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The Bica São Tomé fossil site, Paraná Basin, Rio Grande do Sul, Brazil: A unique window to the dawn of the Mesozoic Era

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Abstract

The Early Triassic is pivotal for understanding the recovery and diversification of post-extinction biotas, marking the initial emergence or early diversification of many modern lineages. This phase holds dual significance as it establishes the groundwork for contemporary biodiversity evolution and provides crucial insights into managing present ecological challenges. Focused efforts on the Sanga do Cabral Formation in the Paraná Basin unveil a critical opportunity for studying Early Triassic vertebrates in South America, offering a unique perspective on Western Gondwana's biotic recovery after the End-Permian Mass Extinction. Here, we review the geology and fossil record of the most important fossiliferous outcrop of the Sanga do Cabral Formation, the Bica São Tomé Fossil Site. Prospections at the outcrop have already recovered over two hundred specimens, including holotypes and representative materials of important Early Triassic taxa. Our review aims to demonstrate the relevance of the site and highlight strategies for its preservation. The site includes an unusual representation of archosauromorphs, although its content is dominated by procolophonids. Among the known localities of the Sanga do Cabral Formation, the Bica São Tomé Fossil Site stands out for the unique presence of well-preserved specimens in articulation, such as the nearly complete skeleton of the archosauromorph *Teyujagua paradoxa*. Even so, most of the record is dominated by fragmentary and reworked specimens. The Bica São Tomé site stands as a beacon for understanding Lower Triassic ecosystems in Latin America, presenting an unparalleled opportunity for Mesozoic exploration in Brazil. The Sanga do Cabral Formation, with its wealth of fossil evidence, promises to enrich our understanding of the Early Triassic period and its significance in shaping modern biodiversity.

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1. Introduction

The path traversed by life in the course of evolution has, at times, been marked by profound revolutions triggered by geological phenomena. Such was the case with the End-Permian Extinction (EPE), an event that led to the decimation of alarming proportions of continental and marine biotas (Erwin, 2008). The impact of the EPE on ecosystems resulted in a revolution in the macroevolutionary history of lineages, so that all current living organisms descend from some of the few survivors of the EPE.

The early moments of the Triassic period thus mark the beginning of the recovery and diversification of post-EPE biotas. This is an event of utmost significance for two reasons. Firstly, the Early Triassic biotic recovery laid the foundation for what we now know as modern life (Romano et al., 2020). Secondly, and no less important, understanding mass extinctions and life's recovery under conditions of profound environmental stress is crucial for managing the current ecological crisis (Payne and Clapham, 2012).

The Triassic was a pivotal moment in the history of continental life, and many of the groups that now populate terrestrial ecosystems, such as birds, turtles, crocodiles, lizards, lissamphibians and mammals, have their origins or initial diversification consolidated in this period (e.g. Simões et al., 2018). The Triassic marks the beginning of the Mesozoic Era (the "Age of Reptiles"), during which dinosaurs eventually became dominant in terrestrial communities (Chen and Benton, 2012; Benton and Wu, 2022).

Despite their relevance, the initial stages of the Triassic remain relatively underexplored, largely due to significant biases in collection and geographic representation. Our understanding of Early Triassic vertebrates is predominantly derived from a limited number of fossil deposits, concentrated mainly in South Africa, Russia, and China (e.g. Benton et al., 2004; Botha and Smith, 2006; Benton et al., 2013). The sparse record adds to the natural scarcity of fossils due to the decline in diversity following the extinction event.

In this context, the Sanga do Cabral Formation (SCF) in the Paraná Basin emerges as a crucial opportunity for the recovery of fossil vertebrates from the Lower Triassic. As a matter of fact, the SCF is the only Lower Triassic unit with informative paleontological content from South America, offering a unique perspective on the biotic recovery of the Early Triassic in Western Gondwana (Dias-da-Silva et al., 2017).

Given its evident relevance, it seems strange that so little effort has been dedicated to systematic paleontological prospecting in the SCF since the first reports of fossil specimens in the 1980s (see Schultz et al., 2020). Three main factors may be hypothesized to explain this apparent lack of interest: First of all, it is not easy to find informative fossils in SCF outcrops. Its deposition resulted from harsh fluvial environments, inhospitable to biological remains (Xavier et al., 2024). SCF fossils are usually found as fragmentary remains, with obvious evidence of transport and reworking, and complete/articulated specimens are exceptionally rare findings. In second place, the productivity and aesthetic appeal of fossils from the overlying Santa Maria and Caturrita formations have eclipsed the SCF record, which has been revealed as the "ugly duckling" of the Brazilian Triassic. A third important factor is related to the distance from productive localities to large urban centers, such as the Rio Grande do Sul state capital, Porto Alegre. Consequently, there has been a significant increase in prospecting within the SCF following the establishment and strengthening of research groups in smaller cities, such as the Laboratório de Paleobiologia at the Universidade Federal do Pampa (Paleobio Unipampa, São Gabriel, RS) and the Laboratório de Estratigrafia e Paleobiologia at the Universidade Federal de Santa Maria (LEP, Santa Maria, RS).

Although the first formal reports of SCF tetrapods were made by Barberena et al. (1981), the first valid nominal taxon described for this unit was *Sangaia lavinai* (Dias-da-Silva et al. 2006). It is important to note that two separate *Procolophon* species, "*P. pricei*" and "*P. brasiliensis*," were erected by Lavina (1983) and Cisneros & Schultz (2002), respectively. However, these were later synonymized to *P. trigoniceps* by Cisneros (2008). A boost in the research on SCF fossil faunas occurred through the discovery and description of new fossil sites (Da-Rosa et al., 2009; Dias-da-Silva and Da-Rosa, 2011) and the growing interest of new research groups, notably the Paleobio Unipampa the LEP (UFSM). These efforts resulted in the recovery of hundreds of new specimens (most of which are still undergoing triage and preparation) and the description of several new taxa, such as the early archosauromorphs *Teyujagua paradoxa* and *Elessaurus gondwanoccidens* (Pinheiro et al., 2016; De-Oliveira et al., 2020), the procolophonid *Oryporan insolitus* (Pinheiro et al., 2021), and the temnospondyls *Tomeia witecki* and *Kwatisuchus rosai* (Fitrik et al., 2016; Pinheiro et al., 2024).

