



## Two new species of ascaridoid nematodes in Brazilian Crocodylomorpha from the Upper Cretaceous



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### ABSTRACT

Two new ascaridoid species, *Bauruascaris cretacicus* n. gen. et n. sp., and *Bauruascaris adamantinensis* n. gen. et n. sp., are described based on the fossils of eggs preserved in 80–70 million year old phosphatized coprolites of Crocodyliformes, chronologically assigned to the Upper Cretaceous (Campanian/Maastrichtian age), collected from sedimentary rocks of the Bauru Group, Adamantina Formation in the municipality of Santo Anastácio, in the southwestern region of the state of São Paulo, Brazil, South America. This paper describes the oldest ascaridoid species ever recorded in Crocodylomorpha. Hence, this article contributes to the body of knowledge about the evolutionary history of this nematode group. It also offers a clue about the composition of the parasite fauna of these reptiles from the Late Cretaceous, which is still unknown despite numerous studies about various aspects of their biology and the pioneering paleoparasitological analysis of animal coprolites by South American researchers.

### 1. Introduction

Nematodes of the superfamily Ascaridoidea are among the most common groups of parasitic helminths of medical and veterinary importance. In their adult form, they usually live in the alimentary tract of the major lineages of vertebrates around the world [1], where they generally consume the food ingested by their final hosts [2]. Ascaridoids normally have simple life cycles, although paratenic hosts are common and some species also require intermediate hosts [3].

These roundworms are typically characterized by their stout body, medium to large size, three developed lips [4] and quasi spherical eggs, cleaved (developing embryo) or not (single cell stage), which adult females lay in large numbers in the feces of their final hosts. The eggs of the species transmitted in aquatic habitats are generally thin-shelled, while those of the species that parasitize terrestrial animals are usually thick-shelled. These morphological features make them highly resistant and long-living in the external environment [2]. In addition, certain species of the Heterocheilidae, Toxocaridae, Ascarididae can show eggs with a characteristic rough outer surface [5], which some parasitologists call a pitted [6] or mammillated outer surface [7].

The origin and evolutionary history of Ascaridoidea are still uncertain and controversial. Phylogenetic studies, however, suggest this clade may have appeared in the Lower Carboniferous (Mississippian Period), approximately 360.47–325.27 million years ago (mya), as a

parasite of terrestrial tetrapods [5]. Nevertheless, the earliest fossil records belong to two later geological periods, the Upper Triassic ( $\pm 240$  mya) and the Lower Cretaceous (100–146 mya). These records describe eggs of different species of the genus *Ascarites* preserved in cynodont [8] and dinosaur [7] coprolites, respectively.

Phylogenetic analysis subdivides this taxon into six monophyletic families, Heterocheilidae, Anisakidae, Raphidascarididae, Acanthocheilidae, Toxocaridae and Ascarididae [5], which are represented by 64 genera and approximately 823 species [9]. The extant Crocodylomorpha reptiles, such as caimans, alligators, crocodiles and gavials, are known to be hosts of the greatest diversity of ascaridoid nematodes, involving almost 50 species belonging to the genera *Dujardinascaris*, *Brevimulticaecum*, *Ortleppascaris*, *Typhlophoros*, *Inguenascaris*, *Gedoelstascaris*, *Hartwichia*, *Multicaecum*, *Trispiculascaris* (Heterocheilidae), *Goezia* (Raphidascarididae), *Terranova* (Anisakidae), and *Orneoascaris* (Ascarididae), which are also the main nematode group that parasitizes these vertebrates [10–29]. Parasitism by some of these species may occasionally be associated with gastric lesions such as ulcers and granulomas, loss of appetite, gradual weight loss, runting and mortality in cases of severe infection of both adult and larval stages [30–33].

