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Re-evaluation of the Permian macrofossils from the Parnaíba Basin: biostratigraphic, palaeoenvironmental and palaeogeographical implications

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Abstract: Although Permian fossils have been known from the Parnaíba Basin for two centuries, and some faunal and flora elements are well known worldwide, research on the fossil assemblages from this basin has lagged relative to other, more accessible basins. In the last decade, however, there has been a significant increase in the study of fossils from the two Permian units of the basin: the Pedra de Fogo and Motuca formations. The goal of this contribution is to synthesize and update the existing data on the Permian macrofossils from these formations, and to use them to address biostratigraphic, palaeoenvironmental and palaeogeographical questions. The Pedra de Fogo and Motuca formations are likely to be Cisuralian in age. Contrary to previous reports, there is more than one stratigraphic interval that preserves petrified fossil plants. The possible marine influence proposed for the Pedra de Fogo Formation must be reassessed based on the strongly terrestrial character of its fossil assemblages. Palaeoenvironmental and palaeoclimatic conditions are inferred to be wetter than is typically predicted for this region of the globe based on climatic modelling. Despite sharing some taxa with the Euramerican and Gondwanan biogeographical provinces, the Parnaíba Basin was likely to have been part of a distinct biogeographical province, as indicated by the high degree of endemism displayed by its Permian floras and faunas.

The Permian Pedra de Fogo (PFF) and Motuca (MF) formations of the Parnaíba Basin are among the most fossiliferous strata exposed in any of the Brazilian Paleozoic cratonic basins (Santos & Carvalho 2009). Fossil plants are especially well known from this interval (Conceição *et al.* 2016*a*; Neregato *et al.* 2017). Indeed, the first fossil plant taxon formally described from Brazil, *Psaronius brasiliensis* Brongniart emend. Herbst (1985), was collected from the PFF. Vertebrate fossils were first collected in the PFF in the late 1940s (Price 1948), and recent discoveries have revealed a diverse assemblage of chondrichthyans, actinopterygians, actinistians, dipnoans, temnospondyl amphibians and reptiles (Cisneros *et al.* 2015).

Although Permian fossils of the Parnaíba Basin have been known since the early nineteenth century, they have received insufficient study in subsequent years. Rocks of the PFF and MF crop out across a vast area, and many of the palaeontological studies of these formations present only preliminary data. This lack of detailed work is due in part to the location of the basin in the inland area of NE Brazil, one of the less developed regions of the country, but also to the low petroleum potential of the Parnaíba Basin, which has caused it to receive little attention from petroleum geologists. This situation has been partially reversed, especially in the last decade, by the hiring of more palaeontologists in institutions located in or near the Parnaíba Basin, as well as the increased interest of oil companies in the petroleum and gas reserves of the basin. New palaeontological discoveries made since the 2000s have revealed clear connections between the fauna and especially the flora of the Parnaíba Basin and the Euramerican biota, despite the basin's location near the southern margin of the Gondwanan tropics. Faunal links to high-latitude regions of Gondwana also are present. The absence of research on terrestrial biotas from adjacent Permian sedimentary basins, such as the South American Parecis and São Francisco basins to the south and the West African Craton to the north, obscures the palaeobiogeographical patterns underlying the assembly of the seemingly unique terrestrial community of the Parnaíba Basin. The uncertain ages of the PFF and MF, stemming from the

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absence of marine index fossils and radiometric dates, makes it difficult to ascertain centres of origin and directions of dispersal for several of the plant and animal taxa found in the fossil assemblages of the basin. The goal of this contribution is to summarize and update information on the fossil content of the Permian units of the Parnaíba Basin, emphasizing the utility of fossils for determining the age of the sedimentary sequences, and for reconstructing palaeoenvironmental and palaeoclimatic conditions.

Geological setting

The Parnaíba Basin is an intracratonic sag basin covering an area of 600 000 km^2 on the Amazonian/Araguaia, Parnaíba and Borborema crustal blocks of the South America Platform (Daly *et al.* 2014; Linol *et al.* 2016). In Brazil, this basin includes parts of the states of Pará, Tocantins, Piauí, Maranhão, Ceará and Bahia (Fig. 1), and closely connects with strata in NW Africa (Góes & Feijó 1994; Milani & Thomaz 2000). During the Permian, the Parnaíba Basin was located in north-central Gondwana (Linol *et al.* 2016).

The sedimentological succession in the Parnaíba Basin is divided into five supersequences (Góes & Feijó 1994; Vaz *et al.* 2007): the Serra Grande Group (Silurian); the Canindé Group (Early Devonian–Carboniferous); the Balsas Group (Carboniferous–Middle Triassic); the Pastos Bons Group (Jurassic); and the Sardinha, Corda, Grajaú, Codó and Itapecuru formations (Early Cretaceous). The first three sequences represent transgressive–regressive cycles resulting from epeiric sea-level fluctuations and global orogenies, whereas the last two are predominantly continental (Vaz *et al.* 2007). From lowest to highest, the Balsas Group is divided into the Piauí, Pedra de Fogo, Motuca and Sambaíba formations (Góes & Feijó 1994). The PFF and MF units are the plant- and vertebrate-bearing strata in this sequence, and therefore are the focus of this contribution.

The PFF was defined by Plummer (1948) to classify strata-bearing chert and the fern *Psaronius* that crop out between the municipalities of Pastos Bons and Nova Iorque (Maranhão State). This formation presents cyclic sedimentation, in which every cycle begins with sandstones, followed by fine-grained sandstones/mudstones, oolitic or concretionary limestone, and finally greenish fossiliferous shales and limestone lenses (Aguiar 1971). In the mid-south region of the basin, Faria & Truckenbrodt (1980*a*, *b*) reported that the PFF forms outcrops up to 100 m thick, with lateral variations and they divided it into three members: the Basal Silex, Middle and Trisidela. Pinto & Sad (1986) mapped the SW border of the PFF and divided the formation into three members, Lower, Middle and Upper, which correlate well with Faria & Truckenbrodt's (1980*a*, *b*) proposed stratigraphy.

In most areas, the Basal Silex Member is separated from the underlying Piauí Formation by a paraconformity. It is approximately 20 m thick, and composed of mudstones and grey/brown/purple shales interspersed with dolomitic layers with some dark chert concretions. The Middle Member has a fine-grained clastic nature, comprising sandstones, mudstones that are occasionally carbonitic, and limestones. The Trisidela Member is 40 m thick, and composed of grey dolomitic layers interspersed with mudstones, greenish-grey carbonate shales, and limestones with concretions and chert layers.

The PFF represents sedimentation in restricted, shallow epeiric seas, and coastal and continental environments, predominantly during warm climatic conditions. Evaporite horizons were formed when hydric balance was negative (Aguiar 1971; Lima & Leite 1978; Faria & Truckenbrodt 1980*a*, *b*; Góes & Feijó 1994), in association with global warming occurring at the time.

The MF also was defined by Plummer (1948) to accommodate reddish shales interspersed with limestone lenses and anhydrite lying above the PFF close to Motuca Farm, between the municipalities of São Domingos and Benedito Leite (Maranhão State). This formation is 300 m thick, and is composed of fine-grained sandstones with tabular or cross-stratification, brown/red sandy siltstones and mudstones, light-green mudstones, and, less frequently, by shales, white anhydrite and rare chert layers. However, the MF lacks the dark shales or limestones seen in the underlying PFF (Góes & Feijó 1994; Vaz *et al.* 2007). Lima Filho (1991) noted that the Motuca Formation is very similar to the PFF, with concentrations of evaporites in the basal part of the unit, but differing in the presence of very thick sandstone bodies.

Traditionally, the PFF has been considered a primarily marine depositional system (Góes & Feijó 1994), whereas the MF has been interpreted as a continental fluvial–aeolian depositional setting, with probable marine incursions principally in its middle portion (Lima & Leite 1978). Góes & Feijó (1994) suggested a desertic environment for the MF with associated lakes, occasionally influenced by the sea. Recent work on the PFF near the eastern margin of the Parnaíba Basin suggests a more terrestrial character for the formation in that area, with abundant lacustrine, floodplain and channel deposits (Cisneros *et al.* 2015).

Collaboration

The authors of this paper comprise a cohesive working group that has collaborated on synergistic research on the Permian macrofossil record of the

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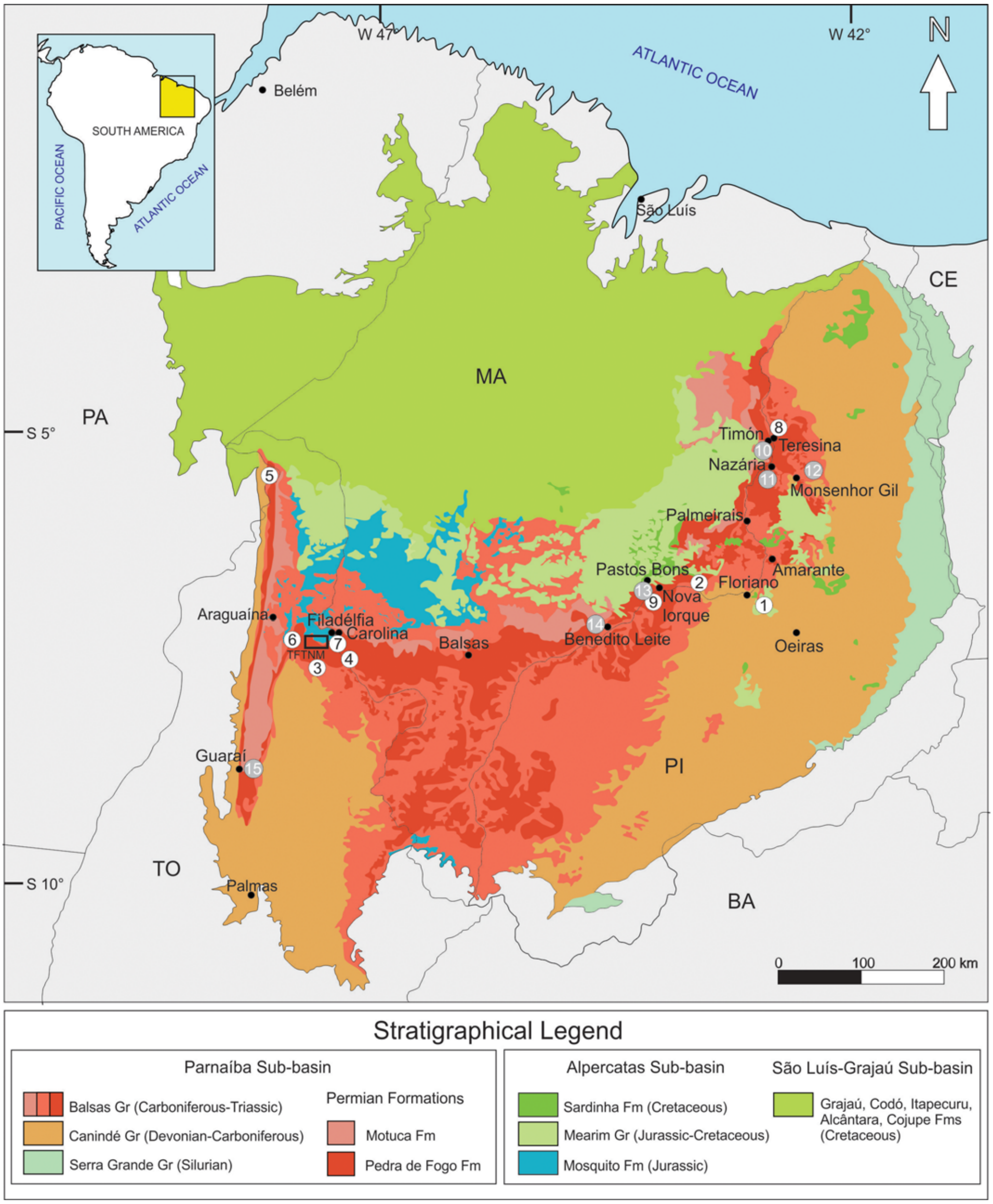

