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Paleo-faunistic checklist of the Tremembé Formation (Oligocene of the Taubaté Basin, Paraíba Valley, Brazil)

CHECKLIST PALEOFAUNÍSTICO DA FORMAÇÃO TREMEMBÉ (OLIGOCENO DA BACIA DE TAUBATÉ, VALE DO PARAÍBA, BRASIL)

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Abstract: **Introduction.** The Tremembé Formation (Oligocene), outcropping in the eastern region of the São Paulo State, Brazil, is the most richly fossiliferous lithostratigraphic unit in the Taubaté Basin, providing numerous records of a diverse flora and fauna from the Paleogene that inhabited the Paraíba Valley. **Objective.** This paper aims to provide an updated checklist of all groups of invertebrates and vertebrates that have been described based on fossils recovered from this geological formation in the last centuries. **Methodology.** A bibliographic survey was carried out in four different databases. **Results.** Over a hundred taxa were reported in the references analyzed, including porifers, nematodes, molluscs, annelids, arthropods, fishes, amphibians, reptiles, birds and mammals. Some invertebrate groups have a remarkable diversity like the paleo-fauna of arthropods. Furthermore, birds and mammals represent most of the taxonomic richness of vertebrates from the Tremembé Formation. **Conclusion.** The faunistic diversity of the Tremembé Formation, described throughout the 20th and 21st centuries, reveals the potential of paleontological discoveries in this geological area and its importance to the Oligocene Brazilian fossil record, providing support for dating processes and correlation with other fossiliferous localities.

Resumo: **Introdução.** A Formação Tremembé (Oligoceno), aflorante na região Leste do estado de São Paulo, Brasil, é a unidade litoestratigráfica mais ricamente fossilífera da Bacia de Taubaté, de onde provêm inúmeros registros de uma diversa flora e fauna do Paleógeno que habitou o Vale do Paraíba. **Objetivo.** O presente artigo visa fornecer uma *checklist* atualizada de todos os grupos de vertebrados e invertebrados que foram descritos com base em fósseis coletados nessa formação geológica, nos últimos séculos. **Metodologia.** Foi realizado um levantamento bibliográfico em quatro distintas bases de dados. **Resultados.** A análise possibilitou encontrar mais de uma centena de taxa nas referências, incluindo poríferos, nematoídeos, moluscos, anelídeos, artrópodes, peixes, anfíbios, répteis, aves e mamíferos. Alguns grupos de invertebrados apresentam diversidade notável, como a paleofauna de artrópodes. Além disso, aves e mamíferos caracterizam a maior parte da riqueza taxonômica dos vertebrados da Formação Tremembé. **Conclusão.** A diversidade faunística dessa unidade litoestratigráfica, descrita ao longo dos séculos XX e XXI, revela o potencial das descobertas paleontológicas nessa área geológica e sua importância para o registro fóssil brasileiro do Oligoceno, fornecendo subsídios para processos de datação e correlação com outras localidades fossilíferas.

Introduction

Despite fossilization being an extremely rare process, Brazil has a range of geological units in which new fossils are routinely discovered, contributing to an increasingly broader understanding of the ancient biodiversity. The Taubaté Basin (Fig. 1) stands out for its expressive paleontological con-

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tent, preserving a great diversity of extinct groups (Couto-Ribeiro, 2010, 2015). It is part of the Continental Rift of Southeast Brazil, being discovered in the first half of the 19th century (Pissis, 1842). It is distributed in the Paraíba Valley, State of São Paulo, and comprises the Resende, Tremembé, São Paulo and Pindamonhangaba Formations, in

addition to some Quaternary deposits (Riccomini, 1989, Riccomini et al., 2004).

Tremembé Formation is considered the most fossiliferous lithostratigraphic unit from the Taubaté Basin, providing numerous insights into the Paleogene fauna and flora that inhabited the Paraíba Valley in the Brazilian territory millions of years ago and its sediments have a lacustrine origin (Chagas et al., 2009). Based on mammals and birds' macrofossils, it has an age between the Upper Oligocene and Lower Miocene and its rocks outcrop in Pindamonhangaba, Taubaté, and Tremembé municipalities (Couto & Mezzalira, 1971, Lima et al., 1985, Bergqvist & Ribeiro, 1998, Alvarenga, 1990, Couto-Ribeiro, 2010, 2015).

