (GenBank accession number: FJ009241) parasitizing the amphibian *Rana temporaria* Linnaeus (Jirků et al., 2009) and Intranuclear coccidium (GenBank accession number: AY728896) parasitizing a turtle (Garner et al., 2006) were the two outgroups chosen (Figure 17) following the study by Xavier et al (2018b). Final sequence alignment had 517 bp and the GTR+G model of sequence evolution (AIC= 2576, -lnL= 1261) was implemented in BI and ML analysis.

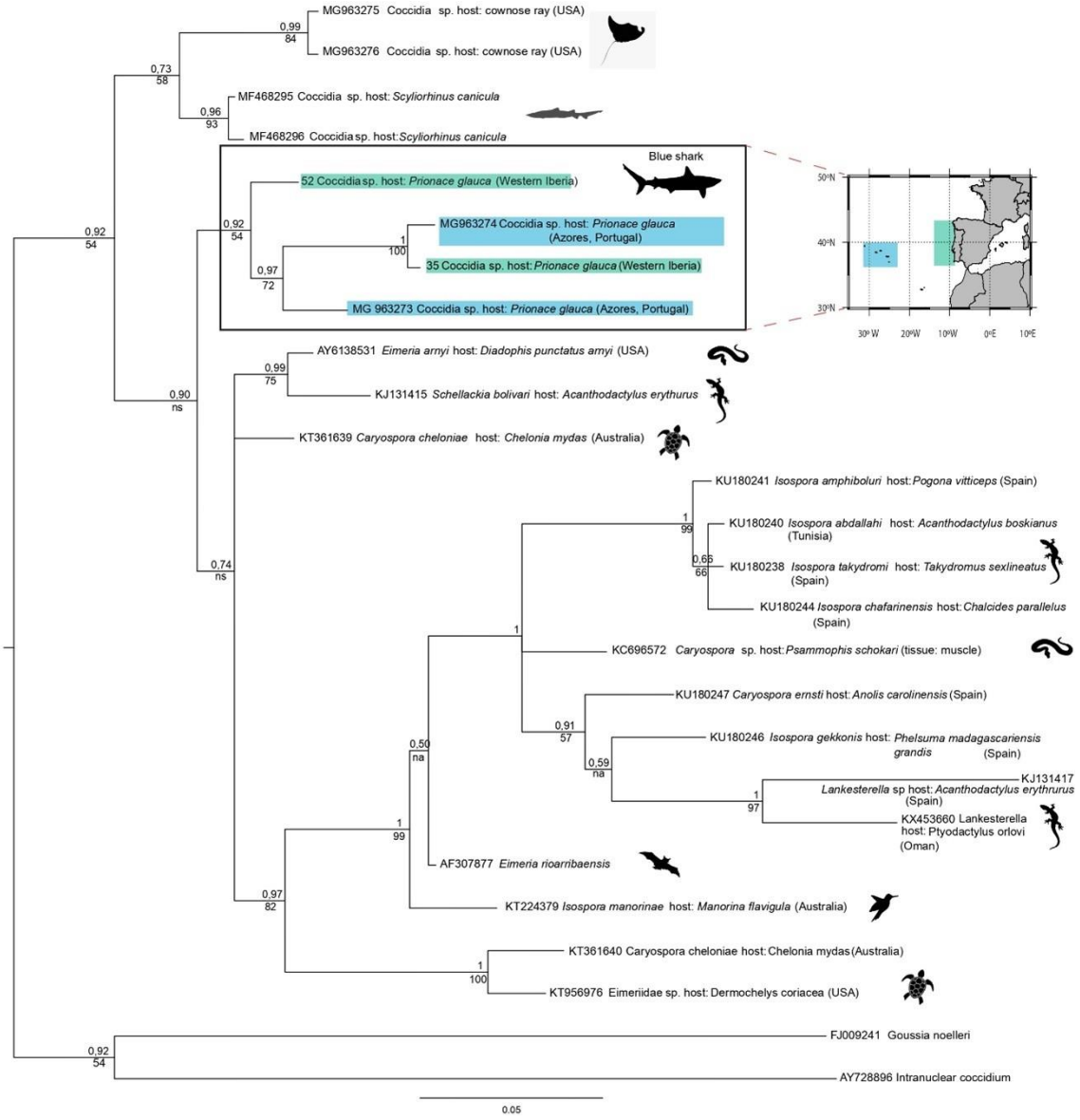

Figure 18: Phylogenetic reconstruction based on partial 18S rRNA gene sequences generated in the present study and those of their closest relatives. The best Bayesian Inference tree is depicted posterior probabilities (BI) and bootstrap values (ML) and are presented above and below each node, respectively. Sequences generated in the present study are highlighted in green. ns- non significant - ML bootstrap supports were lower than 50%.

The topology of the phylogenetic trees recovered by ML and BI analyses was identical and overall concordant with the evolutionary history of their vertebrate hosts, i.e. sequences from *Eimeria* (GenBank accession numbers: AY613853 and AF307877), *Isospora* (GenBank accession numbers: KU180241, KT224979, KU280140, KU180238, KU180244 and KU180246), *Caryospora* (GenBank accession numbers: KC6967572 and KU180247, KT361640) and *Lankesterella* (GenBank accession numbers: KT361639, KJ131417 and KX453660) infecting bats, birds, snakes and lizards were the most

derived. Although the tree topology of the consensus tree derived from BI and the best tree derived from ML analysis was the same, there were some discrepancies between the support values of some branches, and some branches were not fully supported (Figure 17). For example, the monophyly between *Eimeria rioarribensis* (GenBank accession number: AF307877) and the clade that encompasses some *Isospora*, *Caryospora* and *Lankesterella* lineages was not supported by either analyses (50% posterior probability and less than 50 bootstrap support). A similar case is also evident regarding the monophyly of *Isospora gekkonis* (GenBank accession number: KU180246) and the clade including *Lankesterella* sp. lineages in lizards (GenBank accession numbers: KJ131417 and KX453660).

Sequences generated in the present study clustered with other sequences of coccidians obtained from the muscle of Blue sharks captured off Azores, Portugal (GenBank accession numbers: MG963274 and MG963273.1, respectively) (Xavier et al., 2018b). However, while the monophyly of this group was highly supported by the BI analysis (92% posterior probability) it was only weakly supported by the ML analysis (54% bootstrap support). Clustering of sequences within this group did not occur according to geographical origin.

DISCUSSION

The three main objectives of this thesis were to: 1) to compile a list of valid names of fish coccidia and respective synonymies; 2) survey Apicomplexa and Myxozoa parasites in *Engraulis encrasicolus* off Portuguese mainland and perform a morphological and molecular characterization; and 3) investigate the phylogenetic relations of coccidians infecting blue sharks captured off Northwest Iberia, South Africa and Brazil. Unfortunately, in respect to objective 3), extracted samples by Veríssimo et al. (2017) from South Africa and Brazil were too degraded and did not provide good results.

Summary table from literature review (Annex I – Table 11)

As mentioned in the introduction, it is estimated that the diversity of coccidian parasites is still underestimated, especially among fish hosts (Del Campo et al., 2019; Molnár et al., 2012). Annex I presents a list of fish coccidian species, considered valid, along with their synonymies. However, the validity of some synonymies is not consensual among taxonomists. For example, *Eimeria cyprinorum* described by Stankovitch, 1921 was considered a synonym of *Goussia carpelli* pro parte by Dykova and Lom (1983); Similarly, *Eimeria sparis* Sitjà-Bobadilla, Palenzuela and Alvarez-Pellitero, 1996 was considered synonym of *E. spari* Diouf and Toguebaye, 1996, according to Duszynski, Couch and Upton, 2003. In those cases, not only the synonymy is mentioned (according to certain authors), but the species involved are also listed separately in the table. Further studies should investigate whether some of the more recently described species are not synonyms of species already described, as in the case of older species original descriptions of fish Coccidia were generally limited in detail.

Analysis of Figure 12 evidences a peak in the discovery of new species in the 1980s, which could be explained by the high number of studies carried out by a group of specialists dedicated to the study of these parasites, namely Drs. Lom, Molnár and Dyková. Despite the technological advances and the effort to discover new species increasing in the last recent years, graphic 1 (Figure 12) indicates a decreasing number of reports on new fish Coccidia parasites in the last eleven years.

However, molecular data has proven to be an important tool in the discovery and characterization of Coccidian parasites, and is expected to enlighten many of the doubts regarding the taxonomic and diversity of these parasites. In Table 5 are listed the thirty-eight lineages sequenced produced in the last thirteen years (to the best of my knowledge) for valid coccidian name species. Although this corresponds to a small percentage of all species listed in Annex I (16%), it demonstrates the increasing effort

mentioned above. For instance, Molnár and collaborators (2012) sequenced for the first *Eimeria anguillae*, *E. daviesae*, *E. percae*, *E. variabilis*, *E. rutili* and *E. nemethi*, adding further characters for the diagnosis of these species. Similarly, Friend et al. (2016) recently described a novel intestinal coccidian, *Goussia echinata*, and sequenced *G. clupearum* from Atlantic herring *Clupea harengus*, which also included genetic data. Another example is the work of Rosenthal et al. (2016) that sequenced *Calypotospora funduli* and numerous *Eimeria* and *Goussia* specimens; and the work by Couso-Perez et al. (2019) was the first to achieve the genetic characterization of *E. truttae*. Genetic studies of coccidians infecting cartilaginous fish have also been recently performed by Xavier et al. (2018a, b) with high diversity of lineages found infecting these hosts (e.g., cownose ray *Rhinoptera bonasus* Mitchill and the blue shark *Prionace glauca* Linnaeus).

Although there has been an increase in the number of studies carried out resorting to molecular tools, as previously mentioned some of these studies did not include morphological characterization of sequenced parasites and thus taxonomic resolution was rather limited and many lineages remained unnamed. For example, Gibson-Kueh et al. (2011) wasn't able to discern whether a parasite lineage from vietnamese asian seabass *Lates calcarifer* Block belonged to the genus *Eimeria* or *Cryptosporidium*, which reiterates the importance of complementing molecular tools with morphological analysis of tissues, and vice versa. The results presented in this thesis regarding the lineages infecting *P. glauca* is also another example, since it was not possible to ascertain the taxonomy of the parasites of the blue shark, as morphological analysis was hindered.

In some cases, not even the use of both morphological and molecular analyses is sufficient to reach a conclusion about parasite taxonomy. For example, Whipps et al. (2012) discussed the placement of species in the genus *Calyptospora* onto Calyptosporidae or Eimeriidae, due to their phylogenetic affinities with *Goussia*. Another example is the study of Xavier et al. (2020) that reported several parasite lineages infecting the blue whiting, the pout, and the Atlantic chub mackerel which clustered together and were phylogenetic related to *Goussia clupearum* and *Calyptospora* species sequenced so far; however, the morphological differences and genetic distances between the sequences generated precluded a solid conclusion regarding whether some of these lineages corresponded to different species. This study also fits this pattern, as it was not possible to identify with certainty the species of Coccidia infecting the European anchovy, despite the use of both strands of analysis. Nonetheless, the use of both morphological and molecular analysis has proven to be very helpful to the study of some of these parasites, with good results obtained by Rosenthal et al. (2016) that

allowed to definitely move *Eimeria cylindrospora*, *E. leucisci*, *E. siliculiformis*, and *E. subepithelialis* to the genus *Goussia* (see Annex I).

Hence, it is crucial that increasing studies involving molecular and morphological characterization of piscine Coccidia, continue to be carried out, for a clearer characterization of this group and, consequently, an easier understanding of it.

European anchovy

Restrictions imposed to control the pandemic situation caused by Covid-19, specifically the prohibition of commercial fishing for an extended period, thus avoiding an initially intended second sampling (spring 2021) are the cause of the low sampling of the European anchovy in this study. However, it still contributes to the increasingly effort invested by the scientific community in parasitology, particularly regarding fish Coccidia. Coccidia levels of parasitemia indicated in the present work are low, as prevalence was only 1.4%, while *Kudoa* sp. prevalence was 39.6% indicating medium levels of parasitemia. Nonetheless, the usual flesh myoliquefaction post-mortem caused by the presence of *Kudoa* sp. spores in the muscle of fish was not observed, indicating their decent health status. Due to the great demand for fish products, namely sardines, and the restrictions imposed on their fishing, European anchovies have grown in the fishing and canned sectors as a great substitute. If futures studies continue to verify generally low parasitic incidence in *Engraulis encrasicolus* and verifying a good health status in the individuals, gaining even more credibility as a resource, it will be easier to meet the great demand for fish products and, consequently, contribute to the economic growth of fishing and canned sectors.

Surveys of Coccidian infections in marine fish hosts are still quite uncommon, as Annex I evidences a majority of freshwater hosts. According to the literature review carried out in this study, there is only one report on the occurrence of coccidians in the European anchovy, *Eimeria sardinae* (Thélohan, 1890) Reichenow, 1921. There is another report on coccidians parasitizing engraulids by Timi and Sardella (1998), who observed *Eimeria sardinae* (Thélohan, 1890) Reichenow, 1921 in the testes of *Engraulis anchoita*.

The morphological analysis of the Coccidia parasites that infected European anchovies analyzed herein, similarly to the ones in Xavier et al. (2021), fit the general morphology described for *Goussia* species and shared similarities with *G. clupearum*. However, it is relevant to refer that analyses in the present study were performed in thawed tissues, which can potentially represent a slight variation in oocysts size comparing to fresh material.

Despite a limited number of studies, *G. clupearum* and many closely related genetic lineages are increasingly being reported from many marine fish in the North Atlantic (Abollo et al., 2001; Azevedo, 2001; Costa & Mackenzie, 1994; Friend et al., 2016; Kalfa-Papaioannou & Athanassopoulou-Raptopoulou, 1984; Mackenzie, 1981; Morrison & Hawkins, 1984; Tolonen & Karlsbakk, 2003; Xavier et al., 2021; Xavier et al., 2020; Xavier et al., 2018a), namely in the blue whiting (*Micromesistius poutassou* Risso, 1827, Gadidae), Atlantic mackerel (*Scomber scombrus* Linnaeus, 1758, Scombridae), and several *Trisopterus* species (Gestal & Azevedo, 2006). The genetic lineages originated from this coccidians allowed the proposal of a "*Clupearum* group" (sensu Xavier et al 2020). This group encompasses *Goussia* species capable of infecting multiple fish organs, and that are phylogenetically related and morphologically similar to *G. clupearum*, but exhibit significant genetic distances that suggest they are not the same species. The sequences from the coccidians sequenced from the European anchovy fit this description, both at the morphological and phylogenetic level, providing another piece of evidence for the wide host distribution of these lineages.

In this thesis, phylogenetic reconstruction of the "*Clupearum* group", showed that lineages sequenced from each host genera were generally monophyletic, suggesting a degree of host specificity and confirming previous assumption on this group (Xavier et al., 2021). Two main clades were recovered within the *Clupearum* group, one encompassing parasites sequenced from Gadidae (*Trisopterus luscus* and *M. poutassou*), and the other encompassing parasites sequenced from Engraulidae, Clupeidae and Scombridae. In their study, Xavier et al. (2021) further suggested some degree of co-evolution at least at the intra-familiar level, with parasites from each fish family forming distinct clades. However, the inclusion of parasites from Engraulidae hosts changed this view as they clustered within Clupeidae hosts. Anyhow, additional data on other fish-*Goussia* associations as well as other genetic markers is still necessary for a better understanding of the co-evolution between host and these coccidia parasites. To the best of my knowledge, 18S rRNA gene is the sole used molecular marker in studies of fish coccidia and taxon sampling is paramount to fully understand host-parasite co-evolution, so this research area in fish coccidia is still in its infancy.

Nevertheless, results from the present work confirm host-specific lineages within the "*Clupearum* group". This parasite-host specificity may be caused by unique selection pressures both on the parasite and the host to keep up with each other's adaptions (Morris & Costello, 2020). Wide host ranges have been recorded, for example, in fish Coccidia by Lom and Dyková (1992), Davies and Ball (1993) and Sitjà-Bobadilla and Alvarez-Pellitero (2003). Contrary, Fournie and Overstreet (1993) experimentally verified

the host-specificity of *Calyptospora funduli* in hosts mostly in the genus *Fundulus*, and expected more cases of host-specificity in fishes due to the fact that fish parasites are not as protected from environmental conditions as those in homeothermic hosts, leading to a closer relationship and adaptation of the parasite to the host. Similar experiments with the same outcome were carried out with *Eimeria vanasi* (Kim & Paperna, 1992) and *G. cichlidarum* (Kim & Paperna, 1993). Despite the reports of G. *carpelli* in several hosts' genus (Annex I), experiments resorting to cross-infection technique carried out by Molnar et al. (2005) confirmed the host specificity of the parasite species to the common carp *Cyprinus carpio*; their results suggest the presence of morphological similar, but distinct *Goussia* species in cyprinid fishes rather than a single species with a wide host range. All of the studies reporting *G. carpelli* in those hosts were carried out before Molnar et al. (2005) and after that only Rosenthal et al. (2016) sequenced *G. carpelli* from *C. carpio*.

It is worth noticing that *Goussia hupehensis* ("dispersed type" group) did not generate a monophyletic lineage (Figure 16) (GenBank accession numbers: GU679472 and GU479658), in agreement to the results from Rosenthal et al. (2016). *Calyptospora serrasalmi* (GenBank accession numbers: MH167351 and FJ904641) is also not monophyletic according to Figure 16. This suggests taxonomy for these species should be revised. Therefore, as previously stated further efforts are necessary, within and outside the "*Clupearum* group".

