



Diversity of biogenic silica bodies in the stomach of bottom fishes of the upper Paraná River Floodplain

Diversidade de corpos de sílica biogênica no estômago de peixes bentônicos da planície aluvial do alto rio Paraná

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The Upper Paraná River Floodplain includes rivers, channels, and lagoons with distinct limnological features. In this region, benthic fish represent 47% of the ichthyofauna and feed on sediments rich in silt, sand, and organic material. These deposits preserve biogenic silica structures such as sponge spicules, phytoliths, and diatom frustules, which are useful in paleoenvironmental and taxonomic studies. Although biogenic silica in freshwater fish diets is poorly studied, its presence in benthic species may reflect the silica-producing organisms in the environment. Thus, the aim was to identify the diversity of biogenic silica bodies in the stomachs of bottom fish of the Upper Paraná River Floodplain. Phytolith analysis demonstrated morphotypes characteristic of those produced by grasses, tree and shrub species and indicated palm trees' presence. Therefore, the analysis of biogenic silica in the stomachs of bottom-dwelling fish proved to be effective in identifying and analyzing the dispersion of freshwater sponges. The results confirmed the predation of five species of freshwater sponges in the environments and sub-environments sampled and the analysis of phytoliths demonstrated the presence of morphotypes already described for those produced by plant region.

Keywords: biomineralization, phytoliths, freshwater sponge.

A planície aluvial do Alto Paraná inclui rios, canais e lagoas com características limnológicas distintas. Nessa região, os peixes bentônicos representam 47% da ictiofauna e se alimentam de sedimentos ricos em silte, areia e matéria orgânica. Esses depósitos preservam estruturas de sílica biogênica, como espículas de esponjas, fitólitos e frústulas de diatomáceas, que são úteis em estudos paleoambientais e taxonômicos. Embora a sílica biogênica na dieta de peixes de água doce seja pouco estudada, sua presença em espécies bentônicas pode refletir os organismos produtores de sílica no ambiente. Assim, o objetivo deste estudo foi identificar a diversidade de corpos de sílica biogênica nos estômagos de peixes bentônicos da planície aluvial do Alto Paraná. A análise de fitólitos demonstrou morfotipos característicos daqueles produzidos por gramíneas, árvores e arbustos, e indicou a presença de palmeiras. Portanto, a análise de sílica biogênica nos estômagos de peixes bentônicos mostrou-se eficaz na identificação e análise da dispersão de esponjas de água doce. Os resultados confirmaram a predação de cinco espécies de esponjas de água doce nos ambientes e subambientes amostrados, e a análise dos fitólitos demonstrou a presença de morfotipos já descritos para aqueles produzidos pela região da planta.

Palavras-chave: biomineralização, fitólitos, esponja de água doce.

1. INTRODUCTION

Biogenic silica structures, such as sponge spicules, phytoliths, and diatom frustules, serve as valuable tools for research in fluvial environments. These microfossils enable paleoenvironmental and paleontological investigations, as well as studies on sedimentation and erosion processes, and on the composition of regional plant and poriferan communities. Their potential lies in the fact that these structures can persist even in highly oxidized soils, where other organic proxies, such as seeds and pollen grains, typically fail to be preserved [1]. Freshwater sponges possess a body structure composed of spongin fibers associated with

siliceous spicules categorized as megascleres, microscleres, and gemmoscleres [2]. The spicules derived from gemmules (gemmoscleres) hold taxonomic value and can indicate the family, genus, and species of the original organism [3]. Once dissociated from the sponge skeleton in nature, these spicules are commonly preserved in lacustrine and fluvial sediments [4-6].

In plants, the biomineralization of silica results in the formation of phytoliths—microbodies of opaline and amorphous silica ($\text{SiO}_2 \cdot \text{H}_2\text{O}$) precipitated within and between living plant cells [7]. Phytolith morphology typically reflects the shape of the original plant cells [8]. Due to the isometric nature of the source cells, phytoliths are taxonomically informative and particularly useful for identifying families such as Arecaceae and Poaceae [9-11]. After plant death and organic matter decomposition, phytoliths from different plant species can accumulate in sediments, enabling relatively accurate inferences about local vegetation [12]. Another photosynthetic silica biomineralizer is the diatom, whose cell wall — known as a frustule — is composed of biogenic silica [13]. These frustules are taxonomically diagnostic, with each diatom species exhibiting a specific morphology. Their thermal and mechanical resistance favors preservation in sedimentary environments [14].

Silica-biomineralizing organisms, such as plants, have been documented in the diets of various animals. For instance, phytoliths have been recovered from the digestive tracts of ruminants [15]. In addition to plants, sponges can also serve as a source of biogenic silica, and have been shown to be consumed by marine fish [16]. However, the presence of biogenic silica in the diets of freshwater fish remains poorly studied. Nonetheless, sponge spicules have been found in the stomach contents of benthic fish from Itaipu Reservoir [17]. Moreover, the analysis of phytolith morphotypes preserved in the digestive contents of bottom-feeding fish remains an understudied area.

The alluvial plain of the Upper Paraná River begins downstream of the Porto Primavera Dam (Engenheiro Sérgio Motta Hydroelectric Plant) and extends to the backwater zone of the Itaipu Hydroelectric Reservoir. The width of the plain spans a stretch of less than 230 km [18]. The region is part of the Atlantic Forest biome, specifically within the phytogeographic zones of Semi-deciduous Seasonal Forest, Alluvial Semi-deciduous Seasonal Forest, and Pioneer Formation with Fluvial-Lacustrine Influence, all of which are directly influenced by the water regime of the channel and the groundwater table [19].

The Upper Paraná River floodplain is characterized by a mosaic of rivers, channels, and both open and closed lakes, which differ markedly in their limnological characteristics [20, 21]. This floodplain is located in the Neotropical region; which harbors the highest global biodiversity, including freshwater fish species [22]. Benthic fish account for 47% of the total fish fauna in the Upper Paraná River floodplain and are known for their varied diets, which include silt, sand, and the full range of materials found in bottom deposits [23]. Sedimentological studies in this region have demonstrated the preservation of biogenic silica structures such as sponge spicules, phytoliths, and diatom frustules [5].

Live freshwater sponges have been recorded along the margins and bottoms of aquatic bodies in Brazil [22-26]. Due to the limited accessibility of floodplain environments, discovering new sponge species may require complex logistics. In this context, benthic fish may feed on sponges, and analyzing their stomach contents could help detect the presence of specific sponge species in the environment. These fish also ingest bottom-deposited materials [23], which may contain accumulated phytoliths, sponge spicules, and frustules, along with aquatic plants adhered to the substrate. This includes species from the family Podostemaceae, which produce phytoliths of taxonomic significance [27]. In this context, the aim of this study was to identify and quantify the diversity of biogenic silica bodies present in the stomach contents of benthic fish from the Upper Paraná River floodplain, a region recognized for its high biological diversity. Furthermore, this study will provide evidence of the origin of these biogenic silica bodies in the stomach contents of the fish, allowing inferences about the occurrence of freshwater sponge species and riparian plants associated with the environment.