Pivotal to these new discoveries are the systematic collection efforts concentrated on particularly productive SCF sites. This is the case with the Bica São Tomé fossil site in São Francisco de Assis, Brazil (Fig. 1). In its initial report (Da-Rosa et al., 2009), the Bica São Tomé site has already demonstrated an unusual abundance of fossil yields, especially when compared to other SCF localities. The site is also the only SCF locality where fairly complete and articulated specimens have been found (e.g., Pinheiro et al., 2016, 2020; De-Oliveira et al., 2020, 2024). Additionally, four of the six nominal taxa described for the SCF originate from this site (see below). Consequently, the Bica São Tomé site has instigated a revolution in our understanding of the South American Early Triassic, emerging as one of the most relevant localities for Mesozoic research in this continent. In this work, we review the geology and fossil content of this unique locality with the aim of highlighting its significance for understanding the early Mesozoic Era in western Gondwana and proposing potential strategies for its preservation.

Figure 1. Location and geology of the Bica São Tomé fossil site. A, the Paraná Basin in the context of South America; B, simplified geological map of sedimentary units of Rio Grande do Sul State, southern Brazil. C, aerial image detailing the location Bica São Tomé exposures (image from Google Earth Pro); D, aerial image of outcrop BST 5, the most productive exposure of Bica São Tomé fossil site; E, aerial image of BST 3, other productive exposure of the Bica São Tomé fossil site; F, composite geological section of the 6 outcrops of the Bica São Tomé fossil site, indicating the occurrence published fossil specimens. The black numbered bars next to the geological section indicate the outcrops BST 1-6. Church symbol: former location of the Saint Thomas Jesuitic Mission, *ca*. 1632 AD.

2. Comments on the surface exposure of the Sanga do Cabral Formation

Although the Sanga do Cabral Formation (SCF) was designated based on outcrops surrounding the city of Rio Pardo, in the eastern portion of the Triassic exposure in the central region of Rio Grande do Sul State, the fossiliferous sites are primarily situated in the western portion, between the cities of Santa Maria and São Francisco de Assis. There is also a segment of outcrops along the road to Santana do Livramento, and likely extending into Uruguay, prompting Dias-da-Silva et al. (2017) to regard the Buena Vista Formation in that country as part of the Sanga do Cabral Supersequence (Zerfass et al., 2003). However, paleomagnetic data from that formation suggest it predates the Permian-Triassic boundary (Ernesto et al., 2020).

Most of the retrieved fossils from the SCF are fragmentary and/or disarticulated, originating from scattered outcrops in Rio Grande do Sul State, southern Brazil (Table 1). Ramal Abandonado (also referred to as Catuçaba, Campo da Pedra, or Dilermando de Aguiar) likely represents the earliest recognized fossiliferous exposure of the SCF. It comprises a series of exposures of sheet sandstones and conglomerates encased within fine orange sandstones, situated along an abandoned railroad. This outcrop yielded fragmentary specimens of procolophonids, including a partial skull identified as "*Procolophon pricei*," as well as temnospondyl dermal bones (Lavina, 1983; Lavina & Barberena, 1985). Empedrado is an exposure located along road BR 158, exhibiting a similar lithological composition of sheet sandstones/conglomerates embedded in fine orange sandstones, albeit displaying post-depositional fracturing and dyke intrusion, likely associated with the separation of South America and Africa during the onset of the Gondwana breakup. São José da Porteirinha and Cabeceira do Raimundo, also situated along BR 158, exhibit limited lateral expression. Fazenda dos Melos, identified during the geological mapping of the Quarta Colônia Geopark (Zerfass et al., 2008), presents a notable exposure, although no fossils have been recovered thus far. Rincão dos Weiss represents another known outcrop, located adjacent to a rural road near the city of Mata, primarily yielding fragmentary procolophonid remains. A series of small outcrops in the vicinity of Morro do Cruzeiro in Cachoeira do Sul yielded temnospondyl remains described as *Sangaia lavinai* (Dias-da-Silva and Marsicano, 2006). The SCF spans at least 30 m, exhibiting a gradual lithological transition from sheet sandstones/conglomerates embedded in fine orange sandstones to finer lithologies at the top, although a comprehensive description is warranted. Lastly, the exploration of new outcrops led to the discovery of Bica São Tomé (Da Rosa et al., 2009), Côrte, and Granja Palmeiras (Dias-da-Silva and Da Rosa, 2011), significantly enriching the fossil record of the SCF. This last site is the type locality of the temnospondyl *Kwatisuchus rosai*, a recently described taxon for the SCF (Pinheiro et al., 2024).

Considering the scattered outcrops and the characteristic fragmentary nature of SCF fossils, Bica São Tomé (Fig. 1) emerges as a unique and significant site for understanding Early Triassic Gondwanan diversity. Notably, the site stands out as the most productive locality within the SCF in terms of fossil yield.

Table 1. Known fossiliferous outcrops of the Sanga do Cabral Formation.

3. Site characterization, geology and age

The Bica São Tomé is situated within the escarpments of a hill, adjacent to road RS 241, linking the cities of São Francisco de Assis and São Vicente do Sul in Rio Grande do Sul State, Southern Brazil (Fig. 1, 2). It encompasses six outcrops, with most situated along the roadside and two within privately owned areas (Da Rosa et al., 2009). The predominant vegetation consists of open fields utilized for agricultural activities, interspersed with isolated clusters of trees. The exposure of fossiliferous rocks is attributed to road excavation activities or erosional processes within the private areas, likely influenced by extensive cattle grazing.

The name of the fossil site derives from a water fountain (Bica) with religious significance dedicated to Saint Thomas (São Tomé). In fact, a Jesuit mission was founded there on June 13th, 1632, named "Redução Jesuítica São Thomé", agglomerating more than 400 indigenous people till 1838, when it was abandoned prior to the incursions of pillage soldiers from the center of Brazil (Cohen & Colombo 2015).

The six outcrops were arranged in a composite stratigraphic section exhibiting a predominance of orange fine sandstones, interspersed with lenses of intraclastic conglomerates (Da Rosa et al., 2009). A detailed geological profile (Fig. 1) delineates the following:

Outcrop BST 1. situated within a private area, constitutes the basal segment of the composite profile, characterized by approximately three meters of massive, very fine orange sandstones.

Outcrop BST 2. spans both sides of RS 241, positioned at the northwesternmost side, featuring two small cliffs preserving a limited number of fragmentary fossils within lenses of intraformational conglomerates embedded in trough cross-bedded fine orange sandstones.

Outcrop BST 3. located 200 meters southeastwards from the previous outcrop, along the northern margin of the road, exhibits a coarsening upward succession of fine orange sandstones interspersed with medium sandstone levels, carbonate concretions, and lenses of intraformational conglomerates, housing a sparse collection of fragmentary fossils.

