

Chapter 3

A Look into the Past: Fossils from the *Campos Sulinos* Region



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3.1 Introduction

The *Campos Sulinos*, i.e., the grasslands that dominate natural landscapes in the three southernmost states of Brazil, Rio Grande do Sul (SC), Santa Catarina (SC), and Paraná (PR), extend over different geological grounds in southern Brazil: igneous and metamorphic rock from the crystalline basement, fossiliferous sedimentary rocks from the Paraná Basin, volcanic rocks from the top of Serra Geral, and fluvial and coastal sedimentary deposits (Silva and Vaine 2001; Wildner et al. 2008, 2014; see also Menegat 2023, Chap. 2, this volume). This region witnessed important paleogeographic, paleoclimatic, and paleobiotic shifts in the last 300 million years, which will be summarized here (Fig. 3.1). Four major moments can be envisaged in this scenario in southern Brazil. The Permian started with a Gondwanic glaciation, but subsequent deglaciation led to sea level rise, the formation of an internal sea,

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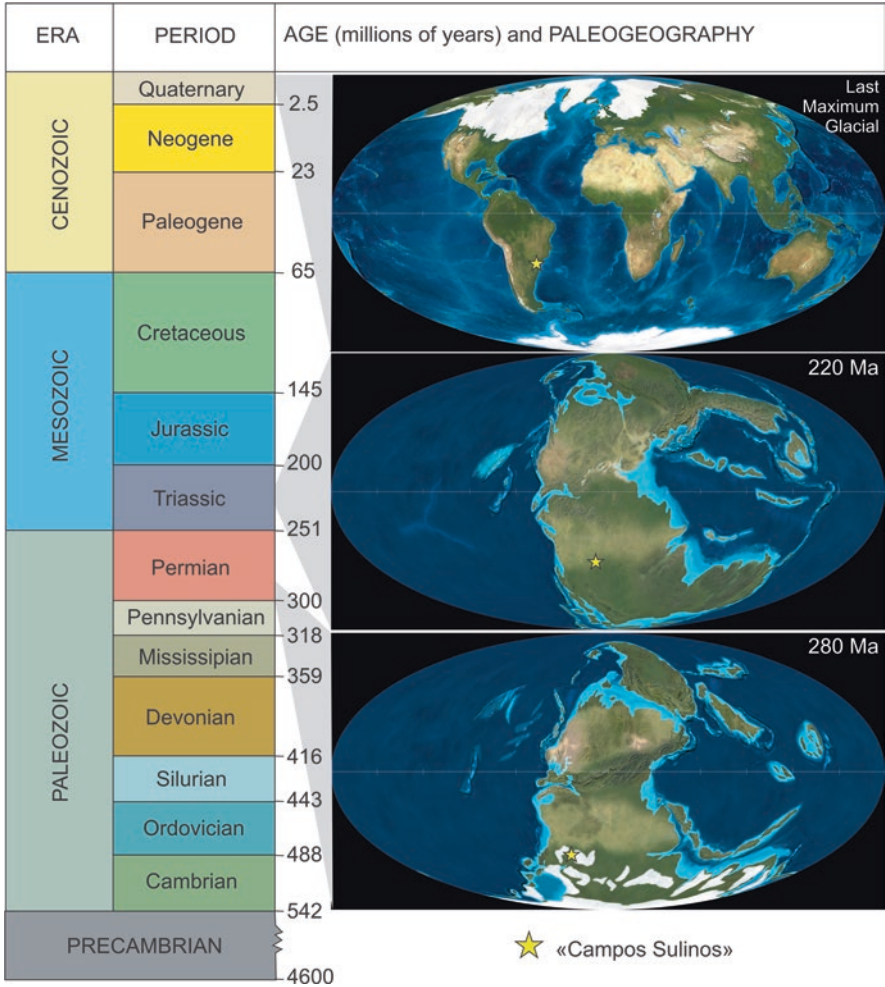


Fig. 3.1 Geological time scale and positioning of “Campos Sulinos” fossiliferous rocks in Permian (280 million years, Ma), Triassic (220 Ma), and Pleistocene (Last Maximum Glacial). (Global reconstructions after Ron Blakey)

and evolution to an alluvial plain in Pangean conditions. The Triassic witnessed the recovery of a massive extinction and development in alluvial plains in Pangean circumstances. The Late Jurassic and Early Cretaceous are known for their desert environments, prior to the breakup of South America and Africa. Finally, the glacial and interglacial cycles of the Pleistocene led to the onset of megamammals and large reptiles, later extinct between the latest Pleistocene and early Holocene, and the establishment of “campos”-forest mosaics.

3.2 Paleogeographic and Paleoenvironmental Reconstruction

Here we present the geobiological transformation over the last 300 million years (Ma), depicting four different periods: the Permian, Triassic, Jurassic-Cretaceous periods, and the Pleistocene Epoch (Fig. 3.1).

3.2.1 Permian

During the Permian, all land masses were gathered in a single, “C”-shaped supercontinent called Pangaea (see Fig. 3.1). This term was coined by Alfred Wegener in 1912 to designate the geological and paleobiological coalescence of present continents into a single supercontinent (Wegener 1912). According to current knowledge, the Pangaea was formed from the convergence of Laurentia, Baltica, and Gondwana during the late Carboniferous (Scotese and Golonka 1997). This supercontinent was bordered by two oceans, the Panthalassa and Tethys.

The Paraná Basin was part of the Gondwanan realm of Pangaea. Its geological history goes from glaciation at the beginning of the Permian period (Itararé Group) and later deglaciation, which led to sea level rise, coastal shift (Rio Bonito and Palermo Formations), and formation of an epicontinental sea (Irati Formation) in the mid-Permian (Holz et al. 2010). During the late Permian, continentalization started, leading to the formation of shallow lakes (Teresina Formation) and alluvial plains (Rio do Rasto Formation). The rocks from the Itararé Group are the record of glacial and postglacial environments, such as glaciomarine or glaciolacustrine settings (Vesely 2007; Weinschütz and Castro 2006). The record of Gondwanan glaciation in Brazil is preserved in some isolate sites, such as the Witmarsun and Salto glacial striations and Mafra dropstones (Santa Catarina), ruiniform relief at Vila Velha State Park (Paraná), and Itu Varvite (São Paulo) (Rocha-Campos 2002a, b; Melo et al. 2002; Pérez-Aguilar et al. 2008). Some outcrops are also known from Rio Grande do Sul.

The Rio Bonito Formation records lagoon-barriers deposited under sea level rise conditions, right after deglaciation. These more humid conditions led to the deposition of peat environments and coal formation (Lavina and Lopes 1987; Castro et al. 1999; Maahs et al. 2019). These rocks include leaf imprints of the *Glossopteris* Flora, which Alfred Wegener used as evidence of continental drift (Iannuzzi 2010; Jasper et al. 2009). The Palermo Formation is formed by mudstones and shales, due to a more prominent sea level rise, only recording rare marine microfossils (Simões and Rocha-Campos 1993). Outcrops are known from São Paulo, Paraná, Santa Catarina, and Rio Grande do Sul.

The Irati Formation records an epicontinental sea with bituminous shales (Chahud et al. 2012). Its fossiliferous content, mainly characterized by crustaceans and mesosaurs, are worthy of mention, as they were also used as evidence of continental drift by Alfred Wegener (Araújo-Barberena et al. 2002; Cerri et al. 2020;

Oleofsen and Araújo 1983a, b, 1987a, b; Ricardi-Branco et al. 2009). Silicified logs are also present (Merlotti 2009). The preservation of almost complete skeletons of mesosaurs is related to winter storms and sea floor erosion (Lavina et al. 1991; Xavier et al. 2018). Outcrops are known from Paraná and Rio Grande do Sul states.

