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RESEARCH ARTICLE

# Tapeworm Eggs in a 270 Million-Year-Old Shark Coprolite

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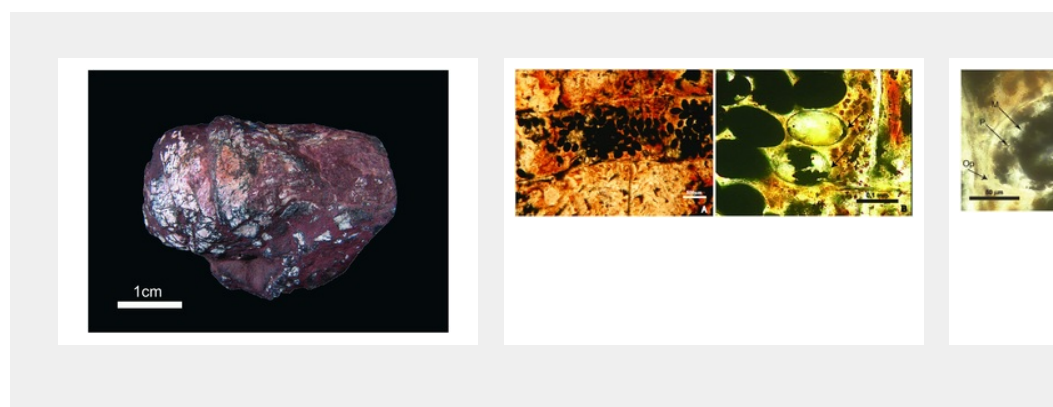
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## Figures



# Abstract

Remains of parasites in vertebrates are rare from the Mesozoic and parasites that live in – or pass through – the gastrointestinal tract or feces (coprolites) or even intestinal contents (enterolites) can even remain. Here we announce the discovery of a spiral shark coprolite bearing a cluster of 93 small oval-elliptical smooth-shelled structures of a tapeworm. The eggs were found in a thin section of an elasmobranch. The eggs are filled by pyrite and some have a special polar swelling suggesting they are non-erupted eggs. One of the eggs contains a larva. The eggs are approximately 145–155  $\mu\text{m}$  in length and 88–100  $\mu\text{m}$  in width and vary little in size within the cluster. The depositional and morphological features of the eggs closely resemble those of cestodes. Not only do the individual eggs resemble those of extant tapeworms, but their deposition all together in an elongate structure is similar to modern tapeworm eggs deposited in mature segments (proglottids). This discovery provides a fossil record of tapeworm parasitism of vertebrates and establishes the evolution of cestodes. This discovery shows that the fossil record of parasites is much older than was hitherto known and that the interaction between tapeworms and vertebrates occurred at least since the Middle-Late

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## Introduction

Paleoparasitology is the study of parasites found in archaeological material [1], [2]. Parasite remains consist mostly of eggs and larvae [3], mainly helminthes, and can provide important diet and disease information to their hosts. Helminthes include nematodes (roundworms), trematodes (tapeworms), and acanthocephalans (thorny-headed worms).

Presently, elasmobranchs carry within their spiral intestines various parasites, being cestodes the most diverse of them [4]. Cestodes have also been found in the viscera and body cavity of numerous large teleosts and from the stomachs of marine mammals. Cestode eggs are characterized by their smooth external surface, polar and equatorial bulges, spines or striations [6].

Extant and fossil tapeworm eggs are morphologically very similar to each other, making it impossible to diagnose a specific infection based only on eggs [3]. Thus, paleoparasitological analyses using them are limited to the phylum level.

Helminth parasites rarely produce eggs with long-lived resistance to environmental stressors. Most of their eggs are fragile, so that they start to decompose soon after being laid outside their host [3]. Eggs of some nematode and cestode parasites have a higher chance of recovery [3]. The crucial factor for the preservation of parasite eggs is the interruption of decay. It usually occurs only under extreme moist, anaerobic environmental conditions [7].

In archeological studies it is usual to find well-preserved remains of intestinal parasites which affected health [3], [8], [9], [10]. However, the older the site, the greater the loss of parasites [9]. In fact, the occurrence of fossil parasites in paleontological material is rare. For the Mesozoic [11], just a single cestode parasite (protozoan cysts and helminth eggs) in a coprolite was described. In the Paleozoic, a mass of possible helminth eggs from the coprolitic rectum of a Pennsylvanian shark, perhaps of cestode origin [12], was described. In the Paleozoic, parasitic platyhelminth hooks were found in acanthodians from the Permian.

Here in we describe the first definite record of cestode parasites in a coprolite from the Paleozoic (about 270 Ma), which is, in fact, the oldest record of cestode eggs in a vertebrate coprolite. The specimen is housed in the Laboratório de Paleontologia de Vertebrados of the Universidade Federal do Rio Grande (FURG), with the collection number UFRGS-PV-429-P. No specific permits were required for the described field studies.