2. MATERIALS AND METHODS

2.1 Study area

The study area is the alluvial plain of the Upper Paraná River, in the subsystems of Ivinhema, Baía and Paraná Rivers. The fish sampling sites were the Patos Lagoon which is located on the Ivinhema subsystem, a Closed lagoon located on the Baía subsystem, the Baía River, the Ivinhema River and the Paraná River main channels (Figure 1). These points were selected due to the occurrence of bottom fish species.

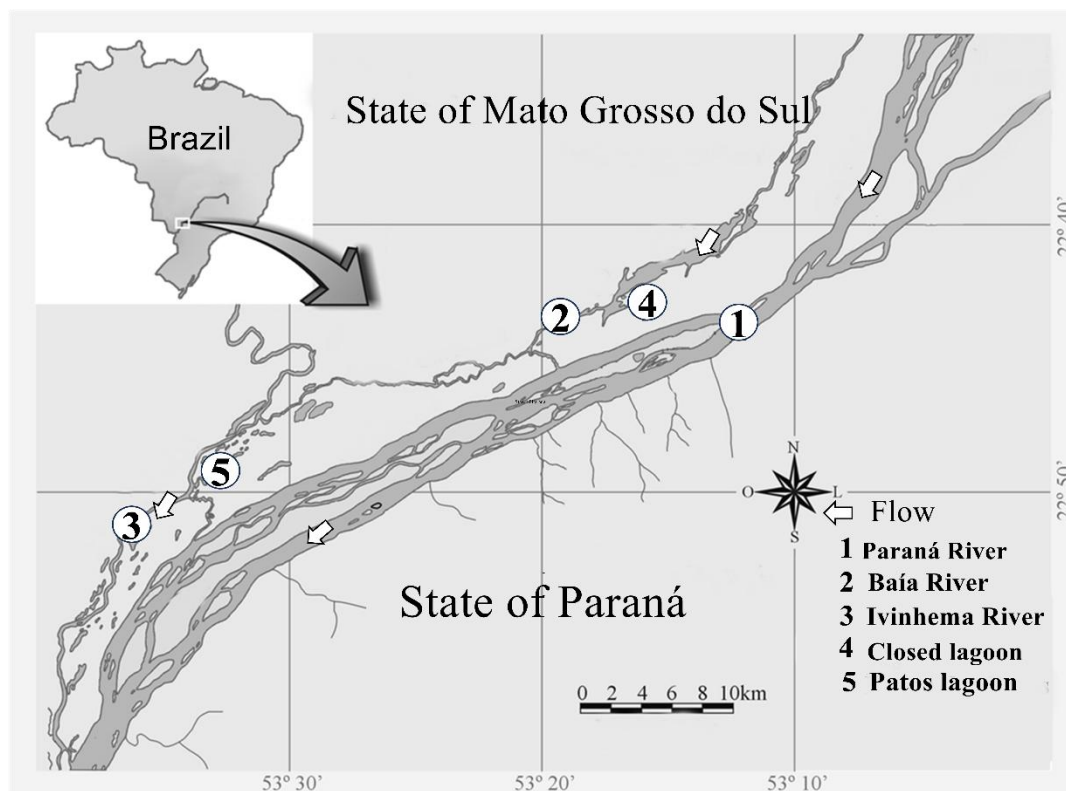


Figure 1: Location of the study area in the Upper Paraná River Floodplain. Source: Adapted from: http://www.peld.uem.br/images/planicie_2010.jpg.

The climate is classified as humid subtropical mesothermal (Cfa) according to the Köppen-Geiger classification, with an average annual temperature of 21.2 °C. February is typically the hottest month, with average highs often exceeding 32 °C, while July is the coldest, with average lows around 11 °C [28]. Rainfall averages more than 30 mm per month throughout the year, with the highest precipitation occurring between September and December, and the lowest between June and August [29].

2.2 Sampling

Five fish species were selected: five *Loricariichthys platymetopon* (Isbrücker & Nijssen, 1979), one *Loricaria* sp., two *Hypostomus regain* (Ihering, 1905), five *Pterygoplichthys ambrosettii* (Holmberg, 1893), and one *Hypostomus cochliodon* (Kner, 1854). The sampled animals are part of the campaigns and collection of the Programa de Pesquisa Ecológica de Longa Duração (PELD) which carries out quarterly collections in different environments. Fourteen individuals whose stomachs contained biogenic silica structures were sampled. Of the total, eight individuals were females and six were males. The sampled animals are part of the

campaigns and collection of the Programa de Pesquisas Ecologicas de Longa Duração (PELD) which carries out quarterly collections in different environments. The fish were captured in a period of high flow in December 2022 through gillnets of different mesh sizes: 2.4, 3, 4, 6, 7, 8, 10, 12, 14 and 16 cm between non-adjacent nodes, 20 m trawl nets and sieves. The fish were anesthetized and euthanized with a standard solution of 100 g of benzocaine in 1 L of ethanol (92%), diluted at the rate of 2 ml per liter of water (according to the 2015 CONCEA Euthanasia Practice Guidelines). They were stored in plastic bags and identified at the Ichthyology Laboratory of the State University of Maringá (UEM), later the stomachs were extracted and fixed in 10% formalin. The sampling was approved by the Ethics Committee on the Use of Animals (CEUA), process No 9251160223.

2.3 Biogenic silica analysis

The biogenic silica bodies were recovered in the following steps: 1) The stomach was treated with HNO₃ (65%) + H₂O₂ (v. 130) on a heating plate for 40 min (200 °C); 2) centrifugation (1000 rpm/3min) followed by washing of the resulting material with distilled water; 3) washing with neutral detergent; 4) washing with alcohol (70%); 5) drying in an oven (24 hours at 75 °C). The resulting material was weighed and alcohol was added, it corresponds to mineral inorganic material and biomineralizations, i.e. recovered inorganic material (RIM). Using a mechanical pipette (50µl), it was collected and deposited on slides that, after drying, were covered with entellan® and coverslip. The analyzed slides were deposited in the Laboratory of Paleoenvironmental Studies of Fecilcam/UNESPAR – LEPAFE/Campus Campo Mourão-Paraná-Brazil.

The slides were analyzed using an Olympus petrographic optical microscope with 10x and 40x magnification, and the images were captured with a 50-megapixel camera. Six transects were analyzed for each slide and for each type of biogenic silica structure (phytoliths and freshwater sponge spicules) were used for the counting and identification of biomineralizations.

Phytoliths were classified according to the morphological descriptions provided by the International Code for Phytolith Nomenclature (ICPN 2.0) [9]. The spicules of freshwater sponges were classified according to the Catalogue of Brazilian Porifera [30].