Fig. 1. Location map. Numbers represent important fossil localities. White circles represent plants; grey circles represent vertebrates: (**1**) Between Oieras and São Gonçalo do Amarante; (**2**) Jaboti Plateau, between Nova Iorque and Floriano; (**3**) right bank of the Tocantins River, approximately 50 km south of Carolina; (**4**) right bank of the Manuel Alves Grande River, near the mouth of the Sereno River; (**5**) left bank of the Araguaia River, Cruzeiro locality; (**6**) between Araguaína and Filadélfia; (**7**) Carolina; (**8**) Poti River in Teresina; (**9**) Nova Iorque; (**10**) Timón; (**11**) between Nazaria and Palmeirais; (**12**) Monsenhor Gil; (**13**) Pastos Bons; (**14**) Benedito Leite; (**15**) Guaraí; (rectangle) TFTNM. Abbreviations: TO, Tocantins State; MA, Maranhão State; PI, Piauí State; BA, Bahia State; TFTNM, Tocantins Fossil Trees Natural Monument. Map by D.M. Conceição and M.G.F. Esperança-Júnior, based on geological data from CPRM (http://geosgb.cprm.gov.br) and stratigraphic divisions according to Góes (1995).

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Parnaíba Basin. Through individual grants and collaborative projects, we have been active for more than a decade, conducting fieldwork for the systematic collection of fossils. The group includes palaeontologists specializing in the different microbial (TF), plant (RI, RR and RR) and animal (JCC, KDA, CM, JF, RMHS, MR, MCL and CFK) groups discovered in the PFF and MF, as well as current and former graduate students (RN, FK, TMVT, DMC, JDP and GAR). As new fossil specimens have been collected representing groups that were previously unknown from the basin, we have added new researchers and/or students to the project. A number of fossil preparators have also contributed to our work.

This contribution represents the first opportunity for all collaborators to publish a summary of the results obtained by former and current members of the working group. In this sense, it constitutes a capstone for our work to date and serves as a baseline upon which our ongoing research will build.

Palaeontology

Flora of the Pedra de Fogo Formation

Petrified Wood in the western Parnaíba Basin: Pedra de Fogo or Motuca Formation? Following Plummer's (1948) establishment of lithostratigraphic units for the Paleozoic sequence of the Parnaíba Basin, all the petrified wood that had been collected up to that point was assigned to the PFF (for a historical review see Dolianiti 1948). Indeed, the occurrence of petrified wood has become one of the main diagnostic features of the PFF. Plummer (1948) noted the presence of the fossil wood at the top of the PFF near the municipality of Balsas (SW Maranhão State), and this stratigraphic occurrence was accepted by subsequent workers until the early 1980s (Barbosa & Gomes 1957; Aguiar 1971). However, Faria & Truckenbrodt (1980*a*) and Caputo *et al.* (2005) considered that besides the PFF, petrified wood also could be found in the overlying MF in the western portion of basin. Pinto & Sad (1986) suggested that the fossil plants occurred in the most basal horizons of the MF in the region between the municipalities of Araguaína and Filadélfia (northern Tocantins State). Later, Dias-Brito *et al.* (2007) agreed with this proposal. The most recent studies have attributed the petrified wood-bearing horizons to the MF (Kurzawe *et al.* 2013*a*, *b*; Neregato *et al.* 2015, 2017), based on the stratigraphic position of fossil material found *in situ* and in the lithofacies described by the previous authors.

Therefore, we conclude that the fossils from the Araguaína-Filadélfia region do not belong to the PFF, but rather to the base of the MF. This includes all fossil materials previously described by Coimbra & Mussa (1984), Herbst (1986, 1999), Mussa & Coimbra (1987) and Rößler & Galtier (2002*a*, *b*, 2003) that were previously referred to the PFF. Most of these fossils were found *ex situ*, either rolled away from their original preservation sites or collected by local people and donated to palaeontologists. Since no petrified wood was found *in situ* in PFF strata in this region, we describe them below as part of the MF flora (see Table 1). The following description of the PFF flora focuses on specimens that can be reliably assigned to that formation.

Historical overview. The first petrified wood described from the PFF was a relatively long stem of a marattialean fern named *Psaronius brasiliensis* by Brongniart (1872) (Fig. 2a), which was collected in the region between the municipalities of Oeiras and São Gonçalo do Amarante (southern Piauí State). In the early twentieth century, Pelourde (1914) studied additional specimens of *Psaronius* collected in Piauí, and proposed the new species *Psaronius arrojadoi* (Fig. 2c). In 1914, Lisboa reported stems attributed to the genus *Psaronius* near the municipality of Teresina (central-western Piauí) (Lisboa 1914). Oliveira (1934) reported fossil wood of unidentified gymnosperms found in association with specimens of *Psaronius* in Piauí. In a classic contribution entitled *Paleobotany in Brazil*, Dolianiti (1948) mentioned the presence of other stems of *Psaronius* from Maranhão and Piauí. In the 1980s, Faria & Truckenbrodt (1980*a*, *b*) found stromatolites in the lowest (Basal Silex Member) to the topmost (Trisidela Member) parts of the PFF in southern Maranhão State (Fig. 3a–d). Caldas *et al.* (1989) described a questionable cycad species, *Teresinoxylon eusebioi*, in association with probable stromatolites (Fig. 3e & f) from the bank of the Poti River in the municipality of Teresina. Recently, new localities containing a large number of petrified fossil stems associated with microbial mats have been mapped in deposits from the eastern rim of the basin (Conceição *et al.* 2016*a*, *b*). However, only the presence of *Psaronius*-type stems and unidentified gymnosperm woods were reported (Conceição *et al.* 2016*a*), and the taxa present have not been described in detail.

Although petrified wood is the most common component of the PFF palaeoflora, compressed/impressed plant fossils also occur in the formation. Among the compressed/impressed fossils, Barbosa & Gomes (1957) reported fragments of '*Pecopteris*' and '*Calamites*' from the right bank of the Tocantins River in NE Tocantins State, which were later confirmed by Iannuzzi & Scherer (2001). In the 1960s, Dolianiti (1962) described a new species of lycophyte, *Cyclostigma brasiliensis* (Fig. 4a & b), based on small compressed stems from the left bank of the Araguaia River (Cruzeiro locality, Pará

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Table 1. *Plant fossils of the Pedra de Fogo and Motuca formations*

Taxon	Higher taxonomic rank	Geological unit	Parnaíba Basin localities and reporting authors	Other records of the genus
Cyclostigma brasiliensis	Lycophyta	Pedra de Fogo	Carolina (Iannuzzi & Scherer 2001)	Gondwana
Psaronius brasiliensis	Marattiales Psaroniaceae	Pedra de Fogo/Motuca	Oieras–Amarante (Brongniart 1872) Araguaína–Filadélfia (Rößler & Noll 2002*a*, *b*)	Paraná Basin, Germany, France, USA and China
Psaronius arrojadoi		Pedra de Fogo/Motuca	Chapada do Jaboti (Pelourde 1914; Herbst 1985) TFTNM (Tavares 2011)	
Psaronius sinuosus		Motuca	Araguaína (Herbst 1999; Rößler & Noll 2002)	
Tietea singularis		Motuca	Araguaína (Herbst 1986; Rößler & Noll 2002) TFTNM (Tavares 2011)	Paraná Basin
Tietea derbyi		Motuca	Carolina (Herbst 1992)	
Buritiranopteris costata	Marattiales	Motuca	TFTNM (Tavares *et al.* 2014)	Endemic
Grammatopteris freitasii	Filicales	Motuca	Araguaína–Filadélfia (Rößler & Galtier 2002*a*)	Germany and France
Dernbachia brasiliensis		Motuca	Araguaína–Filadélfia (Rößler & Galtier 2002*b*)	Endemic
Botryopteris nollii	Filicales Botryopteridaceae	Motuca	Araguaína–Filadélfia (Rößler & Galtier 2003)	Germany, France, Belgian, USA and China
Araguainorachis simplissima	Fern?	Motuca	Araguaína–Carolina (Mussa & Coimbra 1987)	Endemic
Arthropitys cacundensis	Calamitales Calamitaceae	Motuca	Araguaína–Carolina (Coimbra & Mussa 1984)	Germany, France, England, USA and China
Arthropitys isoramis		Motuca	TFTNM (Neregato *et al.* 2015)	
Arthropitys iannuzzii		Motuca	TFTNM (Neregato *et al.* 2015)	
Arthropitys tocantinensis		Motuca	TFTNM (Neregato *et al.* 2017)	
Arthropitys barthelii		Motuca	TFTNM (Neregato *et al.* 2017)	
Sphenophyllum sp.	Sphenophyllales	Pedra de Fogo/Motuca	TFTNM (Neregato *et al.* 2017; this paper)	Cosmopolitan
Cycadoxylon brasiliense	Pteridospermales Cycadoxyleae	Motuca	Araguaína–Carolina (Mussa & Coimbra 1987)	France and England
Teresinoxylon euzebioi		Pedra de Fogo	Teresina (Caldas *et al.* 1989)	Endemic
Rhachiphyllum sp.	Pteridospermales	Pedra de Fogo	Nova Iorque (Iannuzzi & Langer 2014)	Europe, North America, China and SE Asia
Cyclomedulloxylon parnaibense	Pteridospermales?	Motuca	Araguaína–Carolina (Mussa & Coimbra 1987)	Endemic
Amyelon bieloi	Coniferopsida Cordaitales	Motuca	Araguaína–Carolina (Coimbra & Mussa 1984)	England, USA, Scotland, China and France
Carolinapitys maranhensis	Cordaitales?	Motuca	Araguaína–Carolina (Coimbra & Mussa 1984)	Endemic
Parnaiboxylon sp.	Gymnosperm	Motuca	TFTNM (Kurzawe *et al.* 2013*a*)	Endemic
Parnaiboxylon rohnae		Motuca	TFTNM (Kurzawe *et al.* 2013*a*)	Endemic
Scleroabietoxylon chordas		Motuca	TFTNM (Kurzawe *et al.* 2013*a*)	Endemic
Ductoabietoxylon solis		Motuca	TFTNM (Kurzawe *et al.* 2013*a*)	Endemic
Taeniopitys tocantinensis		Motuca	TFTNM (Kurzawe *et al.* 2013*b*)	Antarctica
Taeniopitys sp.		Motuca	TFTNM (Kurzawe *et al.* 2013*b*)	
Kaokoxylon punctatum		Motuca	TFTNM (Kurzawe *et al.* 2013*b*)	India, Australia, South Africa, Argentina, Antarctica
Damudoxylon buritiranaensis		Motuca	TFTNM (Kurzawe *et al.* 2013*b*)	India, Australia, South Africa
Damudoxylon humile		Motuca	TFTNM (Kurzawe *et al.* 2013*b*)	
Damudoxylon roesslerii		Motuca	TFTNM (Kurzawe *et al.* 2013*b*)	