Comparative analyzes between the mammal fauna of the Tremembé Formation and that of other Oligocene-Miocene geological units from other countries in South America (e.g., Argentina, Bolivia, Colombia, Peru and Uruguay), have revealed taxonomic similarities, indicating possible correlation among them and highlighting the importance of this geological area (Couto-Ribeiro, 2010, 2015). Previously, Bernardes-de-Oliveira et al. (2002), Melo (2007) and Couto-Ribeiro (2010, 2015) reported a remarkable paleo-faunistic record in the Paraíba Valley and, considering the emergence of new fossil descriptions in recent years, the present work aims to provide an updated checklist of all groups of invertebrates and vertebrates described for the Tremembé Formation to improves the perception of its paleo-biodiversity and to subsidizing future dating and correlation studies with other fossiliferous localities.

Methods

The paleofauna data collection was obtained from 2020 to 2024 using the combination of the descriptors "Tremembé" and "Formation" with the logical operator "AND" in four different databases (i.e., Scopus, Web of Science, Google Scholar and Science Direct). Articles were selected according to their relevance and consonance with our paleofaunistic studies. References obtained through non-probabilistic sampling methodology were also analyzed when cited in previously read articles and considered essential elements of this research (Zar, 2010).

Results

Paleoinvertebrates

Tremembé Formation has a vast fossil record of invertebrates of the Porifera, Nematoda, Mollusca, Annelida and Arthropoda groups (detailed information on taxa is given in the Table 1). Ferreira (1974) described the presence of decomposed shells, in "chalk appearance", found in bentonite clay; they were assigned to the genera *Lymnaea* Lamarck, 1799 and *Biomphalaria* Preston, 1910 (Gastropoda, Pulmonata). A few decades later, Melo & Bergqvist (2007) recorded the presence of the external mold of a *Biomphalaria* sp. shell in the shales of the Tremembé Formation. Porifera monoaxonic spicules were also reported by Wickert (1974) in these shales. In addition, Fernandes et al. (1987) identified excavations whose genesis is related to the biological activity of aquatic

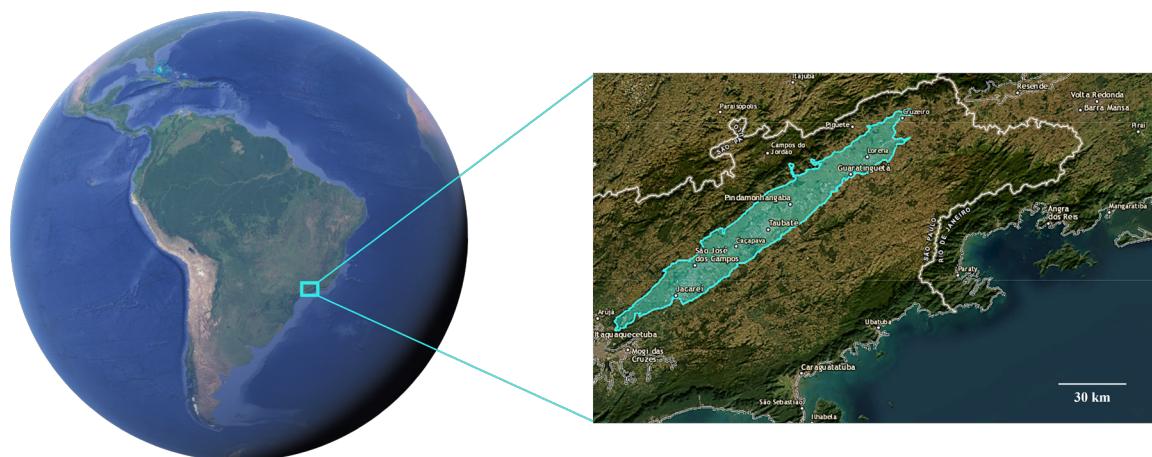


Figure 1. Geographic location of the Taubaté Basin, Paraíba Valley. Modified from Google Earth, 2023 and from SGB/CPRM, 2023

annelids. Carmo et al. (2023) carried out the first paleoparasitological study on bird coprolites from the Tremembé Formation. The authors reported the presence of nematode eggs from the Ascaridina, Spirurina and Trichocephalida groups, in addition to a single egg identified only at the phylum level.