3. RESULTS

Among the five species of analyzed fish, all specimens had biogenic silica in their stomachs. Of the 14 animals sampled, 13 had phytoliths and nine had identified sponge megascleres and gemmoscleres, and diatom frustules were present in all animals.

In the set of analyzed stomachs, an average of 0.84 g ($\pm$ 0.85 g) of inorganic material was recovered, 6.5 ($\pm$ 3.18) phytolith morphotypes and 1.5 ($\pm$ 1.74) of sponge spicules were identified in all animals (Table 1). The male specimens presented an average of 1.25 g ($\pm$ 0.98 g / n=6) of inorganic material, 5.83 ($\pm$ 3.66) of phytolith morphotypes, 0.83 ($\pm$ 0.75) of sponge spicules, and 1 identifiable gemosclera ($\pm$ 0.70). The females had an average of 0.54 ($\pm$ 0.64 / n=8) of inorganic material, 6.7 of phytolith morphotypes ($\pm$ 2.92) and three types of sponge gemmoscleres ($\pm$ 2.12).

Table 1: Fish sampled in the Upper Paraná River floodplain. Acronyms: locality (LL) — Ivinhema River (Rivi), Baía River (Rbai), Paraná River (Rpar), Patos Lagoon (Lpat), and Closed Lagoon (Lclo); total length of the fish (TL); reproductive maturity (RM) — mature (Mat) and immature (Imt); total weight of the fish (TW, g); recovered inorganic material (M, g); sex (S) — female (F) and male (M); phytolith morphotypes (PM); sponge gemmoscleres (SG).

LL	Species	TL	RM	TW g	M g	S	PM	SG
Rpar	<i>Hypostomus regain</i>	23,6	Mat	186.9	0.79	F	BUL_FL A, ACU_BUL and SPH_ORN.	-
	<i>Hypostomus regain</i>	20,5	Imt	83.9	1.04	M	-	-
Rbai	<i>Loricariichthys platymetopon</i>	28,6	Mat	126.6	0.22	F	BIL, ACU_BUL, REC_PSI, SPH_ORN, BLO, BUL_FL A and CLA.	<i>Oncosclera schubarti</i> and <i>Tubella paulula</i> .
	<i>Loricariichthys platymetopon</i>	31,5	Mat	175.1	0.16	F	ELO_FAC, ELO_DEN, ELO_ENT, BLO, BLO_LAC, SPH_ORN, RON, POL, OBL and CLA.	<i>Oncosclera navicella</i> and <i>Oncosclera schubart</i> , <i>Uruguaya corallioide</i> , <i>Tubella paulula</i> and <i>Tubella variabilis</i> .
	<i>Pterygoplichthys ambrosetti</i>	44,1	Mat	707.6	2.90	M	BUL_FL A, SPH_ORN, SPH_PSI, BLO, BLO_PSI, ELO_ENT and BIL.	<i>Oncosclera navicella</i>
Rivi	<i>Loricaria sp.</i>	24,5	Mat	49.7	0.31	F	ELO_ROU, CYL, ELO_ENT, SPH_ORN	-
	<i>Hypostomus cochliodon</i>	21,4	Imt	165.3	0.67	M	CIR_RON, SPH_ORN, SPH_ECY, BIL, ELO_ENT, ACU_BUL, TAB, TAB_PSI and BLO_ROU.	-
Lclo	<i>Loricariichthys platymetopon</i>	29,4	Mat	108	0.05	M	BLO, ELO_ENT and BIL.	<i>Oncosclera navicella</i>
	<i>Loricariichthys platymetopon</i>	29,5	Mat	139.3	0.07	F	BU_FL A and ELO_ENT.	-
	<i>Pterygoplichthys ambrosetti</i>	34,5	Mat	462.6	1.73 20	M	RLO_ENT, SPH_PSI, SPH_ORN, REC_ROU, TAT_PSI, ELO_DEN, BIL and BUL_FL A.	<i>Tubella variabilis</i> and <i>Oncosclera navicella</i> .
	<i>Pterygoplichthys ambrosetti</i>	36,3	Mat	505.2	1.11	M	BLO_PSI, BUL_PSI, ELO_ENT, RON, BIL, SPH_ORN and SPH_ECH.	<i>Tubella variabilis</i> .
	<i>Pterygoplichthys ambrosetti</i>	30,2	Mat	372.7	0.67	F	BUL_FL A, RON, REC_PSI, REC_ROU, ELO_ENT, ACU, BIL, SPH_ORN and CUR.	<i>Tubella paulula</i>
	<i>Loricariichthys platymetopon</i>	28,9	Mat	133	0.11	F	BUL_FL A, TAB_PSI, ELO_SIN; BLO_PSI, ELO_ENT, SPH_ORN, SPH_PSI, BIL and CLA.	<i>Oncosclera navicella</i> , <i>Tubella variabilis</i> and <i>Tubella paulula</i> .
Lpat	<i>Pterygoplichthys ambrosetti</i>	35,6	Mat	438.6	1.98	F	BLO_PSI, ELO_ENT, OBL, SAD, RON, BIL, ACU_BUL, SPH_PSI and SPH_ORN.	<i>Tubella paulula</i> .

3.1 Sampled environments

In the Paraná River, only two individuals of *Hypostomus regani* (Ihering, 1905) were analyzed, and an average of 0.92 g ($\pm$ 0.17 g) of inorganic material was recovered. Three phytolith morphotypes were named, BULLIFORM FLABELLATE (BUL_FL A), ACUTE BULBOSUS

(*ACU_BUL*) and SPHEROID ORNATE (*SPH_ORN*). In the stomach contents of fish from this site, diatom frustules, one sponge spicule of the megasclere type acanthoxea, and another of the acanthostrongyle type were recovered (Figure 2).