Several unidentified fossils of ascaridoid eggs were found during a paleoparasitological investigation of Crocodyliformes coprolites chronologically related to the Upper Cretaceous, approximately 80–70

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Fig. 1. Some phosphatized Crocodyliformes coprolites from the Upper Cretaceous, dated about 80–70 mya, found in the Adamantina Formation, Bauru Group, in the municipality of Santo Anastácio, state of São Paulo, Brazil, South America. These coprolites tested positive for *Bauruascaris cretacicus* n. gen. et n. sp. (black arrows) and *B. adamantinensis* n. gen. et n. sp. (white arrow).

mya, which were collected in the 1980s and 1990s in the Adamantina Formation, Bauru Group in the municipality of Santo Anastácio, southwestern region of the state of São Paulo, Brazil, South America. Two new species of ascaridoids were described based on these egg fossils.

## 2. Materials and methods

Fifty-three phosphatized Crocodyliformes coprolites (Fig. 1), chronologically related to the Upper Cretaceous (Campanian/Maastrichtian age) were analyzed. These ichnofossils, which were associated with Crocodylomorpha bones, were collected previously [34] from sedimentary rocks of the Adamantina Formation, Bauru Group in the municipality of Santo Anastácio, southwestern region of the state of São Paulo, Brazil, South America. They are deposited in the paleobiology collection of the Paulo Milton Barbosa Landim Paleontology and Stratigraphy Museum at São Paulo State University – UNESP, in Rio Claro, state of São Paulo, Brazil, South America.

After measuring the dimensions and weighing the coprolites using a

caliper and a digital balance, respectively, individual macerated samples were obtained from fragments extracted with a Dremel® electric drill from the surface and interior of each coprolite.

Each macerated coprolite sample ( $\cong 1.0$  g) was transferred to a 15 ml Falcon tube, properly identified, to which was added a solution of 10% hydrochloric acid. After the samples were completely dissolved, the chemical reaction was stopped by adding double the volume in distilled water. The resulting solution was washed repeatedly with distilled water, followed by sifting through a Bertel® Tyler 500 mesh sieve.

Lastly, the sediment retained on the sieve was resuspended in distilled water and examined by bright-field microscopy at  $100\times$  and  $400\times$  magnification. Three drops of glycerine were added to each drop of sediment between microscope slide and cover slip.

The descriptions of species were based on the morphological and morphometric features of all the specimens of the two different morphotypes found, which consisted of one and four eggs respectively. Morphological measurements are expressed in micrometers, as mean  $\pm$  standard deviation, while ranges are shown in parentheses,

except for the morphotype for which there was only one specimen. A morphometric analysis was carried out using a Bel Photonics® ocular micrometer, and images were recorded with a Samsung® digital camera coupled to a Nikon® optical microscope.

### 3. Results

Three phosphatized *Crocodyliformes* coprolites (Fig. 1) without visible food remains, 1.4 to 1.8 cm in length, 0.9 to 1.0 cm in width and 4.0 to 7.0 g in weight after paleoparasitological processing, showed two different morphotypes of ascaridoid eggs. The first eggs were recovered from two coprolites and the second from a single coprolite that differed from the former. The two morphotypes are described below.

#### 3.1. Systematics

Phylum: Nematoda (Diesing, 1861) Potts, 1932.  
 Class: Secernentea (von Linstow, 1905) Dougherty, 1958.  
 Order: Ascaridida Skrjabin et Shulz, 1940.  
 Superfamily: Ascaridoidea Railliet et Henry, 1915.  
 Family: Heterocheilidae Railliet et Henry, 1915.  
 Genus: *Bauruascaris* n. gen.  
 Species: *Bauruascaris cretacicus* n. sp.  
*Bauruascaris adamantinensis* n. sp.

#### 3.2. *Bauruascaris* n. gen.

Quasi spherical eggs, cleaved (developing embryo), thick-shelled with outer mammillated surface, extremely or slightly rough, depending on the species. Parasites of Brazilian *Crocodylomorpha* from the Upper Cretaceous.

*Type species.* *Bauruascaris cretacicus* n. sp.

*Etymology.* The name *Bauruascaris* refers to the Bauru Group, a Brazilian lithostratigraphic unit where the species of the new genus were found in fossil *Crocodylomorpha* coprolites, and another sister genus of the superfamily Ascaridoidea (*askaris* [Greek], worms).