TFTNM, Tocantins Fossil Trees Natural Monument.

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State) and from the right bank of the Manuel Alves Grande River, near the mouth of the Sereno River in Maranhão State. However, Dolianiti (1962) attributed the strata containing these lycophytes to the Mississippian Poti Formation, because they also preserved organic matter (unknown in the PFF at that time) and were found below the levels containing *Psaronius* sp. Later, Iannuzzi & Scherer (2001) reanalysed this fossil material and described in detail the rock exposure of one of the sites mentioned by Dolianiti (i.e. in the Manuel Alves Grande River), concluding that the fossils and sediments did indeed belong to the PFF, as originally suggested by Barbosa & Gomes (1957). Recently, Iannuzzi & Langer (2014) reported the occurrence of impressed callipterid foliage similar to *Rhachiphyllum schenkii* (Heyer) Kerp (Fig. 4f & g) in association with fern fronds bearing *Pecopteris*-type pinnules (Fig. 4c) from Nova Iorque (southern Maranhão State). Leaflet whorls of *Sphenophyllum* that have been recovered from the same fossiliferous bed are shown here for the first time (Fig. 4d & e), and complement previous reports of anatomically preserved *Sphenophyllum* axes from the overlying MF (Rößler 2006; Neregato *et al.* 2017).

Palaeoflora summary. The majority of fossil plants described from the PFF were not found *in situ*; exceptions are the compressed/impressed fossils from Cruzeiro, Manuel Alves Grande and Nova Iorque, and the petrified wood from the Poti River in the city of Teresina. Compressed/impressed fossil plants comprise parautochthonous to allochthonous assemblages that were preserved in nearshore regions or transitional settings (e.g. tidal flats, lagoons, coastal marshes) of an epeiric sea or large continental lake (Iannuzzi & Scherer 2001). These assemblages are impoverished, consisting of only one or a few taxa (Iannuzzi & Scherer 2001; Iannuzzi & Langer 2014). In the Poti River site, Teresina, petrified fossil stems are usually found cropping out on the sedimentary rocks in a horizontal position (allochthonous/parautochthonous specimens) or in life-position (autochthonous specimens). These fossil stems are associated with sandstone facies representing beaches and/or coastal aeolian dunes, and siltstone–mudstone intercalations produced in tidal flats (Caldas *et al.* 1989). Finally, the new petrified wood assemblages reported by Conceição *et al.* (2016*a*) are composed of autochthonous and parautochthonous elements, and occur in continental deposits that accumulated in marginal regions of large lakes that occasionally were affected by non-channelized, high-energy fluvial systems, represented by tabular successions of medium- to coarse-grained, planar-bedded sandstones. In these assemblages, the autochthonous elements were covered by episodic sedimentation that allowed rapid burial of still-living plants. The petrified wood assemblages described from the eastern margin of the basin are dominated by autochthonous to parautochthonous (Caldas *et al.* 1989; Conceição *et al.* 2016*a*, *b*) gymnosperm stems; tree-ferns are rare. All of these assemblages usually occur in layers that overlap silicified sandstone horizons, chert breccias, and, to a lesser degree, stromatolites and microbial mats or tepees (Fig. 3c–f) (Conceição *et al.* 2016*a*).

The described PFF palaeoflora is not very diverse, and is composed of a few endemic species: two tree-ferns (*Psaronius brasiliensis*, *P. arrojadoi*) and one dubious cycad (*Teresinoxylon eusebioi*) represented by petrified stems, and one lycophyte (*Cyclostigma brasiliensis*) known from compressed material. In addition, there are reports of impressed remains of *Pecopteris*-type pinnules, the sphenophyte stem ‘*Calamites*’ and leaflet whorls of *Sphenophyllum*, and callipterid foliage similar to *Rhachiphyllum schenkii* (Table 1). Despite the large geographical area over which the PFF crops out, there is still a significant gap in our knowledge of the palaeobotany of the unit. Furthermore, there is persistent uncertainty about the correct stratigraphic positions of the fossil plant assemblages, and the types of facies and sedimentary environments in which their remains were preserved. The only petrified wood-bearing facies that have been extensively described correspond to horizons that are currently thought to belong to the lowermost MF (Faria & Truckenbrodt 1980*a*; Pinto & Sad 1986; Dias-Brito *et al.* 2007).

Fauna of the Pedra de Fogo Formation

In addition to its well-known palaeobotanical record, the PFF also has produced an assemblage of mostly aquatic vertebrates. Chondrichthyans (cartilaginous fishes) in the PFF assemblage include ctenacanthiform, xenacanthid and cladoselachiform sharks (Santos 1946; Santos & Carvalho 2009; Alves 2010; Figueroa & Gallo 2017), the endemic eugeneodontiform holocephalan *Anisopleurodontis pricei* (Fig. 5e) (Santos 1994), and the petalodont holocephalan *Itapyrodus punctatus* (Fig. 5a–c) (Santos 1990). The first published record of actinopterygians in the formation is the poorly-known palaeonisciform *Brazilichthys macrognathus* (Cox & Hutchinson 1991), although disarticulated palaeonisciform scales also have been reported (Alves 2010). Dipnoans and coelacanths have been noted in the literature (Santos 1990), but until now this material has not described in detail. Spiral coprolites are conspicuous in the formation, and are probably attributable to elasmobranch chondrichthyans (Schwanke & Souto 2007). Finally, the temnospondyl amphibian *Prionosuchus plummeri* was described by Price (1948; also see Cox &

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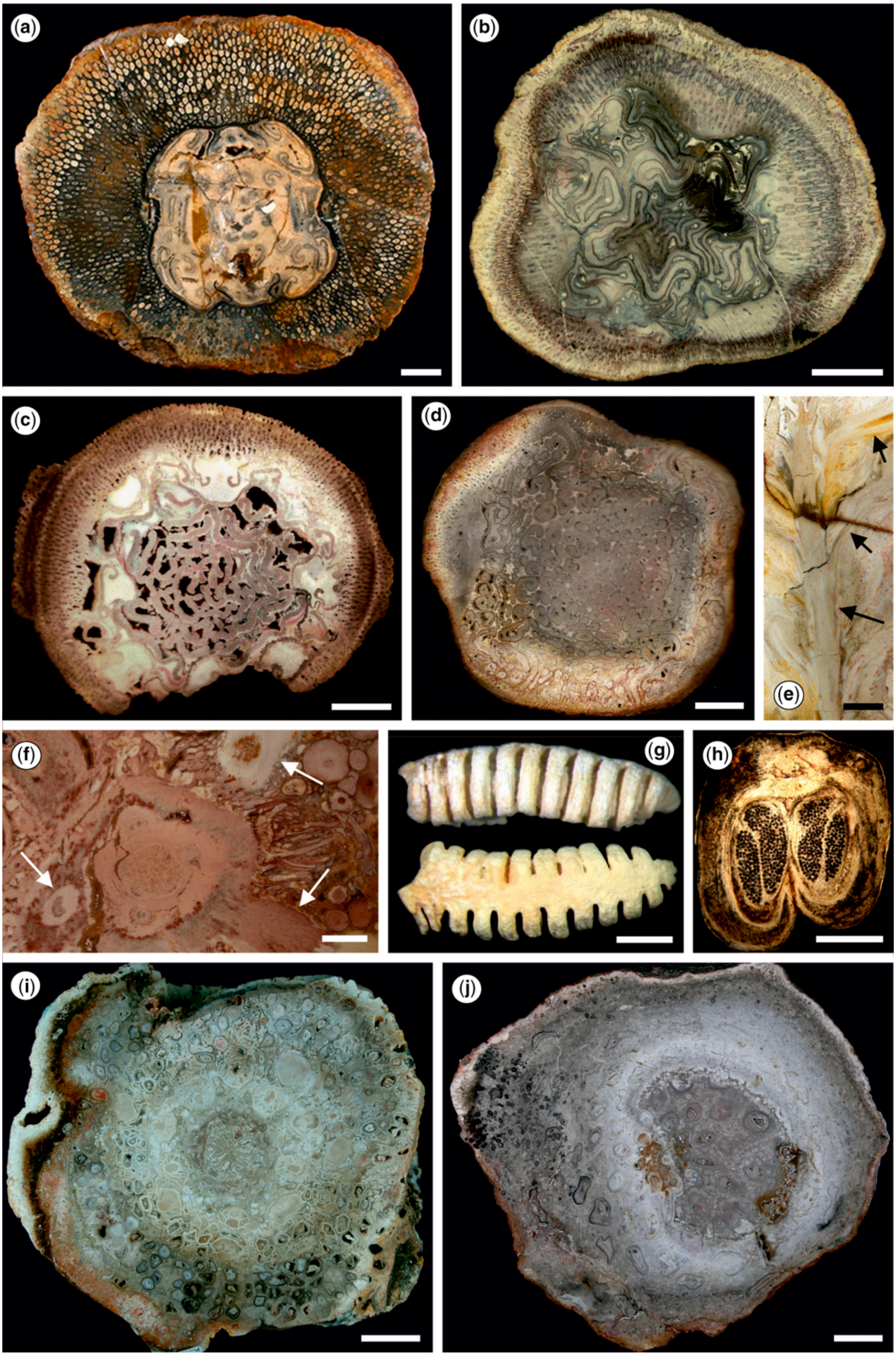

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Hutchinson 1991; Santos & Carvalho 2009). This species is noteworthy because it is not only the first temnospondyl described from South America, but also is one of the largest temnospondyls known, with a maximum estimated skull length of 160 cm and an estimated body length of 5.5 m (Cox & Hutchinson 1991).