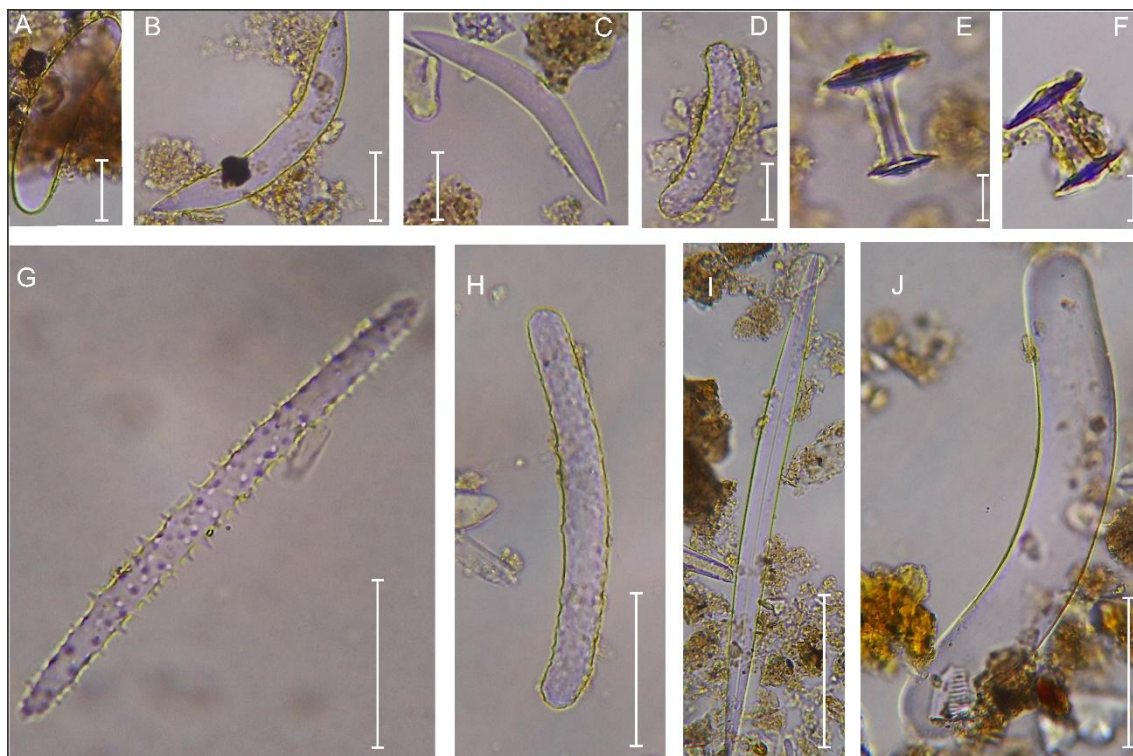


Figure 2: Main gemmoscleres and megascleres of freshwater sponges found in the stomach of bottom-dwelling fish in the alluvial plain of the Upper Paraná River. Images A–F were obtained under a 40× objective lens (scale bar = 15 µm); image G under a 10× objective lens (scale bar = 50 µm); and images H–J under a 40× objective lens (scale bar = 100 µm). Gemmoscleres: A *Uruguaya corallioides*; B and C *Oncosclera navicella*; D *Oncosclera schubarti*; E *Tubella paulula*; F *Tubella variabilis*. Megascleres: G Acanthoxea (*Tubella manauara*); H Acanthostrongyles (*Corvospongilla seckti*); I Oxea; J Strongyle.

The highest average of inorganic material in the stomachs of the fish was recovered in the specimens of the Baía River, with an average of 1.10 g (± 1.56). In this environment, 16 phytolith morphotypes were identified with redundancy for the *SPH_ORN* and BLOCKY PSILATE (*BLO_PSI*) found in all individuals. Four species of sponges (average of 2.67 ± 2.08) were identified, namely: *Oncosclera schubarti* (Bonetto & Ezcurra de Drago, 1967), *Tubella paulula* (Bowerbank, 1863) and *Oncosclera navicella* (Carter 1881) preyed upon by two animals and *Uruguaya corallioides* (Bowerbank, 1863).

In the Closed lagoon, the average inorganic material present in the stomachs of fish was 0.72 g (± 0.71). A total of 15 phytolith morphotypes were identified with ELONGATE ENTIRE (*ELO_ENT*) found in all individuals, while BILOBATE (*BIL*) and *BUL_FLA* were identified in only four individuals. The animals preyed on three species of sponges (average of 1 ± 0.71), which were identifiable as *Tubella variabilis* (Bonetto & Ezcurra de Drago, 1973), *O. navicella* and *T. paulula* (Table 1). In the Ivinhema River, the lowest average of inorganic material was recovered in the stomachs ($0.49 \text{ g} \pm 0.25 / n=2$). And, 12 phytolith morphotypes were identified, *SPH_ORN* and *ELO_ENT* were found in the two sampled individuals. Three megascleres oxea were detected.

In the Patos Lagoon, a greater amount of inorganic material was recovered in the stomachs compared to the previous environment, with an average of 1.05g ($\pm 1.32 / n=2$). At this site, 14 phytolith morphotypes (average of 9 ± 0), and four gemmoscleres (2 ± 1.41) were identified. The most redundant morphotypes were *BLO_PSI*, *ELO_ENT*, *SPH_ORN*, *BIL*, and SPHEROID

PSILATE (*SPH_PSI*), found in both species. The sponge species *T. paulula* was preyed upon by the two animals sampled in this lagoon.

The quantity of gemmoscleres varied between the fish species *L. platymetopon* and *P. ambrosettii*. Gemmoscleres of sponge species *O. navicella*, *T. paulula*, and *T. variabilis* were recorded in the stomach contents of both fish species, whereas *O. schubarti* and *U. corallioides* were found exclusively in the stomach contents of *L. platymetopon* (Figure 3).

A total of 743 megasclere spicules were recorded across the analyzed species, with an average of 96 per individual and a high standard deviation (± 100.85). In *L. platymetopon*, the number of spicules ranged from zero to 267, totaling 480 structures in the five specimens analyzed, with a mean of 96 (± 103.85). In *H. regani*, the two examined individuals contained 11 spicules, with an average of 5 (± 2.12). The single specimen of *Loricaria sp.* presented three megascleres. In *P. ambrosetti*, five individuals accounted for 249 spicules, with an average of 49.8 (± 37). In *H. cochliodon*, however, no spicules were recorded (Figure 4).

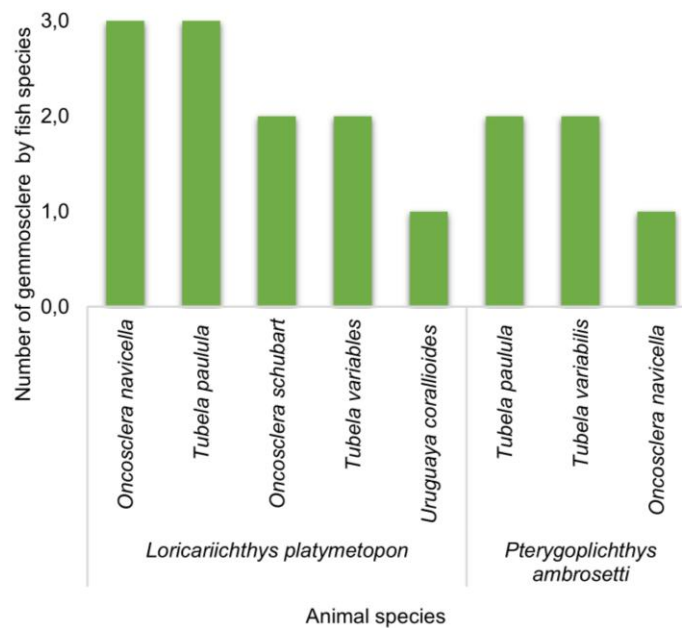


Figure 3: Predation on sponge gemosclera by bottom-dwelling fish species in the alluvial plain of the Upper Paraná River.