#### 3.3. *Bauruascaris cretacicus* n. gen. et n. sp.

(*n* = 4 specimens; Fig. 2)

Quasi spherical thick-shelled egg, cleaved (developing embryo),  $5.6 \pm 1.3$  (5.0–7.5) thick,  $61.3 \pm 4.3$  (57.5–67.5) long by  $51.9 \pm 2.4$  (50.0–55.0) wide, and extremely rough outer mammillated surface.

##### 3.3.1. Taxonomic summary

*Type host.* *Crocodylomorpha* Hay, 1930 (Sauropsida: Diapsida: Archosauromorpha) from the Upper Cretaceous (Campanian/Maastrichtian), possibly from the clades *Notosuchia* Gasparini, 1971 or *Baurusuchidae* Price, 1945.

*Site of infection.* Probably the stomach, but in severe infections, this species can presumably be found from the esophagus to the cloaca, as is the case of the current ascaridoid nematode parasites of modern *Crocodylomorpha*.

*Prevalence.* Two of 53 *Crocodyliformes* coprolites collected (3.8%).

*Type locality.* Phosphatized *Crocodyliformes* coprolites from the Upper Cretaceous (Campanian/Maastrichtian), Adamantina Formation, Bauru Group, in the municipality of Santo Anastácio, southwestern region of the state of São Paulo, Brazil, South America ( $21^{\circ} 58' 30''$  S;  $51^{\circ} 39' 11''$  W).

*Type specimen.* Deposited in the form of permanent glycerol slides in the paleoparasitology collection of the Paulo Milton Barbosa Landim Paleontology and Stratigraphy Museum at São Paulo State University – UNESP, in Rio Claro, state of São Paulo, Brazil, South America.

*Etymology.* The specific name derives from *Creta* [Latin], referring to the Upper Cretaceous, the geological period in which the species lived, parasitizing fossil *Crocodyliformes*.



Fig. 2. Photomicrographs of eggs of *Bauruascaris cretacicus* n. gen. et n. sp. (400× magnification): a – front view, b – side view.



Fig. 3. Photomicrograph of an egg of *Bauruascaris adamantinensis* n. gen. et n. sp. (400× magnification).

#### 3.4. *Bauruascaris adamantinensis* n. gen. et n. sp.

(*n* = 1 specimen; Fig. 3)

Quasi spherical thick-shelled egg, cleaved (developing embryo), 5.0 thick, 30.0 long by 27.5 wide, with slightly rough outer mammillated surface.

##### 3.4.1. Taxonomic summary

*Type host.* *Crocodylomorpha* Hay, 1930 (Sauropsida: Diapsida: Archosauromorpha) from the Upper Cretaceous (Campanian/Maastrichtian), possibly from the clades *Notosuchia* Gasparini, 1971 or *Baurusuchidae* Price, 1945.

*Site of infection.* Probably the stomach, but in severe infections, this species can presumably be found from the esophagus to the cloaca, as is the case of the current ascaridoid nematode parasites of modern *Crocodylomorpha*.

*Prevalence.* One of 53 *Crocodyliformes* coprolites collected (1.9%).

*Type locality.* Phosphatized *Crocodyliformes* coprolite from the Upper Cretaceous (Campanian/Maastrichtian), Adamantina Formation,

Bauru Group, in the municipality of Santo Anastácio, southwestern region of the state of São Paulo, Brazil, South America (21° 58' 30" S; 51° 39' 11" W).

**Type specimen.** Deposited in the form of permanent glycerol slide in the paleoparasitology collection of the Paulo Milton Barbosa Landim Paleontology and Stratigraphy Museum at São Paulo State University – UNESP, in Rio Claro, state of São Paulo, Brazil, South America.

**Etymology.** The name of the new species refers to the Adamantina Formation, a Brazilian geological unit where the species was found in a *Crocodylomorpha* coprolite.