As can be seen from Table 2, most of the research on the vertebrate palaeontology of the PFF has been concentrated on a restricted area near the municipalities of Pastos Bons and Nova Iorque (Maranhão State) (Alves 2010 and Candeiro *et al.* 2015 are exceptions). Beginning in 2011, a research group consisting of JCC and colleagues discovered new vertebrate localities in a number of historical areas (Table 2; Fig. 1), including records of temnospondyls, ctenacanth sharks and *Anisopleurodontis* in the overlying MF at Benedito Leite (Maranhão State), as well as new sites of particular significance in the PFF near the NE margin of the basin in the municipalities of Nazária (Piauí State), Monsenhor Gil (Piauí State), Palmeirais (Piauí State) and Timón (Maranhão State). This work has significantly expanded the tetrapod fauna of the PFF with the addition of the dvinosaurs *Timonya anneae* and *Procuhy nazariensis*, an unnamed rhinesuchid (Fig. 5g), and a captorhinid reptile initially referred to *Captorhinus aguti* (Cisneros *et al.* 2015), but more probably representing *Captorhinikos*. Additional material under study includes new actinopterygians and articulated coelacanths, and a diversity of dipnoan toothplates and skeletal material (Cisneros *et al.* 2015) (Fig. 5d, f & h). Although the presence of shared taxa such as *Prionosuchus*, *Itapyrodus* and rhinesuchid temnospondyls indicates that the new localities in the NE part of the basin are contemporaneous with the historical localities closer to the centre of the basin (Cisneros *et al.* 2015), clear differences exist between the faunal assemblages in the two areas. Tetrapods are more diverse and abundant in the eastern localities, but chondrichthyans and coelacanths are rare. Amniotes are absent near the depocentre of the basin, and temnospondyls are rarer and less diverse, but chondrichthyans are much more abundant. These differences can be interpreted as reflecting an environmental gradient that existed in the Parnaíba Basin, with the animals at the NE localities inhabiting the margins of alkaline continental lakes, ponds, wetlands, and seasonally wet floodplains and fluvial channels (Cisneros *et al.* 2015). Mudflat and nearshore deposits are common at the western localities (Araújo *et al.* 2016), and the vertebrate assemblage from those areas is consistent with a somewhat deeper water habitat.

Flora of the Motuca Formation

Although palaeobotanical studies in the Parnaíba Basin have been carried out since the nineteenth century (Brongniart 1872), only in recent years have plant fossils been recognized as originating in the MF (Dias-Brito *et al.* 2007). In fact, discoveries of petrified stems in northern Tocantins State in the 1980s and 1990s were initially attributed to PFF strata (Coimbra & Mussa 1984; Herbst 1986, 1999; see also the discussion above). This conclusion remains contentious because not all workers accept the placement of these fossils in the MF (Andrade *et al.* 2014). Part of this problem stems from the gradational contact between the PFF and MF (Faria & Truckenbrodt 1980*a*; Pinto & Sad 1986), which creates difficulty in establishing a consistent stratigraphical boundary between these units. Here we accept that all petrified wood from northern Tocantins State originates in the MF, which is the most widely accepted position of researchers working with the fossil plants and strata of the western portion of the basin (Dias-Brito *et al.* 2007; Capretz & Rohn 2013; Kurzawe *et al.* 2013*a*, *b*; Tavares *et al.* 2014; Neregato *et al.* 2015, 2017). Because of the abundance of large petrified stems exposed between the municipalities of Araguaína and Filadélfia–Carolina, in the year 2000 the Tocantins State Government established a 32 000 ha conservation unit in this region named the 'Tocantins Fossil Trees Natural Monument' (TFTNM). It now seems likely that

Fig. 2. Permineralized ferns from the Pedra de Fogo (a) and Motuca (b–h) formations. (**a**) DGM 500, *Psaronius brasiliensis*, transverse section showing vascular bundles. (**b**) K 5495a, *Psaronius sinuosus*, transverse section showing vascular bundles. (**c**) TOF 65-1, *Psaronius arrojadoi*, transverse section showing vascular bundles. (**d**) *Tietea singularis*, transverse section showing vascular bundles. (**e**) K 4880, *Botryopteris nollii*, longitudinal section showing a cauline member (long arrow) and stipes (short arrows). (**f**) K 4880, *Botryopteris nollii*, transverse section showing the main stem and three stipes (arrows). (**g**) TOF 355, *Buritiranopteris costata*, pinnule in lateral (top) and in adaxial view (bottom), showing the deeply incised leaf lamina and the long, narrow lobes. (**h**) TOF 375B, *Buritiranopteris costata*, transverse section of pinnule showing sporangia and spores. (**i**) K 5782, *Dernbachia brasiliensis*, transverse section showing the vascular bundles. (**j**) K 4969a, *Grammatopteris freitasii*, transverse section showing vascular bundles. The specimen in (a) is stored at the Museu Nacional, UFRJ, Rio de Janeiro, Brazil; specimens in (b), (e), (f), (i) and (j) are stored at the Museum für Naturkunde Chemintz, Germany; specimens in (c), (d), (g) and (h) are stored at the Museu de Paleontologia e Estratigrafia Professor Dr Paulo Milton Barbosa Landim, UNESP-Rio Claro, Brazil. (a)–(d) Scale bar= 2 cm; (e) scale bar = 5 mm; (f) & (g) scale bar = 2 mm; (h) scale bar = 1 mm; and (i) & (j) = 3 cm.

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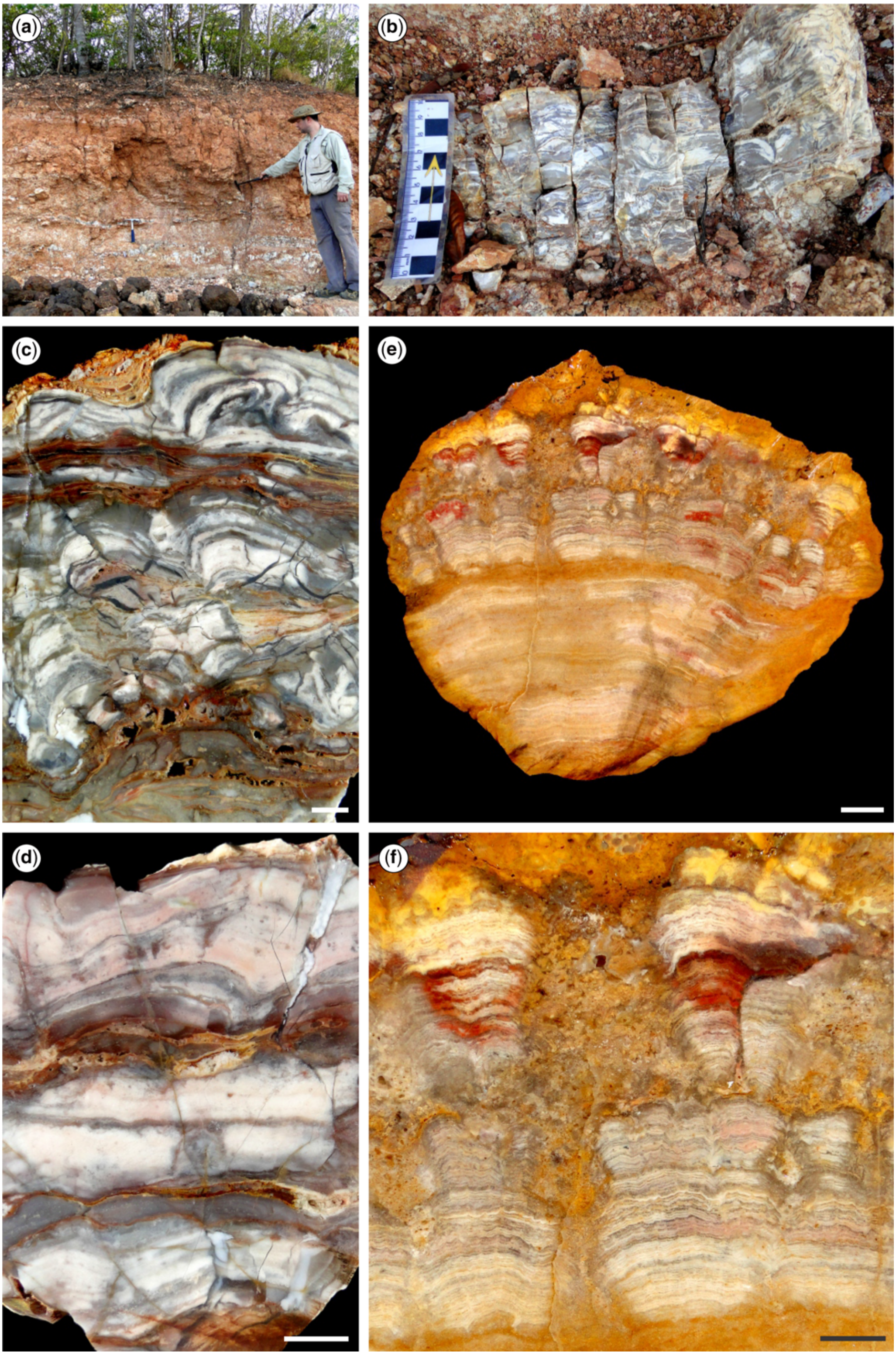

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almost all of the petrified wood from the western basin studied to date came from the TFTNM area or its immediate surroundings.