The morphologic features of myxozoan infecting the European anchovy were compared to the ones in previous studies and fit the generally morphological description of *K. thyrsites* by Eiras et al. (2014), Giulietti et al. (2019) and Cavaleiro et al. (2021). Although there are several reports of *K. thyrsites* parasitizing marine fish hosts (e.g. (Giulietti et al., 2019; Grabner et al., 2012; Henning et al., 2019; Jones et al., 2012; Jones & Long, 2019; Marshall et al., 2016; Meng & Li-Chan, 2007; Whipps et al., 2003; Yokoyama & Itoh, 2005; Yokoyama et al., 2004), among many others), only Langdon et al. (1992) reported *K. thyrsites* in Engraulids (*Engraulis australis* Shaw and *E. japonicus* Temminck & Schlegel). Timi and Sardella (1998) also reported the genus *Sphaeromyxa* (Myxosporea) from *Engraulis anchoita* from the gall bladder. Interestingly, Whipps and Kent (2006) concluded that genetic differences detected in *K. thyrsites* did not correlate with any of the morphological differences between spores from different hosts and locations, implying that spore morphology alone may be inappropriate for intraspecific analyses of myxozoan species. Again, taxonomic revision for the species is warranted. Given what is known for this "species" it is not possible to reject the hypothesis that the *Kudoa* found in the present study corresponds or is related to *K. thyrsites*. Laboratory work was not successful in amplifying the DNA of the observed *Kudoa* parasites. In fact,

several complex amplification methods have been described to amplify *Kudoa* spp., often involving multiple PCRs still coupled the need band excision. Unfortunately, COVID-19 restrictions set in at CIBIO laboratory did not allow for the implementation of all published protocols in a timely manner.

Blue shark

Coccidian parasites infecting sharks are also still very little scrutinized. Attempting to investigate the phylogenetic affinities of this parasite group in the blue shark felt necessary, as that is something little discussed (Veríssimo et al., 2017; Xavier et al., 2018b). Moreover, this work is extremely relevant to understand if parasites populations are panmictic, following the patterns found for their host, and to continue to assess the phylogenetic position of this specific and yet unnamed group of elasmobranchs parasites.

There are only a small number of reports of Coccidian parasites in sharks (Table 11). *Eimeria zygaenae* (Mandal and Chakravarty, 1965) was reported infecting the intestine of winghead shark, *Euphyra blochii* (referred as *Sphyrna blochii*) by Dykova and Lom (1983). Fitzgerald (1975) reported *Goussia squali* (Fitzgerald, 1975) Lom & Dykova, 1922 infecting the intestine's spiral valve spiny dogfish shark *Squalus acanthias* from the Pacific Ocean, coast of Washington (USA). Dykova and Lom (1983) also reported *G. lucida* (Labbé, 1893) Labbé, 1896 in the posterior intestine of small-spotted catshark *Scyliorhinus canicula* in the Mediterranean sea (French coast) and the Atlantic Ocean. Coccidia species from the anal gland, liver and stomach of *S. canicula* were reported by Xavier et al. (2018a, 2018b), however no morphological study was conducted. Until now, and to the best of my knowledge, there was only one report of a coccidia species parasitizing the blue shark (*P. glauca*) (Xavier et al., 2018b).

A panmitic model is practically proven regarding the populational structure of the blue shark in the Atlantic Ocean (King et al., 2015; Leone et al., 2017; Ovenden et al., 2009; Taguchi et al., 2015; Verissimo et al., 2017). The results from the present thesis indicate that the phylogenetic affinities between coccidian lineages parasitizing the blue shark from Azores and western Iberia reflect their host panmixia (Figure 17), with so far no evidences of geographical structuring among parasites from different nursing areas in the Atlantic Ocean. These results do not support the use of coccidian parasite lineages as biomarkers for stock delimitation of blue shark populations. However, the lack of data from the other nurseries – namely South Africa and Brazil – hinders a more robust conclusion.

Also in this case, phylogenetic reconstructions were overall concordant with the ones obtained by Xavier et al. (2018b). Sequences from *Isospora*, *Caryospora* and *Lankesterella* infecting birds, mammals, snakes and lizards were the most derived, in agreement with evolutionary history of vertebrate hosts. By observing Figure 17, coccidians infecting elasmobranchs are quite divergent from those lineages. Although phylogenetic reconstruction in the present study is not as extensive in terms of taxa included in comparison to the study of Xavier et al. (2018b), results still support the conclusions of that study, i.e. most Apicomplexa sequenced from elasmobranchs, explicitly Coccidia, form basal lineages, which is in line with the host's phylogenetic relationships, since elasmobranchs (together with the holocephalans) are the oldest jawed vertebrates on earth. In future studies, morphological analyses of elasmobranchs coccidia are paramount to shed light on the taxonomy of these parasites.

FINAL REMARKS AND FUTURE PERSPECTIVES

The different conclusions drawn from the fulfillment of the three objectives of this work fit into a common general conclusion, the still current need for a greater number of studies focusing on microparasites in fish, especially regarding the Coccidia group, resorting to both morphological and molecular analyses to improve the taxonomy of these groups.

Ideally, in the future, these studies will allow us to identify if whether a particular parasitosis in a certain host is a new occurrence. A better management of fish diseases in wild and cultured fish will be possible, ultimately contributing to the conservation of marine biodiversity and to a more satisfactory fulfillment of the demand for fish products, also benefiting the economic sector.

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ANNEX I

Table 11: Literature review of species of the three main genera of Apicomplexa parasites (*Calyptospora*, *Eimeria* and *Goussia*) reported to date in fish. OC – Oocyst (OCs – Oocysts); Oocyst Residuum – OR; SPC - Sporocyst (SPCs – Sporocysts); SPZ – Sporozoite (SPZs – Sporozoites); Sporocyst Residuum – SR; Stieda Body – SB; Obs. – Observations. *Species or synonymy only referenced by Duszynski, Couch and Upton (2003) in online website(s): https://www.kstate.edu/parasitology/worldcoccidia/SILURIFORMES, https://www.kstate.edu/parasitology/worldcoccidia/PERCIFORMES,https://www.kstate.edu/parasitology/worldcoccidia/CYPRINIFORMES,https://www.kstate.edu/parasitology/worldcoccidia/CLUPEIFORMES, as this information has not been peer reviewed.

Species	Infected organ(s) and characteristics (measures in µm)	Host(s)	Geographical distribution	Bibliographic references
Calyptospora empristica Fournie, Hawkins and Overstreet, 1985	Liver, in hepatocytes and pancreatic acinar cells. OCs spherical 22.3 (19.6-24.5) diameter. SPCs ellipsoid 9.0 × 5.4 (7.0-9.5 × 4.5-7.5). Sporopodium 5.0-7.0 long, supporting membranous veil surrounding SPC. SR Small, granular, 1-4 refractile granules.	*Fundulus nottii*	Mississippi (USA)	Fournie et al. (1985)
Calyptospora funduli (Hawkins, Fournie and Overstreet, 1984) Duszynski, Solangi and Overstreet, 1979 **Syn. *Eimeria funduli*** Hawkins, Fournie and Overstreet, 1984	Liver. OCs spherical 25.0 (20.0-31.0) diameter or ovoid 10.0 (9.0-11.0) × 6.0 (5.0-7.0). SPCs have Stieda and sub-Stieda bodies and a few residual granules. sporopodia 15.0 (10.0-25.0) long high support a transparent membrane that completely surrounds the SPC. SR present. SPZs have one large posterior refractile body. **Obs.:** Second host required *Palaemonetes pugio* (shrimp).	*Fundulus confluentus, F. grandis*, *F. heteroclitus, F. jenkinsi, F. pulvereus, F. similis, Menidia beryllina*, *Opsanus beta*	Halstead Bayou, Ocean Springs, Mississippi (USA) Alabama, Virginia and Mississippi - estuaries (USA)	Hawkins et al. (1984), Duszynski et al. (1979), Dykova and Lom (1983), Fournie et al. (1985), Fournie and Overstreet (1993), Oliveira et al. (1993), Fournie et al. (2000), Rosenthal et al. (2016)
Calyptospora gonzaguensis Silva, Orlanda, Araújo-Costa, Hamoye and Matos, 2020	Liver, in hepatic tissue. OCs ovoid 19.6 diameter. SPCs peripheral 9.2 × 3.9. Sporopodium 2.2 mean length, supporting membranous veil surrounding SPC.	*Triportheus angulatus*	River Tocantins, Amazon (Brazil)	Silva et al. (2020)

Calyptospora paranaidji Da Silva, Silva, Giese, Hamoy and Matos, 2019	Liver, in hepatic tissue. OCs ovoid 22.1 diameter. SPCS piriform 9.7 × 4.6. Sporopodia extending in rows from posterior extension along approximately 2/3 of spore body, supporting membranous veil surrounding SPC. Partial suture located in anterior portion of spore body.	*Cichla piquiti*	River Tocantins, Reservoir of the Estreito Hydroelectric Power Station, Western Maranhão (Brazil)	da Silva et al. (2019)
Calyptospora serrasalmi Cheung, Nigrelli and Riggieri, 1985	Liver, gallbladder and heart. OCs spherical, or pyriform 22.5-25.5 diameter. SPCs pear-shaped 8.2-11.8 × 4.0-6.0. Sporopodium supporting membranous veil surrounding SPC.	*Serrasalmus rhombeus, S. striolatus, Hoplias malabaricus*, *Geophagus proximus*	River Amazon, lagoonal region of Recife and Pernambuco, Pará (Brazil)	Cheung et al. (1986), Casal et al. (2007), Whipps et al. (2012), Negrao et al. (2019)
Calyptospora spinosa Azevedo, Matos and Matos, 1993	Liver, testes and ovary tissue. OCs spherical, or ellipsoid 21.1-23.4 diameter. SPCs ellipsoidal 9.3 (8.9- 9.5) x 3.8 (3.6-4.1). Sporopodium 2.2 long, supporting membranous veil surrounding SPC.	*Crenicichla lepidota*	River Amazon (Brazil)	Azevedo et al. (1993)
Calyptospora tucunarensis Bekesi and Molnar, 1991	Liver. OCs spherical 24.3 (23-26) diameter. SPCs frying-pan shaped 8.3 (7.2-9.1) x 3.7 (3.5-5.0). No SB. Sporopodium 2.7 (2.5-2.9) long, supporting membranous veil surrounding SPC. SR granular (1-2/3-4 refractile granules in young and older SPCs, respectively). SPZs vermiform 5.7 (5.4-6.3) x 1.2 (1.1-1.4).	*Cichla ocellaris*	River Curú - natural waters and fish farms (Northeast Brazil)	Bekesi and Molnar (1991)

Eimeria adioryxi Diouf and Toguebaye, 1994	Testes and digestive tract.	*Adioryx hastatus*	Coast of Senegal	Diouf and Toguebaye (1994b)
Eimeria ambassi Patnaik and Acharya, 1972	"In the dorsal side of the right shoulder, communicating with the intestine". OCs ovoid and thick-walled. Micropyle present.	*Barbus ambassis*	Fish market in India	Dykova and Lom (1983)
Eimeria amudarinica Davronov, 1987	Intestine.	*Scardinius erythrophthalmus*	Uzbekistan	Davronov (1987)
Eimeria amurensis Akhmerov, 1959	Liver and kidney. No SB.	*Pseudorasbora parva*, *Sarcochilichthys sinensis*	USSR – Asian part	Dykova and Lom (1983)
Eimeria anguillae Léger and Hollande, 1922	Intestine, intestinal epithelium, and feces. OCs spherical 8.0-12.8 diameter. OR 1-2 refractile granules of 0.5-1. SPCs ellipsoidal or oval 5.6-8.0 × 2.4-5.0. Micropyle absent. SB present. SR round or ellipsoid 2.3 × 1.6. SPZs vermiform 6.0-7.0 × 1.3-1.8.	*Anguilla anguilla, A. Australis, A. rostrata*	New Zealand Ulla and the Tea rivers (Spain) River Ebro delta (NE Spain) River Ölfusá (Iceland) River Matamek (Quebec) Szczecin Lagoon and river Odra mouth, Baltic Sea	Hine (1974), Molnar and Hanek (1974), Lacey and Williams (1983), Benajiba et al. (1994)
Eimeria aristhichthysi Lee and Chen, 1964	Intestine. No SB.	*Aristichthys nobilis*, *Hypophthalmichthys molitrix*	Hubei province (China)	Dykova and Lom (1983)
Eimeria ashburneri Molnar and Rhode, 1988	Intestinal mucosa and pyloric caeca. OCs round 8.4 (7.7-9.2) diameter. SPCs lemon-shaped 6.4 (5.9-6.7) × 4.2 (3.8-4.6). Small cap-like SB. SR finally granular and ellipsoid 2 × 1.2.	*Macquaria ambigua*, *Pagellus bellottii, Sparus caeruleostictus*	Nerrandera, New South Wales – fish farm (Australia) Coast of Senegal	Molnár and Rhode (1988), Diouf and Toguebaye (1994b)

	SPZs 5.0 (4.8-5.3) × 1.0 (0.8-1.1).			
Eimeria aurati Hoffman, 1965	Anterior intestinal epithelium and feces. OCs spherical, or ovoid 20.1 (16.0-24.0) × 16.3 (14.0-17.0). SPCs ellipsoid 11.0-13.0 × 6.5-8.0. No SB nor SPC residuum. SPZs sausage-shaped, 10.0-13.0 × 2.0-2.5.	*Carassius auratus*	Pennsylvania (USA)	Hoffman (1965), Dykova and Lom (1983)
Eimeria banyulensis Lom and Dyková, 1982	Middle part of the intestine. No SB.	*Coris julis*, *Ctenolabrus rupestris*, Symphodus cinereus, *S. (=Crenilabrus) mediterraneus*	Mediterranean Sea coast, near France	Lom and Dykova (1982b)
Eimeria barbi Davronov, 1987	Intestine.	*Barbus capito*	Uzbekistan	Davronov (1987)
Eimeria baueri Alvarez-Pellitero and Gonzalez-Lanza, 1986	Kidney, spleen, liver, ureter, gall bladder, and heart.	*Carassius carassius*	River Esla (north-west Spain)	Alvarez Pellitero et al. (1986)
Eimeria bouixi Daoudi and Marques, 1987	Intestine.	*Dicentratchus labrax*	Languedoc (France)	Daoudi and Marques (1987)
Eimeria branchiphila Dyková, Lom and Grupcheva, 1983	Kidney, spleen and gills. OCs ellipsoidal 9.0-10 × 19.0-22.0 to elongated 9.0 × 27.0. SPCs ellipsoidal, 4.0-5.0 x 8.0-10.0. SB as a thickening in the form of a wide, low collar (diameter about 1.8) around the anterior end. SR 4.5 diameter consists of coarse granules of 0.5-0.7. SPZs vermiform tapering at both	*Rutilus rutilus*	Batak dam lake (Bulgaria)	Lom et al. (1983)

	ends, with a large vacuole extending a quarter of their length.			
Eimeria brevoortiana Hardcastle, 1944	Intestine, pyloric caeca and testes. OCs spherical 25.1 (17.5-30.0) diameter, or ovoid 26.2 (21.2-30.0) × 22.7 (5.0-27.5). OCs residuum described but not depicted. SPCs elongate, 16.4 × 6.3. SR small. SPZs cigar-shaped, slightly curved, 15.0 × 2.5.	*Brevoortia tyrannus*	Beaufort, North Carolina (USA)	Hardcastle (1944), Upton et al. (1984)
Eimeria carassii Yakimoff and Goussef, 1935	Intestine. Insufficiently described species.	*Carassius auratus, C. carassius*	USSR – European part	Dykova and Lom (1983)
Eimeria carassiusaurati Romero and Rodriguez, 1978	Intestine. SB present.	*Carassius auratus*	Granada (Spain)	Dykova and Lom (1983)
****Eimeria castravetsi*** Moshu, 1992	Intestine.	*Cobitis taenia*	Not documented.	Duszynski et al. (2003c)
Eimeria catalana Lom and Dykova 1981	Testes, middle intestine. OCs spherical 10.5-11.5 diameter. Refractile granules may represent the polar granules. SPCs ellipsoidal 7.7 (7.5-8.5) × 6 (5.5-6.5), with one end slightly tapered. SB encircled by a flat ring-like thickening of the sporocyst wall. SR in the form of lumps of refractile granules and is about 2.5 × 1.2. SPZs C-shaped 2.3 × 9.0.	*Bodianus speciosus, Scarus hoefleri, Symphodus cinereus, S. mediterraneus*	Coast of Senegal Banyuls-sur-Mer (coast of France)	Lom and Dyková (1981), Diouf and Toguebaye (1994b)