The Crustacea, Insecta and Chelicerata groups represent the arthropods. The first Oligocene Con-

chostraca fossils reported in the world were valve molds found in bentonite clay of the Tremembé Formation (Gallego & Mesquita, 2000). They were assigned to the species *Tremembeglypta saadi* Gallego & Mesquita, 2000 (Loxomegallyptidae). Furthermore, *Pseudocaridinella tremembeensis* (Beurlen, 1950), *Propalaemon longispinata* Martins-Neto and Mezzalira, 1991 and *Bechleja robusta* Martins-Neto

Table 1. Fossil invertebrates from the Tremembé Formation

	More specific taxonomic identification	
Porifera	Monoaxonic spicules identified only at the phylum level.	
Nematoda	Ascaridina	
	Spirurina	
	Trichocephalida	
	Egg identified only at the phylum level.	
Mollusca	<i>Biomphalaria</i> sp. (Planorbidae)	
	<i>Lymnaea</i> sp. (Lymnaeidae)	
Annelida	Feeding tracks of aquatic annelids identified only at the phylum level.	
Arthropoda	<i>Tremembeglypta saadi</i> (Loxomegallyptidae)	Specimen identified as belonging to the order Lepidoptera (Fig. 2).
	<i>Propalaemon longispinata</i> (Paleomonidae)	<i>Tremembecarabus rotundus</i> (Carabidae)
	<i>Bechleja robusta</i> (Paleomonidae)	<i>Microbasis longinota</i> (Meloidae)
	<i>Pseudocaridinella tremembeensis</i> (Paleomonidae)	<i>Curculionidae</i> gen. sp.
	<i>Palaega tremembeensis</i> (Cirolanidae)	<i>Hydrophilidae</i> gen. sp.
	<i>Cyprætta</i> sp. (Cyprididae)	<i>Psephenella ferreirai</i> (Psephenidae)
	<i>Strandesia</i> sp. (Cyprididae)	<i>Tremembætalion minutum</i> (Atalionidae)
	<i>Potamocypris</i> sp. (Cyprididae)	<i>Trulaxia primula</i> (Cicadellidae)
	<i>Heterocypris</i> spp. (Cyprididae)	<i>Indusia suguioi</i> (Limnephilidae)
	<i>Eucypris</i> spp. (Cyprididae)	<i>Taubatehymen minuta</i> (Ichneumonidae)
	<i>Herpetocypris</i> spp. (Cyprididae)	<i>Paratilgidops praecursora</i> (Ichneumonidae)
	<i>Eucypris lobatoi</i> (Cyprididae)	<i>Tenthredinidae</i> gen. sp.
	<i>Potamocypris taubatensis</i> (Cyprididae)	<i>Palaeohebrus tremembeensis</i> (Veliidae)
	<i>Cytheridella</i> spp. (Limnocytheridae)	<i>Taubatecoris quadratiformis</i> (Pentatomidae)
	<i>Limnocythere mandubi</i> (Limnocytheridae)	<i>Tremembellina microcelata</i> (Cicadelidae)
	<i>Limnocythere katu</i> (Limnocytheridae)	<i>Taubocicadellina breviptera</i> (Cicadelidae)
	<i>Limnocythere</i> sp. (Limnocytheridae)	<i>Tauborixiellopsis brevidlavata</i> (Corixidae)
	<i>Limnocythere?</i> sp. (Limnocytheridae)	<i>Taubarixa macrocelata</i> (Corixidae)
	<i>Daphnia</i> spp. (<i>Ctenodaphnia</i>) (Daphniidae)	<i>Tauborixella santosae</i> (Corixidae)
	Blattidae gen. sp.	<i>Archaeodrapetius transversa</i> (Hybotidae)
	<i>Kleopatra nemogypsia</i> (Cossidae)	<i>Archaeodrapetius mezzalirai</i> (Hybotidae)
	<i>Kleopatra noctodiva</i> (Cossidae)	<i>Archaeodrapetius nefera</i> (Hybotidae)
	<i>Petisca dryellina</i> (Pyralidae)	<i>Archaeodrapetius elongata</i> (Hybotidae)
	<i>Nepticula? almeidae</i> (Nepticulidae)	<i>Tremembella gracilis</i> (Hybotidae)
	<i>Phyllonoryctes? oliveirae</i> (Gracillariidae)	<i>Eternia papaveroi</i> (Hybotidae)
	<i>Archaeolycorea ferreirai</i> (Nymphalidae)	<i>Taubatempis gracilis</i> (Empididae)
	<i>Neorinella garciae</i> (Nymphalidae)	<i>Taubatempis trompetilia</i> (Empididae)
	<i>Archaeolycorea</i> sp. (Nymphalidae)	<i>Taubatempis elongata</i> (Empididae)
	<i>Philodarchia cigana</i> (Noctuidae)	<i>Tabanus tremembeensis</i> (Tabanidae)
...		<i>Prodiastatinops pulchra</i> (Diastatidae)
		<i>Sackenia? elongata</i> (Mycetophilidae)
		<i>Taubatemyia oligocaenica</i> (Mycetophilidae)
		Chironomidae gen. sp.
		Larval tubes of the Chironomidae family and fragments of cephalic capsules of the subfamilies Chironominæ (<i>Tanytarsus</i> aff. sp.) and Tanypodinæ (Tribe Tanypodini, <i>Tanypus</i> aff. sp.).
		<i>Helius? oligocenicus</i> (Tipulidae)
		<i>Tipula? tremembeensis</i> (Tipulidae)
		<i>Taubaracna maculosa</i> (family incertae sedis)