Historical overview. Faria & Truckenbrodt (1980*a*) were the first to report petrified stems coming from the base of the MF in the municipalities of Araguaína, Filadélfia and Carolina (TFTNM area), northern Tocantins State. However, Coimbra & Mussa (1984) were responsible for the designation of the first taxa formally described from this region. They described two new species and a genus of gymnosperm stem from the 'Cacunda Sandstone': the root *Amyelon bieloi*, the calamitalean stem *Arthropitys cacundensis* and the cordaitalean stem *Carolinapitys maranhensis* (Fig. 6a). One year later, Herbst (1985) emended the diagnosis of *Psaronius arrojadoi* (Fig. 2c) and, in the following year, he recorded the presence of *Tietea singularis* (Fig. 2d) (Herbst 1986), both based on materials allegedly collected in the same region (i.e. near Araguaína), which was later confirmed by Rößler & Noll (2002) and Tavares (2011). Subsequently, Mussa & Coimbra (1987) described three additional species of petrified stems from the rhythmically-layered mudstone–siltstone overlying the 'Cacunda Sandstone' in the Araguaína–Carolina region: the pteridosperm stem *Araguainorachis simplissima*, the putative cycad *Cycadoxylon brasiliense* and the gymnosperm stem *Cyclomedulloxylon parnaibense* (Fig. 6b). In the 1990s, Herbst (1992, 1999) described two new species of tree-fern stems: *Tietea derbyi* from Carolina, and *Psaronius sinuosus* (Fig. 2b) from Araguaína. Rößler & Galtier (2002*a*, *b*, 2003) described two new ferns, *Dernbachia brasiliensis* and *Grammatopteris freitasii* (Fig. 2i & j), and a new species of the fern genus *Botryopteris* (*B. nollii*) (Fig. 2e & f), all from the TFTNM area in Filadélfia. Ten years later, Kurzawe *et al.* (2013*a*, *b*) studied the gymnosperm wood from the TFTNM area in Filadélfia, and erected three new genera and species that are endemic to the Parnaíba Basin: *Ductoabietoxylon solis*, *Scleroabietoxylon chordas* and *Parnaiboxylon rohnae* (Fig. 6c, e, g & h). They also described five new species of the genera *Taeniopitys* (*T. tocantinensis*), *Kaokoxylon* (*K. punctatum*) and *Damudoxylon* (*D. rosslerii*, *D. buritiranaensis* and *D. humile*) (Fig. 6d & f; Table 1). This work stands out as the largest single contribution to the study of gymnosperm stems from the basin. More recently, Tavares *et al.* (2014) and Neregato *et al.* (2015, 2017) examined fossils of spore-producing plants, describing a new genus and species of maratiallean fern (*Buritiranopteris costata*: Fig. 2h) and four species of the calamitalean stem-genus *Arthropitys* (*A. tocantinensis*, *A. iannuzzii*, *A. isoramis* and *A. barthelii*: Fig. 7a–i).

Palaeoflora summary. Anatomically well-preserved silicified specimens are recorded in and around the TFTNM area (northern Tocantins State). These fossils form allochthonous to parautochthonous assemblages that comprise a considerable diversity of taxa, including lycophytes, sphenophytes, ferns and gymnosperms, but are largely dominated by tree-ferns, especially *Tietea* (Capretz & Rohn 2013). Unfortunately, to date there are no records of trees in life-position from these assemblages. Fossil plants are found within sandstone facies representing fluvial channels or in intercalated sandstones and mudstones deposited on floodplains that are referred to the MF (Capretz & Rohn 2013; Tavares *et al.* 2014; but see below).

In terms of palaeofloristic content, there are seven endemic species of fern stems referred to the genera *Psaronius* (2), *Tietea* (2), *Grammatopteris* (1), *Dernbachia* (1) and *Botryopteris* (1). *Buritiranopteris* corresponds to fertile fronds bearing synangia similar to *Scolecopteris* that are attached under *Pecopteris*-type pinnules (see Table 1). Despite their relative scarcity, the sphenophyte and gymnosperm stems are taxonomically diverse. There are five species of the arborescent sphenophyte stem *Arthropitys* and some axes of *Sphenophyllum* growing closely attached to tree-ferns and calamitaleans (Table 1). The diversity of gymnosperm wood is even higher, with four endemic genera (five species) in the basin, *Carolinapitys* (1), *Parnaiboxylon* (2),

Fig. 3. 'Stromatolites' from Pedra de Fogo Formation. (a)–(d) are from an outcrop at the margin of the Boa Esperança reservoir on the Parnaíba River, Municipality of Nova Iorque, Maranhão State. (**a**) Diverse, deformed centimetre-thick beds of chert intercalated with altered pink pelite: silicified microbialitic biostrome (positioned just below the hammer to the left of the outcrop); R. Iannuzzi on the left points to the interval of the greatest abundance of interbedded fossil plants with chert breccia and abundant chert nodules. (**b**) Biostrome (level below the hammer in Fig. 2) made up of silicified low-relief microbial laminites. (**c**) & (**d**) Silicified microbial laminite from the level in previous figures, consisting of two or three horizons of irregularly domed laminites of varied synoptic relief with domes inclined towards the left; note that fine lamination is smooth and the rock is partially brecciated with local dissolution features and filled fractures. (**e**) & (**f**) Teresina Fossil Forest Park, Poti riverbed in Teresina, Piauí State. (e) Silicified microbial laminite, initially gently domed, changes upwards to pseudocolumnar, to incipiently columnar, and finally terminates as a series of irregularly spaced turbinate columnar stromatolites. (f) Detail of the same specimen showing that the fine lamination became more crenulated as sandy sediment entered the system. (c) & (e) Scale bar = 1 cm; (d) & (f) scale bar = 0.5 cm.

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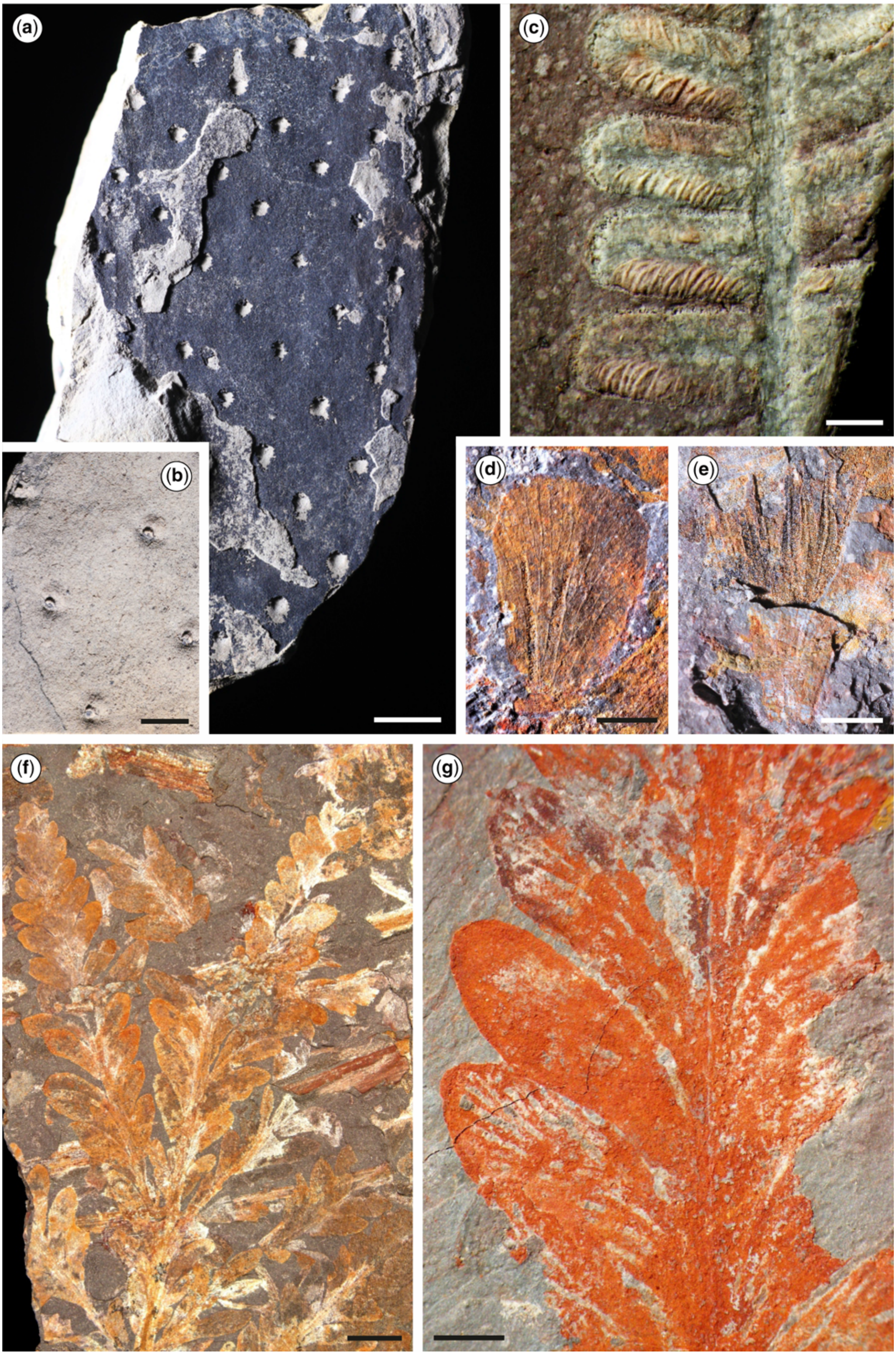