Eimeria catostomi Molnar and Hanek, 1974	Anterior intestine's epithelium and feces. OCs spherical, 7.0 (6.5-7.5) diameter. Polar granule of 0.8 (0.7-0.9) diameter in the center of the OC. SPCs oval, flattened from one side 5.5 (5.2-5.9) × 3.8 (3.6-4.0) × 3.1 (2.9-3.4). No SB. SR round finely granulated 2.3 (2.0-2.6) diameter. SPZs vermiform 4.6 (4.4-4.8) × 1.4 (1.3-1.6).	*Catostomus commersoni*, *Hypentelium nigricans*	Bronte Creek near Milton, river Conestogo near Conestogo, Grand River and Laurel Creek near Waterloo (all in Ontario, Canada)	Molnar and Hanek (1974), Dykova and Lom (1983) Upton et al. (1984)
Eimeria cheilodactyfi Molnar and Rhode, 1988	Intestinal mucosa and pyloric caeca. OCs round 11.2 (10.5-11.5) diameter. Polar granule of irregular shape of 1.6 (1.3-1.8) diameter. SPCs elongated ellipsoidal 9.6 (8.6-10.4) × 4.2 (4.0-4.4), with small SB like thickenings at one end. SPZs vermiform 7.0 (6.8-7.3) × 1.2 (1.1-1.3).	*Cheilodactylus fuscus*	Coifs Harbour, northern New South Wales (Australia)	Molnar and Rohde (1988)
Eimeria cheissini Shulman and Zaika, 1962 **Syn. *Eimeria cheisini*** Izumova, 1977 lapsus	Peritoneum, intestine, swim bladder and gall bladder. No SB.	*Gobio gobio*, *Hemiculter labeo*, *H. leucisculus*	USSR – Asian part	Dykova and Lom (1983)
****Eimeria chenchingensis*** Chen, 1984	Spleen.	*Carassius auratus*	Not documented.	Duszynski et al. (2003c)
Eimeria ciliatae Molnar and Rhode, 1988	Intestinal mucosa and pyloric caeca. OCs round 14.0 (13.4-14.2) diameter, with 1-4 polar	*Sillago ciliata*	Arrawarra Research Station near Coifs Harbour, northern New South Wales (Australia)	Molnar and Rohde (1988)

	granules of 1.7-2.0 diameter. SPCs oval 11.2 (10.9-11.7) × 7.3 (6.7-7.6). SR round, finely granular 2.8 (2.5-3.0). SPZs vermiform 9.2 (9.1-9.3) × 2.6 (2.5-2.8).			
Eimeria citriformis Dogiel, 1948	Pyloric caeca. SB present.	*Tilesina gibbosa*	Sea of Japan - Peter the Great Bay and Lake Biwa	Dykova and Lom (1983)
Eimeria clini Fantham, 1932	Intestinal epithelium.	*Clinus superciliosus*	South Africa	Dykova and Lom (1983)
Eimeria cobitis Stankovitch, 1923	Liver. No SB.	*Cobitis taenia*	River Danube (Yugoslavia)	Dykova and Lom (1983)
Eimeria cotti Gauthier, 1921	Epithelium, in caecal opening. SB present.	*Cottus cognatus, Cottus gobio*	France	Dykova and Lom (1983), Steinhagen et al. (1994)
****Eimeria coreia*** Su and Chen, 1991	Intestine.	*Coreius heterodon*	Not documented.	Duszynski et al. (2003c)
Eimeria credintsi Moshu, 1992	Mucous membrane and intestine's mucus. OCs spherical 13.0 (12.00-14.0) diameter. OR 1-3 amorphous polar granules of 1.0-1.5. SPCs elongate oval, with tapered end, 10.0 (8.5-11.0) × 5.2 (5.0-5.5). Cap-like SB. SR granular, ellipsoidal, 4.0 × 2.5 in younger OCs; but spherical, compact and about 1.5-2.0 in more mature OCs. SPZs vermiform, with one reflexed	*Proterorhinus marmoratus*	River Danube, near Budapest (Hungary)	Molnár (2004)

	end, 13.0 (12.5-13.5) × 3.3 (3.0-3.5).			
Eimeria culteri Lee and Chen, 1964	Intestine. No SB.	*Culter erythropterus*	Hubei province (China)	Dykova and Lom (1983)
Eimeria dakarensis Faye, 1988	Digestive tract and testes.	*Cephalopholis taeniops, Epinephelus alexandrinus*	Coast of Senegal	Diouf and Toguebaye (1994b)
Eimeria daviesae Molnar, 2000	Mucus and anterior intestinal epithelium. OCs spherical 13.4 (13.0-14.0). Amorphous small polar granule of 2 diameter. SPCs short ellipsoidal 8 (7.5-8.2) × 4.9 (4.8-5.2), with a cap-like SB. SPZs vermiform 9.6 (9.5-10) × 2 (1.8-2.3).	*Gobius kessleri, Gobius fluviatilis*, *G. melanostomus*	River Danube (Hungary)	Molnar (2000), Molnar (2006)
Eimeira dicentrarchi Daoudi and Marques, 1987	Anterior region of the intestine, swim bladder and pyloric caeca. OCs round or irregularly shaped 11.3 (10.0-12.2) diameter. A single polar granule of 1.5 (1.2-1.6) diameter. SPCs ellipsoidal, lemon-shaped 8.3 (8.1-8.6) × 4.9 (4.4-5.6), which appeared oval in transverse section. SPZs banana-shaped 5.9 (4.8-6.9) × 1.5 (1.4-1.7). SR 4 or 5 granules dispersed.	*Dicentratchus labrax*	Adriatic Sea (Croatia) Languedoc (France) Mediterranean countries	Daoudi and Marques (1987)
Eimeria dingleyi Davies, 1978	Intestine. OCs spherical 16.1-19.2 diameter, to sub-spherical 13.9-14.2 × 18.8-20.0. 3-5 SPCS per OC; SPCs spherical	*Blennius pholis*, *Cottus bubalis*	Atlantic Ocean, Welsh Coast	Davies (1978), Dykova and Lom (1983)

	to broadly ellipsoid, 5.8-6.1 × 9.4-9.9. No SB. SPZs 2.6-3.1 × 2 8.6-9.0.			
Eimeria dogieli (Dogiel, 1948) Pellérdy, 1963 **Syn. *E. sphaerica*** Dogiel, 1948, *nomem preocc.*	Kidney. No SB.	*Opisthocentrus ocellatus*	Sea of Japan - Peter the Great Bay, Putyatin Island	Dykova and Lom (1981), Lom & Dykova (1983)
Eimeria duszynskii Conder, Oberndorfer and Heckmann, 1980	Intestinal epithelium and feces. OCs irregular in shape, 12.2 (11.6-12.9) diameter. SPCs ovoid, 9.1 × (8.4-10.0) 6.0 (5.2-6.3), with one side slightly flattened. SR compact and coarsely granular, occasionally dispersed. No SB. SPZs 2.1 wide, each with a large, oblong, refractile body near one end.	*Cottus bairdi*	River Provo, Utah (USA)	Dykova and Lom (1983), Upton et al. (1984)
Eimeria dykovae Molnar and Rhode, 1988	Intestinal mucosa and pyloric caeca. OCs round 7.8 (7.2-8.4) diameter. 2 polar granules of 0.7 (0.6-0.8) diameter. SPCs 5.6 (5.1-5.9) × 3.3 (3.2-3.5), with SB. SR round finely granular 1.1 (0.8-1.5). SPZs vermiform with one end reflexed 4.4 (4.3-4.5) × 0.8 (0.7-0.9).	*Cheilodactylus fuscus*	Coifs Harbour, northern New South Wales (Australia)	Molnar and Rohde (1988)
****Eimeria erythroculteri*** Chen, 1984	Kidney.	*Culter erythropterus*	Not documented.	Duszynski et al. (2003c)

Eimeria esoci Shulman and Zaika, 1962 **Syn. *E. patersoni*** Lom, Desser and Dykova, 1989	Intestine, urinary bladder, renal tubule cells, spleen and liver parenchyma. OCs subspherical 11.9 × 10.6, slightly ellipsoidal 11.9 × 9.9 or elongate ellipsoidal 15.8 × 8.6. SPCs ellipsoidal, 10.4 (9.9-11.2) × 3.5 (2.6-4.0), with one end sometimes more broadly rounded than the other and equipped with a lid-like SB. SR consists of 1-3 large granules. Short SPZs elongate, pyriform or irregularly ellipsoidal, 3.6 × 2.0.	*Esox lucius*, *Lepomis gibbosus*	USSR - Asian part Lake Sasajewun, Ontario (Canada)	Lom et al. (1989), Dykova and Lom (1983)
Eimeria etheostomae Molnar and Hanek, 1974	Anterior intestinal epithelium and feces. OCs spherical 9.4 (9.1-10.4) diameter. SPCs coffee-bean-shaped 8.5 (7.8 -9.1) × 5.0 (4.5-5.4) × 4.7 (4.2-5.0). No SB. SR finely granulated, round 3.6 (3.1-3.9) in diameter. SPZs banana-shaped 8.4 (7.8-9.0) × 1.6 (1.4-1.8), each with a round refractile globule.	*Etheostoma exile*, *E. nigrum*	Bronte Creek near Milton and Laurel Creek near Waterloo (all in Ontario, Canada)	Molnar and Fernando (1974), Dykova and Lom (1983)
Eimeria ethmalosae Diouf and Toguebaye, 1994	Digestive tract and testes.	*Ethmalosa fimbriata*	Coast of Senegal	Diouf and Toguebaye (1994b)
Eimeria etrumei Dogiel, 1940	Testes.	*Etrumeus micropus*	Sea of Japan - Peter the Great Bay	Dykova and Lom (1983)
Eimeria evaginata Dogiel, 1948	Pyloric caeca.	*Myxocephallus steleri, Sebastes taczanowski*	Sea of Japan - Peter the Great Bay	Dykova and Lom (1983)

Eimeria fernandoae Molnar and Hanek, 1974	Anterior intestinal epithelium. OCs ellipsoid 8.3 (7.8-9.0) × 6.6 (6.5-7.0). SPCs elongated, ellipsoid 7.2 (6.8-7.5) × 3.0 (2.6-3.4). No SB. SR round finely granulated 2.6 (2.3-3.2) in diameter. SPZs banana-shaped 5.8 (5.2-6.5) × 1.2 (1.0-1.3), each with a round refractile globule.	*Catastomus commersoni, Hypentelium nigricans*	Bronte Creek near Milton, River Conestogo near Conestogo, Grand River near Waterloo (all in Ontario, Canada)	Molnar and Hanek (1974), Dykova and Lom (1983)
Eimeria fluviatili Belova and Krylov, 2001	Feces. OCs 20.0-22.5. OR present. SPCs 7.5 × 12.5. SB present. SR absent.	*Perca fluviatilis*	River Neman (Russia)	Belova and Krylov (2001)
Eimeria gabonensis Diouf and Toguebaye, 1994	Digestive tract and testes.	*Chelidonichthys gabonensis*	Coast of Senegal	Diouf and Toguebaye (1994b)
Eimeria gadi Fiebiger, 1913	Swim bladder. OCs spherical 30.0-35.0 diameter. SPCs both in groups of 4 (OC) and singly, as free SPCs, measuring 15.0 × 10.0. Thick-walled SPCs, containing 2 SPZs each.	*Melanogrammus aeglefinus*	Halifax and Lunenburg, Nova Scotia (Canada)	Odense and Logan (1976)
Eimeria gasterostei (Thelohan, 1890) Donein, 1909 **Syn. *Coccidium gasterostei*** Thelohan, 1890	Liver. OCs spherical 16.0-18.0 diameter. SPCs elongate, narrowing at poles, 10.0-14.3 x 4.0-6.5. No SB. SR large and coarsely granular. SPZs botuliform, each with a large refractile body.	*Gasterosteus aculeatus*	Vancouver, British Columbia Kamchatka, river Paratunka (France)	Dykova and Lom (1981), Dykova and Lom (1983), Upton et al. (1984), Jastrzebski and Komorowski (1990), Rosenthal et al. (2016)
Eimeria gigantea (Labbé, 1986) Reichenow, 1921	Spiral valve.	*Lamna cornubia*	France	Dykova and Lom (1983)

Syn. *Pfeifferela gigantea* (Labbé, 1896) Labbé, 1899 **Syn. *Coccidium giganteum*** Labbé, 1896 **Syn. *Pfeifferia* sp.** Labbé, 1894				
Eimeria glenorensis Molnar and Fernando, 1974	Intestine, intestinal epithelium and feces. OCs spherical 10.5-12.0 diameter. 1 or 2 polar granules of 1.0-2.0. SPCs oval, one end sharply tapered 8.0-9.5 × 5.7-6.0. SB at the tapered end, and consists of a thickening of the SPC wall. SPZs vermiform with one end reflexed 7.5-8.0 × 2.0-2.2 (reflexed portion 2.5-2.7 long). SR rounded, compact, and refractile, of 2.0-2.6 diameter.	*Morone americana*	Bay of Quinte, Ontario (Canada)	Molnar and Fernando (1974), Dykova and Lom (1983)
Eimeria glossogobii Mukherjee and Haldar, 1980	Intestine. SB present.	*Glossogobius giuris*	West Benghal (India)	Dykova and Lom (1983)
Eimeria gobii Fantham, 1932	Intestinal epithelium.	*Gobius nudiceps*	South Africa	Dykova and Lom (1983)
Eimeria haichengensis Chen, 1962	Intestine, No SB.	*Cyprinus carpio*	Hubei province (China)	Dykova and Lom (1983)
Eimeria haneki Molnar and Fernando, 1974	Intestinal epithelium and feces. OCs spherical 7.1-7.8 diameter. 1 or 2 refractile polar granules of 1.0-1.5. No SB. SPCs shortly ellipsoid 5.6-6.5 × 3.9-4.5. SPZs vermiform with one end reflexed. Sporozoite without reflexed portion 5.6-6.0	*Culaea inconstans*	Creek near Bloomfield, Ontario (Canada)	Molnar and Fernando (1974), Dykova and Lom (1983)

	× 1.3-2.0. SR round, compact, non-granulated, refractile, 1.3-1.5 in diameter.			
Eimeria harpodoni Setna and Bana, 1935	Intestine. SB present.	*Harpadon nehereus*	Indian Ocean, Bombay	Dykova and Lom (1983)
****Eimeria hemibarba*** Su and Chen, 1987	Intestine.	*Hemibarbus maculatus*	Not documented.	Duszynski et al. (2003c)
Eimeria hemiculterii Chen and Hsieh, 1964	Intestine. No SB.	*Hemiculter leuscisculus*	Hubei province (China)	Dykova and Lom (1983)
Eimeria hexagona Lom and Dyková, 1981	Pyloric caeca and middle part of intestine. OCs has a membranelike wall stretched closely over the four SPCs, so the shape is not spherical; an average dimension is about 12. SPCs mostly ovoid (ellipsoidal in pyloric caeca), 6 (5.8-6.4) × 7 (6.8-7.2). SB encircled by a ringlike thickening of the wall. Roughly granular SPC residuum, of 2-3.3 x 1.5 lain in size. SPZs sausage-like 8.0 × 1.7.	*Onos tricirratus*	Banyuls-sur-Mer, Mediterranean Sea (near France)	Lom and Dyková (1981), Dykova and Lom (1983)
Eimeria hoffmani Molnar and Hanek, 1974	Anterior intestinal epithelium and feces. OCs ellipsoidal 11.5 (11.0-12.2) × 9.2 (9.1-9.6). 1 polar granule of 0.8 (0.7-0.9). SPCs elongatedly ellipsoid 10.0 (9.6-10.4) × 3.6 (3.4-3.9). No SB. In young OCs, SR elongatedly	*Umbra limi*	Bronte Creek near Milton, Ontario (Canada)	Molnar and Fernando (1974), Dykova and Lom (1983)

	ellipsoid, finely granulated, of 6.4 (6.2-6.6) × 2.0 (1.8-2.2). SPZs vermiform with one end reflexed. SPZs without reflexed portion 8.6 (8.4-8.7) × 1.4 (1.3-1.5).			
Eimeria huanggangensis Su and Chen, 1987	Kidney.	*Misgurnus anguillicaudatus*	Not documented.	Duszynski et al. (2003c)
Eimeria huizhouensis Su and Chen, 1991	Not documented.	*Clarias fuscus = Clarias pulicaris = Macropteronotus fuscus*	Hong Kong (China)	Duszynski et al. (2003a)
Eimeria hybognathi Molnar and Fernando, 1974	Intestinal epithelium and feces. OCs spherical 14.0-14.5 diameter. SPCs ellipsoidal 9.5-10.0 × 5.7-6.0. No SB. SR large finely granulated, usually compact, and oval, 5.8-8.0 × 4.5-5.2 × 2.6-3.0. SPZs banana-shaped with one end slightly reflected 9.0-9.2 × 2.0-2.6, each with a refractile globule.	*Hybognathus hankinsoni*	Laurel Creek, Waterloo, Ontario (Canada)	Molnar and Fernando (1974), Dykova and Lom (1983)
Eimeria hypophthalmichthys Akhmerov, 1959	Kidney. No SB.	*Hypophthalmichthys molitrix*	USSR – Asian part	Dykova and Lom (1983)
Eimeria ictaluri Molnar and Fernando, 1974	Intestinal epithelium and feces. OCs spherical 9.0-10.5 diameter. SPCs ellipsoid, rarely coffee bean-shaped, 7.8-8.4 × 3.6-4.2. No SB. SR oval, compact, and coarsely granulated 5.0-5.3 × 3.0-3.3 × 2.0-2.2. SPZs vermiform with one end reflexed, each with a	*Ictalurus nebulosus*	Laurel Creek, Waterloo, Ontario (Canada)	Molnar and Fernando (1974), Dykova and Lom (1983)

	refractile globule. SPZs without reflexed portion 7.1-7.8 × 1.5-1.8.			
Eimeria insignis Lom and Dyková, 1982	Pyloric caeca. No SB.	*Scorpaena notata*	Mediterranean Sea, near Banylus-sur-mer (France)	Dykova and Lom (1983)
E. intestinalis (Chen, 1956) Schulman and Zaika, 1962 **Syn. *Eimeria cheni*** Chen, 1956, *nomen preocc.*	Anterior part of the intestine. No SB.	*Aristichthys nobilis, Hypophthalmichthys molitrix*, *Mylopharyngodon piceus*	USSR China Hungary	Dykova and Lom (1983)
Eimeria iroquoina Molnar and Fernando, 1974	Intestinal epithelium and feces. OCs spherical 8.6-11.0 diameter. SPCs ellipsoid 6.8-10.3 × 3.0-5.0. No SB. SR finely granulated, round from one side and ellipsoid from other 2.3-4.0 × 2.2-3.0/ ellipsoid/ round/ oval. SPZs vermiform with one end reflexed. SPZs without reflexed portion 4.5-7.7 × 1.3-1.7.	*Nocomis biguttatus, Notropis cornutus, N. heterolepis, N. rubellus, Pimephales notatus, P. promelas*, *Rhinichthys atratulus, Semotilus atromaculatus*	Bronte Creek near Milton, River Conestogo near Conestogo, Grand River and Laurel Creek near Waterloo, River Sauge near Durham (all in Ontario, Canada)	Molnar and Fernando (1974), Dykova and Lom (1983)
Eimeria ivanae Lom and Dykova, 1981	Testes, digestive tract and pyloric caeca. OCs irregularly shaped 10.5 (10-11.5) average diameter. SPCs oval in side view and truncated at one end 4.4 (4-4.6) × 5.8 (5-6.5), with a SB encircled in a circular thickening of the wall. SR is roughly granular and averages 1.6 diameter. SPZs vermiform 6.8 × 8.0, either overlap or lie side by side with flexed ends.	*Serranus cabrilla, S. scriba*	Coast of Senegal Banyuls-sur-Mer, Mediterranean Sea coast (near France)	Lom and Dykova (1981)