#### 4. Discussion

The morphological characteristics of the eggs of both morphotypes, i.e., shape, shell type and internal content, enabled us to identify the specimens as belonging to the superfamily Ascaridoidea (Nematode: Ascaridida). Moreover, after a comprehensive comparative analysis of 44 ascaridoid species of modern *Crocodylomorpha*, excluding only *Trispiculascaris trispiculascaris* because the literature lacks a description of their eggs, the morphology (quasi spherical shape and outer mammillated surface) and morphometry (length and width) of the specimens of the two analyzed morphotypes were found to be similar to those of species of the genus *Dujardinascaris*, which are currently found in caimans, alligators, crocodiles and gavials in every continent. Therefore, *Bauruascaris cretacicus* n. gen. et n. sp. and *B. adamantinensis* n. gen. et n. sp. may be closely related to this genus.

However, *Bauruascaris cretacicus* n. gen. et n. sp. and *B. adamantinensis* n. gen. et n. sp. are distinguishable from all the species of *Dujardinascaris* by their thick shell, which also justifies the creation of this new genus and the two new species. Furthermore, *B. cretacicus* n. gen. et n. sp. is distinguishable from *B. adamantinensis* n. gen. et n. sp. for its different dimensions (length and width) and degree of roughness of its outer mammillated surface.

The thick shell of the eggs of *Bauruascaris* n. gen. allows one to infer that both species lived in a terrestrial habitat, substantiating the speculation, proposed and accepted by most paleobiologists, about the probable environment of the *Crocodylomorpha* of the Upper Cretaceous, belonging to the clades *Notosuchia* and *Baurusuchidae* [35], which may have produced of the coprolites analyzed in this study. The thick shell, which is absent from the eggs of practically all the ascaridoid species of the remaining *Crocodyliformes*, may have disappeared over the evolutionary history of these parasites because it became unnecessary in the semi-aquatic environments of their hosts, whose habitats have less unfavorable conditions for egg viability than terrestrial environments. According to [36], the production of eggs with complex multi-layered shells secreted by the uterine wall involves energy costs for the females of the parasites, thus reducing their oviposition, which may also explain the decreased in eggshell thickness of these nematodes over their evolutionary process.

Based on the general morphological characteristics of the adult parasites of the genus *Dujardinascaris* described in the literature [10,11,20,21,23–26], the species of the genus *Bauruascaris* n. gen. may have had lips with interlocking processes, bodies coiled in a spiral pattern, and a length of 3.0 to 40.0 mm. It is also plausible to infer, based on the morphometry of their eggs, that *Bauruascaris cretacicus* n. gen. et n. sp. was slightly larger than *B. adamantinensis* n. gen. et n. sp. In addition, also extrapolating from the biological cycle of the genus *Dujardinascaris*, according to [30,31], to *B. cretacicus* n. gen. et n. sp. and *B. adamantinensis* n. gen. et n. sp., the two species presumably reached their definitive hosts by preying on small vertebrates, especially amphibians and possibly even fish. These preys contained their infective larvae encysted in tissues, which were acquired by these intermediate hosts after ingesting their eggs from the environment and/or their initial larval forms from inside invertebrates (paratenic hosts), which in turn were also previously infected via their hatched eggs or larvae present in the environment.

The high diversity of ascaridoid genera and species found in modern crocodylians, in contrast to the modest number of species of these hosts, represented by only 23 species, is probably a legacy of the great diversity of *Crocodyliformes* that roamed the planet during the Triassic, Jurassic and Cretaceous periods and the Cenozoic Era. Due to the abundance of different types of hosts in this geological time interval, the ascaridoids of these animals may also have become widely diversified and spread to various regions and ecosystems, generating numerous genera and species. It is probable that the current ascaridoids, which are parasites of modern *Crocodylomorpha*, descended from some of these genera and ancestral species, which, notwithstanding the extinction of a large part of these reptiles in the Cenozoic Era, were able to survive, adapting over their evolutionary history to parasitize species of *Crocodyliformes* from different groups, and/or to coexist in equilibrium with others in the same host species.