## Materials and Methods

The material came from the Rio do Rasto Formation from Paraná Basin, Permian [14] and was collected in the municipality of São Gabriel, Santa Catarina. The formation is characterized by a sequence of fine to medium cross-bedded sandstones, interbedded with siltstones and mudstones, and is interpreted to have formed under fluvio-lacustrine conditions [14]. Its fossil record consists of coprolites, invertebrates and vertebrates [15], [16], [17].

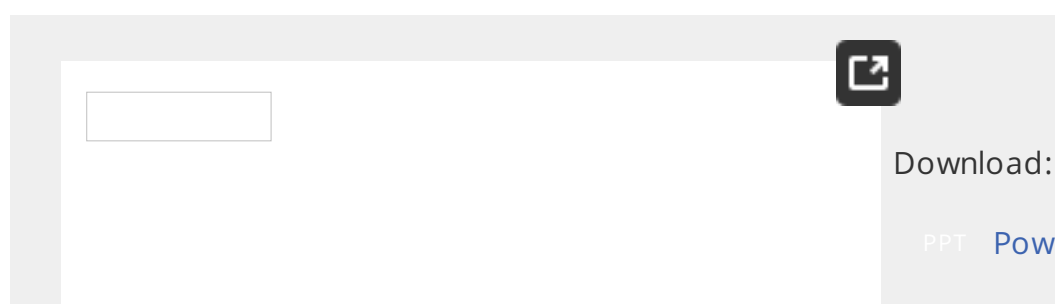
In the same outcrop where UFRGS-PV-429-P was collected, we have

other coprolites in an area of 100 m×30 m [18]. All the specimens were measured and 14 specimens were cut using standard thin section (used for rock samples), in order to search for internal structures, possible inclusions [18], [19]. Longitudinal sections were made in all the 14 specimens approximately in a median plane of each one. In three of them a transverse section was made too. The thin section obtained from the longitudinal cutting of the coprolite showed, under optic microscopy, scales and bone fragments [18], and unusual oval-shaped structures. This coprolite (Fig. 1), with 5 cm in length and 1 cm in diameter, is classified as a spiral heteropolar [20], characterized by closely spaced whorls concentrated in just one end. This morphology (fish scales and bone fragments) are typical features for elasmobranch coprolites.



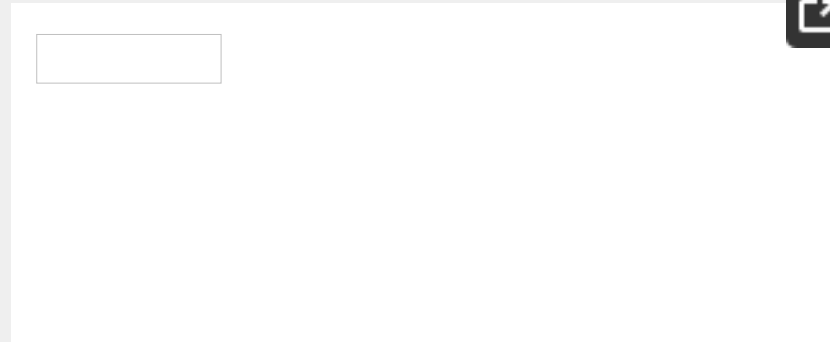
## Results and Discussion

The oval-shaped structures (# =93) are grouped in a segment 4 mm long (Fig. 2A). They reveal structures typical of tapeworm eggs. The eggs are shelled and range from 145–155 µm in length and 88–100 µm in width. They are filled with pyrite and/or hematite. Some eggs appear to have been broken. One egg contains a developing embryophore (Fig. 3). In this egg, only part of the vitelline envelope, composed by a thin shell or “capsule”, remains. The remaining vitelline capsule, apparently underwent apoptosis, as occurs with elasmobranch coprolites [21]. The inner envelope is composed of several layers, the innermost being the embryophore (oncosphere). Portions of the oncospherical membrane are apparent. Within the embryophore is a cluster of small putative somatic cells and some fiber-like objects that could represent early stages of development. Strands of dense material seemingly attached to the embryophore are present. Thickening of the inner envelope [22]. A small slightly protruding operculum is present. Opercula can be better observed on eggs in Fig. 2B.



### Figure 2. Parasite eggs in a shark coprolite.

A - Thin section of the coprolite part containing clustered parasite eggs, the perfect oval shape hole were formed after the filling with resin from the coprolite during the lamination, the arrows show the opening of the eggs. <https://doi.org/10.1371/journal.pone.0055007.g002>



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### Figure 3. Cestode egg.

A - (photo) Cestode egg with a developing embryophore. B - (drawing) reconstruction of egg in A. Abbreviations: C= capsule or shell; E= embryophore (ochosphere); H= putative developing hooklets; I=inner envelope membrane; O=outer envelope; P=putative polar thickening; Op=opercular somatic cells.