Eimeria jadvigae Grabda, 1983	Swim bladder. OR present. SPCs comma-shped, compact, their anterior parts being clearly thicker.	*Coryphaenoides holotrachys*	Falklands (South Atlantic)	Grabda (1983)
Eimeria kassai Molnar, 1978	Intestinal epithelium. No SB.	*Umbra krameri*	Hungary	Molnar (1978), Dykova and Lom (1983)
Eimeria kayarensis Diouf and Toguebaye, 1994	Testes and digestive tract.	*Raja miraletus*	Coast of Senegal	Diouf and Toguebaye (1994b)
Eimeria kotorensis Daoudi, Radujkovic, Marques, and Bouix, 1987	Intestine.	*Spicara maena*, *S. smaris*	Bay of Kotor (Yugoslavia)	Daoudi et al. (1987)
Eimeria kwangtungensis Chen, 1960	Intestine. No SB.	*Channa argus*, *C. maculata*	Hubei province (China)	Dykova and Lom (1983)
Eimeria lairdi Lom and Dyková, 1981	Pyloric caeca. OCs spherical 12.0 (10.0-15.0) diameter. SPCs almost spherical 6.0 (5.0-8.0) diameter, with a SB encircled in a wide collar-like thickening of the wall. Central, roughly granular SR of 3.2. SPZs vermiform 1.5 × 8.0, with the large end of one beside the small end of the other.	*Myoxocephalus scorpius*	Grand Banks, off the coast of Newfoundland	Lom and Dyková (1981)
Eimeria liaoningensis Chen, 1984	Intestine.	*Pseudogobio rivularis*, *Carassius auratus* and possibly *Hypseleotris* sp. and *H. swinhonis*	Not documented.	Duszynski et al. (2003c)

Eimeria lydiae Lukes and Kepr, 1992	Pyloric caeca and intestine. OCs spherical 11.5 (10.6-12.4) diameter. 1 irregular polar granule 1.9 (1.5-2.4) x 1.4 (1.2-1.6). SPCs ellipsoid 8.3 (7.6-9.1) × 4.9 (4.7-5.2), with a small SB on a slightly tapered end. SR composed of 3-5 granules, each 0.5-1.0 diameter. SPZs sausage-like 7.1 (6.7-7.5) × 1.6 (1.4-1.8), each with a single refractile body.	*Salmo trutta m. fario*	Blanice and Volyilka rivers, South Bohemia (Czechoslovakia)	Lukes and Kepr (1992)
****Eimeria macropoda*** Su and Chen, 1991	Intestine.	*Macropodus chinensis*		Duszynski et al. (2003b)
Eimeria maggieae Lom and Dyková, 1981	Middle part of intestine. OCs wall could hardly be seen; diameter of the 4 SPCs bound together averaged 12. SPCs ellipsoidal-to-ovoid 5.3 (4.8-5.7) × 8 (7.5 8.3), with a SB encircled in a knoblike thickening at one wider end. SPC residuum, 2.8 × 1.4, missing in some SPCs. SPZs lie side by side and are twisted in a way that prevents their exact measurement. **Obs.:** In fresh spores, on rare occasions 2 flexed SPZs can be seen lying side by side, with a SR (2.8 × 1.4) between them. In most of the fresh mature SPCs, however, the two sausage-shaped (3 × 1.5) or club-shaped (5-6 × 1.4) SPZs	*Pagellus acarne, P. erythrinus*	Banyuls-sur-Mer, Mediterranean Sea Coast (near France)	Lom and Dykova (1981), Dykova and Lom (1983)

	are accompanied by two spherical structures.			
Eimeria marmorata Molnar, 2004	Mucous membrane and intestine's mucus. OCs spherical 10.2 (10.0-10.5) diameter. SPCs short ellipsoidal, 6.8 (6.5-7) × 5.1 (5.0-5.5). No SB or suture found on SPCs, but one pole bears small thickening. Under coverslip pressure the SPCs left the OCs, and once free their ellipsoidal shape changed to oval and some opened at their tapered end by being divided into 2 equal halves along the longitudinal axis. SPZs vermiform 9.9 (9.5-10.0) × 1.9 (1.5-2.0).	*Proterorhinus marmoratus*	River Danube, near Budapest (Hungary)	Molnár (2004)
Eimeria matskasii Molnar, 1978	Intestinal epithelium. SB present.	*Umbra krameri*	Hungary	Molnar (1978), Dykova and Lom (1983)
Eimeria merlangi Zaika, 1966	Not documented.	*Merlangius merlangus*	Black sea - Sinop, Turkey and Balaklava Bay in Sevastopol (Russia)	Dykova and Lom (1983)
Eimeria meszarosi Molnar, 1978	Intestinal epithelium. No SB.	*Umbra krameri*	Hungary	Molnar (1978), Dykova and Lom (1983)
Eimeria micropteri Molnar and Hanek, 1974	Anterior intestinal epithelium. OCs spherical 12.0 (11.7-12.5) diameter. SPCs ellipsoid 11.4 (11.0-11.7) × 6.2 (6.0-6.5). No SB. SR finely granulated and dispersed. SPZs vermiform with one end reflexed, each	*Micropterus dolomieui*, *M. salmoides*	River Conestogo near Conestogo and Laurel Creek near Waterloo, Ontario (Canada)	Molnar (1974), Dykova and Lom (1983)

	with a round refractile body. SPZs (without reflexed portion) 9.1 (8.9-9.3) × 2.1 (2.0-2.2).			
Eimeria misgurni Stankovitch, 1924	Intestine. No SB.	*Cobitis taenia*, *Misgurnus fossilis*	River Danube (Yugoslavia)	Molnar (1978), Dykova and Lom (1983)
Eimeria molnari Jastrzebski, 1982	Intestine.	*Gobio gobio*	Poland – fish farms	Jastrzębski (1984)
Eimeria moronei Molnar and Fernando, 1974	Intestine, intestinal epithelium and feces. OCs spherical 7.2-8.0 diameter. Polar granule, of 1.0-2.0. SPCs oval 5.7-6.0 × 3.9-4.0, with a distinct knob-like SB on the tapered end. SR rounded, compact, and refractile, 1.5-2.0 diameter. SPZs vermiform crescent-shaped 5.0-5.4 × 1.5-2.0.	*Morone americana*	Bay of Quinte, Ontario (Canada)	Molnar (1974), Dykova and Lom (1983)
Eimeria muraiae Molnar, 1978	Kidney's tubules. No SB.	*Misgurnus fossilis*	Hungary	Molnar (1978), Dykova and Lom (1983)
Eimeria mylopharyngodoni Chen, 1956	Anterior part of the intestine, liver and kidney. No SB.	*Mylopharyngodon piceus*	China	Dykova and Lom (1983)
Eimeria myoxocephali Fitzgerald, 1975	Anterior intestinal mucosa and feces. OCs spherical 37.2 (34.0-40.0) diameter. SPCs composed of a thin membrane stretched tightly around the SPZs. SR present, small, and spherical. SPZs elongated, 16.7 × 3.7, each with a single refractile globule.	*Myoxocephalus polyacanthocephalus*	Pacific Ocean, coast of Washington (USA)	Dykova and Lom (1983)

Eimeria nemethi Molnar, 1978	Spleen, liver, kidney and intestine. SPCs bear a cap-like flat plate at one end of their SPCs, through which SPZS are released. SB present.	*Alburnus alburnus*	Lake Balaton and Lake Valencei (Hungary)	Molnar (1978), Dykova and Lom (1983)
Eimeria nesowai Lom and Dyková, 1995	Pyloric caeca and intestine. Subspherical OCs average 12.9 diameter, the average size of SPCs being 7.0 × 4.2.	*Gerres ovatus*	Australia	Lom and Dykova (1995)
****Eimeria newchongensis*** Chen, 1984	Intestine and liver.	*Carassius auratus, Culter erythropterus*	Not documented.	Duszynski et al. (2003c)
Eimeria nicollei Yakimoff and Gousseff, 1935	Intestine.	*Carassius Carassius*	USSR – European part	Dykova and Lom (1983)
Eimeria nishin Fujita, 1934	Testes. No SB.	*Clupea harengus harengus, C. harengus pallasi*	Japanese coast of the Pacific Ocean North-American Pacific coast	Dykova and Lom (1983)
Eimeria notopteri Chakravarty and Kar, 1944	Intestine. No SB.	*Notopterus notopterus*	Indian Ocean (India)	Dykova and Lom (1983)
Eimeria nucleocola Lom and Dyková, 1981	Pyloric caeca. OCs spherical 13.0 (12.0-14.0) diameter. SPCs ellipsoidal, 5.3 (4.9-6) × 6.8 (6-7.3). SB is hardly visible; under coverslip pressure or after fixation, the SB knob is clearly visible, as if one end of the SPC evaginated a knoblike protrusion. SPZs sausage-like lie side by side.	*Myxocephalus scorpius*	Grand Banks, off the coast of Newfoundland (North America)	Lom and Dykova (1981), Dykova and Lom (1983)

Eimeria ochetobiusi Lee and Chen, 1964	Intestine. No SB.	*Ochetobius elongatus*	Hubei province (China)	Dykova and Lom (1983)
Eimeria ojibwana Molnar and Fernando, 1974	Intestinal epithelium and feces. OCs spherical 10.4-11.0 diameter. SPCs coffee bean-shaped 9.0-9.2 × 5.0-5.8. No SB. SR irregularly granulated and dispersed. SPZs vermiform with one end reflexed, each with a round refractile globule. SPZs without reflexed portion 8.4-8.7 × 2.0-2.5.	*Cottus bairdi*	Creek near Bloomfield, Ontario (Canada)	Molnar and Fernando (1974), Dykova and Lom (1983)
Eimeria ophiocephalae Chen and Hsieh, 1960	Intestine and pyloric caeca.	*Ophiocephalus argus, O. maculatus*	Hubei and Kwantung provinces (China)	Dykova and Lom (1983)
****Eimeria orientalis*** Chen, 1984	Kidney.	*Misgurnus anguillicaudatus*	Not documented.	Duszynski et al. (2003c)
Eimeria osmeri Molnar and Fernando, 1974	Intestinal epithelium and feces. OCs spherical 10.4-1.0 diameter. 1 or 2 polar granules of 1.5-1.7. SPCs oval, end sharply tapered 7.1-7.8 × 4.3-4.7. SB at the tapered end consists of a thickening of the SPC wall. SR rounded, compact, and refractile, 1.3-1.7 diameter. SPZs vermiform with one reflexed end. SPZs without reflexes portion 6.0-7.1 × 1.3-1.7.	*Osmerus mordax*	Bay of Quinte, Ontario (Canada)	Molnar and Fernando (1974), Dykova and Lom (1983)
Eimeria ottojiroveci Dykova and Lom, 1981 **Syn. *Eimeria jiroveci***	Intestinal epithelium and spiral valve's epithelium. SB present.	*Raja miraletus*	Adriatic Sea, coast of Montenegro	Lom and Dykova (1981), Dykova and Lom (1983)

Dykova and Lom, 1983, *nomem preocc.*			Mediterranean Sea coast, near France	
Eimeria parasiluri Chen and Li, 1973	Gall bladder. No SB.	*Silurus asotus*	East Asia (Japan) Hubei province (China)	Dykova and Lom (1983)
Eimeria pastuszkoi Jastrzebski, 1982	Intestine.	*Nemacheilus barbatulus*	Poland – fish farms	Jastrzębski (1984)
Eimeria percae (Dujarrie de la Riviere, 1914) Reichenow, 1921 **Syn. *Coccidium percae*** Dujarrie de la Riviere, 1914	Intestinal epithelium. No SB.	*Dicentrarchus labrax, Perca fluviatilis*	Small creeks in Hungary France USSR – Lake Baikal and Lake Ladoga Poland – fish farms	Dykova and Lom (1983), Jastrzębski (1984), Molnar et al. (2012), Rosenthal et al. (2016)
Eimeria perciformis Diouf and Toguebaye, 1994	Testes and digestive tract.	*Epinephelus goreensis*, *Pomadasys incises*	Coast of Senegal	Diouf and Toguebaye (1994b)
Eimeria philypnodoni Molnar and Rhode, 1988	Intestinal mucosa. OCs spherical 8.9 (8.4-9.2) diameter. 1 amorphous polar granule of 1.2. SPCs oval, tapering toward one end and blunt at the other, 6.4 (5.8-6.7) × 4.0 (3.8-4.2), with a cap-like structure is found at the tapered end. SR granular, in older OCs it is scattered forming small pieces. SPZs vermiform with one end reflexed. SPZs without the reflexed portion 5.0 (4.9-5.2) × 1.5 (1.4-1.7).	*Philypnodon grandiceps*	River Clarence near Grafton, northern New South Wales (Australia)	Molnár and Rhode (1988),
Eimeria pigra Léger and Bory, 1932	Intestinal epithelium. No SB.	*Scardinius erythrophthalmus*	Lyon (France)	Dykova and Lom (1983)
Eimeria piraudi	Intestine.	*Cottus gobio*	Dauphiné (France)	Dykova and Lom (1983)

Gauthier, 1921	No SB.			
Eimeria pleurostici Molnar and Rhode, 1988	Intestinal mucosa. OCs spherical 9.3 (9.1-9.6) diameter. 1 polar granule of 0.7 (0.6-0.8). SPCs short ellipsoidal or oval 6.7 (6.3-7.0) × 4.4 (4.2-4.6), with characteristic plug-like SB on more tapered end. SR round or ellipsoidal, finely granular, 1.5 × 2.5 or 2.5 × 2.5. SPZs vermiform with one end reflexed. SPZs without reflexed portion 3.8 (3.7-3.9) × 1.6 (1.5-1.7).	*Sphaeroides pleurosticus*	Coffs Harbour, northern New South Wales (Australia)	Molnar and Rhode (1988)
Eimeria pneumatophori Dogiel, 1948	Liver. No SB.	*Pneumatophorus japonicus*	Sea of Japan – Peter the Great Bay	Dykova and Lom (1983)
****Eimeria pseudorasbari*** Chen, 1984	Kidney.	*Pseudorasboro parva*	Not documented.	Duszynski et al. (2003c)
Eimeria pungitii Molnar and Hanek, 1974	Anterior intestinal epithelium and feces. OCs ellipsoid 12.5 (12.1-13.0) × 9.8 (8.6-10.4). SPCs elongatedly ellipsoid 10.0 (9.1-10.4) × 3.6 (3.4-3.9). No SB. SR granulated, dispersed, and completely fills the SPC. SPZs banana-shaped 8.7 (8.4-9.1) × 2.3 (2.1-2.4), each with a round refractile globule.	*Pungitius pungitius*	River Matamek, Quebec (Canada) Poland – fish farms	Molnar and Hanek (1974), Dykova and Lom (1983), Jastrzębski (1984)
Eimeira quentini Boulard, 1977	Peritoneal cells.	*Aetobatis narinari*	Indian Ocean (Malaysia)	Boulard (1977), Dykova and Lom (1983)