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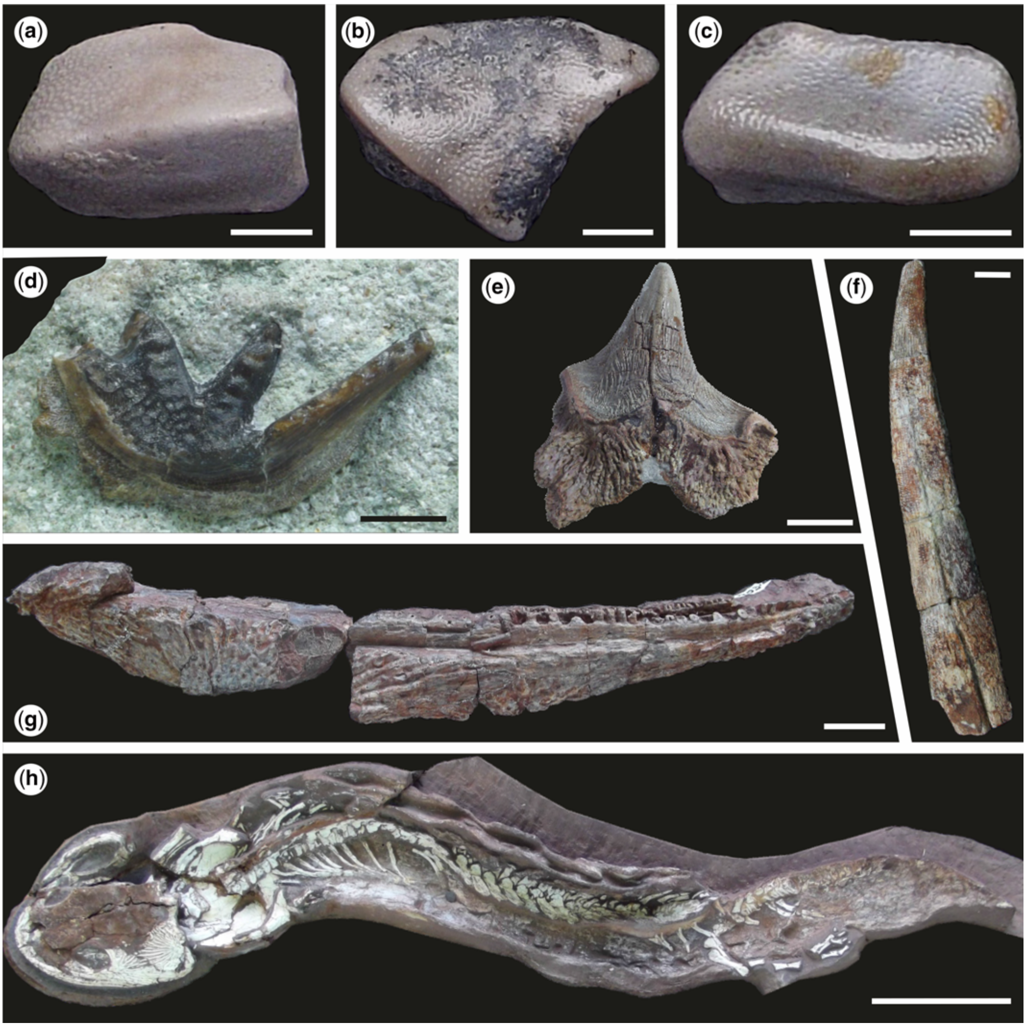

Fig. 5. Vertebrates from the Pedra de Fogo Formation. (**a**)–(**c**) UFPI PV739, *Itapyrodus punctatus* teeth from Pastos Bons (Maranhão), occlusal view. (**d**) UFPI PV849, dipnoan tooth plate from Pastos Bons, occlusal view. (**e**) UFPI PV201, *Anisopleurodontis pricei* tooth from Pastos Bons. (**f**) UFPI PV082, ctenacanth condricthyan spine from Guaraí (Tocantins), lateral view. (**g**) UFPI PV003, rhinesuchid temnospondyl, right jaw, from Pastos Bons, lateral view. (**h**) UFPI PV850, skeleton of a dvinosaur amphibian from Nazária (Piauí), dorsal view. All specimens stored at the Laboratório de Paleontologia, Centro de Ciências da Natureza, UFPI, in Teresina, Brazil. (a)–(c) Scale bar = 2 mm; (d) scale bar = 1 cm; (e), (f) & (g) scale bar = 2 cm; (h) scale bar = 5 cm.

Fig. 4. Compressed–impressed plant fossils from the Pedra de Fogo Formation. (**a**) MP-Pb 5275, *Cyclostigma brasiliensis*, stem showing leaf cushions. (**b**) MP-Pb 5276, *Cyclostigma brasiliensis*, details of the leaf cushions. (**c**) LPRP/USP 0060, *Pecopteris* sp., detail of pinnules showing venation pattern. (**d**) PAB 074.2, *Sphenophyllum thonnii*, detail of leaflet showing venation pattern. (**e**) PAB 071.3, *Sphenophyllum thonnii*, detail of leaflet showing dissected apex. (**f**) LPRP/USP 0122, *Rhachiphyllum* sp., partial view of a frond. (**g**) LPRP/USP 0075, *Rhachiphyllum* sp., detail of pinnules showing venation pattern. Specimens in (a) & (b) are stored at the Museu de Paleontologia, Instituto de Geociências, UFRGS, Brazil; specimens in (c), (f) & (g) are stored at the Coleção de Paleontologia, USP-Riberião Preto, Brazil; specimens in (d) & (e) are stored at the Laboratório de Paleontologia, Centro de Ciências da Natureza, UFPI, in Teresina, Brazil. (a) & (f) Scale bar = 1 cm; (b) scale bar = 5 mm; (c) scale bar = 1 mm; (d), (e) & (g) scale bar = 2 mm.

Table 2. *Vertebrate genera and species of the Pedra de Fogo Formation*

Taxon	Higher taxonomic rank	Geological unit	Parnaíba Basin localities and reporting authors	Other records of the taxon
Anisopleurodontis pricei	Chondrichthyes Holocephali	Pedra de Fogo/ Motuca	Benedito Leite (this work) Pastos Bons (Santos 1990) Nova Iorque (this work)	Endemic
Itapyrodus punctatus		Pedra de Fogo	Pastos Bons (Santos 1994) Palmeirais (Cisneros *et al.* 2015) Benedito Leite, Nova Iorque (this work)	Irati Formation, Paraná Basin (Chahud *et al.* 2010)
Glikmanius sp.	Chondrichthyes Elasmobranchii	Pedra de Fogo	Guaraí (Richter 2008; Alves 2010)	Russia, UK and USA (Ginter *et al.* 2005)
Sphenacanthus maranhensis		Pedra de Fogo	Pastos Bons (Santos 1946)	Endemic
Taquaralodus albuquerque		Pedra de Fogo	Pastos Bons (Santos 1946)	Irati Formation, Paraná Basin (Chahud & Petri 2010)
Rubencanthus diplotuberculatus		Pedra de Fogo	Pastos Bons (Figueroa & Gallo 2017)	Endemic
Sphenacanthus ignis		Pedra de Fogo	Pastos Bons (Figueroa & Gallo 2017)	Endemic
Bythiacanthus lopesi		Pedra de Fogo	Pastos Bons (Figueroa & Gallo 2017)	Endemic
Brazilichthys macrognathus	Actinopterygii 'Palaeonisciformes'	Pedra de Fogo	Pastos Bons (Cox & Hutchinson 1991)	Endemic
Prionosuchus plummeri	Temnospondyli Platyoposauridae	Pedra de Fogo	Pastos Bons (Price 1948; Cox & Hutchinson 1991) Nazária (Cisneros *et al.* 2015)	Endemic
Timonya anneae	Temnospondyli Dvinosauria	Pedra de Fogo	Nazária, Timon (Cisneros *et al.* 2015) Palmeirais (this work)	Endemic
Procuhy nazariensis		Pedra de Fogo	Nazária (Cisneros *et al.* 2015)	Endemic
Captorhinikos sp. (*Captorhinus aguti* of Cisneros *et al.* 2015)	Reptilia Captorhinidae	Pedra de Fogo	Nazária (Cisneros *et al.* 2015)	North America (various authors)

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Scleroabietoxylon (1) and *Ductoabietoxylon* (1), and six endemic species referred to the genera *Amyelon* (1), *Taeniopitys* (2), *Kaokoxylon* (1) and *Damudoxylon* (3) (Table 1).

Discussion

Ages of the Pedra de Fogo and Motuca formations

Pedra de Fogo Formation. The age of the PFF has long been debated, although all workers agree that the unit is of Permian age (Mesner & Wooldridge 1964). The palynological content was initially regarded as indicative of an early Permian age (Müller in Mesner & Wooldridge 1964). However, an analysis carried out by Dino *et al.* (2002) dated the upper Trisidela Member as ?Guadalupian (middle Permian). This result was based on correlations using the overall character of the assemblage as well as some specific index taxa. The total content of the miospore assemblage is comparable to that of the *Tornopollenites toreutos* Palynozone of the Andirá Formation in the Amazonas Basin, and that is quite similar to assemblage recovered from the Flowerpot Formation in Oklahoma, USA (Dino *et al.* 2002). The *T. toreutos* Palynozone is not precisely dated by any other independent method, which only allows a Permian age assignment. The Flowerpot Formation was previously considered to be middle–late Permian, but is now thought to be Kungurian (=Leonardian: Nelson & Hook 2005). Additional Kungurian occurrences of index-pollen grain *T. toreuto* are known from Gondwana (Dino *et al.* 2002). Excepting *T. toreutos*, the stratigraphic ranges of the remaining nine index taxa emphasized by Dino *et al.* (2002) have recently been extended to the beginning of the Permian (Asselian–early Artinskian), based on radiometric dates obtained from the Copacabana Formation, in the Apillapampa section of the Peru–Bolivia Basin, central Bolivia (di Pasquo *et al.* 2014). Therefore, the palynological content of the PFF is consistent with a Permian age for the formation, and possibly an early Permian age within the Artinskian–Kungurian interval.

Plant macrofossils suggest similar age constraints for the PFF. Iannuzzi & Langer (2014) reported the occurrence of callipterid foliage very similar to *Rhachiphyllum schenkii* (Heyer) Kerp in the PFF. Callipterids are a seemingly natural group of plants that ranges from the late Pennsylvanian to the late Permian, the distribution of which appears to have been strongly influenced by local climatic and environmental conditions. Following their initial appearance in Europe, callipterids spread widely throughout the palaeotropical belt during the early Permian, with records extending from SE North America (first appearance in the late Moscovian = Asturian of Illinois: DiMichele *et al.* 2005, 2013) to SE Asia (Booi *et al.* 2009; Wang *et al.* 2013). The morphogenus *Rhachiphyllum* first appears in Central and Western Europe in the late Pennsylvanian, with *R. schenkii* occurring from the late Pennsylvanian to the early Permian Rotliegendes interval (Kerp 1988). Its range in other geographical areas appears to be restricted to Pennsylvanian–early Permian deposits as well (DiMichele *et al.* 2005, 2013; Wang *et al.* 2013).