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Besides the similar morphology, the mass deposition of these fossil eggs in a single segment is typical of modern tapeworm eggs deposited in mature proglottids. A proglottid of an extant tapeworm proglottid is full of eggs, it breaks off in the stomach of the host and eventually passes out of the body with the feces [23]. Nourishment of the eggs occurs only after this separation, so fully mature eggs occur only in the feces [24].

Since the fossil egg contains both yolk and a well-developed shell, it has extensive vitellaria. This is characteristic of the pseudophyllidean eggs in the Pseudophyllidea, Trypanorhyncha and Tetraphyllidea, all of which are parasitic on vertebrate hosts [21], [25], [26].

Tapeworm taxonomy is confusing and controversial. Typically four orders of tapeworms parasitize elasmobranchs, the Diphyllidea, Lecanicephala, and Trypanorhyncha [6], [27]. Unfortunately very little information is available on the internal structure in these orders. Even the few measurements given are incomplete and were made on eggs in segments still attached to the parasite and in which the eggs continue to develop (and enlarge) after the proglottids are released from the host [24].

The larger size of the fossil eggs described herein distinguish them from modern tapeworm eggs. In size and shape the fossil eggs most closely resemble

shark parasite, *Disculiceps pileatum* (Linton) (= *Discocephalum pileatum*) which has oval, brown eggs measuring 110 µm long by 80 µm wide. The systematic placement of this species is controversial. It was considered a "new species" and originally described as a new order, the Heterophyllida, but was later transferred to the Tetraphyllida [25]. Since the size of the great rhabdionch tapeworm eggs are unknown, some extant forms could fall within the range of the fossils. Then again, the large egg size could be characteristic of Permian cestodes.

Although it is not possible to assign the fossil eggs to any extant tapeworm, the characters (operculum, egg shape and size) are reminiscent to those of the Tetraphyllida. This is the most widespread order of cestodes found in the Permian, with some 540 extant species.

In some fish parasites (nematodes species) the mature eggs contain stage larvae, which do not hatch spontaneously in the external environment. In other groups are uncleaved at the time of oviposition, and the larvae hatch in the external environment, where they undergo their first moult inside the egg. This could explain why we did not find larvae in all of the eggs.

The presence of pyrite in the coprolites indicates anoxic environments, which probably were responsible for the preservation of both coprolites. A similar pattern occurs in feces of Neolithic Age, in which some parasitic embryos inside the egg, filled with crystals of pyrite [9], [29].

The possibility of the fossil eggs belonging to a trematode or nematode is also considered. However, eggs of digenetic trematodes are deposited singly and not in masses, as in the case of the present fossils. They also do not demonstrate hook formation for development. Most trematodes associated with sharks are ectoparasites of the body cavity (pericardial and coelomic cavities). While the spiral valve is usually full of cestodes, there are almost never digenetic trematodes [31], [32].

Nematodes are also rare in sharks and while species of *Acanthostrongylus* Mawson, 1954 occur in the alimentary tract, they are found singly, not in masses [33].

The crowding of individuals of a population in a restricted area favors the preservation of parasites [9], which enhance the possibility of its preservation, as occurred in the present case. As mentioned above, the coprolite is composed of more than 500 specimens found in a restricted area. It was interpreted as a site where many fishes became entrapped for some time, probably during a storm, which could explain the great number of coprolites of different shapes and sizes, as well as the anoxia in the bottom of the water column (evidenced by the presence of pyrite in the coprolites and also by the high number of preserved coprolites).

Many extant tapeworms require several hosts to complete their development. Often an invertebrate that is eaten by a second host, normally a frog, and the maturation continues through the next stage [34]. Tapeworms react

(developing eggs) when that animal is eaten by a third, and final, host. This coprolite has fish scales and bone fragments allowing us to infer that this tapeworm was a fish.

Even in Holocene remains only a small amount of coprolites contain parasite eggs, which depend on the method of processing and observation selected. The finding of parasite eggs in a coprolite of about 270 Ma is an amazing discovery because no special method was used to find the parasite eggs.

Infectious diseases have been poorly reported for vertebrates from the Paleozoic as a whole. Even extensive studies of inclusions in coprolites have not found any parasite. The fossil parasite eggs presented here corroborate the hypothesis that parasitism was present since the advent of life [37].

This is the earliest fossil record of tapeworm parasitism of vertebrates, marking a key point in the timeline for the evolution of cestodes. Analyses of tapeworm phylogeny and on parasite phylogeny and the mapping of host groups, there is no evidence that eucestodes existed in archaic sharks and rays [26]. While it is impossible to know which vertebrate group served as the original hosts to tapeworms, the primitive elasmobranchs (neoselachians), were hosts of tapeworms some 270 Ma. The lacustrine environment could well have been the ancestral habitat of primitive elasmobranchs as their primitive final hosts.

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## Author Contributions

Field and laboratorial support: AEQF, BH. Analyzed the data: PCD-D, GP, AEQF. Wrote the paper: PCD-D, GP, AEQF.

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