These parasitic strategies are still visible today in the ascaridoid species that parasitize crocodylians. For example, *Multicaecum agile*, which is found in Oceania, Asia and Africa, may parasitize crocodylians of the family *Crocodylidae*, such as *Crocodylus johnstoni* (freshwater crocodile), *C. palustris* (mugger crocodile), *C. niloticus* (Nile crocodile) and *Mecistops cataphractus* (West African slender-snouted crocodile) and also of the family *Gavialidae*, such as *Gavialis gangeticus* (true gavia) [37]. Moreover, the ascaridoids *Dujardinascaris dujardini*, *D. gedoelsti*, *D. madagascariensis*, *D. puylaerti*, *Ingwenascaris asymetrica*, *I. sprenti*, *Gedoelstascaris vandenbrandeni*, *Ortleppascaris nigra*, *Hartwichia rousseloti*, *T. trispiculascaris*, *Orneoascaris chrysanthemoides*, and even *M. agile*, can simultaneously inhabit the digestive tract of the species *C. niloticus* (Nile crocodile) [28,29,37]. Therefore, species of stenoxenous ascaridoids and/or ascaridoids that were unable to survive in sympatry inside the same host probably became extinct in the Cenozoic Era.

This present paper therefore describes the oldest species of Ascaridoidea nematodes reported to date in *Crocodylomorpha*. These species can be considered the third most ancient fossil record of Ascaridoidea parasitizing vertebrates that have been published in the literature.

#### Declaration of Competing Interest

None.

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#### References

- [1] S.A. Nadler, D.S.S. Hudspeth, Phylogeny of the Ascaridoidea (Nematoda: Ascaridida) based on three genes and morphology: hypotheses of structural and sequence evolution, *J. Parasitol.* 86 (2000) 380–393, [https://doi.org/10.1645/0022-3395\(2000\)086\[0380:POTANA\]2.0.CO;2](https://doi.org/10.1645/0022-3395(2000)086[0380:POTANA]2.0.CO;2).
- [2] R.C. Anderson, *Nematode Parasites of Vertebrates: Their Development and Transmission*, second ed., CABI Publishing, Wallingford, 2000.
- [3] L.S. Roberts, J. Javony-Jr, *Foundations of Parasitology*, eighth ed., McGraw-Hill, New York, 2009.
- [4] G. Hartwich, R.C. Anderson, A.G. Chabaud, S. Willmott (Eds.), *Keys to the Nematode Parasites of Vertebrates: Archival Volume*, CABI Publishing, Wallingford, 2009, pp. 309–323 *Keys to genera of the Ascaridoidea*.
- [5] L. Li, L. Lü, S.A. Nadler, D.I. Gibson, L.P. Zhang, H.X. Chen, W.T. Zhao, Y.N. Guo, Molecular phylogeny and dating reveal a terrestrial origin in the Early Carboniferous for ascaridoid nematodes, *Syst. Biol.* 67 (2018) 888–900, <https://doi.org/10.1093/sysbio/syy018>.
- [6] J.F.A. Sprent, Ascaridoid nematodes, in: G.L. Hoff, F.L. Frye, E.R. Jacobson (Eds.), *Diseases of Amphibians and Reptiles*, Springer Science & Business Media, Berlin, 1984, pp. 219–245.
- [7] G. Poinar, A.J. Boucot, Evidence of intestinal parasite of dinosaurs, *Parasitology*. 133 (2006) 245–249, <https://doi.org/10.1017/S0031182006000138>.
- [8] P.A. Silva, V.H. Borba-Nunes, J.M. Dutra, D. Leles, A.A. Stock Da-Rosa, L.F. Ferreira, A.A. Araújo, New ascarid species in cynodont coprolite dated of 240 million years,