Attempts at vertebrate biostratigraphy have produced conflicting age estimates for the PFF. The archegosaurid temnospondyl *Prionosuchus plummeri* (Price 1948) was considered evidence for a Cisuralian age (Petri & Fulfaro 1983), although later Cox & Hutchinson (1991) suggested that its very long snout represented an evolutionary grade more typical of a late Permian age (at that time including the Guadalupian). The PFF chondrichthyan genus *Itapyrodus* also is known from the Irati Formation of the Paraná Basin (Chahud *et al.* 2010). The latter unit was radiometrically dated to 278.4 ± 5 Ma (Santos *et al.* 2006), which corresponds to an earliest Kungurian age in the current geological timescale (Cohen *et al.* 2013; updated on the website). The presence of the ctenacanth genus *Glikmanius* in the PFF indicates an age between the Carboniferous and the Guadalupian (Ginter *et al.* 2005), whereas the recent discovery of *Captorhinikos* sp. (initially identified as *Captorhinus aguti* by Cisneros *et al.* 2015), a reptile known from strata attributed to the Kungurian in North America (Olson 1958, 1970; Modesto *et al.* 2014), supports a Kungurian age for this unit. Therefore, based on the few biostratigraphically-informative vertebrates, we follow Cisneros *et al.* (2015) in tentatively proposing a Kungurian (late Cisuralian) age for the PFF.

Motuca Formation. There is no consistent age assessment for the MF. The underlying PFF has produced palynomorphs, plants and vertebrates that are probably no younger than middle Permian (=Guadalupian; see the discussion above). Aside from the extremely fragmentary vertebrate remains noted above (also see Table 2), only fossil plants are present in the MF, but a few biostratigraphically-informative taxa are present among the petrified stems (Dias-Brito *et al.* 2007). The filicalean fern stem *Grammatopteris* is potentially the best index fossil for the unit. Besides the Brazilian species (*G. freitasii*), there are only two other species assigned to the genus, which are restricted to the early Permian in Germany and France (Autunian) (Rößler & Galtier 2002*a*). Of particular interest is the fact that in Germany, *Grammatopteris* was recovered from the Chemnitz fossil forest, which was radiometrically dated to 290.6 ± 1.8 Ma (Rößler *et al.* 2012). This age corresponds to the latest Sakmarian–earliest

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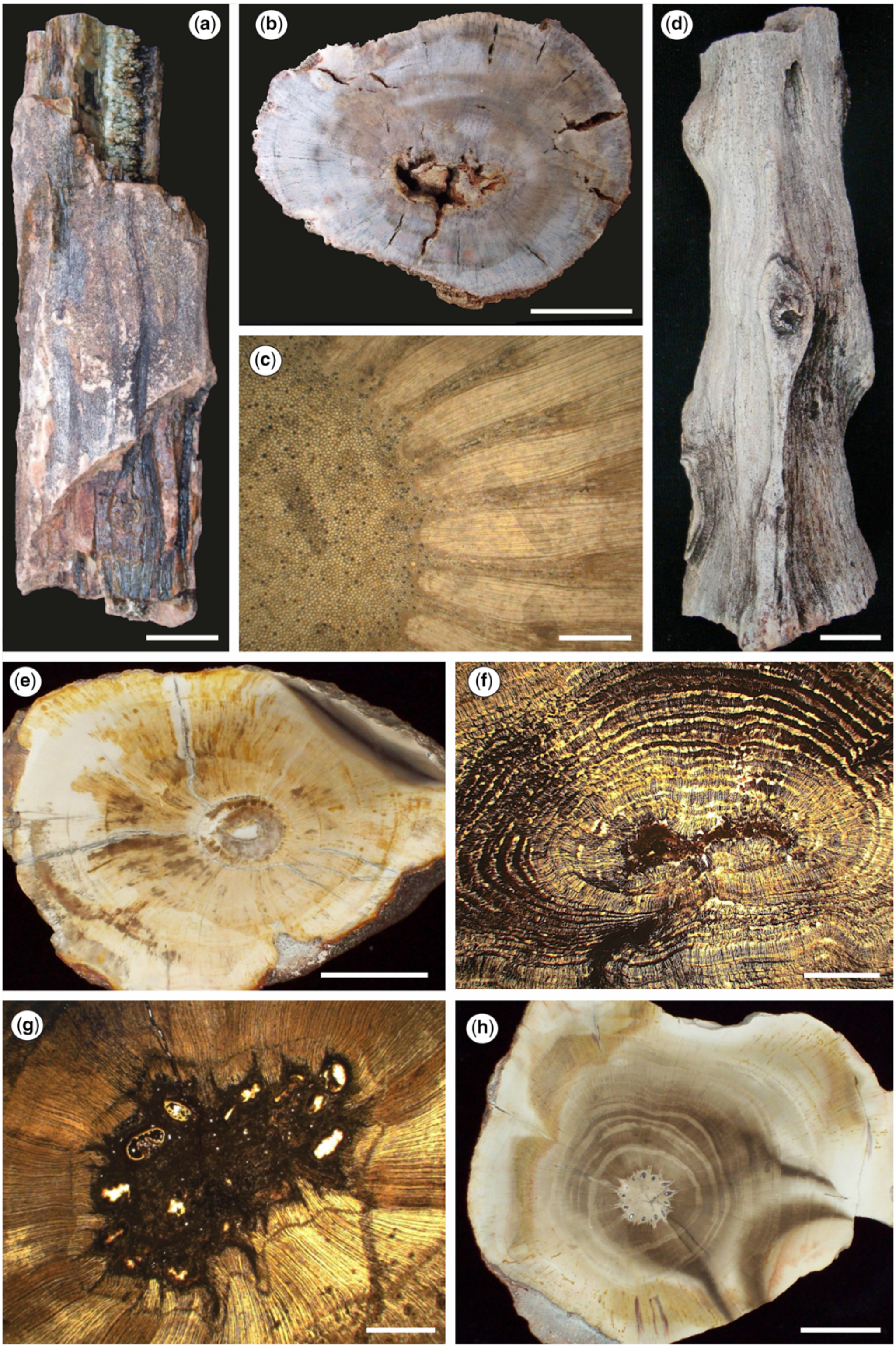

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Artinskian stages (Cohen *et al.* 2013; updated on the website).

Two other genera of plants from the MF are of biostratigraphic interest: *Botryopteris* and *Tietea*. *Botryopteris* is a filicalean fern stem typically found in Euramerica, ranging from the latest Mississippian up to the early Permian, and it is most abundant in Pennsylvanian equatorial floras (Rößler & Galtier 2002*b*). At the beginning of the Permian it became rarer, but during this period the genus radiated and expanded beyond the Euramerican region to the Döhlen Basin, in Germany, and one deposit in China (Hilton *et al.* 2001), in addition to the present record in the Parnaíba Basin.

Despite the fact that the tree-fern stem *Tietea* is the most abundant taxon of the rich fossiliferous region of northern Tocantins State, it is an endemic South American taxon and has a limited geographical range. Besides its presence in the Parnaíba Basin, *Tietea* stems only occur in Permian strata of Paraguay (Herbst 1986), and in the Tatuí and Corumbataí formations of the northern Paraná Basin in SE Brazil (Chahud & Petri 2009; Tavares 2011). The Tatuí crops out in the northern portion of basin and is equivalent to the Rio Bonito Formation (Holz *et al.* 2010). Radiometric ages obtained from distinct tonstein layers found in the middle Rio Bonito suggest a time of deposition between the early Sakmarian and the mid-Artinskian (see Simas *et al.* 2012). The Corumbataí Formation is equivalent to the Teresina Formation that overlies, in stratigraphic order, the Irati (early Kungurian) and the Serra Alta formations. Its tentative age is estimated to be early Guadalupian, varying from the Wordian to the Roadian (Holz *et al.* 2010).

Palaeoenvironmental interpretation

The fossil plant-bearing horizons of the PFF have been interpreted by Andrade *et al.* (2014) as terrestrial, deposited in nearshore regions of large continental lakes that were affected by high-energy, non-channelized flows generated by associated fluvial systems. These flows formed suspension lobes after reaching the flat bottoms of the lake basins, splaying extensively and producing tabular-bedded successions with sheet-like geometries. These deposits were subsequently covered by suspension-deposited mudstones, following an aggradational arrangement as energy in the depositional system decreased (Andrade *et al.* 2014). The presence of horizontal silicified gymnosperm stems within the sandstone beds is compelling evidence of high-energy events in the associated fluvial systems. Autochthonous plant assemblages are likely to have accumulated on the lake-shore areas, which facilitated rapid burial of the material by episodic sedimentation associated with permanent and/or ephemeral fluvial systems.

There are few good outcrops of the MF in the Araguaína–Fildelfia region because of the relatively low relief, vegetation cover and intense weathering. The most typical facies are white to reddish fine sandstones with tabular or trough cross-stratification, which may be stacked to form up to 10 m-thick sandstone intervals (Rößler 2006; Dias-Brito *et al.* 2007). Siltstones (up to 5–10 m thick) may occur as lateral equivalents of some sandstones (Dias-Brito *et al.* 2007) or overlie upwards-fining sandstones (Rößler 2006). According to Rößler (2006), the facies are arranged as approximately 10 m-thick fluvial cycles. The sandstones at the base of the cycles correspond to single or stacked channel bodies. They are succeeded by mottled sandstones with muddy intercalations, which represent floodplain deposits and, in part, palaeosols, indicating seasonally-alternating wet and dry conditions. The siltstones, especially some beds with bivalve mollusks, are considered lacustrine. The upper part of the MF in the TFTNM region, above the fossiliferous interval, includes a 2–3 m-thick gypsum bed (Dias-Brito *et al.* 2007). Evaporites and aeolian sandstones also are known in other areas of the Parnaíba Basin (Lima Filho 1998), and these lithologies substantiate interpretations that the MF represents sabkha or playa environments (Faria 1984; Lima Filho 1998).