Outcrop BST 4. extends southwards from the preceding outcrop, showcasing a maximal coarsening trend with abundant conglomeratic lenses, evidence of phreatic hydromorphism (manifested as lateral discoloration levels), yet yielding few fragmentary fossils.

Outcrop BST 5. situated within a private area, features an erosional escarpment displaying at least four beds of fining upward fine to medium orange sandstones, adorned with carbonate nodules. Notably, two of these beds exhibit the highest productivity in fossil preservation, yielding the majority of retrieved fossils.

Outcrop BST 6. records medium pink sandstones with trough cross-bedding, attributable to the Guará Formation (Upper Jurassic).

The only SCF nominal taxon with a precise and undisputed correlation to other, better temporally anchored sedimentary basins is the parareptile *Procolophon trigoniceps* (see below). The presence of this species enables a reliable correlation of the SCF with the *Lystrosaurus declivis* Assemblage Zone of the South African Karoo Basin (Katberg Formation) (Botha and Smith, 2020). In well-described, complete sections of the Katberg Fm., the first remains of *P. trigoniceps* occur 116 m above the Permo-Triassic boundary (Botha and Smith, 2006). This correlation, along with the temporal range of other taxa (from a more inclusive taxonomic perspective), indicates a late Induan/Olenekian age for the SCF. It is worth noting, however, that absolute dating of the SCF is already underway. Furthermore, the apparently highly time-averaged SCF assemblage may suggest the possibility of wide temporal gaps between fossil elements present in different sedimentary facies, thus necessitating an in-depth taphonomic assessment of the SCF. For a more detailed account of the SCF biostratigraphy, please refer to Dias-da-Silva et al. (2017).

4. Taphonomic remarks

Fossils collected from the Bica São Tomé Fossil Site are divided into two distinct modes of preservation, associated with different sedimentary facies and also differing in numerical representativeness. The most common occurrences are characterized by isolated, disarticulated bone elements (especially vertebrae, mandibular fragments, and long bones) in varying degrees of fragmentation. These occurrences are usually associated with intraformational conglomerate levels. The common preservation of fragile structures might indicate, according to Holz & Souto-Ribeiro (2000), the pre-fossilization and reworking of elements sharing these taphonomic signatures.

Much more rarely, some specimens show moderate to high degrees of articulation. These include vertebral sequences, limbs, or skeletal portions in varying degrees of completeness (e.g., *Elessaurus gondwanoccidens* - De-Oliveira et al. 2020) (Fig. 3, F, H). A single occurrence of a skull associated with a reasonably complete postcranium is known—the holotype of the archosauromorph *Teyujagua paradoxa* (De-Oliveira et al. 2024) (Fig. 3, C, E). Articulated or semi-articulated specimens are normally associated with fine sand facies, sometimes preserved as cores of carbonate concretions (see Dias-da-Silva et al. 2017).

The different modes of preservation and the possibility of reworking of specimens recovered from conglomeratic levels highlight the potential for substantial time averaging at the fossil site. An accurate assessment of this temporal dimension requires a more in-depth taphonomic study.

Figure 2. Bica São Tomé fossil site. A, aerial view of outcrop BST 5, exposing the most fossiliferous layers of the locality; B, Sanctuary in honor of Saint Thomas, a water fountain area suitable for picnics and camping.

5. Fossil content

The first fossils from the Bica São Tomé site were presented alongside the formal introduction of the locality by Da-Rosa et al. (2009). At that time, the authors illustrated and preliminarily described numerous fossils belonging to Temnospondyli, Procolophonidae, Cynodontia, and Archosauromorpha. It is worth noting that specimens presented as Cynodontia were reevaluated by Dias-da-Silva et al. (2017) as belonging to Procolophonoidea. Among the materials reported by Da-Rosa et al. (2009), only *Procolophon trigoniceps* was identified at the specific level. Some of the materials presented by the authors were further described in posterior contributions, and Da-Rosa et al. (2009) already recognized the uniqueness of the Bica São Tomé site due to the quality of preservation and the occurrence of articulated elements.

Given that the Bica São Tomé site is a recent addition to the Brazilian Triassic, systematic and exhaustive collections at the locality are relatively recent, and the collection effort intensified from the year 2016. Although the locality already boasts hundreds of recovered specimens (mostly fragmentary), the materials that have been sorted, prepared, and identified are scarce compared to those still waiting for preparation. Therefore, this review will focus on those specimens that have already been formally presented and described for the site.

5.1 Temnospondyli

The temnospondyls are the most diverse group of non-amniote tetrapods in Paleozoic and Mesozoic ecosystems, with a large stratigraphic range that spans from the Carboniferous until nowadays (when considering that lissamphibians belong to the clade) (Schoch, 2013). The main adaptive radiation of temnospondyls occurred in the aftermath of the End-Permian Extinction, and the group is one of the major components of Early Triassic continental ecosystems (Romano et al., 2020).

Although bone fragments of Temnospondyli are not rare occurrences at the Bica São Tomé site, few materials have been formally reported for the site. Many collected specimens still require preparation, identification, and formal presentation.

The first materials belonging to the clade for the site were presented by Da-Rosa et al. (2009). These are specimens UFSM 11408, UFSM 11447, UFSM 11455, UFSM 11451, UFSM 11450, UFSM 11473, UFSM 11477. Da-Rosa et al. (2009) highlighted the relevance of specimen UFSM 11408. In this initial article, the material was illustrated as a sequence of cranial bones found in association, some of them showing fitting surfaces.

The same specimen (UFSM 11408) was formally presented as a new species of temnospondyl by Eltink et al. (2017). It consists of a partial skull, represented by its posterior portion, along with several fragmented cranial roof bones and jaw fragments (Fig 3, A). The animal was named *Tomeia witecki* and was recovered as belonging to the Capitosauroidea, one of the major stereospondyl lineages that diversified during the Triassic. Approximately ten years after the discovery of the holotype of *T. witecki*, a cranial fragment was found near the location where the first material was discovered. After laboratory preparation, it became evident that, surprisingly, this second piece fits perfectly with the holotype, being attributable to the same specimen. The holotype of *T. witecki*, including new anatomical information contributed by the new material, is undergoing reassessment and study.