- An. Acad. Bras. Ciênc. 86 (2014) 265–269, <https://doi.org/10.1590/0001-3765201320130036>.
- [9] M. Hodda, Phylum Nematoda Cobb 1932, in: Z.Q. Zhang (Ed.), *Animal Biodiversity: An Outline of Higher-Level Classification and Survey of Taxonomic Richness*, Magnolia Press, Auckland, 2011, pp. 63–95.
- [10] L. Travassos, Sobre os Ascaroidea parasitos dos crocodylos sul-americanos, *An. Acad. Bras. Ciênc.* 5 (1933) 153–169.
- [11] J.F.A. Sprent, Ascaridoid nematodes of amphibians and reptiles: *Dujardinascaris*, *J. Helminthol.* 51 (1977) 253–287, <https://doi.org/10.1017/S0022149X00007586>.
- [12] J.F.A. Sprent, Ascaridoid nematodes of amphibians and reptiles: *Goezia*, *J. Helminthol.* 52 (1978) 91–98, <https://doi.org/10.1017/S0022149X00005174>.
- [13] J.F.A. Sprent, Ascaridoid nematodes of amphibians and reptiles: *Gedoelestascaris* n. g. and *Ortleppascaris* n. g., *J. Helminthol.* 52 (1978) 261–282, <https://doi.org/10.1017/S0022149X00005460>.
- [14] J.F.A. Sprent, Ascaridoid nematodes of amphibians and reptiles: *Multicaecum* and *Brevimulticaecum*, *J. Helminthol.* 53 (1979) 91–116, <https://doi.org/10.1017/S0022149X00005782>.
- [15] J.F.A. Sprent, Ascaridoid nematodes of amphibians and reptiles: *Terranova*, *J. Helminthol.* 53 (1979) 265–282, <https://doi.org/10.1017/S0022149X00006088>.
- [16] T.L. Deardorff, R.M. Overstreet, *Goezia lacerticola* sp. n. (Nematoda: Anisakidae) in *Alligator mississippiensis* from Florida, *J. Helminthol.* 53 (1979) 317–320, <https://doi.org/10.1017/S0022149X00006167>.
- [17] J.F.A. Sprent, Ascaridoid nematodes of amphibians and reptiles: *Typhlophorus*, *Hartwichia* and *Trispiculascaris*, *J. Helminthol.* 57 (1983) 179–189, <https://doi.org/10.1017/S0022149X00009457>.
- [18] J.F.A. Sprent, Ascaridoid nematodes of amphibians and reptiles: *Orneoascaris*, *Ann. Parasitol. Hum. Comp.* 60 (1985) 33–55, <https://doi.org/10.1051/parasite/198560133>.
- [19] J.F.A. Sprent, Some ascaridoid nematodes of fishes: Heterocheilinae, *Syst. Parasitol.* 16 (1990) 149–161, <https://doi.org/10.1007/BF00009613>.
- [20] M. Machida, J. Araki, P.A. Regoniel, F.A. Pontillas, Three species of ascaridoid nematodes from crocodile in the Philippines, *Bull. Natl. Sci. Mus.* 18 (1992) 95–102.
- [21] J.F.A. Sprent, E.A. McKeown, M. Cremin, *Dujardinascaris* spp. (Nematoda: Ascaridoidea) in Old World crocodylians, *Syst. Parasitol.* 39 (1998) 209–222, <https://doi.org/10.1023/A:1005934614630>.
- [22] J.F.A. Sprent, Species of *Typhlophorus* von Linstow, 1906 (Nematoda: Ascaridoidea) in Old World crocodylians, *Syst. Parasitol.* 43 (1999) 229–236, <https://doi.org/10.1023/A:1006117822808>.
- [23] F. Moravec, Some helminth parasites from Morelets crocodile, *Crocodylus moreletii*, from Yucatan, Mexico, *Folia Parasitol.* 48 (2001) 47–62.
- [24] Š. Mašová, V. Baruš, M. Seifertová, J. Malala, M. Jirků, Redescription and molecular characterisation of *Dujardinascaris madagascariensis* and a note on *D. dujardini* (Nematoda: Heterocheilidae), parasites of *Crocodylus niloticus*, with a key to *Dujardinascaris* spp. in crocodylians, *Zootaxa*. 3893 (2014) 261–276, <https://doi.org/10.11646/zootaxa.3893.2.6>.