and Mezzalira, 1991 (Paleomonidae, Decapoda) were found in pyrobituminous shale, in addition to the species *Palaega tremembeensis* Martins-Neto, 2001 (Cirolanidae, Isopoda) (Beurlen, 1950, Martins-Neto & Mezzalira, 1991, Martins-Neto, 2001). Bergue et al. (2015b; 2018) recorded a great diversity of ostracod taxa in the genera *Cypræta* Vavra, 1895, *Strandesia* Stuhlmann, 1888, *Potamocypris* Brady, 1870, *Heterocypris* Claus, 1892, *Eucypris* Vavra, 1891, *Cytheridella* Daday, 1905 and *Limnocythere* Brady, 1868. Finally, trace fossils from *Daphnia* spp. (Ctenodaphnia, Branchiopoda) also occur in this geological unit (Bergue et al., 2015a).

Although Crustacea is well represented, the Insecta class is the group of invertebrates with the most remarkable diversity of the Tremembé Formation, having individuals in the Coleoptera, Trichoptera, Hymenoptera, Orthoptera, Diptera, Lepidoptera, Hemiptera and Homoptera orders. The paleoentomological taxa are listed in the Table 1 and were inventoried based on the works of Martins-Neto (1989, 1997a, 1997b, 1998a, 1998b, 1998c, 1999, 2001), Martins-Neto et al. (1992a, 1992b, 1993), Martins-Neto & Mezzalira (1991) and Morraye (2003). It is worth noting that a Lepidoptera specimen was housed at the Museu de História Natural de Taubaté and has not been described formally, being reported here for the first time (Fig. 2). To date, the species *Taubaracna maculosa* Martine et al., 2023 is the only taxon representing the Chelicerata group in the Tremembé Formation and the first arachnid described from the Paleogene of the South American territory (Martine et al., 2023).

Paleovertebrates

Tremembé Formation preserved fossils of fish, amphibians, reptiles, birds and mammals (Table 2, Figs, 3, 4). The ichthyofauna consists of Siluriformes species, found in bentonite clay and pyrobituminous shales, and taxa from the Characiformes, Cichliformes and Centrarchiformes orders, found in pyrobituminous shales (Woodward, 1898, Schaeffer, 1947, Travassos & Santos, 1955, Figueiredo & Costa-Carvalho, 1999a, 1999b, Malabarba & Lundberg, 2007). Woodward (1898) was a pioneer in the description of fish fossils from the Tremembé Formation, and the paleontological material of these animals is abundant and preserved almost in its totality, revealing the similarities of these animals with some taxa of living Neotropical fish (Malabarba, 1998, Figueiredo & Costa-Carvalho, 1999b).