Figure 3. Representative fossil specimens from the Bica São Tomé fossil site. A, *Tomeia witecki* (Temnospondyli), holotype (UFSM 11408), posterior skull in ventral view; B, *Procolophon trigoniceps* (Procolophonoidea) (CAPPA/UFSM 0189) skull in

right lateral view; C, *Teyujagua paradoxa* (Archosauromorpha), holotype skull (UNIPAMPA 653) in right lateral view; D, *Oryporan insolitus* (Procolophonoidea), holotype skull (UFSM 11443) in left lateral view; E, *T. paradoxa*, holotype (UNIPAMPA 653) skull and postcranium; F, *Elessaurus gondwanoccidens* (Archosauromorpha), holotype (UFSM 11471) left hindlimb and axial bones; G, *T. paradoxa*, skeletal reconstruction (mirrored from De-Oliveira et al, 2024); H, *Elessaurus gondwanoccidens*, holotype (UFSM 11471) left foot. Art in G by Voltaire D. P. Neto.

5.2 Procolophonoidea

Procolophonoidea is a fairly diverse group of parareptiles, exclusively composed of small-sized animals. Among Parareptilia, procolophonoids were the only clade to survive the EPE, indicating a pulse of diversification in the Early Triassic (Modesto et al., 2011). Within procolophonoids, the taxon with the most abundant and geographically well-distributed records is undoubtedly the procolophonid *Procolophon trigoniceps*. This species is abundantly represented in outcrops of the Sanga do Cabral Formation, being the primary biostratigraphic proxy for the unit and enabling its correlation with other Lower Triassic strata worldwide (see Dias-da-Silva et al., 2017).

Da-Rosa et al. (2009) attribute several cranial and mandibular materials recovered from the Bica São Tomé site to *Procolophon trigoniceps* (UFSM 11409a, UFSM 11443, UFSM 11448, UFSM 11449, and UFSM 11454), citing the diagnostic presence of "bicuspid, labio-lingually expanded and highly meso-distally compressed molariforms'' as justification for the assignment. Among these materials, a comparatively enormous skull stands out, possibly constituting the largest known specimen for the species (UFSM 11409a). This material would later be described in greater detail by Dias-da-Silva et al. 2017. It is worth noting that specimen UFSM 11443 would later be recognized as representing another genus and species of procolophonid by Pinheiro et al. (2021). Other materials attributed to Procolophonoidea by Da-Rosa et al. include a fragmentary vertebra (UFSM 11469), a long bone fragment identified as a femur (UFSM 11453), and a mandibular fragment (UFSM 11474). The latter exhibits a peculiar morphology, and its assignment to Procolophonoidea lacks a more in-depth evaluation.

As reported earlier, the work by Dias-da-Silva et al. (2017) describes in greater detail the specimen UFSM 11409a. This specimen is of great significance, as it appears to be the largest specimen ever reported for *Procolophon trigoniceps*, surpassing even the largest African specimens (see Dias-da-Silva et al. for further details). The assignment of UFSM 11409a to the species was based on the recognition of bicuspid molariform teeth and a large subtemporal emargination, being also supported by phylogenetic analysis (Dias-da-Silva et al., 2017). Two other specimens attributable to Procolophonoidea were presented for the Bica São Tomé site by Dias-da-Silva et al. (2017). The first of these is a well-preserved, large dorsal vertebra (UNIPAMPA 0655). Its morphology is similar to what has been previously described for procolophonids from the Sanga do Cabral Formation. (as in Dias-da-Silva et al., 2006). A second specimen (UNIPAMPA 0680) is a fragment of a right mandibular ramus bearing bicuspid molariform teeth, a typical characteristic of *Procolophon trigoniceps*.

The specimen, which is likely the best-preserved *Procolophon trigoniceps* for the Sanga do Cabral Formation, also found at the Bica São Tomé site, was described in detail by Silva-Neves et al. (2018). It concerns CAPPA/UFSM 0189, a virtually complete skull with the mandible still in occlusion (Fig 3, B). Its morphology is characteristic of the taxon, not differing significantly from similar-sized South African specimens.

One of the most intriguing specimens of Procolophonoidea recovered from the Bica São Tomé site was described in detail by Pinheiro et al. (2021). This is specimen UFSM 11443, which had previously been identified as *P. trigoniceps* by Da-Rosa et al. (2009) (Fig. 3, D). A more detailed study, aided by images from computed microtomography, allowed recognition that the specimen belongs to a unique taxon of early-diverging procolophonid, only distantly related to *P. trigoniceps*. The new taxon was named *Oryporan insolitus*, and differs from *P. trigoniceps* in a series of cranial and dental characteristics. According to Pinheiro et al. (2021), *O. insolitus* is phylogenetically one of the earliest procolophonids to show clear adaptations to herbivory, contributing substantially to the understanding of the group's evolution.

One last contribution presenting new materials of Procolophonoidea for the Bica São Tomé Site is the recognition, by Bohmann et al. (2024), of the presence of temporal fenestration in a large specimen of *P. trigoniceps*. Although confirmed in some rare South African materials, such structure had never been recorded in Brazilian specimens of the species. Temporal fenestration is considered an anomalous feature for *P. trigoniceps* by the authors.

We emphasize that Procolophonoidea is the most represented taxon in the Bica São Tomé Site and in the Sanga do Cabral Formation as a whole. Thus, beyond the already published works, literally hundreds of specimens collected at the Bica São Tomé site await screening, preparation, and cataloging, especially in the collection of the Laboratório de Paleobiologia at Unipampa. The majority of these materials consist of fragmented cranial and post-cranial remains, providing limited anatomical/taxonomic information. Nevertheless, a detailed evaluation of the recovered fragmentary specimens is underway.

5.3 Archosauromorpha

Archosauromorpha are defined as all those Diapsida more closely related to crocodilians and birds than to lizards and snakes (see De-Oliveira et al. 2020 for a review). Although they may appear restricted in terms of diversity of body plans today, archosauromorphs formed the dominant group in Mesozoic terrestrial ecosystems, with immense diversity of early groups, as well as significant adaptive radiations of clades more closely related to both crocodilians and birds.

The relevance of archosauromorphs in both current and Mesozoic ecosystems, exemplified by the dominance of dinosaurs during that era, makes the origins and early diversification of the group a highly significant topic. Although the origin of Archosauromorpha is traced back to the Permian, their first major diversification event, including an increase in relative abundance in ecosystems and the emergence of new groups, occurred after the end-Permian extinction (e.g. Pinheiro et al., 2016). Therefore, rocks from the Early Triassic are exceptionally relevant for understanding the onset of the clade's dominance (De-Oliveira et al. 2020).

The first records of Archosauromorpha for the Bica São Tomé site were already presented by Da-Rosa et al. (2009).