The Serra Alta Formation is composed of regressive facies of dark gray mudstones (Warren et al. 2015), recording bivalves (Matos et al. 2017a, b), ostracods (Bergue et al. 2020), and silicified logs (Merlotti 2009). The Teresina Formation is characterized by gray siltstones, intercalated with micritic carbonate and stromatolites, representing the transition from marine environments to marine zones with shallow water influenced by storms (Rohn 2001; Silva and Vaine 2001; Callefo et al. 2015), with fossils restricted to palynomorphs (Neregatto et al. 2008), pelecypods (Silva and Vaine 2001), ostracods (Bergue et al. 2020), and microbial mats (Callefo et al. 2015).

The Rio do Rasto Formation facies are diverse, with fluvial, aeolian, and lacustrine environments (Schemiko et al. 2014). Their sedimentary evolution indicates the formation of a large confined water body and the accumulation of a transgressive-regressive sequence at its lower portion, eventually recording storm conditions, while the progradational character of the upper portion led to the colmatation of the water body with deltaic and aeolian deposition (Warren et al. 2008). The Rio do Rasto Formation was considered Lopingian (Malabarba et al. 2003). However, a recent U-Pb age repositioned it to Guadalupian (Francischini et al. 2018).

3.2.2 *Triassic*

Still under the overall condition of continental agglutination, the Triassic witnessed a slight northern displacement of Pangea (Fig. 3.1), maintaining the paleoequator at the inflection of the boomerang-like structure (Golonka et al. 2018). At the end of the Triassic (Norian and Rhaetian), a massive bulging took place at that point, leading to the formation of a magmatic province, namely the Central Atlantic Magmatic Province (CAMP; Marzoli et al. 2018), which is related to the opening of the Atlantic Ocean and the extinction of several land vertebrates (Davies et al. 2017).

The Triassic record of the Paraná Basin is restricted to its southern portion, in Rio Grande do Sul. Here, two depositional packages were recognized, the Sanga do Cabral Supersequence, composed of the arenaceous rocks of the homonymous geological formation, and the Santa Maria Supersequence, integrating the Santa Maria and Caturrita formations (Zerfass et al. 2003). More recently, Horn et al. (2014) subdivided the Santa Maria Supersequence into third-order sequences: Pinheiros-Chiniquá (Ladinian?), Santa Cruz (early Carnian), Candelária (late Carnian to Norian), and Mata (Rhaetian?).

The Sanga do Cabral Supersequence records fine sandstones with intercalated intraformational conglomerates, deposited in broad alluvial plains (Da Rosa et al. 2009a, b), while the Santa Maria Supersequence (SMS) presents a more complex organization (Da Rosa 2015). The lower part of the SMS, i.e., the

Pinheiros-Chiniquá, Santa Cruz, and the lower portion of the Candelária sequences, records the intercalation of sandstones and fine-grained lithologies, deposited at low energy, high sinuosity rivers, representing channels, levees, overbank deposits, shallow and temporary lakes, loess, and paleosols (Da Rosa et al. 2004a, b, 2005; Horn et al. 2013). On the other hand, the upper portion of the SMS shows a predominantly sandy deposition in high energy, low sinuosity rivers, with channels and overbank deposits (Müller et al. 2015).

3.2.3 *Jurassic/Cretaceous*

The time interval between the end of the Jurassic and the beginning of the Cretaceous is characterized by the continuation of the Pangaea breakup, with main interest in the separation of South America and Africa circa 135 Ma ago. In the Paraná Basin, the Guará Formation consists of fine to conglomeratic sandstones of whitish to reddish color, with trough cross-stratification from small to large size and horizontal lamination. The facies associations characterize fluvial to fluvio-aeolian deposits, with a distinctive change throughout its exposure, the northern part consisting of facies associations of braided fluvial systems and the southern part showing a tendency to replace the predominant fluvial facies by aeolian associations (Scherer and Lavina 2005). These fluvial-aeolian sandstones are correlated to the Tacuarembó Formation in Uruguay and placed at the end of the Jurassic based on their faunal content (see Sect. 3.3.3).

3.2.4 *Pleistocene*

The main Cenozoic units from Rio Grande do Sul are restricted to the Quaternary Period (2.58 million years ago to the present), more precisely between the Middle Pleistocene and the Holocene. During the Pleistocene, the continents were already organized in their present condition (Fig. 3.1), with rapidly changing environments due to glacial cycles and subsequent sea level fall, the imposition of dry climates, and the shift of river profiles and coastal lines (Golonka 2009). The Pleistocene deposits, mostly formed in fluvial environments, are found in western RS (WRS – Alegrete, Quaraí, and Uruguaiana) (Lopes et al. 2020), central region (Caçapava do Sul, Pantano Grande), and Coastal Plain (CPRS – Santa Vitória do Palmar). In addition to these locations, there are several others with sparse records, such as São Gabriel and Jaguarão. Different methodologies, such as Carbon-14 (^{14}C), Accelerated Mass Spectrometry (AMS), Electron Spin Resonance (ESR), and Optically Stimulated Luminescence (OSL), have been applied to time-calibrate fossils and Pleistocene sediments. Radiometric ages from WRS (Touro Passo Creek, Uruguaiana; Quaraí River, Quaraí; Sanga da Cruz and Ibicuí River, Alegrete) are placed between ~42 and 10 ka (Bombin 1976; Miller 1987; Kotzian et al. 2005;

Milder 2000; Ribeiro and Scherer 2009; Kerber et al. 2011a, b, c), while deposits from the CPRS include older sediments. Chuí Creek sedimentary strata (Santa Vitória Formation, Santa Vitória do Palmar) were deposited between ~190 and ~30 ka, with most fossils dated between 50 and 30 ka (Lopes et al. 2014a, b, 2019, 2020). The fossils from onshore deposits found in Balneario Hermenegildo (Santa Vitória do Palmar) are even older, dated between 650 and 18 ka (Lopes et al. 2010). Concerning the record of tetrapods, the fossils found in these locations show a certain taxonomic uniformity (although some peculiarities are observed; see Sect. 3.4) and mostly represent fossils of large mammals (Mammalia) known as the Pleistocene megafauna. However, other small vertebrates, such as lizards, birds, and fishes, are also recorded.

3.3 Biodiversity and Paleocological Reconstruction of Fauna and Flora

Here, we summarize the faunistic (tetrapods) and floristic biodiversity and paleoecological inferences of the studied time intervals, i.e., Permian, Triassic, Jurassic/Cretaceous, and Pleistocene.

3.3.1 Permian

Almost all Permian rocks in the *Campos Sulinos* region have a fossil record restricted to fish, invertebrates and/or plant fossils. However, exceptions are the Irati and Rio do Rasto formations, which present tetrapods in a more complex food chain. Few fossils are known from the Itararé Group, and they consist of invertebrates (Matos et al. 2017a; Neves et al. 2014; Taboada et al. 2016), fish fragments and ichnofossils, such as annelid and trilobite trackways (Netto et al. 2009; Lima et al. 2015; Wilner et al. 2016; Noll and Netto 2018). The Irati Formation is remarkable for its exceptional record of mesosaurs, i.e., parareptiles adapted to an aquatic way of life, such as thickened bones (especially ribs) and characteristic teeth. Three mesosaur species were proposed for the Irati Formation, *Mesosaurus brasiliensis*, “*Stereosternum tumidum*”, and “*Brazilosaurus saopaulensis*”. Piñeiro et al. (2021), however, recognized only the former as valid. Mesosaurs seem to have fed on fish and pygocephalomorph crustaceans in the Irati-Whitehill Sea.