Figure 2. Lepidoptera specimen (MHNT-VT-2015) housed at the Museu de História Natural de Taubaté. Scale bar: 2.2 cm. Photographer: Fabio Colombini

The herpetofauna of the Tremembé Formation has a smaller number of taxa than the ichthyofauna. The amphibian group is represented by a caecilian specimen of the family Typhlonectidae and by two anurans, one assigned to the Pipidae family and the other identified as belonging to the Hyloidea (= Bufonoidea) superfamily, having osteological characteristics common to the families Leptodactylidae and Hylidae (Riff & Bergqvist, 1999, Campo et al., 2016, Santos, 2020, Santos et al., 2024). Species of the orders Crocodylia, Squamata and Testudines represent the reptiles found in bentonite clay and pyrobituminous shale (Chiappe, 1988, Kischlat, 1993, Capilla, 1994).

The ancient avifauna of the Tremembé Formation is quite diverse in terms of the number of species described in the families Anhimidae, Phoenicopteridae, Opisthocomidae, Cathartidae, Palaelodidae, Quercymegapodiidae, Phorurhacidae and Teratornithidae. Some of these families have become completely extinct, while others still have living species in the Holocene biota. Among the avian fossils already reported, Alvarenga (1982; 1993a) described fragmented bones found in bentonite clay that belonged to a bird identified as *Paraphysornis brasiliensis* (Alvarenga, 1982) about two meters tall (in forced extension, it reached three meters), whose wings were tiny and the hind limbs were robust, while the head and the jaw were well developed. The osteological characteristics reveal a carnivorous bird, slow and incapable of running, possibly a scavenger (Alvarenga, 1982).

The Tremembé Formation also had in its avian fauna the species of medium-sized vulture called *Brasilogyps faustoi* Alvarenga, 1985, found in bentonite clay (Alvarenga, 1985). The unit also includes the *Taubacrex granivora* Alvarenga, 1988, a terrestrial bird that fed on grains, described through bone fragments and impressions found in pyrobitumi-