They consisted of a well-preserved dorsal vertebra (UFSM 11394) attributed to cf. Archosauromorpha, along with less well-preserved vertebrae, found either isolated or in association (UFSM 11467, UFSM 11475, UFSM 11458, UFSM 11460), and an ilium (UFSM 11444) attributed to cf. Archosauriformes. All the reported materials indeed allow their assignment to Archosauromorpha; however, they require a more detailed anatomical assessment to recover their classification at less inclusive taxonomic levels.

By far, the most relevant archosauromorph specimen ever recovered at the Bica São Tomé site (as well as at the whole Sanga do Cabral Formation) is *Teyujagua paradoxa*. Its skull, associated with some cervical vertebrae (UNIPAMPA 653) (Fig. 3, C), was discovered during an expedition to the site in 2015. The specimen was preserved as the core of a "rolled" carbonate concretion, making it impossible to identify the exact stratigraphic level from which the specimen originated. The taxon was described the following year by Pinheiro et al. (2016), with a detailed osteology published by Pinheiro et al. (2020). Throughout 2016, several similarly rolled concretions were also recovered by the Unipampa team near the location where the skull was found. Laboratory preparation revealed that one of these concretions enclosed a significant portion of the postcranial skeleton of *T. paradoxa*, which was described by De-Oliveira et al. (2024) (Fig. 3, E, G).

In addition to being the most complete and well-preserved specimen ever recovered in the Sanga do Cabral Formation, *T. paradoxa* holds special evolutionary significance. Its anatomy exhibits a mosaic of features typical of early archosauromorphs combined with traits typically found in archosauriforms (Pinheiro et al. 2016, 2020). In the evolutionary tree of archosauromorphs, *T. paradoxa* is recovered as one of the closest relatives of the archosauriforms, illuminating the early morphological evolution of this important clade.

An additional archosauromorph species was described based on material collected at the Bica São Tomé site by De-Oliveira et al. (2020). This specimen (UFSM 11471) is well-preserved and includes an almost complete hind limb, as well as the pelvic girdle and sacral and caudal vertebrae (Fig. 3, F, H). The animal was recovered as the sister taxon to the enigmatic Tanystropheidae and was named *Elessaurus gondwanoccidens* (De-Oliveira et al. 2020). If the relationships of *E. gondwanoccidens* with the tanystropheids is confirmed, as it appears to be the case (Spiekman et al. 2021), the specimen also proves to be of deep macroevolutionary interest, as it would correspond to one of the oldest records of the group, being also the only one ever recovered in South America.

De-Oliveira et al. (2022) delved deeper into the investigation of the diversity of archosauromorphs from the Sanga do Cabral Formation, presenting four interesting specimens collected at the Bica São Tomé site. Some of them proved to be diagnostically significant, allowing their inclusion in a phylogenetic matrix. One of the specimens, UNIPAMPA 750, is a peculiar anterior cervical vertebra identified by the authors as cf. *Chasmatosuchus*. A second vertebra, this time belonging to the dorsal series (UNIPAMPA 684), was recovered as cf. *Proterosuchus*. Additionally, De-Oliveira et al. (2022) presented fragmentary elements (a parietal portion of a cranial roof and a neural spine), identifying them as Archosauriformes indet. The work of De-Oliveira et al. (2022) is relevant for presenting the first unequivocal records of Archosauriformes for the Sanga do Cabral Formation, substantially expanding the diversity of Archosauromorpha for the Brazilian Lower Triassic. Some of the specimens presented by De-Oliveira et al. (2022) were reassessed by Ezcurra et al. (2023). The latter allocates the specimens UNIPAMPA 750 and UNIPAMPA 684 to the new clade Chasmatosuchinae (Archosauriformes: Proterosuchidae).

5.4 General comments on the fossil diversity of the site

The Bica São Tomé site showcases an unequivocal diversity of at least three taxa of archosauromorphs, representing the majority of the clade's diversity within the Sanga do Cabral Formation. It is noteworthy that all described species of archosauromorphs from the Sanga do Cabral Formation have their holotypes recovered from this site, and numerous new specimens (potentially including new species) are currently under evaluation.

It is important to note that the majority of specimens collected at the Bica São Tomé fossil site are still undergoing sorting and preparation, without precise taxonomic identification. Nonetheless, the site presents a considerably high number of collected specimens (256), deposited in the scientific collections of the Universidade Federal do Pampa and the Universidade Federal de Santa Maria. Among the identified specimens, Procolophonidae are the most represented, followed by Archosauromorpha and Temnospondyli. Fragments of fish (not described in detail) have also been reported, and these are currently undergoing study. The taxa thus far reported for the site are representative of a typical Early Triassic disaster fauna (Fig. 4, 5). The absence of synapsids, which are common in localities of the same age in Russia, India, and South Africa, remains enigmatic and unexplained.

Figure 4. Taxonomic representation of fossil groups found at the Bica São Tomé fossil site. Silhouette credits: Procolophonidae, Felipe A. Elias; Temnospondyli, Dmitry Bogdanov; fish, Tree of Life App; Archosauromorpha, Márcio Castro. Images used under permission or licensed via Wikimedia Commons.

Figure 5. Artistic reconstruction of the Bica São Tomé fossil assemblage. 1. Proterosuchidae indet; 2. *Elessaurus gondwanoccidens*; 3. *Tomeia witecki*; 4. *Teyujagua paradoxa*; 5. *Procolophon trigoniceps*; 6. *Oryporan insolitus*. Artwork by Voltaire Neto.

6. Geoconservation

Considering the importance of this site for scientific purposes, including its participation in the Geopark Raízes de Pedra Project, several geoconservation measures are proposed here.

Outcrops Bica 1 and 5 are situated in private areas, with the latter being the most significant in terms of fossil representation. Therefore, we suggest that these outcrops be reserved exclusively for scientific purposes, with tourism activities discouraged. The remaining outcrops can be utilized for tourism and educational purposes, with special emphasis on the water fountain area due to its existing infrastructure.

The water fountain area currently includes a parking and camping area (see Fig. 2, B), but better visual organization is necessary. This could involve the installation of educational

signs, both for paleontological information and urban usage guidance. Outdoor signs and totems represent feasible solutions that could be implemented by the municipal government or private entrepreneurs. One challenge to address is providing access for buses and large vehicles, which may require the involvement of the state government responsible for roads and tourism management. Expansion of the entrance and parking area, along with improved organization of visitor activities, is essential.