A complex and diversified fauna inhabited the aquatic environments associated with the deposition of the Rio do Rasto Formation. The unit already yielded abundant actinopterygian remains, even though those are often represented by fragmentary bones and isolated “paleonisciform” scales. Exceptions to these highly transported, mainly uninformative materials come from the Serrinha Member, known for its representativeness of low-energy depositional environments (e.g.,

Milani et al. 2007). Perhaps the best-preserved actinopterygian so far recovered from the Rio do Rasto Formation is the bizarre *Paranaichthys longianalis*, a laterally flattened fish with flamboyant anal fins (Dias 2012). *Paranaichthys* is known solely from its holotype, a superbly preserved specimen recovered in Paraná state. *Rubidus pascoalensis*, another Rio do Rasto actinopterygian known from a complete specimen, had a more elongated body, displaying several rows of diamond-shaped scales (Richter 2002).

The diagnostic nature of isolated shark teeth and fin spines made it possible to recognize three nominal shark species for the Rio do Rasto Formation, all known by fragmentary specimens. Two of these, *Xenacanthus ragonhai* and *Triodus richterae* (Pauliv et al. 2014, 2017), belong to the Xenacanthiformes, eel-like sharks with long and low dorsal fins and strong denticulated fin spines. Xenacanthiform teeth are easily recognized by their tricuspoid crowns, with long lateral cusps flanking a smaller central one. Recent findings suggest that xenacanthiforms may be at least partially responsible for producing the exceptional coprolite concentrations found in Rio do Rasto outcrops (e.g., Dentzien-Dias et al. 2012a, b). A third shark species, *Sphenacanthus riorastoensis*, belongs to the enigmatic Sphenacanthidae, and is only known from isolated fin spines (Pauliv et al. 2012).

Sharks were not the apex predators in mid- and late-Permian freshwater bodies. At that time, this role was played by the Temnospondyli, an extraordinarily diverse clade of early-diverging tetrapods commonly referred to as “amphibians” (Schoch 2013). With a wide range of sizes and an obligate carnivorous diet, temnospondyls may have played an ecological role similar to that of modern-day crocodylians, even though several representatives were adapted to feed in terrestrial environments (Clack 2012). Several temnospondyl nominal species are known from the Rio do Rasto Formation, this being by far the best-represented group in this sedimentary unit. Like modern caimans, some Rio do Rasto temnospondyls, such as *Rastosuchus hammeri* (Dias et al. 2020) and *Parapytanga catarinensis* (Strapasson et al. 2015) had short and broad snouts, while the bizarre *Australerpeton cosgriffi* and *Bageherpeton longignathus* had exceptionally long and slender snouts, completely filled with small (but sharp) needle-shaped teeth (Dias and Barberena 2001; Pacheco et al. 2016; Azevedo et al. 2017).

Synapsids, the mammal forerunners, were abundant during the Permian period, dominating most land ecosystems and occupying several ecological roles that ranged from primary consumers to apex predators. In the Rio do Rasto Formation, herbivore synapsids belong to the clade Anomodontia. Anomodonts were diverse forms of mainly tusked herbivores that prospered during most of the late Permian and Triassic times. Early-diverging anomodonts are rare in the fossil record. Among these, the most striking is certainly *Tiarajudens eccentricus*, a saber-toothed pig-sized animal known by an almost complete skull and some postcranial remains from a Rio do Rasto Formation outcrop. Besides long canines, *Tiarajudens* had strong molariforms adapted to macerate vegetation (Cisneros et al. 2011, 2015). The saber-like canines of *Tiarajudens* likely evolved as display structures, perhaps also being used during intraspecific agonistic interactions, similar to what is seen today in musk deers (Cisneros et al. 2015).

Dicynodontia, the most diverse anomodont subclade, has two representatives in the Permian of Brazil. Among these, the best-known is *Rastodon procurvidens*, a diminutive (~40 cm long) dicynodont that lacked teeth except for two small forward-directed banana-shaped tusks (Boos et al. 2016; Simão-Oliveira et al. 2019). *Rastodon* is known from a single, superbly preserved specimen, including an almost complete skull and several postcranial bones. As can be extrapolated from other Permian dicynodonts, *Rastodon* was probably gregarious and excavated burrows for protection (Simão-Oliveira et al. 2019). The second Rio do Rasto Formation dicynodont, *Endothiodon* sp., is known only from a crushed and incomplete skull from Paraná (Barberena and Araújo 1975; Boos et al. 2013). Despite fragmentary, *Endothiodon* is a key taxon to understanding Rio do Rasto Formation geochronology, allowing a direct correlation with the better-studied South African Karoo Basin.

The remaining synapsids recovered from the Rio do Rasto Formation belong to the clade Dinocephalia. Medium to large animals, dinocephalians apparently had a wide range of feeding habits and were first reported from the Rio do Rasto Formation through isolated teeth and jaw fragments (Langer 2000). Only in 2012 the first reasonably complete specimen was introduced, the complete (albeit crushed) skull of the medium-sized carnivore *Pampaphoneus biccai* (Cisneros et al. 2012). This specimen so far represents the largest land predator of the Brazilian Permian, probably occupying an apex position in its food chains. A second, more complete *Pampaphoneus* specimen was recently recovered from the same outcrop where the holotype was found (Costa Santos et al. 2023). This new specimen contributes with information on the anatomy of this carnivorous dinocephalian. Still unpublished, this specimen will contribute with information on the anatomy of this carnivorous dinocephalian. The Rio do Rasto Formation also yielded a single herbivorous dinocephalian specimen (Boos et al. 2015). Albeit not sufficiently complete to allow a specific attribution, the material confirms the presence of the dome-headed tapinocephalid dinocephalians in the Brazilian Permian. A summarized scenery of the Rio do Rasto Formation is available in Fig. 3.2.

The taphoflora preserved in the Rio do Rasto Formation deposits is characterized by the latest records of the *Glossopteris* Flora, which dominated most environments during the Permian Period, before the formation of desertic landscapes at the end of the Paleozoic. The *Glossopteris* Flora represents one of the most important paleofloras preserved over geological time. In addition to its wide paleogeographic distribution, which attests to the continental drift proposed by Alfred Wegener in 1912, this flora also witnessed the most important environmental and climatic changes that occurred in the course of the Permian Period, from the transition of the icehouse to the greenhouse stage and the aridization of previously moist environments, culminating in the Earth's greatest mass extinction.

The main floristic elements that characterize the *Glossopteris* Flora were diagnosed mainly through impressions of leaves and stems of *Glossopteris*, *Gangamopteris*, *Rubidgea*, and *Buriadia* (Guerra-Sommer and Cazzulo-Klepzig 2000a, b). Other groups still present in today's environments, such as the lycophytes *Cyclodendron* sp. (Herbst 1986) and *Lycopodiopsis* sp. (e.g., Martins and Sena-Sobrinho 1951; Ferraz et al. 2021), the sphenophyte *Shenophyllum* sp. (e.g., Rohn



Fig. 3.2 Permian. Faunistic elements depicted, from front to back: *Australerpeton*, *Bageherpeton*, *Rastodon*, *Tiarajudens*, *Provelosaurus*, *Pampaphoneus*, and indeterminate tapinocephalian. (Floristic records: Equisetales and Cycadaceae. Artwork: Voltaire Dutra Paes Neto)

and Rösler 1990; Iannuzzi 2010), and the pteridophytes *Pecopteris* sp. (e.g., Cazzulo-Klepzig 1978; Rohn and Rösler 1986; Ferraz et al. 2021), *Schizoneura* sp. (e.g., Cazzulo-Klepzig 1978; Cazzulo-Klepzig and Correia 1981), *Dichophyllites* sp. (Bortoluzzi 1975; Rohn 1988), and *Paracalamites* sp. (Bortoluzzi 1975; Rösler and Rohn 1984), have also been documented.