Table 2. Fossil vertebrates from the Tremembé Formation

	Order	More specific taxonomic identification
PISCES	Characiformes	<i>Brycon avus</i> (Characidae)
		<i>Lignobrycon ligniticus</i> (Characidae)
		<i>Megacheirodon unicus</i> (Characidae)
		<i>Plesiocurimata alvarengai</i> (Curimatidae)
		<i>Cyphocharax mosesi</i> (Curimatidae)
	Cichliformes	<i>Tremembichthys pauloensis</i> (Cichlidae)
	Centrarchiformes	<i>Santosius antiquus</i> (Percichthyidae)
	Siluriformes	<i>Taibateia paraiba</i> (Loricariidae)
		<i>Steindachneridion iheringi</i> (Pimelodidae)
		<i>Steindachneridion silvasantosi</i> (Pimelodidae)
AMPHIBIA	Anura	Specimen identified as belonging to the superfamily Hyloidea, with Leptodactylidae and Hylidae characteristics.
		Pipidae gen. sp.
	Gymnophiona	<i>Ymboirana acrux</i> (Typhlonectidae)
REPTILIA	Crocodylia	<i>Caiman tremembensis</i> (Alligatoridae) ¹
	Testudines	<i>Phrynnops (Phrynnops) geoffroanus</i> (Chelidae)
	Squamata	Specimen identified as belonging to the Ophidia group.
NEORNITHES	Phoenicopteriformes	<i>Agnopterus sicki</i> (Phoenicopteridae)
		<i>Palaelodus aff. P. ambiguus</i> (Palaeodidae)
	Galliformes	<i>Taubacrex granívora</i> (Quercymegapodiidae)
		<i>Ameripodius silvasantosi</i> (Quercymegapodiidae)
	Pelicaniformes	Ardeidae? gen. sp.
	Cariamiformes	<i>Paraphysornis brasiliensis</i> (Phorurshacidae)
	Cathartiformes	<i>Brasiliogyps faustoi</i> (Cathartidae)
	Anseriformes	<i>Chaunoides antiquus</i> (Anhimidae)
		Anatidae? gen. sp.
	Opisthomocomiformes	<i>Hoazinavis lacustris</i> (Opisthomocomidae)
	Suliformes	Phalacrocoracidae? gen. sp.
	Podicipediformes	Podicipedidae? gen. sp.
	Order incertae sedis	<i>Taubatornis campbelli</i> (Teratornithidae)
Avian coprolites identified only at the Neornithes subclass level.		
A bird footprint identified at the Neornithes subclass level, probably produced by a taxon from the Opisthomocomidae, Rallidae or Quercymegapodiidae families.		
MAMMALIA	Chiroptera	<i>Mormopterus (Neomops) faustoi</i> (Molossidae)
	Rodentia	<i>Sallamys? minutus</i> (Família incertae sedis)
		<i>Paulacoutomys paulista</i> (Echmyidae?)
	Notoungulata	<i>Rhynchippus brasiliensis</i> (Notohippidae)
		<i>Taubatherium paulacoutoi</i> (Leontiniidae)
		Leontiniidae gen. sp.
	Cingulata	<i>Eocoelophorus glyptodontoides</i> (Dasypodidae)
	Liptoterna	Proterotheriidae gen. sp.
	Pyrotheria	Pyrotheriidae gen. sp.
	Astrapotheria	Specimen identified as belonging to the Astrapotheriinae subfamily.
	Metatheria	Hathliacynidae gen. sp.
		Proboryhaenidae gen. sp.
		Specimen identified only at the order level.

1 Fortier et al. (2014) argue that the material used in the description of the species (a fragmented left dentary, isolated vertebrae, osteoderms and a humerus fragment) in fact, has characteristics of a caimanine, however, they contest the diagnosis of *Caiman tremembensis*, proposing that the species be treated as a *nomen dubium*



Figure 3. Vertebrates from the Tremembé Formation (Oligocene from the Taubaté Basin, São Paulo, Brazil). A and B: *Paraphysornis brasiliensis* holotype (MHNT-VT-5000 / DGM 1418-R) – Mandible (A) and left tarsometatarsus (B). C: *Brasilogyps faustoi* holotype – Proximal fragment of the right tarsometatarsus (C1) and distal fragment of the right tibiotarsus (C2) (MNRJ-4045-V). D: Astrapotheria incisor tooth in labial view (DGM-1090-M). E: *Taubatornis campbelli* holotype – Distal fragment of the right tibiotarsus (MHNT-VT-5154). F: *Taubatornis campbelli* paratype – Proximal fragment of the left ulna (MHNT-VT-5155). G: *Chaunoides antiquus* paratype – Left tibiotarsus (MNRJ-4629-V). H: Lower left canine tooth of Astrapotheria in labial view (MHNT-VT-883). I: *Chaunoides antiquus* holotype – Left coracoid (MNRJ-4619-V) in ventral (J1) and dorsal (J2) view. J: *Caiman tremembensis* (*nomen dubium*) holotype – Anterior dentary fragment; left hemimandible (MHNT-VT-2180 / DGM 1444-R). K: *Taubatherium paulacoutoi* holotype – Fragment of the right maxilla with P2-4 (occlusal view) and alveoli of P1 and C (DGM 1087-M). L: Left hemimandible of a *Taubatherium paulacoutoi* adult individual (MHNT-VT-2074), containing the alveoli of i1-3 and the teeth p1-m3 in their respective positions. Scale bar: 5 cm

nous shales (Alvarenga, 1988). Bone fragments found in bentonite clays were used to describe the flamingo taxa *Agnopterus sicki* Alvarenga, 1990 and *Palaelodus* aff. *P. ambiguous* Milne-Edwards, 1871 and the feeding of these animals possibly consisted of ostracods and decapods that were abundant in the Tremembé paleolake, which could reach expressive saline concentrations because it received water from tributary rivers but did not communicate with the ocean (Alvarenga, 1990).