Eimeria radae Moshu, 1992	Kidney.	*Cobitis taenia*	Not documented.	Duszynski et al. (2003c)
Eimeria raibauti Daoudi, Radujkovic, Marques and Bouxi, 1989	Pyloric caeca's epithelium. OCs spherical 28.8-33.0 or ellipsoidal 37.2-32.2 × 30.5-27.1. SPCs ovoid or ellipsoidal 16.7-17.7 × 8.5-10.3. SB and Stieda sub-body (4.0 × 3.0) present. When present, SR granular. SPZs vermiform 15.0 × 3.5, curved at their ends.	*Trisopterus esmarki, T. minutus*	Mediterranean Sea Northern North Sea (Norway) Banyuls-sur-Mer et Sète (France) Adriatic Sea (Yougoslavia)	Daoudi et al. (1989), Costa et al. (1991)
Eimeria rohdei Kandilov, 1975 **Syn. *Eimeria sericei*** Levine, 1988	Intestine and pyloric caeca. OCs spherical 7.5 average diameter. SPCs 5.1 × 3.0.	*Monacanthus chinensis, Rhodeus sericeus*	Australia USSR – Azerbhaidzhan River Kura (mountains of Asia)	Dykova and Lom (1983), Lom and Dykova (1995)
Eimeria roussillona Lom and Dyková, 1981	Middle part of the intestine. OCs irregularly shaped 11.0 (10.0-12.0) diameter. SPCs are elongated ellipsoids,4.1 (3.5-4.5) × 7.8 (7.5-8.5), with a flat thickening of the SB at one end. SR consists of a few refractile granules. SPZs sausage-like 10.6 × 1.2, with one flexed end.	*Labrus turdus*	Banyuls-sur-Mer, Mediterranean Sea coast (near France)	Lom and Dyková (1981)
Eimeria rouxi (Elmassian, 1909) Reichenow, 1921 **Syn. *Coccidium rouxi*** Elmassian, 1909 **Syn. *E. rouxi*** (Elmassian, 1909) Stankovitch, 1921	Intestine. No SB.	*Tinca tinca*	France	Dykova and Lom (1983)

Eimeria rutili Dogel and Bychovski, 1938 **Syn. *E. branchiphila*** Dykova, Lom and Grupcheva, 1983, * **according to Duszynski, Couch and Upton, 2003**	Kidney and liver. OCs 8.0-13.0 diameter. SPCs bear a cap-like flat plate at one end, through which SPZs are released. SB present.	*Abramis brama*, *Chondrostoma polylepis polylepis*, *Leuciscus cephalus cabeda*, *Rutilus rutilus caspius*	River Danube USSR - Asian part River Esla (north-west Spain) Lake Balaton (Hungary)	Dykova and Lom (1983), Alvarez Pellitero et al. (1986), Molnár and Székely (1995), Molnar et al. (2012)
Eimeria ryptici Diouf and Toguebaye, 1994	Testes and digestive tract.	*Rypticus subbifrenatus*	Coast of Senegal	Diouf and Toguebaye (1994)
Eimeria salvelini Molnar and Hanek, 1974	Anterior intestinal epithelium. OCs spherical 12.0 (11.7-12.5) diameter. SPCs oval 9.2 (9.0-9.4) × 5.1 (5.0-5.3), with cap-like SB 1.1 (0.9-1.3) long at the tapered end. SR round, compact, 1.8 (1.5-2.1) diameter. SPZs vermiform 6.8 (6.5-7.1) × 1.5 (1.3-1.7), which are characteristically interlaced.	*Salvelinus fontinalis*	River Matamek (Canada)	Molnar and Hanek (1974), Dykova and Lom (1983)
Eimeria sardinae (Thélohan, 1890) Reichenow, 1921 **Syn. *E. oxiphila*** Dobel, 1919 **Syn. *E. oxyspora*** Dobel, 1919 **Syn. *E. anijdersi*** Dobell, 1920 **Syn. *E. patagonensis*** Timi and Sardella, 1998 **Syn. *E. snijdersi*** Dobell, 1920 **Syn. *Eimeria* sp.**	Testes, ovaries and digestive tract. OCs spherical 10.5-60.0 diameter. OR in a form of a few scattered granules or big OR 12.7 (11.9-13.0) × 15.5 (15.1-16.5. SPCs cigar-shaped 25.0-35.0 × 7.0-8.2 or fusiform 7.7 × 29.5 × 3.5-7.8, with a plaque-like thickening situated the opposite of the SR in longitudinal sections. SR consists of amylopectin granules, refractile bodies, and	*Alosa fallax, Clupea harengus*, *C. harengus membras, C. pilchardus, Engraulis anchoita*, *E. encrasicolus*, *Merlangius merlangus*, *Sardinella aurita*, *S. maderensis, Sardinops sagax*, *Sprattus sprattus*	Portuguese coast Norwegian Sea Northern Norway - wintering areas in fjords South African coast Adriatic Sea (Montenegro) Senegal coast Tunisian coast Nova Scotia (Canada) Mediterranean Sea Western North Atlantic Ocean, North Sea Estonian Archipelago and	Pinto (1956), Sindermann (1961) in Sindermann (1960), Kabata (1963), Dykova and Lom (1983), Morrison and Hawkins (1984), Dykova and Lom (1983), McGladdery (1987), Morrison (1991), Turovsky et al. (1993), Diouf and Toguebaye (1994a), Draoui et al. (1995), Timi and Sardella (1998), Reed et al. (2012), Ozer et al. (2015), Ssempa (2013)

of Morrison and Marryatt, 1990	other cytoplasmatic organelles, of 5.1 (4.1-6.2) diameter. SPZs with developing conoid apparatus and rhoptries laying at the anterior end, 10.3 (8.2-12.4) × 5.3 (4.1-6.2).		Gulf of Finland (Baltic Sea, Barents Sea) Black Sea, White Sea and Japan Sea Coast of Argentina and Uruguay	
Eimeria saroetobramae Allamuratov and Iskov, 1970 **Syn*. Eimeria capoetobramae*** Allamuratov, 1966, nomem nudum	Kidney.	*Capoetobrama kuschakewitschi*	USSR – Azerbaizhan River Surkhandari (Uzbekistan)	Dykova and Lom (1983)
Eimeria saurogobii Chen, 1964	Intestine. No SB.	*Ctenopharyngodon idella*	Hubei province (China)	Dykova and Lom (1983)
Eimeria schizothoraci Davronov, 1987	Intestine.	*Schizothorax intermedius*	Uzbekistan	Davronov (1987)
Eimeria schulmani Kulemina, 1969	Intestine. No SB.	*Leuciscus cephalus, L. idus*	USSR – European part Seliger Lake (Russia) Poland – fish farms	Dykova and Lom (1983), Jastrzębski (1984)
Eimeria scorpaenae Zaika, 1966	Intestine. SB present.	*Scorpaena porcus*	Black Sea – USSR Coast at Sevastopol (Ukraine)	Dykova and Lom (1983)
Eimeria scyllii Chen, 1956 **Syn. *Coccidium scyllii***, 1902, nomem nudum	Intestine. No SB. Micropyle present in OCs wall.	*Aristichthys nobilis*, *Hypophthalmichthys molitrix*	China USSR Hungary	Dykova and Lom (1983)
Eimeria sillaginis Molnar and Rhode, 1988	Intestine, intestinal mucosa and pyloric caeca's mucosa. OCs spherical 8.9 (8.4-9.2) diameter. 1-4 polar granules of 1. SPCs oval, with small	*Sillago ciliata*	Arrawarra Research Station near Coifs Harbour, northern New South Wales (Australia)	Molnar and Rohde (1988), Lom and Dykova (1995)

	thickenings on tapered end, 6.8 (5.9-7.6) × 4.3 (3.8-5.0). SR round, finely granular, of 1.8 (1.6-2.3). SPZs vermiform with one end reflexed. SPZs without reflexed portion 4.2 (4.1-4.4) × 1.8 (1.6-2.0).			
Eimeria siluri Davronov, 1987	OCs ellipsoidal. SPZs stubby similar to *Eimeria varicorhini* Davronov, 1987 and *Eimeria patersoni* Lom and Dykova, 1989.	*Silurus glanis*	Uzbekistan	Davronov (1987), Lom et al. (1989)
Eimeria smaris Daoudi, Radujkovic, Marques and Bouxi, 1989	Middle portion of the intestine.	*Spicara smaris*	Mediterranean Sea	Daoudi et al. (1989)
Eimeria soufiae Stankovitch, 1921 **Syn. *E. sontlae*** Stankovitch, 1921, lapsus	Middle portion of the intestine. No SB.	*Leuciscus souffia agassizi*	Dauphiné (France)	Dykova and Lom (1983)
Eimeria southwelli Halawani, 1930	Intestine, pancreas, peritoneal lining and liver. OCs polymorphic 15.0-63.0 × 10.0-15.0. SPCs pear-shaped 10.0-12.0 long, with a ridge-like structure along the length. Polar SB present. SPZs 5.0-10.0 × 2.0.	*Aetobatus narinari*, *Rhinoptera bonasus*	Atlantic coast	Dykova and Lom (1983), Stamper et al. (1998)
Eimeria spari Diouf and Toguebaye, 1996	Intestine. OCs spherical 10.6 ± 1.2 diameter. 3 polar granules present. SPCs pear-shaped 6.8 ± 0.7 × 3.9 ± 0.4, and their surface presents ridges in electron microscopy. SB split-	*Sparus aurata*, *S. caeruleostictus*	North Lake, Tunis (Tunisia) Coast of Senegal	Diouf and Toguebaye (1996)

	like at the tapered end of the SPC.			
Eimeria sparis Sitjà-Bobadilla, Palenzuela and Alvarez-Pellitero, 1996 **Syn. *E. spari*** Diouf and Toguebaye, 1996, *** according to Duszynski, Couch and Upton, 2003**	Intestine. OCs spherical 9.4-14.6 diameter. When present, OCs residuum consisted of 1 or 2 refractile bodies. SPCs ellipsoid or oval 6.0-9.7 × 4.0-6.5. A Stieda-like body as an enlargement of the SPC wall. When present, SR varying from a single body to a mass of granules, depending on the maturation stage. SPZs placed longitudinally, with one reflexed end.	*Sparus aurata*, *S. caeruleostictus*	Spain – maricultures	Sitjà-Bobadilla et al. (1996), Alvarez-Pellitero et al. (1997), Bahri (2012)
Eimeria strelkovi Schulman and Zaika, 1962	Kidney. No SB.	*Pseudorasbora parva*	USSR – Asian part	Dykova and Lom (1983)
Eimeria syacii Diouf and Toguebaye, 1994	Testes and digestive tract.	*Syacium micrurum*	Coast of Senegal.	Diouf and Toguebaye (1994b)
Eimeria symphodi Daoudi, Radujkovic, Marques and Bouxi, 1989	Posterior region of intestine.	*Symphodus rostratus*	Mediterranean Sea	Daoudi et al. (1989)
Eimeria syngnathi Yakimoff and Gousseff, 1936	Intestinal mucosa. No SB.	*Syngnathus nigrolineatus*	USSR – European part	Dykova and Lom (1983)
Eimeria syrdarinica Davronov, 1987	Intestine.	*Ctenopharyngodon idellus*	Uzbekistan	Davronov (1987)
Eimeria tedlai Molnar and Fernando, 1974	Intestinal epithelium and feces. OCs spherical 9.5-10.0 diameter. Refractile polar granule 1.0-1.5 diameter.	*Perca flavescens*, *P. fluviatilis*	Bay of Quinte, Ontario (Canada) Poland – fish farms	Molnar and Fernando (1974), Dykova and Lom (1983), Upton et al. (1984), Jastrzębski (1984)

	SPCs oval 8.4-8.7 × 4.5-4.7, with a cap-like SB at its tapered end, 1.5-2.0 long. SR rounded or ellipsoid, compact, and refractile, 1.5-2.0 × 1.5-2.6. SPZs vermiform with one reflexed end. SPZs without the reflexed portion 6.0-6.5 × 1.6-2.1.			
Eimeria triglae Daoudi, Radujkovic, Marques and Bouxi, 1989	Pyloric caeca.	*Trigla lucerna, T. lyra*	Mediterranean Sea	Daoudi et al. (1989)
Eimeria truttae (Léger and Hesse, 1919) Stankovitch, 1921 **Syn. *Goussia truttae*** Léger and Hesse, 1919	Pyloric caeca, anterior intestinal epithelium and feces. OCs spherical 12.8 (12.3-13.0) diameter. A single polar granule present, 0.9 (0.7-1.0) diameter. SPCs oval, 10.1 (9.3-1 1.0) × 6.0 (5.0-6.5), with a disc-like SB 2.7 (2.6-2.8) diameter at its tapered end. SR finely granulated, round, 2.8 (2.6-3.0) diameter. SPZs vermiform with one reflexed end. SPZs without reflexed portion 8.5 (7.8-9.0) × 1.6 (1.3-2.0).	*Oncorhynchus masou, Salmo trutta, Salvelinus fontialis*	River Matamek, Quebec (Canada) France	Molnar and Hanek (1974), Dykova and Lom (1983), Couso-Perez et al. (2019)
Eimeria vanasi Landsberg and Paperna, 1987	Intestine. Immature OCs: 12.0-19.0 diameter, sporoblast 4.0-6.0 × 12.0-14.0. Mature type I: OCs 16.2 (14.0-18.0) × 13.3 (12.0-15.0), SPCs 12.7 (11.0-15.0) × 5.2 (4.0-6.0); SPZs 11.8 (8.0-14.0) × 3.2 (2.0-4.0).	*Oreochromis aureus*, *O. mossambicus, O. niloticus*, *Pscudocrenilabris philander, Sarotherodon galilaeus Tilapia sparrmanii*	Israel South Africa	Landsberg and Paperna (1987), Paperna (1990), Kim and Paperna (1992)

	Mature type II: OCs 10.0 × 10.0; SPCs 7.5 × 4.5.			
Eimeria variabilis (Thélohan, 1893) Reichenow, 1921 **Syn. *Goussia variabilis*** (Thélohan, 1893) Labbé, 1896 **Syn. *Coccidium variabilis*** Thélohan, 1893	Intestine, pyloric caeca and rectum. OCs more commonly spherical 11.9-14.6 diameter, or subspherical 9.2-10.9 × 13.9-14.3. SPCs 8.5-9.2 × 5.0-5.5, with a prominent plug resembling a SB at one pole. SPZs elongated.	*Dicentratchus labrax*, *Blennis pholis*, *Cottus bubalis*, *Crenilabus melops*, *Taurutus bubalis*, *Gobius bicolor*, *G. paganellus,* and probably *Anguilla anguilla* and *Lepadsgaster gouanii*	Coast of Portugal North Atlantic Sea Saint George channel, Welsh coast French coast at Roscoff	Davies (1978), Davies (1990), Dykova and Lom (1983)
Eimeria varicorhini Davronov, 1987	Intestine.	*Capoeta capoeta*	Uzbekistan	Davronov (1987), Lom et al. (1989)
Eimeria anguillae Léger and Hollande, 1922 **Syn. *Epieimeria anguillae*** (Léger and Hollande, 1922) Dykova and Lom, 1983	Intestine.	*Anguilla anguilla*, *A. australis, A. dieffenbachi*, *A. rostrata*	Mediterranean Sea, Coast of Corsica New Zealand Vistula Lagoon, Baltic Sea (Russian part) Rivers Ulla and Tea. Galicia (northwest Spain) River Tiber, Rome (Italy) Lake Balaton (Hungary)	Dykova and Lom (1983), Lacey and Williams (1983), Orecchia et al. (1987), Benajiba et al. (1994), Molnár and Székely (1995), Aguilar et al. (2005), Rodjuk and Shelenkova (2006)
Eimeria zygaenae Mandal and Chakravarty, 1965	Intestine. OCs spherical 12.1-14.3 diameter. SPCs about 8.8 × 5.5.	*Euphyra blochii* (referred as *Sphyrna blochii*)	Indian Ocean	Dykova and Lom (1983)
Epieimeria isabellae Lom and Dyková, 1982	Middle portion of the intestine.	*Conger conger*	Mediterranean Sea coast near Banylus-sur-Mer (France) Adriatic Sea (Montenegro)	Lom and Dykova 1982, Dykova and Lom (1983), Daoudi (1987), Daoudi et al. 1986, 1989, Radujkovic and Raibaut (1990)
Epieimeria puytoraci	Anterior portion of the intestine.	*Symphodus tinca*	Mediterranean Sea	Daoudi et al. (1989)