Although vegetation records in the Rio do Rasto Formation predominantly indicate hygrophilic and mesophilic habits (Rohn 1988), the slow process of aridization during this period was documented through the reduction of floristic diversity. Records of pteridophytes become rarer, lycophytes are represented only by arborescent and shrubby forms, and *Glossopteris* species show changes in their leaf structure, with a reduction in limb dimensions and secondary venation of leaves. These signs suggest a warm and semi-arid climate, with long dry seasons alternating with rainy seasons of moderate rainfall (Guerra-Sommer and Cazzulo-Klepzig 2000a, b).

Due to environmental disturbances in the Permian (Guadalupian), including forest fires (Manfroi et al. 2015), there was a significant change in the floristic landscape, also affecting the cohabiting fauna. For example, evidence of insect–plant interactions in these deposits was seen in *Glossopteris* sp. with damaged leaf edges, indicating phytophagy and climatic cyclicality (Rohn 1988). Likewise, herbivorous vertebrates that fed on the existing vegetation on the edges of Permian lakes suffered from the reduction of available plant biomass, such as recorded for the *Equisetales*. This may have caused a disturbance in the entire food chain, which, along with other factors, later resulted in the end of the Paleozoic Era.

3.3.2 Triassic

The tetrapod biodiversity of the Brazilian Triassic is summarized into five assemblage zones (AZs) of biostratigraphic relevance (Schultz et al. 2020). Each AZ can be regarded as a different fauna. The AZs are organized in time, so that their succession represents the evolution of land communities from the devastated, postextinction Early Triassic environments toward the mature, stable Late Triassic ecosystems in which the first dinosaurs dwelt.

The diverse ecomorphological adaptations present in vertebrates from each AZ suggest the presence of complex ecological interactions and food chains during the time intervals recorded in the southern Brazilian fossil record (see evidence of trophic relationships in Schwanke and Kellner 2009). The earliest Brazilian Triassic assemblage zone is the *Procolophon* AZ. Albeit still poorly sampled, this AZ has recently been shown to hold an important and relatively diverse tetrapod fauna. The archosauromorph *Teyujagua paradoxa* and temnospondyl amphibians (e.g., *Sangaia lavinae* and *Tomeia witecki*) played their roles as carnivores in Early Triassic times (Pinheiro et al. 2016, 2019; Eltink et al. 2016). At the same time, the parareptiles *Procolophon trigoniceps* and *Oryporan insolitus* were probably omnivore/herbivore animals (Pinheiro et al. 2021). The proterosuchid archosauriforms and the tanystropheid *Elessaurus gondwanaoccidens* were probably specialized faunivores (De-Oliveira et al. 2020, 2022). Although inferring Early Triassic food chains is not an easy task, the increasing number of specimens recovered will certainly improve our knowledge of ecosystem dynamics in this period.

The second, younger Brazilian Triassic assemblage zone is the *Dinodontosaurus* AZ (Schultz et al. 2020). This AZ records a more complex ecosystem, where huge

archosaurs such as *Prestosuchus chiniquensis* (~12 m long) were the apex predators. In contrast, smaller archosaurs (e.g., *Decuriasuchus quartacolonina*, *Pagosvenator candelariensis*, *Archeopelta arborensis*, and indeterminate proterochampsids and raiusuchians) may have played a secondary role as carnivores. In this AZ, non-mammaliaform cynodonts become very diversified in the fossil record of Rio Grande do Sul. The herbivore/omnivore cynognathians are represented by several traversodontids: *Massetognathus ochagaviae* and *M. pascuali*, *Traversodon stahleckeri*, *Protuberum cabralense*, *Luangwa sudamericana*, and *Scalenodon ribeiroae* (von Huene 1936; Abdala and Teixeira 2004; Liu et al. 2008; Reichel et al. 2009; Melo et al. 2017). The last two taxa have coeval species recorded in African Triassic strata. Probainognathians (mostly carnivore/insectivore cynodonts) include *Chiniquodon theotonicus*, *Protheriodon estudianti*, *Candelariodon barberenai*, *Aleodon cromptoni*, and *Bonacynodon schultzi* (von Huene 1936; Bonaparte et al. 2006; Oliveira et al. 2011; Martinelli et al. 2016, 2017a). Dicynodonts were herbivores of large (*Stahleckeria potens*) and medium size (*Dinodontosaurus*) (von Huene 1935; Schultz et al. 2020). The owenettid parareptile *Candelaria barbouri* seems to have been faunivorous, probably insectivorous.

The next assemblage zone (*Santacruzodon* AZ) has a still scarce fossil record, which can be attributed to sampling bias or a possible co-occurrence with the older *Dinodontosaurus* AZ. This biozone has produced a number of traversodontid and probainognathian cynodonts, but raiusuchian and proterochampsid archosaurs are also present. The traversodontid *Santacruzodon hopsoni*, which names the AZ, is the most abundant cynodont (Abdala and Ribeiro 2003), but there are also records of *Massetognathus ochagaviae*, *Menadon besairiei*, and the probainognathians *Santacruzognathus abdala* and *Chiniquodon* sp. (Melo et al. 2015; Martinelli et al. 2016; Schmitt et al. 2019). Interestingly, the Malagasy *Menadon besairiei* is a Triassic cynodont with hypsodont postcanines (indicating the presence of specialized adaptations in herbivores as a result of the arid Triassic environments), previously described from the 'Isalo II' group of Madagascar (Melo et al. 2015, 2019). Aside from indeterminate proterochampsids (Hsiou et al. 2002; Raugust et al. 2013; Ezcurra et al. 2015), a single large-sized predator archosaur was recorded for the *Santacruzodon* AZ. *Dagasuchus santacruzensis*, known solely from a fragmentary pelvis (Lacerda et al. 2015), was a medium-sized raiusuchian, probably very similar to its "cousin" *Prestosuchus chiniquensis*.

The *Hyperodapedon* AZ was probably the most diverse assemblage zone, in which several carnivores disputed the same geographic area (Garcia et al. 2019). Archosaurs such as proterochampsids, raiusuchians, silesaurids, and early dinosaurs (herrerasaurids and basal sauropodomorphs) were the main predators. The most common herbivores were rhynchosaurs, but cynodonts were also present, as well as clevosaurid sphenodontians. Procolophonians were never recorded from this time interval, but a new taxon is currently under study (Silva-Neves *in prep*). Regarding the cynodonts, the cynognathians are represented by the traversodontid *Exaeretodon riograndensis*, one of the most abundant fossils of this association, *Gomphodontosuchus brasiliensis*, represented by few remains, and the recently described *Santagnathus mariensis* (von Huene 1928; Hopson 1985;

Abdala et al. 2002; Schultz et al. 2020; Schmitt et al. 2023). Probainognathians are more diverse and include the enigmatic *Charruodon tetracuspoidatus*, the large body-sized ecteniid *Trucidocynodon riograndensis*, and the small prozostrodonians, probably insectivorous or carnivores, *Prozostrodon brasiliensis*, *Therioherpeton carnigini*, and *Alemoatherium huebneri* (Barberena et al. 1987; Abdala and Ribeiro 2000; Oliveira et al. 2010; Martinelli et al. 2017b; Kerber et al. 2020, 2022; Stefanello et al. 2023). In addition, two other cynodonts may be included in this AZ, or alternatively in the younger *Riograndia* AZ, or even at an as-yet-unknown interval: the traversodontid *Siriusgnathus niemeyerorum* and the probainognathian *Agudotherium gassenae*, both recovered from outcrops in Agudo municipality in central RS, but without index fossils so far (Pavanatto et al. 2018; Miron et al. 2020; Martinelli et al. 2020). The fossil content of these two localities appears to be endemic when compared to other Brazilian Triassic outcrops.