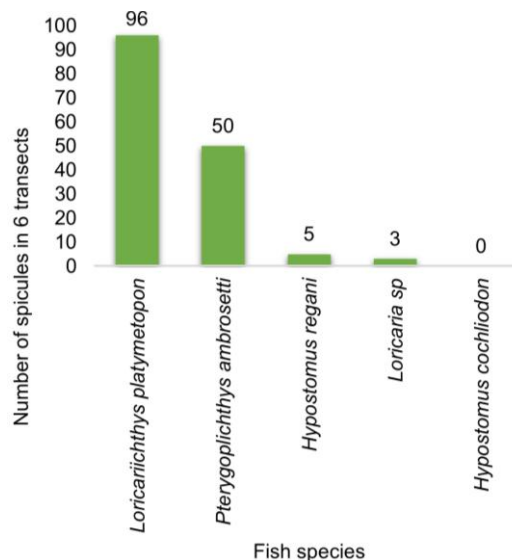


Figure 4: Number of sponge spicules quantified in the stomach material of benthic fish along six transects per slide.

3.2 Phytolith diversity

A total of 27 identifiable phytolith morphotypes were recovered. The most common was the *ELO_ENT* (n = 110) found in the stomachs of 11 animals. In *P. ambrosetti* 19 morphotypes were found, in *L. platymetopon* 19 morphotypes, in *H. cochliodon* 10 morphotypes, and in *H. regani* five morphotypes. Other phytolith morphotypes were also found, increasing the diversity recorded in this study (Figure 5). In addition, a pollen grain was identified (See Table 2).

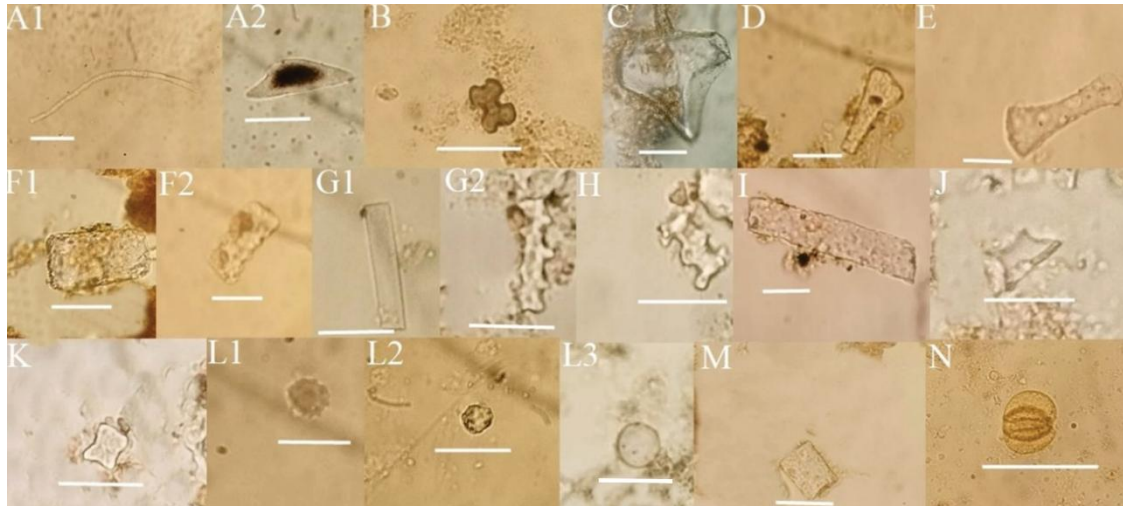


Figure 5: Main morphotypes of phytoliths and pollen grains found in the stomach of fish exploring the bottom of the alluvial plain of the Upper Paraná River, observed under a 40× objective lens; scale bar = 5 μm: A1 - ACU; A2 - ACU_BUL; B - BIL; C - BUL_FLA; D - CLA; E - CYL; F1 - BLO; F2 - BLO_ROU; G1 - ELO_ENT; G2 - ELO_DEN; H - POL; I - REC_ROU; J - RON; K - SAD; L1 - SPH_ECH; L2 - SPH_ORN; L3 - SPH_PSI; M - TAB; N - Pollen.

Table 2: Abundance and diversity of phytolith morphotypes identified in the stomach contents of benthic fishes from the Upper Paraná River floodplain, classified according to the International Code for Phytolith Nomenclature 2.0 (ICPN 2.0), with corresponding morphotype codes and absolute frequencies (n).

Morphotype Name	International Code for Phytolith Nomenclature 2.0	Quantity (n)
ACUTE	ACU	1
ACUTE BULBOSUS	ACU_BUL	109
BILOBATE	BIL	99
BLOCKY	BLO	29
BLOCKY LACUNATE	BLO_LAC	1
BLOCKY PSILATE	BLO_PSI	14
BLOCKY ROUGH	BLO_RUG	7
BLOCKY SINUATE	BLO_SIN	1
BULLIFORM FLABELLATE	BU_FLA	54
CIRCULAR	CIR	1
CLAVIFORM	CLA	5
CYLINDER	CIL	3
ELONGATE CURVED	ELO_CUR	1
ELONGATE DENTATE	ELO_DEN	3
ELONGATE ENTIRE	ELO_ENT	110
ELONGATE FACETATE	ELO_FAC	2
OBLONG	OBL	3
POLYLOBATE	POL	1

RECTANGULAR PSILATE	<i>REC_PSI</i>	5
RECTANGULAR ROUGH	<i>REC_RUG</i>	6
RONDEL	<i>RON</i>	19
SADDLE	<i>SAD</i>	3
SPHEROID ECHINATE	<i>SPH_ECH</i>	4
SPHEROID ORNATE	<i>SPH_ORN</i>	261
SPHEROID PSILATE	<i>SPH_PSI</i>	261
TABULAR	<i>TAB</i>	26
TABULAR PSILATE	<i>TAB_PSI</i>	5

4. DISCUSSION

Female fish showed a lower value of inorganic material compared to males, and presented a higher average diversity of phytolith morphotypes and also sponge spicules. This confirms that the amount of inorganic material does not imply the diversity of biogenic silica bodies and that not all inorganic matter is biogenic silica. This also happens in plants, in studies with plants from the Upper Paraná River Floodplain, they have already demonstrated that a quantity of material resistant to acid burning does not imply a diversity of phytolith morphotypes and that not all recovered material is necessarily bodies of biogenic silica [31, 32].

There was a higher concentration of inorganic material found in the stomach of fish from the Baía River compared to the specimens from Paraná and Ivinhema Rivers, confirming the studies of these same environments [33]. *Uruguaya corallioides* was found exclusively in the Baía River. This freshwater sponge inhabits deep lotic environments, with rocky and protected bottoms [22]. This species had already been described in the Tietê River, adhered to *Limnoperna fortunei* (golden mussel) in the Upper Paraná River and its gemmoscleres observed in sediments of fluvial islands of the Paraná River [34-36].

The low concentration of inorganic material found in the Closed Lagoon confirms that the current is essential for the transport of organic and inorganic particulate matter (Sh 1985). For Silveira (2004) [37], the river's flow conditions exert a significant influence on the ecosystem processes of energy transport and matter cycling.