Daoudi, Radujkovic, Marques and Bouix, 1989				
Goussia acerinae Pellérdy and Molnár, 1971	Intestine.	*Acerina cernua*	Rivers Danube and Balaton (Hungary) Poland – fish farms	Jastrzębski (1984), Molnár and Székely (1995)
Goussia acipenseris Molnar, 1986	Intestinal mucus membrane, intestinal epithelium and pyloric caeca. OCs short-ellipsoidal 9.6-10.7 × 7.5-9.7. Polar granule of 0.5-1.0. SPCs elongated ellipsoidal 6.6-8.8 × 3.0-4.3. SR 2.5 × 1.3. SPZs vermiform with one reflexed end, with a large refractile body. SPZs without the reflexed end 7.2-8.0 length × 1.1-1.6 thickness.	*Acipenser ruthenus*	River Danube (Hungary)	Molnar (1986)
Goussia aculeati Jastrzebski, 1984	Intestinal epithelium.	*Gasterosteus aculeatus*	Inland Fishery Institute, Zabieniec (Poland)	Jastrzebski (1989)
Goussia alburni (Stankovitch, 1920) Yakimoff, 1929 **Syn. *Eimeria alburni*** Stankovitch, 1920	Peri-intestinal adiposal tissue.	*Gobio gobio*, *Rutilus rutilus, Scardinius erythrophthalmus*	France Czechoslovakia	Dykova and Lom (1983)
Goussia alosii Lovy and Friend, 2015	Posterior intestine. OCs elongated and ovoid 25.3 ± 1.9 (21.6-28.8) × 14.1 ± 1.3 (11.4-16.2). SPCs ellipsoidal 11.8 ± 1.1 (9.9-14.1) × 3.6 ± 0.3 (2.8-4.3). **Obs.:** OCs wall relatively thin, but thicker OC wall than *G. ameliae*. The OCs wall was smooth and created a uniform	*Alosa pseudoharengus*	River Maurice, New Jersey (USA)	Lovy and Friend (2015)

	elongated and ovoid OC shape, compared to the thin, irregular OC wall of *G. ameliae.*			
Goussia ameliae Lovy and Friend, 2015	Pyloric caeca. OCs round to slightly ovoid, irregular shape 13.6-20.4 × 11.1-15.7 or spherical 21.0-30.0 diameter. SPCs elongated 5.6-8.8 × 3.0-4.7. SR abundant.	*Alosa pseudoharengus*	River Maurice, New Jersey (USA)	Lovy and Friend (2015), Rosenthal et al. (2016)
Goussia anopli Molnar, Avenant-Oldewage and Székely 2004	Intestinal epithelium and feces. OCs spherical 8.0–9.0 (8.3 ± 2.3) diameter. SPCs ellipsoid 3.4-7.2× 3.3-4.5. 2 SPC valves are connected by indistinct, longitudinal suture. No SB. SR globular or short ellipsoidal, finely granulated, 1.5 × 1.5 or 2.0 × 1.5. SPZs vermiform, with reflexed end, 6.6-8 × 1.5-2.0. **Obs.:** In its SPC morphology this species resembles the 'carpelli'-like coccidia [*G. carpelli* (Leger and Stankovitch, 1921), *G. legeri* Stankovitch, 1920 and *G. iroquoina* (Molnár and Fernando, 1974)], but its SPCs are less compact.	*Barbus anoplus*	River Nile, Limpopo Province (South Africa)	Molnar et al. (2004)
Goussia arinae Belova and Krylov, 2001	OCs 12.5-17.5. OR present. SPCs 5.0-7.5. No SB.	*Pelecus cultratus*	River Nema (Russia)	Belova and Krylov (2001)
Goussia arrawarra Molnar and Rhode, 1988	Intestinal mucosa.	*Sillago ciliate*	Arrawarra Research Station near Coffs Harbour,	Molnar and Rohde (1988), Diouf and Toguebaye (1993)

	OCs ellipsoidal 14.5 (14.3-15.1) × 10.7 (10.1-10.9). SPCs elongated ellipsoidal 9.4 (9.3-9.6) × 4.8 (4.6-5.0). SR finely granular, lentiform or scattered 4.2 in diameter and 1.5 in thickness. SPZs banana-shaped 8.8 (8.4-9.2) × 2.4 (2.2-2.5).		northern New South Wales (Australia)	
Goussia auxidis (Dogiel, 1948) Dykova and Lom, 1983 **Syn. *Eimeria auxidis*** Dogiel, 1948	Liver, kidney and spleen. OCS with a thin membranous wall. SPCs 8.7-12.0 × 6.1. No SB. SPZs elongated, curving around each other. SR granular, but not often seen in sectioned material.	*Allothunnus fallai, Auxis maru, Cololabis saira, Katsuwonus pelamis, Scomber australasicus*, *Thunnus alalunga*, *T. albaeares,*	Western and central South Pacific Ocean Sea of Japan - Peter the Great Bay	Dykova and Lom (1983), Jones (1990)
Goussia bayae Matsche, Adams and Blazer, 2019	Hepatic bile ducts and gallbladder. OCs subspherical 26.2 × 21.8. Micropyle present. SPCs ellipsoidal 12.6 × 7.8. No SB. SPZs present.	*Morone americana*	North Atlantic - Chesapeake Bay	Matsche et al. (2019)
Goussia balatonica Molnar, 1989	Intestine. OCs short and ellipsoidal 18.7 (17.0-22.0) × 17.0 (15.0-19.0). SPCs elongated and ellipsoidal, 13.2 (12.0-17.0) × 5.8 (5.0-7.0). SPC wall is thin and composed of 2 equal valves joined by a suture line. SR finely granulated. SPZs banana-shaped 12.0 (10.0-12.5) × 2.3 (2.0-2.5), with a large refractile nuclei each.	*Abramis brama*, *Blicca bjoerkna*, *Rutilus rutilus*	River Danube and Lake Balaton (Hungary)	Molnar (1989), Molnar and Baska (1992), Rosenthal et al. (2016)

Goussia bettae Molnar, Shaharom and Székely, 2003	Intestinal epithelium. OCs spherical 7.5-8.5 (8.0 ± 0.4) diameter. SPCs elongatedly ellipsoidal 6.5-7 (6.7 ± 2.11) × 2-3 (2.5 ± 0.28). 2 SPC valves are connected by indistinct, longitudinal suture. No SB. SR globular, finely granulated. SPZs vermiform, with one reflexed end, 6.0-6.5 × 1.0 (6.3 ± 0.21 × 1.0). **Obs.:** OCs of *Goussia bettae* n. sp. resembles *G. sinensis* (Chen, 1956), a parasite of the silver carp *Hypophthalmichthys molitrix* C. & V., but it is smaller in size and the taxonomic position of the hosts is different.	*Betta splendens*	Small streams in Kuala Terengganu (Malaysia)	Molnár et al. (2003)
*** *Goussia bigemina*** (Labbe, 1896) Yakimoff, 1929 **Syn. *Eimeria bigemina*** Labbe, 1896	Intestine.	*Ammodytes tobianus*		Duszynski et al. (2003b)
Goussia biwaensis Molnar and Ogawa, 2000	Mucus and intestinal epithelium. OCs spherical 8.5 (8.0-9.0) diameter. Polar granule amorphous, small but bright, with diameter of 1, located in most cases in center of OC. SPCs ellipsoidal slightly pointed at ends 5.6 (5.0-6.0) × 3.8 (3.5-4.0). 2 SPC valves are connected by indistinct, longitudinally running suture.	*Pseudogobio esocsinus*	Lake Biwa (Japan)	Molnar and Ogawa (2000)

	No SB. SPZs vermiform, with reflexed end, 6.7 (6.5-7.0) × 1.4 (1.0-1.5). **Obs.:** In its morphology and size *Goussia biwaensis* n. sp. resembles species of the "carpelli type" [G. carpelli Leger and Stankovitch, 1921, *G. legeri* Stankovitch, 1920, *G. iroquoina* (Molnár and Fernando, 1974)] but differs from them by having a bright, distinct polar granule.			
Goussia bohemica Lukes, 1994	Intestine. OCs subspherical 14.6 (13.4-15.7) × 13.3 (12.8-13.9) or spherical 8.0-13.0 diameter. SPCs with slightly tapered ends and a poorly discernable longitudinal suture in their wall, 11.5 (10.6-12.4) × 5.7 (5.3-6.1). SR large and irregular, composed of small, scattered granules. SPZs elongated 10.8 (10.1-11.4) × 2.4 (2.3-2.5), with a single centrally located refractile body.	*Blicca (=Abramis) bjoerkna, Gobio gobio*	Cernovicky Brook in Sobeslav, South Bohemia (Czech Republic) Tapolca creek (Hungary)	Lukes (1994), Rosenthal et al. (2016)
Goussia callinani Molnar and Rhode, 1988	Intestinal mucosa. OCs spherical 8.8 (8.4-9.2) diameter. SPCs ellipsoidal 6.0 (5.8-6.3) × 4.0 (3.8-4.2). SR oval and finely granular, 2.5-1.5 (2.2-2.7 × 1.4-1.7). SPZS vermiform, with one reflexed end, 5.2 (5.0-5.4) × 1.2 (1.1-1.3).	*Hypseleotris compressa*	River Clarence near Grafton, northern New South Wales (Australia)	Molnar and Rhode (1988)

Goussia carpelli (Léger and Stankovitch, 1921) Dykova and Lom 1983 **Syn. *Eimeria cyprini*** Phlen, 1924 **Syn. *Eimeria carpelli*** Léger and Stankovitch, 1921	Liver, intestine, intestinal epithelium, mucus, gallbladder and feces. OCs spherical 8.0-14.0. SPCs ovoid 7.0-10.4 × 5.0-6.0. SR of 2.1-3.1 (2.7 ± 0.4). SPZs 7.3-9.4 × 1.5-6.0.	*Acheilognathus rhombeus*, *Alburnus alburnus*, *Aristrichthys nobilis, Asprocottus megalops, Barbus barbus, Batrachottus baicalensis, Carassius auratus, C. carassius*, *C. cuvieri*, *C. gibelio*, *Chondrostoma polylepis*, *Clupea harengus*, *Cottus kessleri*, *Cyprinus carpio, Gnathopogon strigatus*, *Gobio gobio*, *Hypophthalmichthys molitrix, Leucaspius delineatus*, *Leuciscus cephalus*, *L. leuciscus, Paracottus kessleri, Phoxinus phoxinus, Pseudorasbora parva*, *Rutilus rutilus, Scardinus erythrophthalmus*, *Sphyrna blochii*, *Tinca tinca*	Agricultural University, Wageningen - artificially bred (Netherlands) Europe (Spain and others) USSR Poland Lake Balaton (Hungary) Bulgaria Yugoslavia Indian Ocean	Lom and Dykova (1982a), Dykova and Lom (1983), Steinhagen et al. (1989), Steinhagen and Koerting (1990), Lom et al. (1991), Jendrysek (1993), Jendrysek et al. (1994), Steinhagen (1995), Molnár and Székely (1995), Oesterreich and Tieraerztliche Hochschule (1996), Steinhagen and Hespe (1997), Steinhagen et al. (1997), Hemmer et al. (1998), Rosenthal et al. (2016)
Goussia caseosa Lom and Dyková, 1982	Swim bladder, gas gland, gall bladder, intestinal contents and mesenteric blood vessels. OCs irregularly shaped 42.0 (40.0-47.0) diameter. SPCs ellipsoid, 19.2 × 13.6 (18.0-20.3 by 12.0-15.5). SPZS partially curled one another, 26.0 × 7.0.	*Macrourus berglax*	Grand Banks, Atlantic Ocean - Newfoundland (Canada)	Lom and Dykova (1982b), Upton et al. (1984), Khan (2009)
Goussia cernui Belova and Krylov, 2001	OCs 15.0-22.5. SPCs 5.0-12.5. No SB.	*Gymnocephalus cernuus*	River Neman (Russia)	Belova and Krylov (2001)
Goussia chalupskyi Lukes, 1995	Posterior intestine and feces.	*Leuciscus cephalus*	River Blanice, Southern Bohemia (Czech Republic)	Lukes (1995), Rosenthal et al. (2016)

	OCs spherical 11.0 (10.5-11.5) diameter. SPCs oval to subspherical 7.7 (7.0-8.5) × 5.7 (5.0-6.5). Longitudinal suture of SPC wall indistinct. No SB. SR small composed of 2-4 granules. SPZs elongate, 6.5 × 1.5.		River Danube (Hungary)	
Goussia cichlidarum Landsberg and Paperna, 1985	Swim bladder lining epithelium. OCs spherical 29.0-37.0 diameter. SPCs ellipsoidal 13.0-15.0 × 9.0-10.5, consisting in 2 valves divided by a thin suture line occasionally visible. SPZs curved at their midpoints 14.4-21.8 × 3.5-5.2.	*Oreochromis aureus*, *O. niloticus, Sarotherodon galilaeus*	Lake Kinneret and fish ponds, Jordan Valley (Israel)	Landsberg and Paperna (1985), Paperna et al. (1986), Kim and Paperna (1993)
Goussia clupearum (Thelohan, 1894) Labbe, 1896 **Syn. *Eimeria wenyoni*** Dobell, 1919 **Syn. *Eimeria clupearum*** (Thelohan, 1894) Doflein, 1909 **Syn. *Coccidium clupearum*** Thelohan, 1894 **Syn. *Coccidium* sp.** Thelohan, 1892	Liver, liver parenchyma and intestinal wall. OCs spherical 8.0-31.3 large diameter or 4.0-10.0 small diameter. Polar granule present. SPCs ellipsoidal 8.7-14.2 × 5.0-10.8. SR consisting of refractile granules. SPZs vermiform, not coalescing, with 1-4 refractile bodies each.	*Alosa kessleri pontica, Auxis rochei, Belone belone, Caranx rhonchus, Clupea harengus, C. harengus pallasi, C. pilchardus, Diplodus prayensis, D. vulgaris,* *******Engraulis encrasicolus, Etrumeus micropus, Euthynnus alletteratus, Micromesistius poutassou*, *Psetldupeneus prayensis, Sardina pilcharuds*, *Sardinella aurita, S. maderensis, Selene vorner, Scomber japonicus, S. scombrus, Sparus pagrus pagrus, Spicara melanurus,*	Atlantic Ocean: Scottish waters (Nova Scotia), Galician waters, Norwegian Sea, North Sea, North Aegean Sea (Greece), Coast of Senegal Mediterranean Sea	Kalfa-Papaioannou and Athanassopoulou-Raptopoulou (1984), Costa and Mackenzie (1994), Azevedo (2001), Tolonen and Karlsbakk (2003), Shukhgalter (2004), Shukhgalter (2013), Friend et al. (2016)

		Trisopterus esmarkii, T. minutus, Trachurus mediterraneus, T. trachurus, T. picturalis		
Goussia cruciata (Thelohan, 1892) Labbe, 1896 **Syn. *Eimeria cruciata*** (Thélohan, 1892) Yakimoff, 1929 **Syn. *Coccidium cruciatum*** Thelohan, 1892	Branchial and body cavities, and viscera (stomach, intestine and intestine's wall, liver and liver parenchyma, gonads, pancreas, and pyloric caeca). OCs spherical 4.0-26.0 diameter. SPCs ellipsoidal, arranged as a symmetrical cross shape or a triradiate star, 7.0-12.5 × 5.7-8.4. Longitudinal suture line of two shell valves sometimes difficult to discern. No SB. SR as a cluster of coarse refractile granules. SPZs worm-shaped.	*Caranx trachurus, Clupea pilchardus, Pseudocaranx dentex, Trachurus lathami, T. mediterraneus, T. murphyi, T. picturatus, T. trachurus*	North Aegean Sea (Greece) Adriatic Sea (coast of Montenegro) Australia Moroccan Mediterranean coasts Galician waters (north-west Spain) Portuguese North Atlantic coast Madeira and Canary Islands Central Chilean coast Argentinean and Brazilian coasts (Southwestern Atlantic Ocean)	Dykova and Lom (1983), Kalfa-Papaioannou and Athanassopoulou-Raptopoulou (1984), Daoudi et al. (1987), Gonçalves (1996), Diouf et al. (2000), Abollo et al. (2001), Diouf et al. (2005), Gestal and Azevedo (2005), MacKenzie et al. (2008), Braicovich et al. (2012), Costa et al. (2013), Gonzalez-Kother and Gonzalez (2014)
Goussia cultrati Belova and Krylov, 2001	OCs 22.5-30.0. SPCs 12.5-15.0. No SB.	*Pelecus cultratus*	River Neman (Russia)	Belova and Krylov (2001)
Goussia cylindrospora (Stankovitch, 1921) Rosenthal, Dunams-Morel, Ostoros and Molnar, 2016 **Syn. *Eimeria cylindrospora*** Stankovitch, 1921	Intestinal epithelium. OCs 8.0-19.0 diameter.	*Alburnus alburnus*	France Lake Balaton (Hungary)	Dykova and Lom (1983), Rosenthal et al. (2016)
Goussia cyprinorum Stankovitch, 1921 **Syn. *Eimeria cyprinorum*** Stankovitch, 1921 **Syn. *Goussia carpelli*** ******pro parte*****, according to Dykova and Lom, 1983**	Intestinal epithelium.	*Alburnus alburnus*, *Abramis brama, Barbus barbus, Leucaspius delineatus, Phozinus phoxinus, Rhodeus sericeus amarus*, *Rutilus rutilus, Scardinius erythrophthalmus*	Eastern and central France Lake Kis-Balaton (Hungary) Poland – fish farms	Dykova and Lom (1983), Jastrzębski (1984), Rosenthal et al. (2016)