Archosauromorph diapsids were also a major component of the *Hyperodapedon* AZ. As mentioned before, the most abundant herbivores were the rhynchosaurs, bizarre pig-sized early archosauromorphs bearing beak-like projections on their jaws. Two rhynchosaur taxa are known for this AZ: the widespread genus *Hyperodapedon* and the smaller, more recently described species *Teyumbaita sulcognathus* (Montefeltro et al. 2010). The bulky aetosauroids were armored omnivore archosaurs, represented by the taxa *Aetosauroides scagliai* and *Aetobarbakinoidea brasiliensis* (e.g., Desojo et al. 2012; Brust et al. 2018; Paes-Neto et al. 2021). Aside from these species, *Hyperodapedon* AZ archosauromorphs are also represented by the proterochampsids *Rhadinosuchus gracilis* (von Huene 1938), *Cerritosaurus binsfeldi* (Price 1946) and *Proterochampsia nodosa* (Barberena 1982), as well as the rausuchian *Rausuchus tiradentes* (von Huene 1938). Most interestingly, the *Hyperodapedon* AZ preserves a wealth of early dinosaurs, most of which being forerunners of the long-necked sauropods, such as the sauropodomorphs *Buriolestes schultzi* (Cabreira et al. 2016), *Saturnalia tupiniquim* (Langer et al. 1999), *Bagualosaurus agudoensis* (Pretto et al. 2018), and *Pampadromaeus barberenai* (Cabreira et al. 2011). Typical carnivores are represented by the Herrerasauridae, medium-sized apex predators bearing sharp teeth and hooked hand claws (*Staurikosaurus pricei* and *Gnathovorax cabreirai*) (Colbert 1970; Pacheco et al. 2019). Finally, *Ixalerpeton polesinensis* was a small dinosaur-related gracile archosaur, recently proven to be akin to the pterosaurs (Cabreira et al. 2016; Ezcurra et al. 2020). Figure 3.3 illustrates some taxa of the *Hyperodapedon* AZ.

Unlike the Carnian strata, the Norian fossil record of synapsids in the subsequent *Riograndia* AZ is characterized by the return of large-sized dicynodonts to the Brazilian fossil record. The only known taxon is the stahleckerioid *Jachaleria candelariensis* (Kannemeyeriiformes), which represents one of the last South American dicynodonts (Araújo and Gonzaga 1980; Martinelli et al. 2020). Although almost all fossils point to fully terrestrial forms, two aquatic vertebrates are present: a fragmentary interclavicle of a Stereospondyli (Dias-da-Silva et al. 2009) and part of a snout of an indeterminate phytosaur (Kischlat and Lucas 2003). On the other hand, except for putative records of traversodontids (Ribeiro et al. 2011) plus the records mentioned above (pending further geochronological studies), the confident fossil



Fig. 3.3 Triassic. Faunistic elements, from front to back: *Hyperodapedon*, *Exaeretodon*, *Gnathovorax*, and *Dinamigosuchus*. (Floristic records: *Dicroidium*, Cycadaceae. Artwork: Márcio L. Castro)

record of cynodonts is exclusively of small prozostrodonts, which include the “ictidosaur” *Riograndia guaibensis*, and the tritheledontids *Irajatherium hernandezi*, *Botucaratherium belarminoi*, and *Brasilodon quadrangularis*, the sister-group to Mammaliaformes (Bonaparte et al. 2003, 2005; Martinelli et al. 2005, 2017c; Soares et al. 2011, 2014; Kerber et al. 2022). These forms are important for understanding the origin and early evolution of Mammaliaformes and, consequently, provide evidence for the reconstruction of mammalian history.

Dinosaurs were also present in the *Riograndia* AZ strata, albeit were less diversified than in the older *Hyperodapedon* AZ. Three dinosaur taxa are currently known, two of them belonging to the Sauropodomorpha (*Macrocollum itaquii* and *Unaysaurus tolentinoi*) (Leal et al. 2004; Muller et al. 2018), while the third species (*Guaibasaurus candelariensis*) has disputed affinities (Bonaparte et al. 1999; Langer et al. 2010). Other *Riograndia* AZ archosauromorphs include the pterosauriforms *Faxinalipterus minima* and *Maehary bonapartei* (Bonaparte et al. 2010; Kellner et al. 2022) and the dinosaur-like silesaurid *Sacisaurus agudoensis* (Ferigolo and Langer 2021).

The Triassic period has witnessed one of the main vegetation transitions in the Earth’s history, with environments dominated by the *Dicroidium* Flora gradually replacing the *Glossopteris* Flora, abundant during the Permian. The *Dicroidium* Flora was composed of plants better adapted to the new climatic conditions, significantly warmer and drier than in the previous period. Among them are the Corytospermales (*Xylopteris*, *Dicroidium*, and *Jonstonia*), which, despite being morphologically very similar to ferns (pteridophytes), produced seeds (spermatophytes) as the gymnosperms (Guerra-Sommer et al. 1999; Pankaj et al. 2014).

In RS deposits, remarkable fossiliferous assemblages that reveal the taphoflora, mainly of conifers of the group *Araucarioxylon*, are associated with the last fossil records of Triassic tetrapods. The herbivores at the time probably fed on shrubs and small arboreal plants of the *Dicroidium* Flora. The changes that occurred in the composition of the flora due to lower rainfall and higher temperatures are pointed out as one of the reasons for the substitution of the cynodont and dicynodont fauna, which did not adapt to the new vegetation, thus leaving room for the domain of rhynchosaurs and first dinosaurs (Guerra-Sommer et al. 1998; Guerra-Sommer and Cazzulo-Klepzig 2007; Langer et al. 2007; Schultz and Langer 2007; Horn et al. 2014).

The Triassic plains in western Gondwana (where southern Brazil is located today) were filled not only by plant groups that are now extinct, such as Corytospermales, but also by plants that still have extant representatives, e.g., the phyllicophytes (*Todites*, *Clapophlebis*, and *Asterotheca*), ginkgophytes (*Ginkoites*, *Baiera*, and *Stenorachis*), sphenophytes (*Neocalamites*), conifers (*Araucarioxylon*, *Podozamites*, and *Rissikia*), and cycads (*Pseudoctenisi*, *Otozamites*, and *Taeniopteris*). This taphoflora is found in the fossil record through the impression of fronds, leaves, and stems in clayey sediments and silicified stems in clayey and sandy sediments (e.g., Guerra-Sommer et al. 1999; Da Rosa et al. 2009a, b; Barboni and Dutra 2015). These distinct taphonomic and depositional processes have been the subject of debate up to the present. The so-called *Dicroidium* Flora, preserved

through normally articulated impressions, is associated with a low-energy depositional environment. On the other hand, the Coniferous Flora, or “*Araucarioxylon* Flora”, is represented by phytofossils of silicified stems associated with high energy deposition. The Coniferous Flora was composed of floristic elements with overall small leaves, such as the Araucariaceae, Taxodiaceae, and Cheiropodiaceae. The difficulty in performing the biostratigraphy insertion of this palaeoflora results from the fact that the fossiliferous record is rarely found in situ. However, Guerra-Sommer et al. (1999) suggest that the *Dicroidium* Flora and the Coniferous Flora preserved in RS deposits were contemporary floristic communities and belonged to the same depositional system, but preserved in different faciolgies. The *Dicroidium* Flora is related to a depositional system proximal to the fluvial plain, due to its hygromesophilic features, and the *Araucarioxylon* Flora, with mesoxerophilic features, is associated with distal deposits of the flooding plain.