In addition to the measures mentioned above, it is crucial to implement specific strategies for the effective protection of fossil outcrops. This may include installing physical barriers around the most sensitive areas to prevent damage caused by unaware visitors. Furthermore, regular surveillance by trained personnel can help prevent illegal fossil collection and other harmful impacts on the environment. Environmental education and public awareness also play a crucial role, highlighting the importance of fossil outcrops for science and the need to preserve them for future generations. Collaboration between local authorities, landowners, and communities may be essential for the development and effective implementation of these protection measures. It is also important to emphasize that none of the conservation measures suggested here will impact land productivity or its use for agricultural purposes.

7. Final remarks

The Bica São Tomé fossil site within the Sanga do Cabral Formation has played a crucial role in enhancing our understanding of the Early Triassic period in South America. As we continue to uncover new insights into post-extinction biotic recovery, it is essential to prioritize measures for the preservation and controlled scientific exploration of such fossil sites.

Implementing strategies to safeguard these valuable resources will ensure their long-term conservation and sustainable utilization for scientific research. By adopting responsible practices in exploration and preservation, we can uphold the integrity of these sites and continue to advance our knowledge of Earth's evolutionary history.

Acknowledgements

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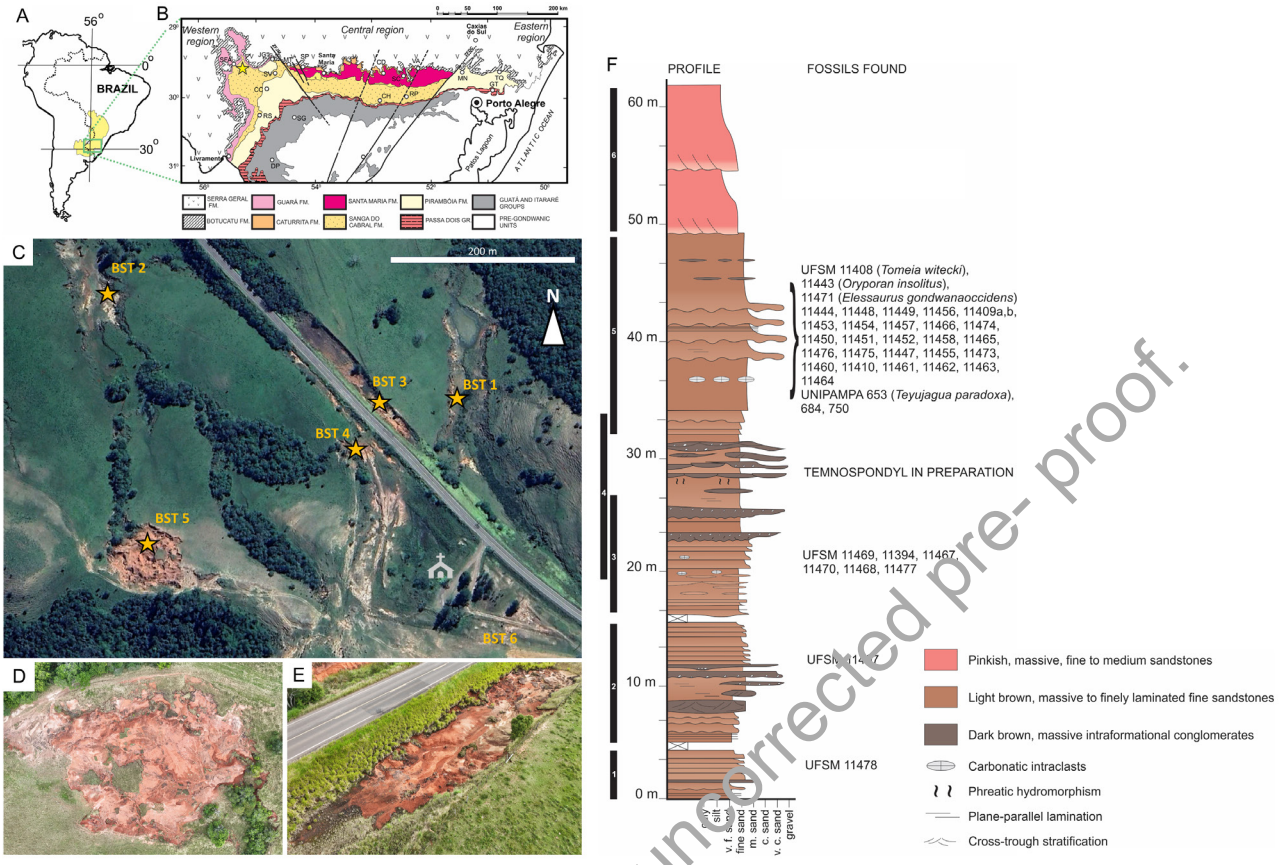

Figure 1. Location and geology of the Bica São Tomé fossil site. A, the Paraná Basin in the context of South America; B, simplified geological map of sedimentary units of Rio Grande do Sul State, southern Brazil. C, aerial image detailing the location Bica São Tomé exposures (image from Google Earth Pro); D, aerial image of outcrop BST 5, the most productive exposure of Bica São Tomé fossil site; E, aerial image of BST 3, other productive exposure of the Bica São Tomé fossil site; F, composite geological section of the 6 outcrops of the Bica São Tomé fossil site, indicating the occurrence published fossil specimens. The black numbered bars next to the geological section indicate the outcrops BST 1-6. Church symbol: former location of the Saint Thomas Jesuitic Mission, *ca*. 1632 AD.