A higher amount of inorganic material was found in the fish from the Patos Lagoon than in those from the Ivinhema River. Ragonha and Takeda (2014) [38], had already shown that the Patos Lagoon also had a higher concentration of organic material in the sediment when compared to the Ivinhema River. This is since open lagoons such as the Patos have a direct connection channel with the river, which, in turn, favors the entry and increase of nutrient contents. As a consequence, there is a homogenizing effect that increases the diversity of biological species [39].

The specimens of *H. regani* captured in the Paraná River did not exhibit ingestion of gemmoscleres but revealed the presence of megascleres of the acanthoxea type, morphologically similar to those described for *Tubella manauara* (Nunes, Custódio & Pinheiro, 2024), recorded in the Amazon Basin [40].

Gemmoscleres belonging to both *O. navicella*, *T. paulula* and *T. variabilis* were found in the specimens of *L. platymetopon*, while in *P. ambrosettii* there was a preference for *T. paulula* and *T. variabilis*. However, *T. variabilis* was preyed upon less frequently by both species. *Tubella variabilis* occurs in both lotic and lentic environments and can be associated with macrophytes and also adhered to the soil [41, 42].

Loricariichthys platymetopon showed exclusivity in the predation of *O. schubarti* and *U. corallioides*. This finding indicates a preference for sponge species among fish inhabiting the Upper Paraná River floodplain. The occurrence of *O. navicella* in both lotic and lentic environments has also been reported in the Piquiri River (Paraná State) and in Venezuela [22, 43, 44, 45]. Gemmoscleres of *O. navicella* were also found in sediments from Paraná State, near the study area [46]. In the stomach contents of a *L. platymetopon* individual from the Paraná River, megasclere spicules of the Acanthostrongyle type were found, similar to those described

for *Corvospongilla seckti* Bonetto & Ezcurra de Drago, 1966 [47], were recorded; however, gemmoscleres of this species were absent.

The *ELO_ENT* was the most common phytolith, this morphotype is considered to have no taxonomic value, being produced by several species of monocots and eudicots [31, 32]. The other morphotypes: *BUL_FLA* and *ACU_BUL* are considered characteristic of grasses that indicate water stress [48], *SAD* and *BIL_ROM* that indicate C4 grasses [49, 50], *TAB* indicates broadleaf trees [1, 51], *SPH_ORN* is found in woody species [52] and *SPH_ECH* is characteristic of Arecaceae and Bromeliaceae [10, 53]. The phytolith morphotypes preserved in the fish stomachs are similar to those produced by plant species located in the region [30, 31]. It is worth noting that, since this is a fluvial environment with constant flow, some morphotypes may have been transported from other regions by the river and/or by flood pulses, and were subsequently deposited in the sediments of the studied area and, consequently, ingested by benthic fish. The high number of preserved phytolith morphotypes demonstrated that the stomach activity of freshwater fish does not interfere with the morphological preservation of biogenic silica bodies.

The literature indicates that *L. platymetopon* [54, 55], *H. regain* [56], species of the genus *Loricaria* [57], *P. ambrosettii* [58], and *H. cochliodon* [59] share a predominantly benthic trophic pattern, with diets based on detritus, algae, sediment, and substrate-associated invertebrates. The data from the literature demonstrate that the four species and the genus *Loricaria* exhibit primarily benthic and detritivorous feeding habits. Such that the occurrence of sponges (*Porifera*) in the stomach contents constitutes a novel record for these taxa. Additionally, this study provides the first detailed description of the occurrence and preservation of phytoliths in the stomach contents of freshwater fishes and the second in the stomach contents of freshwater aquatic vertebrates [60]. However, no new species of freshwater sponges or new phytolith

5. CONCLUSION

The males had a higher rate of inorganic material and a lower quantity and diversity of phytoliths and sponges. On the other hand, females had a lower rate of inorganic material and a higher diversity of phytoliths and sponges. This demonstrates that the amount of inorganic matter ingested by fish does not reflect the quantity and diversity of biogenic silica bodies. Considering this analysis and identification of the gemmoscleres, the presence of five species of sponges in the sampled environments and subsystems was recorded. Regarding phytoliths, although the river channel may have transported morphotypes, the subsystems presented similarity in the morphotypes of phytoliths produced by vegetables in the region, both size and morphology were maintained and preserved in the stomach of bottom fish. Therefore, the analysis of the stomachs of these fish species can serve as indicators of the presence of sponges in different environments. Future studies should be conducted to confirm this hypothesis, increasing knowledge about the biodiversity of the Upper Paraná River Floodplain, the interactions between organisms and to ensure the conservation of ecosystems.