Regarding the conifer taphoflora in the Triassic deposits of RS, there are very few records of leaf branches of Araucariaceae (Crisafulli and Dutra 2009; Barboni and Dutra 2013), and all other records of this conifer flora are thus far only constituted by silicified wood, with no other records of associated macro- or microfossils (Horn et al. 2014). This assembly of silicified woods of *Araucarioxylon* preserved in conglomeratic sandstones that characterize the Mata Sequence represents one of the most important paleobotanical sites in South America and, although its deposition is evidently associated with high-energy fluvial events, being an allochthonous taphocoenosis, the analysis of the anatomical structures of these woods corroborates a climate with low seasonality as inferred for the Triassic in these latitudes (Pires and Guerra-Sommer 2004; Pires et al. 2005; Dos Santos et al. 2023).

3.3.3 *Juro-Cretaceous*

The Brazilian Jurassic is predominantly represented by aeolian sedimentary units, so the scarcity of body fossils is remarkable. As such, most of what we know about Jurassic faunas that thrived in southern Brazil comes from ichnological evidence – especially footprints and burrows (e.g., Dentzien-Dias et al. 2007, 2012a, b; Francischini et al. 2015, 2017). These have been recovered from the Guar Formation (Upper Jurassic), a geographically restricted unit with a predominance of aeolian and fluvial deposition (Scherer and Lavina 2005). The Guar Formation crops out in the southwestern portion of Rio Grande do Sul, with aeolian exposures concentrated toward the south (Scherer and Lavina 2005). However, it is noteworthy that the Guar Formation has a lateral correlation with the Uruguayan Tacuaremb Formation, from which a large number of somatic (i.e., body fossils) occurrences have already been reported (e.g., Perea et al. 2009; Soto et al. 2021).

Dinosaurs are the main components of the Guar Formation ichnoassemblage. Their footprints are found in both sand dune and sand sheet deposits (Dentzien-Dias et al. 2012a, b), especially within the boundaries of Santana do Livramento and Rosrio do Sul municipalities. The first Guar Formation dinosaur footprints were

formally reported by Scherer and Lavina (2005). Subsequently, Dentzien-Dias et al. (2007) conducted the first detailed assessment of dinosaur tracks and small-sized vertebrate burrows. These authors recognized a diverse assemblage composed of sauropods, theropods, and ornithopods. In a later contribution, Dentzien-Dias et al. (2012a, b) quantified Guara Formation occurrences, recognizing the presence of 60 dinosaur tracks. Footprints from which a conclusive identification can be made reveal an ichnoassemblage dominated by sauropods ($n = 22$) and theropods ($n = 15$), with a smaller contribution of ornithopods ($n = 6$).

The most recent contribution to the knowledge of the southern Brazilian Late Jurassic faunas was the recognition by Francischini et al. (2017) of the presence of ankylosaur tracks in a Guara Formation outcrop. Besides the scarcity of ankylosaur fossils in South America, the Guara Formation occurrence represents the oldest record of this clade in the western portion of Gondwana. The discovery of this new and unexpected ichnotaxon highlights the underexplored potential of the Guara Formation in revealing clues from the elusive Brazilian Jurassic faunas.

3.3.4 *Pleistocene*

The fossil record of Pleistocene tetrapods, especially mammals, shows a mixture of taxa from lineages with different biogeographic origins: mainly forms that evolved in South America during the Paleogene (in addition to caviomorphs, of African origin) and Neogene, and tetrapods that immigrated from the northern hemisphere (Central and North America) during the Great American Biotic Interchange (GABI) (see Woodburne 2010; Goin et al. 2012; Forasiepi et al. 2014; Carrillo et al. 2015; O’Dea et al. 2016). This biogeographic event, which is perhaps primarily responsible for the emergence of the modern fauna of the South American continent (Carrillo et al. 2015), was the biotic interchange between South America and North and Central America. It began during the Late Miocene (~10–7 Ma), with the arrival of the first immigrants (i.e., procyonids and cricetid rodents, also called “island hoppers”, in reference to the fact that the isthmus was not fully formed), and was intensified between the end of the Pliocene (2.7 million years) and the Pleistocene (Woodburne 2010; Goin et al. 2012; O’Dea et al. 2016). Before the Pliocene, terrestrial organisms could not pass freely between these continents because the Isthmus of Panama had not yet been fully formed. As a result, South America was virtually isolated from the northern hemisphere by land routes during part of the Cenozoic. After the formation of this terrestrial connection, several organisms migrated from one region to another, significantly modifying the biotic composition of the continent’s ecosystems. This mixture of organisms resulted in the so-called South America Pleistocene Megafauna (Fig. 3.4), characterized by the presence of several large-sized mammals (>300 kg), such as giant sloths, glyptodonts, pampatheres, toxodonts, macrauchenias, horses, cervids, large carnivores, and mastodonts, among others. Apart from a few exceptions, megamammals disappeared at the end

of the Pleistocene. So far, all mammals found in RS are placentals, as marsupials are still unknown in the fossil record. These placentals represent four large groups: Xenarthra, Laurasiatheria, Euarchontoglires, and Afrotheria (Asher et al. 2009). Some iconic fossils from the Pleistocene Megafauna are shown in Fig. 3.4.

Concerning autochthonous South American mammals present in the Pleistocene of RS, a first group is Xenarthra the only placental lineage with extant species originating in South America. This is one of the most emblematic groups of the Cenozoic of this continent because of their great taxonomic diversity, abundant fossil record, and endemism (Gaudin and Croft 2015). During the Pleistocene of RS, xenarthrans were represented by two groups: pilosans (ground sloths) and cingulates (glyptodonts, armadillos, and pampatheres). Both megatheriid and mylodontid ground sloths have been found in RS Pleistocene deposits (Oliveira 1992, 1996). Megatheriid



Fig. 3.4 Late Pleistocene landscape of Rio Grande do Sul, showing from left to right the glyptodont *Glyptodon clavipes*, the ursid *Arctotherium*, the toxodontid *Toxodon platensis* (behind), and the megatheriid *Megatherium americanum*. The predominance of herbaceous vegetation is also evident, typical of parts of the landscape with a less significant presence of Araucaria Forest. (Artwork Julio Lacerda)

records include the co-occurrence of *Megatherium americanum* and *Eremotherium laurillardii* in at least two localities: Arroio Seival, Caçapava do Sul (Oliveira et al. 2002) and Chui Creek, Santa Vitória do Palmar (Lopes et al. 2019). This is the only Brazilian territory with records of both megatheriids, because *M. americanum* had an austral distribution and *E. laurillardii* had an intertropical distribution. Hence, RS was possibly a geographic boundary in the distribution of both species. The large mylodontid *Lestodon armatus* was reported from Caçapava do Sul and Chuí Creek (Vargas-Peixoto et al. 2021). Other ground sloths from the coastal plain of RS (CPRS) include the mylodontids *Myiodon darwini*, the only record of this species in Brazil, *Glossotherium robustum*, and the scelidotheriine mylodontid *Catonyx* cf. *C. cuvieri* (Oliveira 1992; Lopes and Pereira 2010; Pitana et al. 2013). In western RS (WRS), ground sloths are rarer than in CPRS. Only records of the mylodontid *Glossotherium robustum* have been confidently reported (Pitana et al. 2013). Cingulates, especially glyptodonts, are common in RS Pleistocene deposits. However, most records are based on isolated osteoderms. The glyptodonts *Glyptodon clavipes* and *Panochthus* are present in most fossiliferous assemblages (Kerber and Oliveira 2008a; Pereira et al. 2012; Kerber et al. 2014a, b). Recently, large portions of carapaces, probably of *G. clavipes*, were found in the Ibicuí River, Alegrete, and Jaguarão, but the material is still undescribed (LK, pers. obs.). *Panochthus* from CPRS is represented by two species: *P. tuberculatus* and *Panochthus* cf. *P. greslebini* (Ferreira et al. 2015). *Doedicurus* is present only in deposits of the CPRS (Pereira et al. 2012), and rare material of *Neuryurus* was recorded from Garupá Creek, Quaraí (Kerber and Oliveira 2008b). The record of the enigmatic cingulate *Pachyarmatherium* is only based on isolated osteoderms from Balneário Hermenegildo (Lopes and Buchmann 2010). The pampatheres *Pampatherium humboldti* and *Holmesina paulacoutoi* have been documented from several Pleistocene deposits (Oliveira and Pereira 2009; Ferreira et al. 2018), although the species of *Pampatherium* of WRS is unknown (Kerber et al. 2014a, b). Dasypodids are the rarest cingulates, probably because of their smaller size, which makes it difficult to find their fossils. *Propraopus grandis* fossils have been mentioned for several localities (Pitana and Ribeiro 2007) and *Dasypus* sp. for the Chuí Creek (Oliveira and Pereira 2009).