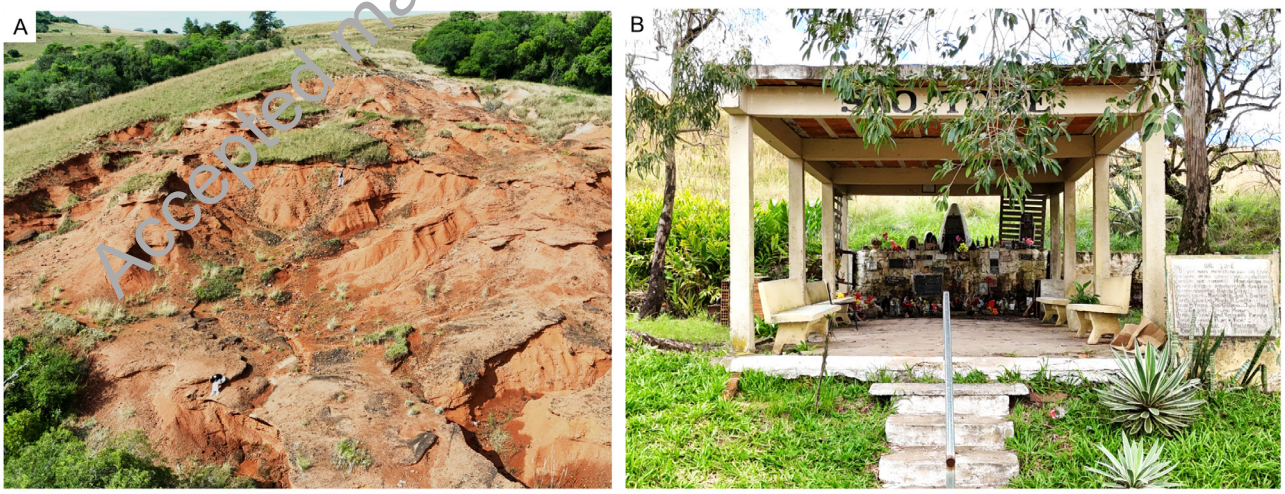

Figure 2. Bica São Tomé fossil site. A, aerial view of outcrop BST 5, exposing the most fossiliferous layers of the locality; B, Sanctuary in honor of Saint Thomas, a water fountain area suitable for picnics and camping.

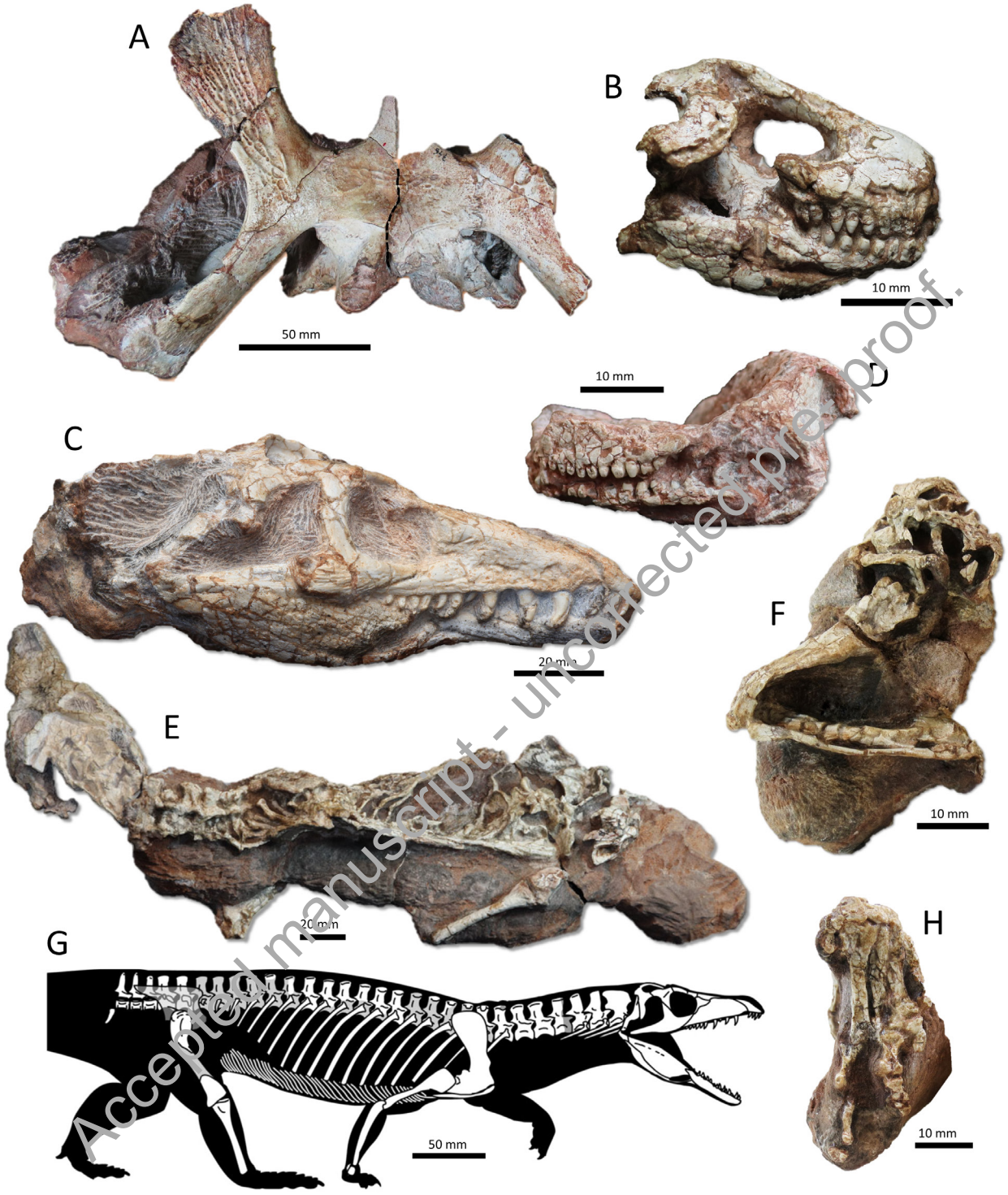

Figure 3. Representative fossil specimens from the Bica São Tomé fossil site. A, Tomeia witecki (Temnospondyli), holotype (UFSM 11408), posterior skull in ventral view; B, Procolophon trigoniceps (Procolophonoidea) (CAPPA/UFSM 0189) skull in right lateral view; C, Teyujagua paradoxa (Archosauromorpha), holotype skull (UNIPAMPA 653) in right lateral view; D, Oryporan insolitus (Procolophonoidea), holotype skull (UFSM 11443) in left lateral view; E, T. paradoxa, holotype (UNIPAMPA 653) skull and postcranium; F, Elessaurus gondwanoccidens (Archosauromorpha), holotype (UFSM 11471) left hindlimb and axial bones; G, T. paradoxa, skeletal reconstruction (mirrored from De-Oliveira et al, 2024); H, Elessaurus gondwanoccidens, holotype (UFSM 11471) left foot. Art in G by Voltaire D. P. Neto.