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7. BIBLIOGRAPHIC REFERENCES

1. Ge Y, Lu H, Wang C, Gao X. Phytoliths in selected broad-leaved trees in China. *Sci Rep*. 2020 Sep;10(1):15577. doi: 10.1038/s41598-020-72547-wDd
2. Kalinovsk ECZ, Parolin M, Souza Filho EE. Esponjas de água doce na América do Sul: O estado da arte da produção científica no Brasil. *Terrae didactica*. 2016 May;12(1):4-18. doi: 10.20396/td.v12i1.8645963
3. Rueda J, Gálvez Á, Castillo-Escrivà A, Bonilla F, De Manuel B, Morales L, et al. Nuevas aportaciones sobre las esponjas de agua dulce (Porifera: Spongillidae) en aguas temporales de Costa Rica. *Limnetica*. 2024 Jan;43(1):45-57. doi: 10.23818/limn.43.04
4. Harrison FW. Utilization of freshwater sponges in paleolimnological studies. *Palaeogeogr Palaeoclimatol Palaeoecol*. 1988 Jan;62:387-97. doi: 10.1016/0031-0182(88)90063-6
5. Rasbold GG, McGlue MM, Stevaux JC, Parolin M, Silva A, Bergier I. Enhanced middle Holocene organic carbon burial in tropical floodplain lakes of the Pantanal (South America). *J Paleolimnol*. 2021 Oct;65(2):181-99. doi: 10.1007/s10933-020-00159-5
6. Rasbold GG, Calheira L, Domingos-Luz L, Pessenda LC, Pinheiro U, McGlue MM. A morphological guide of Neotropical freshwater sponge spicules for paleolimnological studies. *Front Ecol Evol*. 2023 Jan;10:1067432. doi: 10.3389/fevo.2022.1067432
7. Piperno DR. *Phytolith analysis: an archaeological and geological perspective*. 1. ed. San Diego (US): Academic Press; 1988.
8. Coe HHG, Chueng KF, Gomes JG. Reconstituições da vegetação e inferências de paleoclimas através da utilização dos indicadores fitólitos e isótopos de carbono—exemplos de estudos no Brasil. *Rev Geonorte*. 2012 Jun;3(4):248-61.
9. International Committee for Phytolith Taxonomy (ICPT). Katharina N, Strömberg CAE, Ball T, Albert RM, Vrydaghs L, Cummings LS. International code for phytolith nomenclature (ICPN) 2.0. *Ann Bot*. 2019 Jul;124(2):189-99. doi: 10.1093/aob/mcz064
10. Witteveen NH, Hobus CEM, Philip A, Piperno DR, McMichae CNH. The variability of Amazonian palm phytoliths. *Rev Palaeobot Palynol*. 2022 May;300:104613. doi: 10.1016/j.revpalbo.2022.104613
11. Vargas-Machuca BD, Piperno DR, Böhnert T, Stoll A, Maldonado A, Arancio G, et al. Regional phytoliths from the Coastal Cordillera of the Atacama Desert, Chile, and their potential for paleoecological reconstructions. *Quat Int*. 2024 Jan;681:33-43. doi: 10.1016/j.quaint.2024.01.005
12. Speranskaya NY, Zhembrovskaya TA, Bobkova DG. Comparative analysis of phytolith spectra of steppe and forest phytocoenoses. *Acta Biol Sib*. 2021 Dec;7:505. doi: 10.3897/abs.7.e72839
13. Iatskiu P, Nardelli MS, Cristina E, Bartozek R, Bueno NC, Peres CK. Biodiversidade de diatomáceas em riachos subtropicais com diferentes níveis de impacto antrópico. *Rev MultidiscEduc Meio Amb*. 2023 Jan;1(4). doi: 10.51189/ii-eonline/13724
14. Hata GY, Da Trindade LG, De Lima Lourenço RBG, Barrera-Alba JJ, Mazzo TM. Óxido de zinco e biosilica de diatomáceas: potencias fotoeletrodos? *Braz J Develop*. 2020 Oct;6(10):80712-9. doi: 10.34117/bjdv6n10-477
15. Vandevenne FI, Barão AL, Schoelynck J, Smis A, Ryken N, Van Damme S, et al. Grazers: biocatalysts of terrestrial silica cycling. *Proc R Soc B: Biol Sci*. 2013 Dec;280(1772):20132083. doi: 10.1098/rspb.2013.2083
16. Wulff JL. Parrotfish predation on cryptic sponges of Caribbean coral reefs. *Mar Biol*. 1999 Jul;129:41-52. doi: 10.1007/s002270050144
17. Volkmer-Ribeiro C. Esponjas. In: Joly CA, Bicudo CEM, organizadores. *Biodiversidade do Estado de São Paulo: síntese do conhecimento ao final do século XX*. São Paulo: FAPESP Invertebrados de água doce; 1999. p. 1-9.
18. Murphy KJ, Dickinson G, Thomaz SM, Bini LM, Dick K, Greaves K, et al. Aquatic plant communities and predictors of diversity in a sub-tropical river floodplain: the upper Rio Paraná, Brazil. *Aquatic Bot*. 2003 Dec;77(4):257-76. doi: 10.1016/S0304-3770(03)00108-6
19. Oliveira SC, Pupim FN, Stevaux JC, Assine ML. Luminescence chronology of terrace development in the Upper Paraná River, Southeast Brazil. *Front Earth Sci*. 2019 Dec;7:200. doi: 10.3389/feart.2019.00200
20. Menin M. Amazônia: diversidade biológica e história geológica. *Reptilia*. 2007 Feb;708:273.
21. Abelha MCF, Agostinho AA, Goulart E. Plasticidade trófica em peixes de água doce. *Acta Sci*. 2001 May;23(2):425-34.
22. Volkmer-Ribeiro C, Pauls SM. Esponjas de água doce (Porifera, Demospongiae) de Venezuela. *Acta Biol Venez*. 2000 Mar;20(1):1-28.

23. Volkmer-Ribeiro C, Parolin M, Fürstenau-Oliveira K, Menezes ER. Colonization of hydroelectric reservoirs in Brazil by freshwater sponges, with special attention on Itaipu. *Interciencia*. 2010 May;35(5):340-7.
24. Santos JCA, Parolin M. Distribuição de esponjas continentais no Rio Mourão. *GEOMAE*. 2011 Jun;2:13-22.
25. Da Costa FG, Pellegrini MO, Bove CP. Diversidade de corpos de sílica em Mourera Aublet (*Podostemaceae*) e suas aplicações filogenéticas, paleobotânicas e taxonômicas. *Rev Paleobot Palinol*. 2021 Dec;295:104509. doi: 10.1016/j.revpalbo.2021.104509
26. Hayakawa EH, Couto EV, Souza-Filho EE, Prado BR, Paula PF. Análise temporal da planície de inundação do Alto Rio Paraná (região de Porto Rico, PR) através de dados de sensoriamento remoto. *Bol Geogr*. 2010 Sep;28(1):115-26. doi: 10.4025/bolgeogr.v28i1.8086
27. Roderjan CV, Galvão F, Kuniyoshi YS, Hatschbach GG. As unidades fitogeográficas do estado do Paraná, Brasil. *Ciênc Amb*. 2002 Jan;24(1):75-92.
28. Instituto de Desenvolvimento Rural do Paraná (Iapar). Cartas climáticas do Estado do Paraná. Londrina; 2019 (accessed on 2023 Sep 12). Available at: <https://www.idrparana.pr.gov.br/system/files/publico/agrometeorologia/medias-historicas/Londrina.pdf>.
29. Instituto de Desenvolvimento Rural do Paraná (Iapar). Cartas climáticas do Estado do Paraná. Palotina; 2011 (accessed on 2023 Set 12). Available at: <http://www.idrparana.pr.gov.br/system/files/publico/agrometeorologia/medias-historicas/Palotina.pdf>.
30. Muricy G, Lopes DA, Hajdu E, Carvalho MS, Moraes FC, Klautau M, et al. Catalogue of Brazilian Porifera. Rio de Janeiro: Museu Nacional; 2011.
31. De Oliveira LM, Calegari MR, Leli IT, Romagnolo MB. Production of phytoliths in woody plants of the Atlantic Forest in islands of the Paraná River, Brazil. *Quat Int*. 2024 Jan;681:24-32. doi: 10.1016/j.quaint.2023.12.006
32. De Oliveira LM, Leli IT, Ferreira ML, Romagnolo MB, Calegari MR. Phytolith production in non-woody plants from the Atlantic Forest on islands of the Paraná River, Brazil. *Quat Int*. 2025 Jul;738:109858. doi: 10.1016/j.quaint.2025.109858
33. Esper Amaro de Faria AC, Benedito E. Quality and digestibility of food ingested by various trophic fish groups in the Upper Paraná River floodplain. *Rev Biol Trop*. 2011 Aug;59(1):85-101.
34. Pinheiro US, Hajdu E, Caballero ME. Três novos registros de esponjas (Porifera, Demospongiae) para águas continentais do Estado de São Paulo. *Bol Mus Nac*. 2003 Jan;498:1-14.
35. Rasbold GG, Stevaux JC, Parolin M, Leli IT, Luz LD, Guerreiro RL, et al. Sponge spicules as indicators of paleoenvironmental changes in island deposits—Upper Paraná River, Brazil. *Paleogeogr Palaeoclimatol Palaeoecol*. 2019 Dec;536:109391. doi: 10.1016/j.palaeo.2019.109391
36. De Medeiros Fortunato HF, Figueira RMA. Freshwater sponges overgrow the invasive golden mussel *Limnoperna fortunei* in the Upper Paraná River, Brazil. *Mard Freshw Res*. 2022 Dec;73(11):1393-8. doi: 10.1071/MF22023
37. Silveira MP. Aplicação do biomonitoramento para avaliação da qualidade da água em rios. Embrapa Meio Ambiente; 2004.
38. Ragonha FH, Takeda AM. Does the richness of Oligochaeta (Annelida) follow a linear distribution with habitat structural heterogeneity in aquatic sediments? *J limnol*. 2014 Aug;73:1. doi: 10.4081/jlimnol.2014.791
39. Rodrigues L, Bicudo DC. Limnological characteristics comparison in three systems with different hydrodynamic regime in the Upper Paraná River Floodplain. *Acta Limnol Bras*. 2001;13(1):39-49.
40. Nicacio G, Pinheiro U. Biodiversity of freshwater sponges (Porifera: Spongillina) from northeast Brazil: new species and notes on systematics. *Zootaxa*. 2015 Jul;3981(2):220-40. doi: 10.11646/zootaxa.3981.2.4
41. Nunes G, Custodio MR, Pinheiro U. A new species of *Tubella* (Porifera: Spongillidae) for the Brazilian Amazon: how misidentification can mask a potential species complex. *Acta Amaz*. 2024 Nov;54, e54bc24187. doi: 10.1590/1809-4392202401873
42. Docio L, Rasbold GG, Da Silva ALC, Parolin M, Caxambu MG, Pinheiro U. An assessment of the wealth of information given by sponge spicules as a paleoenvironmental tool: The case of two lakes in the northeast (Brazil). *J South Am Earth Sci*. 2021 Apr;107:103099. doi: 10.1016/j.jsames.2020.103099
43. Bonetto AA, De Drago IE. Esponjas del noreste argentino. *Acta Zoologica Lilloana*. 1967 Dez;(23):331-47.
44. Tavares-Frigo MC, Volkmer-Ribeiro C, De Oliveira AEZ, Machado VS. Freshwaterspongefrom Pampa Biome, Brazil. With description of a new species of *Oncosclera*. *Neotrop Biol Conserv*. 2015 Dec;10(3):110-22. doi: 10.4013/nbc.2015.103.01