Goussia dakarensis Diouf and Toguebaye, 1993	Liver and intestine. OCs spherical 15.0 (13.0-17.0) diameter. SPCs ellipsoidal 8.0 (7.5-9.5) × 6.9 (6.0-7.5), with surface smooth with a suture line. SR in the form of a few refringent granules. SPZs falciform, one extremity wider than the other.	*Brachydeuterus auritus*, *Cephalopholis taeniops*, *Epinephelus fasciatus*, *Galeoides decadactylus, Pomadasys peroteti*	Coast of Senegal (Dakar)	Diouf and Toguebaye (1993)
Goussia decapteri Diouf and Toguebaye, 1993	Liver. OCs spherical 16.1 (13.0-18.5) diameter. Polar granule present. OCs containing sporoblasts observed. SPCs ellipsoidal 7.9 (7.0-8.5) × 5.9 (5.0-7.0), usually arranged two by two in two perpendicular planes. SR occurs in the form of a single compact mass. SPZs falciform with overlapping extremities.	*Decupterus rhonchus*	Coast of Senegal (Dakar)	Diouf and Toguebaye (1993)
Goussia degiustii (Molnar and Fernando, 1974) Dyková and Lom, 1983 **Syn. *Eimeria spleni*** Degiusti and Hnath, 1968, *nomen nudum* **Syn. *Eimeria degiustii*** Molnar and Fernando, 1974	Spleen, kidney, pancreatic islets and swim bladder. OCs spherical 19.0-22.0 dimeter, subspherical 15.0-25.2 × 14.0-23.5, or ellipsoidal 24.4 (22.8- 25.2) × 18.8 (17.5-19.3). 1-2 polar granules of 1.0-2.0 diameter. SPCs ellipsoidal 12.0-17.0 × 4.5-8.5, with suture line. SR large, coarsely granulated, compact 9.0-10.0 × 7.0-8.0 × 4.5-5.5, sometimes confined within a delicate membrane. SPZs banana-shaped 10.5-13.0 ×	*Campostoma anomalum*, *Notropis cornutus*, *Pimephales notatus*, *P. promelas*	Eramosa Creek and Lake Sasajewun, Ontario (Canada)	Molnar and Fernando (1974), Lom and Dyková (1981), Upton et al. (1984), Lom and Dykova, 1983, Lom et al. (1989)

	2.5-3.1, sometimes with a spherical refractile body each.			
Goussia desseri Molnar, 1996	Intestine, in epithelium, nodules and pyloric sacs. Unsporulated OCs spherical 17.0-20.0 diameter, or nearly spherical 14.1-21-3 × 12.9-18.2. SPCs ellipsoidal 9.8-14.9 × 4.8-7.8, composed of 2 valves. SPZs banana-shaped.	*Lepomis macrochirus, Sander lucioperca, S. volgensis*	Lake Balaton (Hungary) Lake Assunpink, Monmouth County, New Jersey (USA)	Molnar (1996), Rosenthal et al. (2016), Lovy et al. (2019)
Goussia echinata Friend, Lovy and Hershberger, 2016	Anterior intestine and pyloric caeca. OCs 18.7 (18.0−19.3) ± 0.5 × 11.1 ± 0.9, with the presence of 3 long 15.1 ± 5.1 spiny projections on both ends. SPCs 9.2 ± 0.9 × 4.1 ± 0.5. No SB. A line drawing of the sporulated OC is shown.	*Clupea harengus*	Northwest Atlantic Ocean, New Jersey (USA)	Friend et al. (2016)
Goussia emissolei Diouf and Toguebaye, 1993	Intestine. OCs 19.3 × 15.25. SPCs ovoid and even spherical, 9.2 x 8.9 with thin suture line. SR composed of few refringent granules.	*Leptocharias smithii*	Coast of Senegal (Dakar)	Diouf and Toguebaye (1993)
Goussia exoceti Diouf and Toguebaye, 1993	Liver. OCs 26.1 × 22.9. SPCs ellipsoidal, 12.3 × 8.7 with projections. SR composed of few refringent granules.	*Hirundichthys affinis*	Coast of Senegal (Dakar)	Diouf and Toguebaye (1993)
Goussia gadi Fiebiger, 1913 (Dyková and Lom, 1981)	Swim bladder and swim bladder wall.	*Enchelyopus cimbrius, Gadus aeglefinus, G. virens, Molva vulgaris*	North Atlantic Sea	Dykova and Lom (1981), Dykova and Lom (1983),

Syn. *Eimeria gadi* Fiebiger, 1913	OCs spherical 26.0-28.0 diameter. OC residuum sometimes present. SPCs ovoid, 11-15 × 7.5-10.0, with apical pore and longitudinal ridges extending length of SPC. SR present. SPZs 16.0 × 4.0, with 1 or more refractile bodies each.			Morrison et al. (1993a), Morrison et al. (1993b)
Goussia girellae Kent, Fournie, Snodgrass and Elston, 1988	Intestinal epithelium, liver, gills and spleen. OCs elongated 18.1-18.8 × 12.5-16.3. SPCs ellipsoidal 6.8-13.5 × 4.0-5.6. SR consisting of 5-10 small refractile granules. Suture in SPC wall poorly defined. SPZs with one refractile body near posterior end.	*Girella nigricans*, *Leuciscus leuciscus*	La Jolla, California (USA) - tide pools Czechoslovakia	Kent et al. (1988), Lukes and Dykova (1990)
Goussia grygieri Molnar and Ogawa, 2000	Mucus and intestinal epithelium. OCs spherical 10.4 (10.0–11.0) diameter. SPCs ellipsoidal in upper view, while in side view one of their longitudinal sides is flattened. SPCs 9.5 (9.0-10.0) × 5.0 (4.5-5.5). 2 SPC valves are connected by indistinct, longitudinally running suture. No SB. SR globular or ellipsoidal, finely granulated, 3.0 × 2.5 in younger OCS. SPZs vermiform, with one reflexed end, 12.0 (11.0-13.0) × 1.5 (1.0-2.0).	*Pseudogobio esocinus*	Lake Biwa (Japan)	Molnar and Ogawa (2000)

	Obs.: OCs of *Goussia grygieri* n. sp. resembles *G. laureleus* (Molnar and Fernando, 1974), a parasite of the yellow perch, but it is smaller in size and the hosts are unrelated.			
Goussia guamaensis Da Silva, Araújo, Silva, Hamoy and Matos, 2019	Gastric mucosa of the intestine. OCs spherical 16.5 ± 0.9 (14.9-17.6) diameter. SPCs elliptical, with slightly pointed poles, 8.4 ± 0.6 (7.2–9.8) × 7.1 ± 0.7 (6.2-8.2). No SB. SR present. SPZs vermiform with 2 refractile bodies each.	*Thoracocharax stellatus*	River Guamá (Northern Brazil)	Da Silva et al. (2019b)
Goussia gymnocephali Belova and Krylov, 2001	OCs 25.0 × 25.0. SPCs 10.0 × 12.5. No SB.	*Gymnocephalus cernuus*	River Neman (Russia)	Belova and Krylov (2001)
Goussia hupehensis (Chen and Hsieh, 1964) Rosenthal, Dunams-Morel, Ostoros and Molnar, 2016 **Syn. *Eimeria hupehensis*** Chen and Hsieh, 1964	Intestine. OCs 8.0-13.0 diameter.	*Carassius auratus, C. gibelio*	Hubei province (China) Lake Balaton and pond farm (Hungary)	Dykova and Lom (1983), Rosenthal et al. (2016)
Goussia janae Lukes and Dyková, 1990	Intestine (epicellular position). OCs irregularly ellipsoidal 18.1 (14.2-22.0) × 12.7 (11.0-14.5) or spherical 14.0-19.0 diameter. SPCs ellipsoidal 13.5 (12.5-14.5) x 5.0 (4.3-5.8). Suture line connecting the 2 valves of the SPC wall, observed by TEM. SPZs elongated 10.7 (10.0-11.5) × 2.8 (2.5-3.2).	*Leuciscus cephalus, L. leuciscus*, *Perca fluviatilis*	Malse, Vltava and Blanice rivers, South Bohemia (Czech Republic) Balatonszemes (Hungary)	Lukes and Dykova (1990), Lukes and Stary (1992), Rosenthal et al. (2016)

Goussia kessleri Molnar, 2000	Mucus and intestinal epithelium. OCs spherical 8.1 (7.0-8.5) diameter. SPCs ellipsoidal 5.8 (5.0-6.0) × 3.9 (3.8-4.0). SR finely granulated and globular. SPZs vermiform, with one reflexed end, 7 × 1.5.	*Gobius kessleri*, *G. fluviatilis*	River Danube and Lake Balaton (Hungary)	Molnar (2000), Rosenthal et al. (2016)
Goussia koertingi Baska, 1997	Intestine. OCS 15.8-16.5 × 12.8-13.5. 4 SPC showing typical *Goussia* structure. Sporozoite cylindrical, not tapered at apical end, with centrally located nucleus easily discernible.	*Barbus barbus*	River Danube (Hungary)	Baska (1997), Rosenthal et al. (2016)
Goussia kuehae Borkhanuddin, Shaharom, Embong and Molnar, 2013	Mucus and epithelium of the anterior part of intestine. OCs ellipsoidal, 37.0-40.0 (37.9 ± 1.49) × 28-30.3 (29.3 ± 0.97). 2 or 3 pale rounded OR-like bodies 7.0-8.5 (7.8 ± 0.54) in size and some round or amorphous compact 1.0-3.5 diameter. SPCs ellipsoidal 15.2-17.0 × 5.7-8.0 (16.2 ± 0.7 × 6.7 ± 0.8). 2 SPC valves connected by an indistinct, longitudinally running suture. No SB. SR rough scattered dots (0.8–1.2). SPZs elongate, banana-shaped 14.0-15.7 × 2.3-2.7 (14.7 ± 0.71 × 2.6 ± 0.19).	*Lates calcarifer*	Brackish water cages at Setiu Wetland, Terengganu State (Malaysia)	Szekely et al. (2013), Rosenthal et al. (2016)

Goussia langdoni Molnar and Rhode, 1988	Intestinal mucosa and pyloric caeca. OCs spherical 11.2 (10.5-12.0) diameter. 1 amorphous polar granule of 0.8. SPCs elongated, cylindrical, tapering towards the ends, but blunt ended, 8.2 (8.1-8.4) × 4.4 (4.2-4.6). Valves and suture line not distinctly visible. SR coarsely granular, fills the whole space between SPZs in young SPCs and scattered, forming 5-7 granules 0.4 diameter in old SPCs. SPZs vermiform, with one reflexed end. SPZs without the reflexed portion 6.9 (6.7-7.1) × 1.2 (1.1-1.3).	*Macquaria ambigua*	Fish farm near Narrandera, New South Wales (Australia)	Molnár and Rhode (1988)
Goussia laureleus (Molnar and Fernando, 1974) Li and Desser, 1985 **Syn. *Eimeria laureleus*** Molnar and Fernando, 1974	Intestinal epithelium and feces. OCs spherical 11.0-12.0 diameter. SPCs coffee bean-shaped, from certain angles they appear oval, and measure 9.2-1 1.0 × 5.0-5.8. No SB. SR finely granulated and dispersed. SPZs vermiform 9.0-10.0 × 1.5-2.0, each with a round refractile globule.	*Perca flavescens*	Laurel Creek, Waterloo, Ontario (Canada)	Molnar and Fernando (1974), Dykova and Lom (1983)
Goussia stankovitchi (Pinto, 1928) Levine, 1983 ***Syn. Eimeria stankovitchi*** (Stankovitchi, 1920) Pinto, 1928 **Syn. *Eimeria legeri*** (Stankovitch, 1920) Pinto, 1928 ***Syn. Goussia legeri*** Stankovitch, 1920 non ***Eimeria legeri***	Intestine. OCs spherical 10.0 diameter. SPCs ellipsoidal 7.0 × 5.0, without OR.	*Abramis brama, Alburnus lucidus, Aspius aspius, Leucaspius delineates, Leuciscus brandti, Rutilus rutilus, Rhodeus sericeus amarus, Scardinius erythrophthalmus*	France USSR Poland Lake Balaton (Hungary) Yugoslavia	Dykova and Lom (1983), Diouf and Toguebaye (1993), Molnár and Székely (1995)

(Simond, 1901) Reichenow, 1921				
Goussia lepomi Lovy, Friend and Lewis, 2019	Intestine. OCs nearly spherical 9.2-13.8 × 8.4-12.2. SPCs ellipsoidal 5.4-9.4 × 3.9-6.2. SPZs elongated 6.1-8.1 × 1.8-3.0.	*Lepomis macrochirus*	Lake Assunpink, Monmouth County, New Jersey (USA)	Lovy et al. (2019)
Goussia leucisci (Schulman and Zaika, 1964) Lom, Desser, and Dykova, 1989 **Syn. *Goussia scardinii*** (Pellerdy and Molnar, 1968) Molnar, 1996 **Syn. *Eimeria scardinii*** Pellerdy and Molnar, 1968 **Syn. *Eimeria freemani*** Molnar and Fernando, 1974 **Syn. *Goussia freemani*** (Molnar and Fernando, 1974) Lom, Desser, and Dykova, 1989 **Syn. *Eimeria leucisci*** Schulman and Zaika, 1964	Kidney, kidney tubules, renal haemopoietic tissue and gall bladder. OCs ellipsoidal 22.0-32.0 × 16.6-28.2 or spherical 30.0-35.0 diameter. OR polar granule of 1.0-2.0. SPCs ellipsoidal 11.3-17.0 × 4.7-7.2. SR ellipsoidal, finely granulated, 5.1-6.1 × 2.7-3.6, located at one end or centrally; a few loose granules may be present. SPZs slightly arched along the SPC wall or moderately sinuous, 5.6-13.0 × 3.5-5.6, each with a large refractile globule (paranuclear body) at the wider end and a smaller one in the middle portion.	*Abramis brama, Alburnus alburnus, Barbus barbus bocagei*, *Blicca bjoerkna*, *Carassius auratus gibelio*, probably *Chondrostoma nasus*, *Leuciscus baicalensis*, *L. cephalus*, *Notropis cornutus*, *Rutilus rutilus, Scardinius erythtophthalmus*	Lake Baikal, Lake Velencei and Lake Balaton (Hungary) River Esla (north-west Spain) Lake Sasajewun and Laurel Creek, Ontario (Canada) Lake in northern Greece Poland – fish farms	Pellérdy and Molnar (1968), Molnar and Hanek (1974), Dykova and Lom (1981), Dykova and Lom (1983), Jastrzębski (1984), Lom et al. (1989), Alvarez Pellitero et al. (1986), Athanassopoulou and Vlemmas (1986), Molnár and Székely (1995), Rosenthal et al. (2016)
Goussia lomi Molnar and Rhode, 1988	Intestinal mucosa. OCs spherical 16.0 (14.3-16.8) diameter. OCS residuum large and lentiform 9.2 (8.4-10.4) diameter. SPCs ellipsoidal 9.2 (8.8-9.6) × 5.0 (4.9-5.2). Valves and suture indistinctly visible. SR finely granular, round, 2.6 (2.5-2.7) diameter; in older SPCs, compact with 1-	*Maccullochella peeli*	New South Wales- hatchery (Australia)	Molnár and Rhode (1988), Philbey and Ingram (1991), Rosenthal et al. (2016)

	3 residues. SPZs vermiform, with one end reflexed. SPZs without the reflexed portion 8.0 (7.6-8.4) × 1.9 (1.8-2.0).			
Goussia luciae Lom and Dyková, 1982	Intestine. OCs spherical 10.0 diameter. SPCs ellipsoidal 7.5 × 5.5, with residuum.	*Mullus barbatus*	France	Lom and Dykova (1982b), Dykova and Lom (1983)
Goussia lucida (Labbé, 1893) Labbé, 1896 **Syn. *Eimeria lucida*** (Labbé, 1893) Reichenow, 1921 **Syn. *Coccidium lucidum*** Labbé, 1893 **Syn. *Nucleogoussia lucida*** Daoudi, Radujković, Marques and Bouix, 1989	Posterior intestine.	*Acanthias vulgaris, Mustelus canis, M. vulgaris, Scyliorhinus canicula, S. stellaris*, *Squalus blainville*	Atlantic Ocean Gulf of Lion, Southern France Adriatic Sea, coast of Montenegro (Mediterranean Sea)	Dykova and Lom (1983)
Goussia luciopercae Belova and Krylov, 2001	OCs 30.0-35.0 × 30.0. SPCs 12.5-15.0 × 10.0-12.5. No SB.	*Stizostedion lucioperca*	River Neman (Russia)	Belova and Krylov (2001)
Goussia lusca Gestal and Azevedo, 2006	Liver. OCs 31.69 (28.8-35.4) diameter. SPCs ellipsoidal, in an aleatory position and, 13.7 (13.1-14.4) × 9.24 (8.52-9.84).	*Trisopterus luscus*	Northwest Spain Portuguese North Atlantic coast	Gestal and Azevedo (2006)
Goussia malayensis Molnar, Shaharom-Harrison and Székely, 2003	Intestinal epithelium. OCs spherical 33-38 (35.3 ± 2.1) diameter. SPCs elongated and ellipsoidal, 21.0-26.0 (23.9 ± 1.9) × 5.0-6.5 (5.6 ± 0.63). 2 SPC valves are connected by indistinct, longitudinal suture. No SB. SR finely granulated, globular or amorphous. SPZs	*Apocheilus panchax*	Kuala Terengganu – small stream (Malaysia)	Molnár et al. (2003)

	stout, pointed only at one end, 12.0-16.0 (14.0 ± 1.3) × 5.0-6.0 (5.4 ± 0.5). **Obs.:** By its large OC size *G. malayensis* resembles OCs of *G. scardinii* Pellérdy and Molnár, 1968, a renal parasite of cyprinid fishes, but it differs from them by the lack of polar granules. It also resembles *G. trichogasteri* Székely and Molnár, 1992, but it has larger OCs and has no OR.			
Goussia metchnikovi (Laveran, 1897) Dykova and Lom, 1983 **Syn. *Eimeria metschnikovi*** of Molnar, 1981, lapsus **Syn. *Eimeria macroresidualis*** Shulman and Zaika, 1962 **Syn. *Eimeria metchnikovi*** (Laveran, 1897) Reichenow, 1921 **Syn. *Coccidium metchnikovi*** Laveran, 1897	Spleen, liver, kidney and intestine. OCs spherical 20.0-27.0 diamter. SPCs thin-walled, bluntly elliptic 10.5-15.0 × 5.0-9.0. SR bulky and refractive, of up to 2.0 diameter, or coarsely granular of 5.2-6.5 diamey	*Gobio albipinnatus, G. albipinnatus tennuicorpus, G. gobio*, *G. kessleri*	USSR – Asian part River Lee (England) Hungary Poland – fish farms	Pellérdy and Molnar (1968), Dykova and Lom (1983), Jastrzębski (1984), Ball et al. (2012)
Goussia microcanthi Molnar and Rhode, 1988	Intestinal mucosa. OCs short oval 12.2 (11.7-13.5) × 10.9 (10.1-11.7). 1 small polar granule of 0.8. SPCs elongated ellipsoidal 11.0 (10.9-11.2) × 4.6 (4.5-4.7). SR scattered, forming small pieces. SPZS banana-shaped 9.6 (9.2-10.0) × 2.5 (2.4-2.6), with large refractile nuclei.	*Microcanthus strigatus*	Arrawarra Research Station near Coffs Harbour, northern New South Wales (Australia)	Molnar and Rohde (1988), Diouf and Toguebaye (1993)