Furthermore, *Ameripodius silvasantosi* Alvarenga, 1995, a small-sized chicken with relatively short and robust wings, was described in the pyrobituminous shales of the Tremembé, as well as the anseriform *Chaunoides antiquus* Alvarenga, 1999, found in bentonite clay (Alvarenga, 1995, 1999). Tremembé Formation's paleo-avifauna also includes the species *Taubatornis campbelli* Olson and Alvarenga 2002 found in bentonite clay and described in the Teratornithidae family, characterized by large

birds, supposedly predators or scavengers (Olson & Alvarenga, 2002). Notably, this avian species was unique for having a reduced size compared to the other family members. *T. Campbelli* and *B. faustoi*, may have benefited from periodic mortalities of large amounts of small fish due to the alternation between dry and wet seasons in the Tremembé Formation (Olson & Alvarenga, 2002). *Hoazinavis lacustris* Mayr et al., 2011 is another taxon that inhabited the Paraíba Valley. This bird species had some folivory eating habits and limited flight capacity and its ancestral lineage may have emerged in Africa and arrived in America, being transported by floating vegetation islands (Mayr et al., 2011).

Several bird fossils were housed at the Museu de História Natural de Taubaté and have not been described formally, being only mentioned by Castro et al. (1988) and Alvarenga (1993b, 1997). Based on the preliminary identification efforts in the 20th century, individuals of the families Phalacrocoracidae, Anatidae, Ardeidae and Podicipedidae were reported. However, they must be better studied in order to improve their taxonomic classification (Couto-Ribeiro, personal communication). Avian coprolites, identified only at the Neornithes subclass level, and a bird footprint, probably produced by

members of the families Opisthocomidae, Rallidae or Quercymegapodiidae, were also described (Castro et al., 1988, Carmo et al., 2023, Lima et al., 2023).

The mammalian fauna has a great diversity of species, being represented by the Rodentia, Notoungulata, Cingulata, Liptoterna, Pyrotheria, Astrapotheria and Metatheria orders, whose fossils occur in bentonite clays, in addition to a specimen of the order Chiroptera, which occurs in pyrobituminous shales from the Tremembé Formation (Couto, 1956, Couto & Mezzalira, 1971, Soria & Alvarenga, 1989, Vucetich et al. 1993, Oliveira et al. 1997, Vucetich & Ribeiro, 2003, Alvarenga et al., 2005, Couto-Ribeiro et al., 2005).

Conclusions

Brazil has only a few Paleogene lithostratigraphic units, but most of them house numerous fossils. In this sense, it is crucial to highlight the importance of updated reviews related to the paleobiota from this geological period, as these efforts improve the understanding of the global Cenozoic ancient fauna.

The faunistic diversity of the studied geological unit, described throughout the 20th and 21st centuries reveal its importance for the Brazilian