- [25] J.H. Zhao, L. Li, Y.N. Guo, L.P. Zhang, *Dujardinascaris gigantea* sp. n. (Nematoda: Ascaridida) from the critically endangered crocodile *Alligator sinensis* Fauvel (Reptilia: Crocodylia), *Parasitol. Res.* 114 (2015) 801–808, <https://doi.org/10.1007/s00436-014-3980-z>.
- [26] J. Nacar-Muñoz, V. León-Règagnon, J.L. Cifuentes-Lemus, H. Hernández-Hurtado, P. Hernández-Hurtado, R.M. Chávez-Dagostino, *Dujardinascaris helicina* (Nematoda: Ascaridida) parásito de *Crocodylus acutus* (Reptilia: Crocodylidae) en Puerto Vallarta, Jalisco, México, *Rev. Mex. Biodivers.* 87 (2016) 1010–1014, <https://doi.org/10.1016/j.rmb.2016.07.017>.
- [27] J.H. Zhao, S.S. Wang, G.J. Tu, Y.K. Zhou, X.B. Wu, Morphological and molecular characterization of *Ortleppascaris sinensis* sp. nov. (Nematoda: Ascaridoidea) from the Chinese alligator *Alligator sinensis*, *J. Helminthol.* 90 (2016) 303–311, <https://doi.org/10.1017/S0022149X15000255>.
- [28] K. Junker, Y. Mutafchiev, *Ingwenascaris* n. g. (Nematoda: Ascaridida: Heterocheilidae) established for *I. sprenti* n. sp. and *I. asymmetrica* (Ortlepp, 1932) n. comb., parasites of African crocodiles, and an identification key to the genera of the Heterocheilidae, *Syst. Parasitol.* 94 (2017) 849–859, <https://doi.org/10.1007/s11230-017-9748-y>.
- [29] K. Junker, Y. Mutafchiev, *Typhlophorus kwenae* n. sp. (Nematoda: Ascaridida: Heterocheilidae), a gastric parasite from the Nile crocodile *Crocodylus niloticus* Laurenti (Reptilia: Crocodylidae) in South Africa, *Syst. Parasitol.* 94 (2017) 971–978, <https://doi.org/10.1007/s11230-017-9757-x>.
- [30] F.W. Huchzermeyer, *Crocodyles, Biology, Husbandry and Diseases*, first ed., CABI Publishing, Wallingford, 2003.
- [31] E. Jacobson, *Infectious Diseases and Pathology of Reptiles: Color Atlas and Text*, first ed., CRC Taylor & Francis, Boca Raton, 2007.
- [32] A.M.C. Cardoso, A.J.S. Souza, R.C. Menezes, W.L.A. Pereira, R. Tortelly, Gastric lesions in free-ranging black caimans (*Melanosuchus niger*) associated with *Brevimulticaecum* species, *Vet. Pathol.* 50 (2012) 582–584, <https://doi.org/10.1177/0300985812459337>.
- [33] J.H. Zhao, S.S. Wang, G.J. Tu, Y.K. Zhou, X.B. Wu, C. Li, Histopathology of gastric wall in Chinese alligator *Alligator sinensis* infected with *Ortleppascaris sinensis* (Nematoda: Ascaridoidea), *Nutr. Hosp.* 32 (2015) 1180–1183, <https://doi.org/10.3305/nh.2015.32.3.9344>.
- [34] R.J. Bertini, *Paleobiologia do Grupo Bauru, Cretáceo Superior continental da Bacia do Paraná, com ênfase em sua fauna de amniotas*, PhD Tesis IG/UFRJ, Rio de Janeiro, 1993.
- [35] D. Riff, R.G. Souza, G.M. Cidade, A.G. Martinelli, J.P. Souza-Filho, *Crocodylomorfos: a maior diversidade de répteis fósseis do Brasil*, *TERRÆ* 9, (2012), pp. 12–40.
- [36] R. Gaugler, A. Bilgrami, *Nematode Behaviour*, first ed., CABI Publishing, Wallingford, 2004.
- [37] M. Tellez, *Checklist of Host-Parasite Interactions of the Order Crocodylia*, first ed., University of California Press, Los Angeles, 2013.