Goussia minuta (Thélohan, 1892) Labbé, 1896 **Syn. *Eimeria minuta*** (Thélohan, 1892) Doflein, 1909 **Syn. *Coccidium minutum*** Thélohan, 1892	Spleen, liver and kidney.	*Tinca tinca*	France	Lom and Dykova (1893)
Goussia molnarica El-Mansy, 2008	Mucus and intestinal epithelium. OCs elliptical or irregularly shaped 14.4 (13.6-16.3) × 10.9 (9.7-13.9). SPCs ellipsoidal 7.8 ± 1.3 (7.5-10.6) long × 5.6 ± 0.9 (3.9-7.0). No SB. SR in young spores was a large globule, of 1.2-2.0 (2.0 ± 0.5); in elder spores composed of small, scattered granules, 0.5-1.1 (0.7 ± 0.3) × 1.6-2.3 (1.9 ± 0.3), 0.3-0.7 (0.5 ± 0.2) diameter. SPZs vermiform, with reflexed ends, 6.8 ± 1.1 (5.5-9.1) × 1.7 ± 0.5 (0.7-2.1).	*Clarias gariepinus*	River Nile (Egypt)	El-Mansy (2008)
Goussia motellae (Labbé, 1893) Labbé, 1896 **Syn. *Eimeria motellae*** (Labbé, 1893) Yakimoff, 1929 **Syn. *Coccidium motellae*** Labbé, 1893	Pyloric caeca.	*Motella tricirrata*	Atlantic Ocean French Coast	Dykova and Lom (1983)
Goussia nipponica Molnar and Ogawa, 2000	Mucus and intestinal epithelium. OCs spherical 11.0 (10.0-12.0) diameter. SPCs cylindrical, slightly pointed at ends, 8.0 (7.8-8.5) × 2.8 (2.5-3.0). 2 SPC valves are connected by indistinct, longitudinally	*Tribolodon hakonensis*	Lake Biwa (Japan)	Molnar and Ogawa (2000)

	running suture. No SB. SR globular or short ellipsoidal, finely granulated, 2.0 × 2.0 or 2.0 × 1.0. SPZs vermiform, with reflexed ends, 8.5 (8.0-9.0) × 1.3 (1.0-1.5). **Obs.:** In its SPC morphology this species resembles the SPCs of *G. cylindrospora* (Stankovitch, 1921), *G. alburni* Stankovitch, 1920 and *G. siliculiformis* (Schulman and Zaika, 1962); differs from the last two species by its smaller size. Same size SPCs as *G. cylindrospora*, a specific parasite of the bleak *Alburnus alburnus* L., but *G. nipponica's* they are less slender and compact.			
Goussia noternigonica Li and Desser, 1985	Kidney, spleen, swim bladder and ureter. OCs 21.0 (19.0-25.5) diameter. SPCs rod-shaped 11.5 × 5.0. SR finely granulated.	*Notemigonus crysoleucas*	Canada	Diouf and Toguebaye (1993)
Goussia pannonica Molnar, 1989	Intestine. OCs ellipsoidal 15.0 (14.0-16.0) × 12.2 (11.0-14.0) or spherical 14.0-19.0 diameter. SPCs elongated ellipsoidal 11.8 (11.0-13.0) × 4.0 (3.0-4.5), with thin walls and are composed of 2 equal valves. SR is finely granulated. SPZs banana-shaped 9.5 (8.5-10.5)	*Abramis brama*, *A. sapa*, *Blicca bjoerkna*	Lake Balaton and River Danube (Hungary) Sobeslav, South Bohemia (Czech Repubic)	Molnar (1989), Lukes (1992), Molnar and Baska (1992), Molnár and Székely (1995), Rosenthal et al. (2016)

	long and 2.1 (2-2.5), with large refractile nuclei.			
Goussia peleci Belova and Krylov, 2001	OCs 37.5-45.0 × 35.0-42.5. SPCs 20.0-22.5 × 15.0-17.5. SB absent. SR present.	*Pelecus cultratus*	River Neman (Russia)	Belova and Krylov (2001)
Goussia piekarskii Lom and Dyková, 1995	Small intestine. OCs spherical or subspherical 9.2 average diameter. SPCs 7.6 × 4.2 average size.	*Gambusia holbrooki*	Australia	Lom and Dykova (1995)
Goussia pogonognathi Molnar, Shaharom-Harrison and Székely 2003	Intestinal epithelium. OCs spherical 10.0-13.0 (11.1 ± 1.16) diameter. SPCs ellipsoidal 8.0-11.0 (9.0 ± 1.0) × 4.0-5.0 (4.5 ± 0.5). 2 SPC valves are connected by indistinct, longitudinal suture. No SB. SR globular or short ellipsoidal, finely granulated. SPZs vermiform, with reflexed ends, 8.0-9.0 (8.4 ± 0.5) × 1.5-2.0 (1.8 ± 0.25). **Obs.:** SPC morphology resembles the 'carpelli' type coccidia (*G. carpelli* Leger and Stankovitch, 1921, *G. legeri* Stankovitch, 1920 and *G. iroquoina* Molnár and Fernando, 1974), but its SPCs are less slender and less compact.	*Hemirhamphodon pogonognathus*	Kuala Terengganu – small streams (Malaysia)	Molnár et al. (2003)
Goussia senegalensis Faye, 1988	Liver. OCs spherical 17.4 (15.5-19.0) diameter. Polar granule present. SPCs ovoid (9.5-10.5) 9.8 × 8.7 (8.0-9.0), usually	*Apsilus fuscus*, *Pagellus bellotii*	Coast of Senegal (Dakar)	Diouf and Toguebaye (1993)

	arranged in the form of a cross, with suture and some longitudinal lines. SR consists of dense granules. SPZS peripheral falciform, each with transverse band one-third of the way from the posterior end.			
Goussia siliculiformis (Schulman and Zaika, 1962) Dykova and Lom, 1981 **Syn. *Eimeria siliculiformis*** Schulman and Zaika, 1962	Swim bladder, intestine, mesentery, kidney and testes. OCs spherical 15.0-17.0 diameter. SPCs coffin-shaped, 12.0-13.0 x 5.0-7.0. **Obs.:** Resembles *G. leucisci* (Schulman and Zaika, 1964) Lom, Desser, and Dykova, 1989 and nodular type coccidians, but is distinguished by its affinity for serous membranes.	*Abramis brama*, *Alburnus alburnus*, *Gobio albipinnatus fenuicorpus, G. gobio*, *Rutilus rutilus*, *Scardinius erythrophthalmus*	USSR Lake Balaton (Hungary) Poland – fish farms	Dykova and Lom (1983), Jastrzębski (1984), Rosenthal et al. (2016)
Goussia sinensis (Chen, 1956) Rosenthal, Dunams-Morel, Ostoros and Molnar, 2016 **Syn. *Eimeria sinensis*** Chen, 1956	Intestinal epithelium. OCs spherical 8.5-10.5 diameter. Small polar granule at the periphery of the OC. SPCs prismatic and end bluntly 8-9.5 × 3.4-4.0. SR granular, elongated oval in shape. SPZs worm-like, recurved at one end, 8.0-9.0 × 1.5.	*Aristichthys nobilis, Hypophthalmichthys molitrix*	Russia Lake Balaton and pond farm (Hungary)	Molnár (1976), Dykova and Lom (1983), Molnár and Székely (1995), Rosenthal et al. (2016)
Goussia soumbediounensis Diouf and Toguebaye, 1993	Intestine. OCs spherical 11.8 (10.0-14.5) diameter. SPCs spherical roughly 6.8 (5.0-9.5) diameter, with suture line. SR consists of a few refringent granules. SPZs falciform arranged in the	*Leptocharias smithii*	Coast of Senegal (Dakar)	Diouf and Toguebaye (1993), da Silva et al. (2019)

	shape of a cross, all with tips folded over in the same manner.			
Goussia sparis Sitjà-Bobadilla, Palenzuela and Alvarez-Pellitero, 1996	Intestine. OCs ellipsoidal 16.0-21.0 (17.4 ± 1.5) × 13.0-18.0 (14.4 ± 1.7). SPCs ellipsoidal 8.6-10.3 (9.5 ± 0.5) × 5.7-7.4 (6.5 ± 0.5), with a suture line that was scarcely visible. SR consists of several granules. SPZs vermiform 9.2-9.7 (9.3 ± 0.2) × 3.2-3.5 (3.2 ± 0.1).	*Sparus aurata*	Spain – maricultures	Sitjà-Bobadilla et al. (1996)
Goussia spraguei Morrison and Poynton, 1989	Kidney and kidney tubules. OCs more or less spherical 16.0-17.6 diameter. SPCs ovoid 10.8-13.0 × 6.4-8.5. SR small. SPZs usually with one reflexed end.	*Gadus morhua, Melanogrammus aeglefinus*	Halifax Harbour, Nova Scotia (Canada)	Morrison and Poynton (1989), Diouf and Toguebaye (1993), Gestal and Azevedo (2006), da Silva et al. (2019)
Goussia subepithelialis (Moroff and Fiebiger, 1905) Dykova and Lom, 1983 **Syn. *Eimeria subepithelialis*** Moroff and Fiebiger, 1905	Intestine and intestinal wall. OCs 17.0-22.0 diameter. SPCs 13.0-16.0 × 5.0-8.0. SPZs 12.0-16.0 × 1.5-4.0, with granular residual body.	*Cyprinus carpio*	South Bohemian (Czech Republic) and North German - ponds Hungary	Pellérdy and Molnar (1968), Dykova and Lom (1983), Steinhagen et al. (1990), Steinhagen (1991), Rosenthal et al. (2016)
Goussia squali (Fitzgerald, 1975) Lom and Dyková, 1992 **Syn. *Eimeria squali*** Fitzgerald, 1975	Spiral valve's mucosa and feces. OCs ovoid or ellipsoid 24.0-36.0 × 20.0-29.0. Large OR present of 12.4. SPCs ellipsoid 19.6 × 5.9. SR consisting of several small, spherical granules. SPZs slender, spindle-shaped, 13.6 × 2.2, slightly twisted in a head to tail arrangement.	*Squalus acanthias*	Pacific Ocean, coast of Washington (USA)	Fitzgerald (1975), Lom et al. (1992), Dykova and Lom (1983)

***Goussia szekely*i** Molnar, 2006	Mucus and anterior intestinal epithelium. OCs spherical 14.0-15.5 (14.7 ± 0.59), short ellipsoidal 13.8-16.7 (15.7 ± 0.7) × 13.1-15.2 (14.1 ± 0.65). SPCs ellipsoidal 9.3-11.7 (10.2 ± 0.8) × 4.9-6.6 (5.8 ± 0.44), with indistinct, longitudinal suture line. SR small, rough scattered dots (0.8-1.2) arranged in the SPC on opposite sides, partially obscuring the SPZs. No SB. SPZs banana-shaped 8.0-9.3 (8.7 ± 0.43) × 2.3-3.0 (2.5 ± 0.44).	*Gobius fluviatilis*, *G. melanostomus*, *Rutilus rutilus*	River Danube and Lake Balaton (Hungary)	Molnar (2006), Rosenthal et al. (2016)
Goussia thelohani Labbé, 1896 **Syn. *Eimeria thelohani*** (Labbé, 1896) Yakimoff, 1929 **Syn. *Coccidum* sp.** Thélohan, 1894	Liver parenchyma.	*Acanthopagrus australis*, *Labrus* sp. *Symphodus tinca*, *Rhabdosargus sarda*	Adriatic Sea, coast of Montenegro Australia	Dykova and Lom (1983)
Goussia trachinoti Diouf and Toguebaye, 1993	Liver. OCs spherical 10.9 (9.5-12.0) diameter; smears OCS are often found enveloped in 'yellow body', a product of degeneration of host cells. SPCs oval 5.9 (5.5-6.5) × 4.5 (4.0-5.0). SR consists of 6 refringent granules. SPZs vermiform, peripheral.	*Trachinotus ovatus*	Coast of Senegal (Dakar)	Diouf and Toguebaye (1993), da Silva et al. (2019b)
Goussia trichogasteri Székely and Molnár, 1992	Intestinal epithelium. OCs spherical 14.0-21.0 diameter. SPCs ellipsoidal 4.7-	*Trichogaster pectoralis trichopterus*, *T. trichopterus*	Budapest (Hungary) Kuala Terengganu – streams (Malaysia)	Szekely and Molnar (1992), Kim and Paperna (1993),

	5.5 × 3.5-4.9, with 2 equal valves connected by a longitudinal suture. SPZs banana-shaped 7.1 (5.5-8.3) × 1.8 (1.6-2.4).			Molnár et al. (2003), da Silva et al. (2019b)
Goussia vanasi (Landsberg and Paperna, 1987) Lom and Dyková, 1992 **Syn. *Eimeria vanasi*** Landsberg and Paperna, 1987	Feces and intestinal epithelium. OCs spherical 15.0-17.0 (16.4 ± 0.4) × 11.0-13.0 (12.4 ± 0.6). SPCs elongated-ellipsoidal, length 11.0-12.0 (11.6 ± 2.11) × 3.0-4.5 (3.6 ± 0.38) wide and thickness, with 2 valves connected by indistinct, longitudinal suture. No SB. SPZs banana-shaped 10.0-11.0 (10.3 ± 0.21) × 1.5-2.0 (1.6 ± 0.31).	*Tilapia sparrmanii*	River Klein Nile, Limpopo Province River Magalies, Northwest Province Padda Dam, Johannesburg, Gauteng Province (South Africa)	Molnar et al. (2004)
Goussia vargai Molnar, 1986	Intestinal mucus membrane and pyloric caeca. OCs spherical 12.6-20.0 or short-ellipsoidal 15.0-20.0 × 14.0-19.0. 2 amorphous polar granules of 1.0-1.5. SPCs elongated ellipsoidal 10.5-14.0 × 4.5-6.0. SR 3.0 × 4.0. SPZs vermiform with one reflexed end, with a large refractile body. SPZs without the reflexed end 9.0-11.5 length × 1.7-2.2 thickness.	*Acipenser ruthenus*	River Danube (Hungary)	Molnar (1986), Rosenthal et al. (2016)
Goussia vimbae Belova and Krylov, 2001	OCs 15.0-22.5. SPCs 5.0-7.5. No SB.	*Vimba vimba*	River Neman (Russia)	Belova and Krylov (2001)

Goussia wakabayashii Molnar and Ogawa, 2000	Content of anterior intestine. OCs spherical 8.5 (8.0-9.0) diameter. SPCs ellipsoidal 7.0 (6.5-7.5) × 4.1 (3.8-4.3), with 2 valves are connected by indistinct, longitudinal suture. No SB. SR globular. SPZs vermiform, with one reflexed end, 7.5 (7.0-9.0) × 1.3 (1.0-1.5).	*Tridentiger kuroiwae brevispinis*	Lake Biwa (Japan)	Molnar and Ogawa (2000), El-Mansy (2008), da Silva et al. (2019b)
Goussia washuti Lovy, Friend and Lewis, 2019	Intestine. OCs nearly spherical 24.4-38.7 × 15.6-33.4. SPCs ellipsoidal 11.3-24.4 × 5.2-8.1. SR present, less prominent as OCs matured. SPZs elongated 11.5-14.8 × 2.7-4.8, with a centrally located refractile body.	*Lepomis macrochirus*	Lake Assunpink, Monmouth County, New Jersey (USA)	Lovy et al. (2019)
Goussia zarnowskii Jastrzębski, 1982	Anterior and middle intestine. Young OCs elongated-oval 8.0-16.4 × 4.1-8.0, with new single membrane external to the pellicle, under which a material of electron dense inclusions was deposited. Developed OCs with a wall consisting of three membranes external to the tri-membranous pellicle.	*Gasterosteus aculeatus*	Poland - fish farms Sulak creek, Erd (Hungary)	Jastrzębski (1984), Jastrzebski and Komorowski (1990), Rosenthal et al. (2016)

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