Other iconic Cenozoic South American mammals are the native ungulates (Croft et al. 2020). These animals, possibly related to perissodactyls (horses, tapirs, rhinos, etc.; Laurasiatheria) (Buckley 2015; Croft et al. 2020), have five major lineages. The native ungulates from the Pleistocene of RS belong to two groups: notoungulates (toxodontids) and litopterns (protherotheriids and macraucheniiids). Toxodontids are large herbivores, hippo-like mammals, and are represented by *Toxodon platensis* found in most Pleistocene localities of RS (Pereira et al. 2012; Kerber et al. 2014a, b). Protherotheriids are litopterns with more plesiomorphic morphological traits and are smaller than macraucheniiids, which are characterized by elongated necks and nasal retraction. Fossils of the protherotheriid cf. *Neolicaphrium recens*, the only Quaternary survivor of the lineage (Bond et al. 2001), were found in the Hermenegildo Beach (Santa Vitória do Palmar) (Scherer et al. 2009). Like

T. platensis, the macraucheniid *Macrauchenia patachonica* has also been found in several localities (Scherer et al. 2009).

Euarchontoglires is represented by rodents. Two groups are found in Pleistocene sediments of RS: caviomorphs (African origin) and cricetids (Holarctic origin). Together, both lineages compose the most diversified lineage of South American mammals (D'Elía et al. 2019). The Pleistocene record of caviomorphs includes the capybara (*Hydrochoerus hydrochaeris*) and the coypu (*Myocastor coypus*) in deposits from WRS and CPRS (Kerber and Ribeiro 2011; Kerber et al. 2014a, b). A fossil of the cavy *Galea* sp. (absent in the RS modern mastofauna) was found in deposits of the Touro Passo Creek (Kerber et al. 2011b). Similarly, in the fossiliferous assemblage from the Chuí Creek, three rodents that currently inhabit drier areas of southern South America have been found: the cavy *Microcavia*, the vizcacha *Lagostomus* cf. *maximus*, and the mara Dolichotinae indet. (Ubilla et al. 2008; Kerber et al. 2011c). The fossil record of cricetids is scarce, represented by remains of *Reithrodon auritus* from Balneário Hermenegildo (Rodrigues and Ferigolo 2004) and *Holochilus brasiliensis* from WRS and CPRS (Kerber et al. 2012).

Like cricetids, other mammalian lineages recorded in Pleistocene deposits of RS have a Holarctic origin, and their ancestral lineages arrived during the Plio-Pleistocene GABI (see Woodburne 2010; Goin et al. 2012). Most of them had wide geographic distributions in the South American Pleistocene. Artiodactyla is the most diverse clade of laurasiatherians, with three groups: tayassuids, camelids, and cervids. Tayassuids (peccaries) show records of the extant white-lipped peccary *Tayassu pecari* at Touro Passo Creek, and of the large extinct *Brasiliochoerus stenocephalus* in WRS as well as in CPRS (Gasparini et al. 2009; Kerber et al. 2014a, b; Copetti et al. 2021). Camelids, the llamas and guanacos, are represented by three species in several localities: the extant guanaco *Lama guanicoe* and the vicuña *L. aff. gracilis*, and extinct *Hemiauchenia paradoxa* (Scherer 2006; Scherer et al. 2007). Cervids (deers) have records of indeterminate species of the extant genus *Mazama* in the CPRS, and the extinct genus *Morenelaphus*, and the large *Antifer* in several localities (Kerber et al. 2014a, b; Pereira et al. 2012; Fontoura et al. 2020).

Perissodactyls include two species of horses, *Equus neogeus* and *Hippidion principale*, and the tapir *Tapirus* cf. *terrestris*, which were widely distributed (Pereira et al. 2012; Holanda et al. 2012; Kerber et al. 2014a, b). The fossil record of carnivores is rare, and most fossils come from the CPRS. Few specimens of the canid *Dusicyon* cf. *D. avus*, and the large hypercarnivore forms *Procyon troglodytes* and cf. *Theriodictis* are recorded from the CPRS, as well as the iconic saber-toothed cat *Smilodon popularis* and the jaguar *Panthera onca* (Rodrigues et al. 2004; Lopes et al. 2020). Ursids are known from undescribed bones from Quaraí River, an isolated tooth from Pantano Grande, and a canine assigned to cf. *Arctotherium* from Chuí Creek (Pereira et al. 2012). Afrotherians are represented by proboscids, with records of mastodont *Notiomastodon platensis* from several localities (Marcon 2008).

Other continental tetrapods are much less abundant and studied. From the Touro Passo Creek, there are some records of chelonians, not described in detail, such as *Hydromedusa tectifera* (Maciel et al. 1996; Hsiou 2009), the endemic extinct teiid

lizard *Tupinambis uruguaianensis* (Hsiou 2007), and the tropical stork *Mycteria* cf. *M. americana* (Ribeiro et al. 1995; Hsiou 2009). Finally, the tropical stork *Ciconia* is recorded from Chuí Creek (Lopes et al. 2019).

Due to the geographic location of RS, the Pleistocene fossils are in the geographic boundary between two biogeographic regions, the Pampean and Intertropical regions (Oliveira 1999; Oliveira et al. 2002; Oliveira and Pereira 2009; Kerber et al. 2014a, b; Lopes et al. 2019, 2020). For this reason, their taxonomic composition show a mix of taxa predominantly recorded in the southernmost parts of South America (e.g., *Doedicurus* and *Macrauchenia*) and forms of intertropical affinities (e.g., *Eremotherium*). Most large mammals were extinct at the end of the Pleistocene and early Holocene. During the Holocene, the taxonomic composition of the modern faunas originated (see Hadler et al. 2008, 2009, 2016; Lopes et al. 2020 and references therein for a review). Although the causes of this extinction event of continental proportions are still debated, it is inferred that the extinctions were not simultaneous, but occurred over the course of a few thousand years. (Lopes et al. 2020). According to the model proposed by Lopes et al. (2020), the most recent study on RS extinctions, large mammals disappeared in at least two phases, which can be related to climatic changes in the Late Pleistocene. The first phase occurred around 30 ka in the CPRS, predating the arrival of humans into the region by about 25 ka. A second phase eliminated taxa that survived until about 12.7 ka in reduced suitable environments associated with perennial rivers of the WRS. This phase coincides with the transition from glacial to interglacial conditions. Finally, it was suggested that early human occupations may have contributed to environmental modifications. No confident archaeological records of humans' coexistence or exploitation of extinct mammals have been documented in RS yet, although there are plenty of them in South America (Bampi et al. 2022). However, early inhabitants may have contributed to environmental changes through the use of fire for agricultural purposes (Behling et al. 2009).