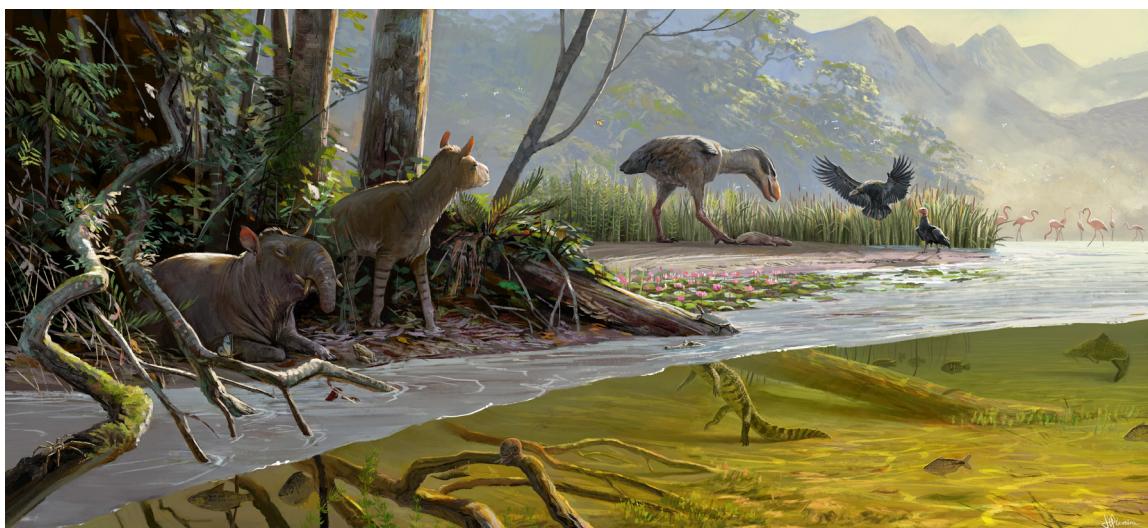


Figure 4. Paraíba Valley Oligocene landscape. On land: the arachnid species *Taubaracna maculosa*, and the lepidopteran *Archaeolycorea ferreira*, both on tree trunks (left side of the figure); Astrapotheria specimen lying next to the vegetation and *Taubatherium paulacoutoi*, both close to an anuran individual (left side of the figure); the cheloniid *Phrynos (Phrynos) geoffroanus* on a tree trunk, closer to the water (center of the figure); *Paraphysornis brasiliensis*, and the vultures *Brasilogyps faustoi* (on land) and *Taubatornis campbelli* (flying), interacting with a *Rhynchosaurus brasiliensis* carcass (center of the figure); a group of *Agnopterus sicki* and *Palaelodus* aff. *P. ambiguus* flamingos (background, right side of the figure). In the Tremembé paleolake: the alligator *Caiman tremembensis (nomen dubium)* and the fish *Cyphocharax mosesi* (center of the figure); the taxa *Steindachneridion silvasantosi* (one single individual) and *Tremembichthys pauloensis* (four specimens) (background, right side of the figure); *Biomphalaria* sp. and *Bechleja robusta*, both on tree trunks underwater, and two *Plesiocurimata alvarengai* fishes (left side of the figure). Paleoartist: Júlia d’Oliveira

Paleontology as well as for the global Paleogene fossil record. Currently, over a hundred taxa have been reported and some invertebrate groups have remarkable diversity similar to the paleo-fauna of arthropods. Furthermore, birds and mammals have evolved and diversified into different groups that inhabited the Paraíba Valley during the Paleogene, characterizing most of the taxonomic diversity of vertebrates from the Tremembé Formation and telling an important story of the deep time. Despite this great diversity of paleontological remains, some fossils have not been identified to lower taxa (i.e. genera, species) due to the loss of biological information related to the fossilization process itself or due to the need for further taxonomic studies.

Taxonomia CRedit: • Authors' contribution: Conceptualization; Data curation; Investigation; Validation; acquisition of data through Primary Survey; Review & Editing – original draft; Writing – Review & Editing: Gustavo Macêdo do Carmo. Validation; Resources; Supervision: Sueli de Souza Lima. Validation; Resources; Supervision: Hermínio Ismael de Araújo-Júnior; Ralph Maturano Pinheiro; Diogo Jorge de Melo; Graziella Couto-Ribeiro. • Conflicts of interest: The authors certify that they have no commercial or associative interest that represents a conflict of interest in relation to the manuscript. • Ethical approval: Not applicable. • Availability of data and material: Available in the text itself. • Acknowledgments: Not applicable. • Financing: Coordenação de Aperfeiçoamento de Pessoal de Nível Superior, Brazil (CAPES), Financial Code 001.

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- In addition, some of these materials are ichnofossils preserved in the absence of their zoological origin, such as coprolites and feeding tracks, which makes the taxonomic analysis even more difficult. Therefore, new efforts are necessary in order to identify these fossils and to provide precise quantitative analyzes of the taxonomic diversity, which inhabited the Oligocene paleoenvironments of the Paraíba Valley. This article updated the state of art of paleo-faunistic occurrences in the Tremembé Formation, expanding our perception of its paleobiodiversity and providing subsidies for future dating and correlation studies with other fossiliferous localities, especially in South America.
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