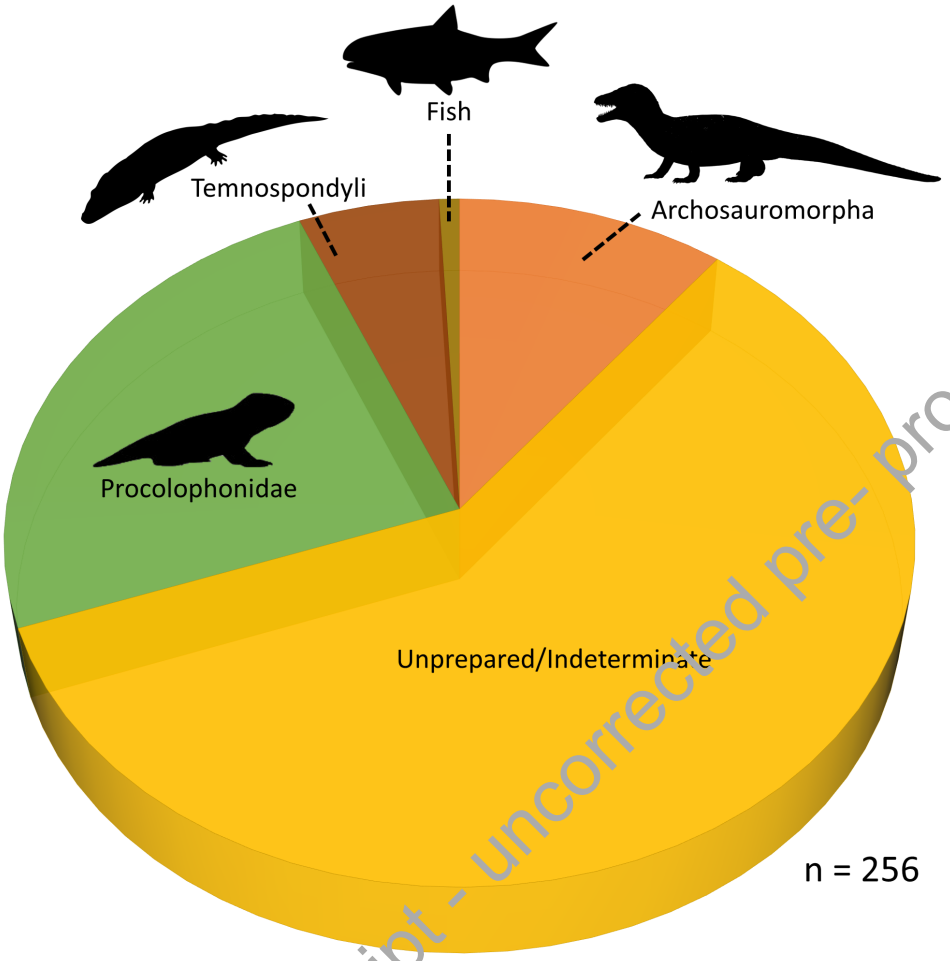

Figure 4. Taxonomic representation of fossil groups found at the Bica São Tomé fossil site. Silhouette credits: Procolophonidae, Felipe A. Elias; Temnospondyli, Dmitry Bogdanov; fish, Tree of Life App; Archosauromorpha, Márcio Castro. Images used under permission or licensed via Wikimedia Commons.

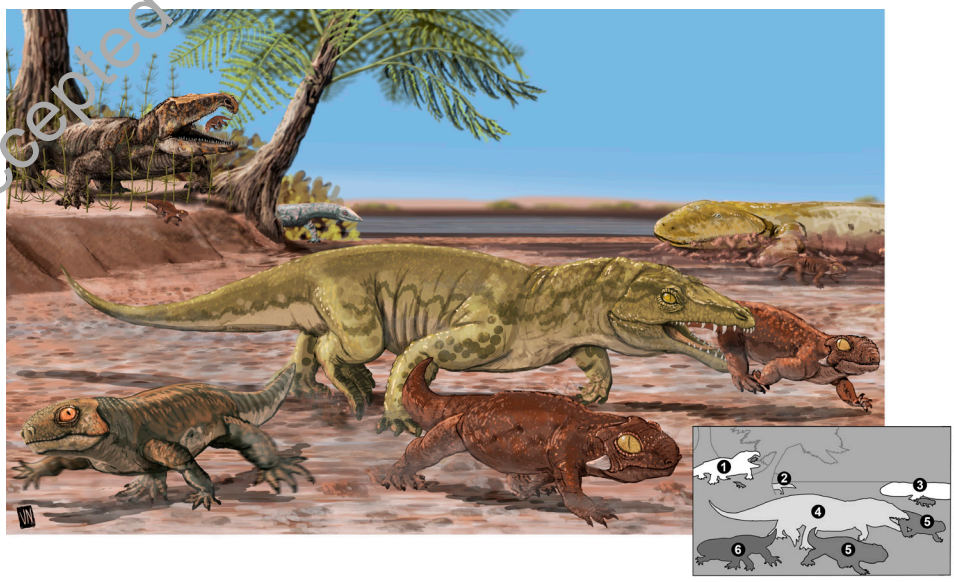

Figure 5. Artistic reconstruction of the Bica São Tomé fossil assemblage. 1. Proterosuchidae indet; 2. Elessaurus gondwanoccidens; 3. Tomeia witecki; 4. Teyujagua paradoxa; 5. Procolophon trigoniceps; 6. Oryporan insolitus. Artwork by Voltaire Neto.

Table 1. Known fossiliferous outcrops of the Sanga do Cabral Formation.

Outcrop	Municipality	Fossils	References
Ramal abandonado (also Catuçaba or Dilermando de Aguiar)	Dilermando de Aguiar	*"Procolophon pricei"*, temnospondyl dermal bones	Lavina 1983; Lavina & Barberena 1985
Empedrado	Dilermando de Aguiar	Procolophonid jaw, undescribed fragments	
São José da Porteirinha	Dilermando de Aguiar	Indeterminate fragments	
Cabeceira do Raimundo	Santa Maria	Procolophonid fragments	Da Rosa, 2004
Fazenda dos Melos	Restinga Seca	Indeterminate remains	Zerfass et al, 2008
Morro do Cruzeiro	Cachoeira do Sul	*Sangaia lavinai*	Dias-da-Silva and Marsicano, 2006
Rincão dos Weiss	Jaguari	Procolophonid and temnospondyl fragments	
São Vicente do Sul	São Vicente do Sul	Indeterminate fragments	
Trevo para Cacequi	São Vicente do Sul	Indeterminate fragments	
Côrte	Rosário do Sul	Indeterminate fragments	
Granja Palmeiras	Rosário do Sul	Fish, procolophonid, temnospondyl and archosauriform frgments, *Kwazusuchus rosai*	Dias-da-Silva and Da Rosa, 2011; Pinheiro et al., 2024
Bica São Tomé	São Francisco de Assis	Procolophonid, temnospondyl and archosauriform fragments, *Teyujagua paradoxa*, *Tomeia witecki*, *Elessaurus gondwanaoccidens*, *Oryporan insolitus*	Da Rosa et al, 2009; Eltink et al, 2016; Pinheiro et al, 2016, 2022; De-Oliveira et al., 2020