It is clear that it was the climatic variation over time that outlined the environmental mosaic of the *Campos Sulinos* region. Different studies confirm that grassland vegetation is much older than forests in the Pleistocene phytogeography of southern Brazil. During much of the Pleistocene, the landscape that made up these environments was predominantly grassland vegetation, with rivers not accompanied by riparian forests. These open areas were populated by megafauna and had a humid and cold climate for most of the year (Scherer and Da Rosa 2003; Behling et al. 2009). The presence of megafauna also played an important role in vegetation dynamics, and herbivory action guided the process of plant evolution and their morphological patterns. Studies carried out in savannah areas of South America and Africa show that the vegetation coexisting with the past megafauna developed specific protection mechanisms, such as thorns and smaller and rigid leaves, including the production of unpalatable chemical substances to minimize predation (Dantas and Pausas 2022). Thus, large herbivorous mammals also maintained grassland vegetation for a long time during the Pleistocene. After the extinction of the megafauna, an opportunity for the expansion of forest was created (Behling et al. 2009; Dantas and Pausas 2022). The development of vegetation cover in southern Brazil can be

traced from the palynological record of peats recovered in different locations in the southern states of Brazil: Paraná (Behling 1997), Santa Catarina (Behling 1995), and Rio Grande do Sul (Roth and Lorscheitter 1993; Behling et al. 2001, 2004), which abundantly preserve pollen from the Pleistocene, including species of Poaceae, Cyperaceae, and Asteraceae, all typical of grassland communities. On the other hand, the presence of forests in the region, especially the Araucaria Forest, and their expansion over grasslands vegetation is only verified from 3 ka AP on, associated with the increase and frequency of rainfall. At first, forests were restricted to areas close to water bodies; later, they advanced over grassland vegetation in areas farther away (Behling et al. 2009). In addition, the presence of charcoal in palynological slides (e.g., Behling et al. 1995, 2005; Ribeiro et al. 2020) is evidence of paleowildfires during the Pleistocene in the *Campos Sulinos* (Behling et al. 2009). Fire is one of the key modeling elements of past ecosystems (e.g., Scott and Stea 2002; Scott and Damblon 2010; Manfroí et al. 2023), and can be compared to herbivory as a modifier of different biomes over time (Bond and Keeley 2005). In the *Campos Sulinos*, we thus conclude that both fire and herbivory were instrumental in restricting forest expansion over grasslands during much of the Pleistocene (see also Behling et al. 2023, Chap. 4, in this volume).

3.4 Summary and Conclusions

3.4.1 Earlier Ecosystems

Permian ecosystems are directly related to Pangean conditions, ranging from glacial to desert environments, including epicontinental marine forms. In these scenarios, the fossils from early Permian (Sakmarian-Artinskian) of southern Brazil record several ecosystems, from glacial and postglacial highlands and lowlands covered with shrubs and forests, to coastal lagoons and sandy barriers coupled with peat environments, and recurrent wildfires. Middle Permian deposits only record an epicontinental sea and its coastal environments, but no continental succession is known so far. The late Permian sediments record the continentalization of Gondwana, and the formation of complex food chains of amniotes and temnospondyls in flat alluvial plains covered with shrubs and small forests, also subject to wildfires.

Triassic ecosystems also relate to Pangean conditions, but resulted from environmental and biotic recovery after the most massive extinction event, and later the continental breakup forming Laurasia and Gondwana. The early Triassic deposits (Olenekian) gave rise to alluvial plain ecosystems, with fish, temnospondyls, and archosauriforms, in a food chain not yet detailed. Middle and Late Triassic deposits can be related to two different fluvial scenarios: low energy, high sinuosity rivers, and related floodplain environments (Ladinian and Carnian), and high energy rivers with restricted overbank deposits (Norian). There is a dominance of archosaurs and synapsids (cynodonts and dicyodonts) at first, in *Dinodontosaurus* and

Santacruzodon Assemblage Zones (AZ's), followed by the disappearance of dicynodonts or their substitution by specialized herbivores and the irradiation of more agile carnivores, respectively, rhynchosaur and dinosaurs, in *Hyperodapedon* AZ. The *Riograndia* AZ records the return of dicynodonts, but in ecosystems mainly occupied by cynodonts and sauropodomorph dinosaurs as main herbivores, and a plethora of carnivores, such as cynodonts, dinosaurs, and archosaurs. The twofold scenario is also recorded by the presence of shrubby plants of the *Dicroidium* Flora that are later replaced by the Conifer Flora, more related to forests.

Late Jurassic land faunas are known only by their ichnological remains, found in association with typically aeolian deposits, a result of arid desertic environments. Despite that, the yet poorly known fossil record of this timespan reveals the presence of an association of medium to large-sized herbivore and carnivore dinosaurs. More data on southern Brazil Jurassic faunas are needed in order to better understand the ecological dynamics of ecosystems.

3.4.2 Pleistocene and Modern Ecosystems

The present relief of southern Brazil is a post-Cretaceous construction that formed after the breakup of South America and Africa. Most rivers started flowing inward and later toward the Atlantic Ocean, forming the coastal plain and continental platform (Potter 1997). The result of fluvial erosion is recorded in the Pelotas Basin's Cretaceous, Paleogene, and Neogene succession (Anjos-Zerfass et al. 2008).

Along the last 400 ka, the intercalation of glacial and interglacial cycles led to the formation of a mosaic of forests and grasslands, each cycle favoring a specific environment and associated flora and fauna. The onset of interglacial cycles led to sea level rise, and the continental onward shift of the coastline, preserving lagoons and sandy barriers at the coastal plain of Rio Grande do Sul. In contrast, the glacial cycles shifted the same coastline basinward, i.e., at least 100 km from the present shoreline, depositing fluvial sediments along the submerged continental platform (Lopes et al. 2021). On the continental side, the glacial cycles reinforced fluvial erosion, due to river profile lowering. In contrast, the interglacial cycles favored fluvial deposition, through progressive drowning of the river profile (see references in Maahs et al. 2019).

Some ecological processes are considered important in shaping the *Campos Sulinos* landscapes, both in the past and today. The action of fire on vegetation, for example, is recognized as an important controller in the maintenance of ecosystems, and evidence of fire exist especially in the more recent past (the last 600 years), despite humid climatic conditions during this period. Likely, occurrence of fire is related to human populations, did not allow for widespread development of forests and keeping grassland vegetation as the predominant system (e.g., Behling et al. 2009; Piperno and Becker 1996; see also Behling et al. 2023, Chap. 4 in this volume). Along with fire, the influence of herbivore animals is likely equally important in the dynamics of the *Campos Sulinos* landscapes. Whether large herbivore

mammals that inhabited the region until 8500 years ago (Scherer and Da Rosa 2003) or cattle introduced by the Jesuits in the seventeenth century (Porto 1954), herbivores consume plants and prevent the expansion of woody vegetation, while also limiting the accumulation of biomass and thus preventing the availability of fuel for larger fires (Behling et al. 2009). Clearly, human occupation has had an influence on natural environments from their earliest beginnings.

The fossil record of the region known today as the *Campos Sulinos* is extremely rich and dates back to 300 million years ago. These fossils testify important paleogeographic, paleoclimatic, and paleofaunistic shifts, and provide evidence for the origin and evolution of the different ecosystems. It is impossible to study the region's biodiversity without considering its past, including biotic and abiotic events that occurred during the Cenozoic and probably acted as shaping agents of environments and current biodiversity.

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