45. Dos Santos JCA, Parolin M. Distribuição de esponjas continentais no rio Mourão. *Rev Geomae-Geografia Meio Ambiente e Ensino*. 2011 Mar;2(1):13-22.
46. Parolin M, De Oliveira LM, Dos Santos JCA, Gasparetto NVL. Caracterização paleoambiental do baixo curso do rio Mourão, Paraná–Brasil. *Rev Geoc Nordeste*. 2026 Apr;12(1):231-42. doi: 10.21680/2447-3359.2026v12n1ID42566
47. Pinheiro U, Docio L, Nicacio G, Hajdu E. A reassessment of neotropical species of *Corvospongilla* (Porifera: Spongillidae). *J Nat Hist*. 2012 Jun;47(37-38):2373-84. doi: 10.1080/00222933.2013.798700
48. Kondo R, Childs CW, Atkinson IAE. *Opal Phytoliths of New Zealand*. Lincoln (NZ): Manaaki Whenua Press; 1994.
49. Chueng KF, Coe HHG, Fagundes M, Vasconcelos AMC, Ricardo SDF. Reconstituição paleoambiental da área arqueológica de Serra Negra, face leste do Espinhaço Meridional (Minas Gerais), através da análise de fitólitos. *Rev Bras Geogr Física*. 2019 Jan;11(7):2260-75. doi: 10.26848/rbgf.v11.07.p2260-2275
50. De Oliveira LM, Parolin M, Dos Santos JCA, Caxambu MG. Fitólitos de *Andropogon bicornis* L. e *Andropogon leucostachyus* Kunth in Humb., Bonpl. & Kunth. (Poaceae). *Obs Econ Latinoam*. 2023 Jun;21(8):7880-90. doi: 10.55905/oelv21n8-007
51. Chen W. A Review on diagnostic phytoliths for the application in paleovegetation reconstruction and environmental archaeology in East Asia. *Int J Geosci*. 2024 Jun;15(6):479-92. doi: 10.4236/ijg.2024.156026
52. Bremond L, Alexandre A, Hély C, Guiot J. A phytolith index as a proxy of tree cover density in tropical areas: calibration with Leaf Area Index along a forest–savanna transect in southeastern Cameroon. *Glob Planet Change*. 2005 Mar;45(4):277-93. doi: 10.1016/j.gloplacha.2004.09.002
53. Piperno DR. *Phytoliths: a comprehensive guide for archaeologists and paleoecologists*. Lanham (MD): Altamira Press; 2006.
54. Fugi R, Agostinho AA, Hahn NS. Trophic morphology of five benthic-feeding fish species of a tropical floodplain. *Rev Bras Biol* 2001 Apr;61:27-33. doi: 10.1590/S0034-71082001000100005
55. Bennemann ST, Casatti, L, Oliveira DCD. Alimentação de peixes: proposta para análise de itens registrados em conteúdos gástricos. *Biota Neotrop*. 2006 Dez;6(2):1-8. doi: 10.1590/S1676-06032006000200013
56. Villares-Junior GA, Cardone IB, Goitein R. Comparative feeding ecology of four syntopic *Hypostomus* species in a Brazilian southeastern river. *Braz J Biol*. 2016 May;76:692-9. doi: 10.1590/1519-6984.00915
57. Silva GH, Zeni JO, Langeani F. Head morphology and diet of whiptail catfishes (Loricariidae: Loricariinae). *Neotropl Ichthyol*. 2025 Apr;23(01):e240113. doi: 10.1590/1982-0224-2024-0113
58. Reinas GCZ, Silva JC, Bialetzki A. Coexistence patterns between native and exotic juvenile Loricariidae in a Neotropical floodplain: an approach to resource partitioning. *Hydrobiologia*. 2022 Feb;849(7):1713-26. doi: 10.1007/s10750-022-04816-w
59. Watts JE, McDonald R, Daniel R, Schreier HJ. Examination of a culturable microbial population from the gastrointestinal tract of the wood-eating loricariid catfish *Panaque nigrolineatus*. *Diversity*. 2013 Aug;5(3):641-56. doi: 10.3390/d5030641
60. De Oliveira LM, Parolin M, Grou CEV, Scoarize MMR, Benedito E. First record of biogenic silica in the stomach contents of South American freshwater turtles. *Acta Herpetol*. 2026 Jan;21. doi: 10.36253/a_h-18063