There are several indicators in the Permian floral record from Parnaíba Basin pointing to a seasonally

Fig. 6. Petrified gymnosperms from the Motuca Formations. (**a**) MN-Pb 1655, *Carolinapitys maranhensis* (Coimbra & Mussa 1984), longitudinal view. (**b**) MN-Pb 1751, *Cyclomedulloxylon parnaibense* (Mussa & Coimbra 1987), transverse section. (**c**) K 5503aTS, *Ductoabietoxylon solis* (Kurzawe *et al.* 2013*a*), transverse section showing pith with ducts and secretory cells (black dots), projections of the pith and secondary xylem. (**d**) TOF 195, *Damudoxylon roessleri* (Kurzawe *et al.* 2013*b*), longitudinal view. (**e**) K 5869, *Scleroabietoxylon chordas* (Kurzawe *et al.* 2013*a*), transverse section. (**f**) TOF 125TR, *Damudoxylon buritiranaense* (Kurzawe *et al.* 2013*b*), transverse section showing pith and secondary xylem with growth rings and shear zones. (**g**) TOF 221, *Parnaiboxylon rohnae* (Kurzawe *et al.* 2013*a*), transverse section showing pith with canals and secondary xylem with shear zones. (**h**) K4861a, *Parnaiboxylon* sp. 1 (Kurzawe *et al.* 2013*a*), transverse section. Specimens in (a) & (b) are stored at Museu Nacional, UFRJ, Rio de Janeiro, Brazil; specimens in (c), (e) & (h) are at the Museum für Naturkunde Chemintz, Germany; specimens in (d), (f) & (g) are at the Museu de Paleontologia e Estratigrafia Professor Dr Paulo Milton Barbosa Landim, UNESP – Rio Claro, Brazil. (a) Scale bar = 2 cm; (b) scale bar = 1 cm; (c) scale bar = 2 mm; (d) & (e) scale bar = 1 cm; (f) & (g) scale bar = 2 mm; (h) scale bar = 1 cm.

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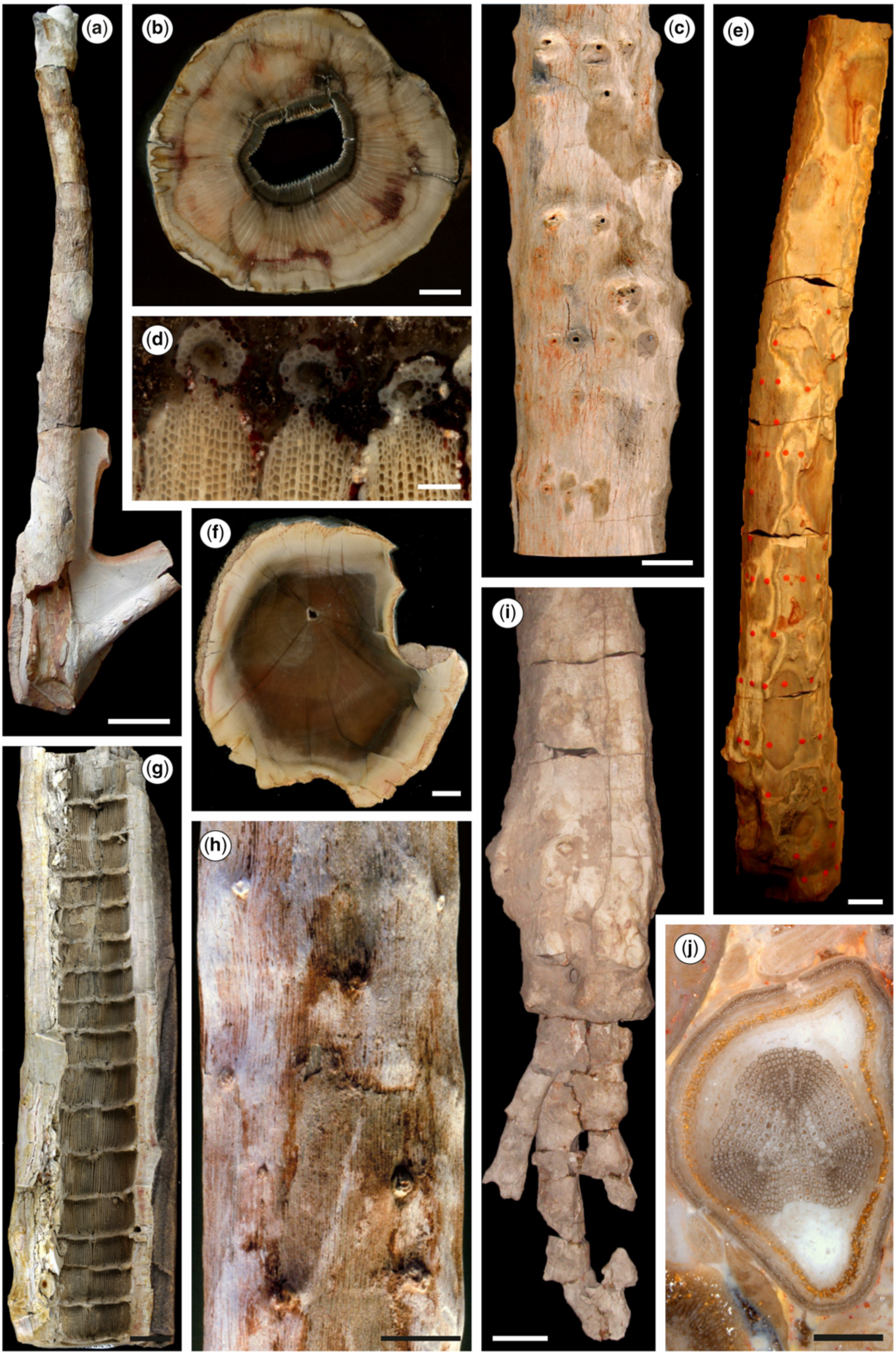

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dry climate, such as: (a) the probable occurrence of climate-driven silicification processes (Matysová *et al.* 2010); (b) the presence of flash-type fluvial systems (Capretz & Rohn 2013; Andrade *et al.* 2014); (c) the occurrence of evaporites and gypsum deposits (Faria & Truckenbrodt 1980*a*); (d) the prominent xeromorphic characteristics of the fronds of the fern *Buritiranopteris costata* (Tavares *et al.* 2014); and (e) the growth-ring-like patterns found in *Arthropitys* stems (Neregato *et al.* 2015), roots (Rößler *et al.* 2012) and in associated gymnosperms (Kurzawe *et al.* 2013*a*, *b*; Benício *et al.* 2015). However, it is also clear that a reliable water supply must have been available annually to support the diversity of plant groups observed and the arborescent growth forms of the tree-ferns, arborescent calamitaleans and most of the gymnosperms. The majority of those trees likely grew over several years to attain their large dimensions, both in diameter (e.g. gymnosperm logs more than one metre in diameter) and in height (e.g. some tree-fern stems are *c.* 10 m long). Moreover, the diverse aquatic vertebrate community described by Cisneros *et al.* (2015) would have required permanent water sources. Based on all these considerations, the Permian palaeoflora and vertebrate faunal assemblage of the Parnaíba Basin fits best with the modern 'tropical summerwet' biome of Rees *et al.* (2002). However, this conclusion contradicts the predictions of climate models for this region of northern South America during the Permian. Model results suggest that the region should have experienced a semi-arid climate regime unsuitable for the development of forests comprised of mostly spore-producing plants (Rees *et al.* 1999, 2002). The richness of plant types and the number of arborescent taxa is also not fully compatible with the palaeoenvironmental interpretations made from the facies analysis, because they appear to overestimate the aridity of the environments, whereas the plants and animals indicate the existence of milder, more humid environmental conditions that allowed continuous growth of plants throughout their lives. In this scenario, dry episodes associated with deposition of evaporites and gypsum may not have been annual but instead followed multi-year cycles. This would permit the development of arborescent growth forms in plants that colonized the coastal plains adjacent to lakes and along river courses, and the aquatic vertebrates that lived in these bodies of water.

Palaeobiogeography

During the early Permian, the Parnaíba Basin was positioned between two major floristic provinces, the Euramerican to the north and the Gondwanan to the south (Fig. 8). Mussa & Coimbra (1987) noted that interactions between the Parnaíba Basin floral assemblage and the classical Gondwanan assemblages are to be expected, but it is also important to investigate the potential influences of the Euramerican and/or Cathaysian floral assemblages on the Parnaíba Basin floras. The cluster analysis performed by Neregato *et al.* (2017) showed that the Parnaíba Basin Permian palaeoxylofloras (i.e. petrified wood from the PFF and MF) do not have strong similarities to any other anatomically-preserved palaeoflora from the Pennsylvanian–Permian interval. This result reflects the fact that although the Parnaíba flora shares a considerable number of higher taxa with palaeoxylofloras from the Euramerican tropics and the Gondwanan floristic province, it also has a high degree of endemism at the specific and generic levels. The Parnaíba Basin palaeoxyloflora was even quite distinct from that of the Irati Formation from the Paraná Basin, the most geographically proximate fossil xyloflora in Gondwana.

One possible explanation for this dissimilarity may lie in differences in the palaeoclimatic regimes in the respective basins. Whereas the Parnaíba Basin was located in the palaeotropical belt in the early Permian, the Paraná Basin was characterized by a mid-latitude temperate climate based on the climate modelling of Rees *et al.* (2002), which would have limited the exchange of taxa between the two

Fig. 7. Petrified sphenophytes from the Motuca Formation. (**a**) K 5266, *Arthropitys tocantinensis* (Neregato *et al.* 2017), longitudinal view. (**b**) K 5394, *Arthropitys iannuzzii* (Neregato *et al.* 2015), transverse section showing secondary body. (**c**) K 5867, *Arthropitys iannuzzii* (Neregato *et al.* 2015), longitudinal view. (**d**) K 4486, *Arthropitys isoramis* (Neregato *et al.* 2015), transverse section showing the carinal canals. (**e**) K 5787, *Arthropitys barthelii* (Neregato *et al.* 2017), longitudinal view showing nodes with branch scars (red dots). (**f**) K 4874, *Arthropitys barthelii* (Neregato *et al.* 2017), transverse section showing secondary body and the reduced pith cavity. (**g**) K 5407, *Arthropitys isoramis* (Neregato *et al.* 2015), longitudinal view showing pith cavity and nodal diaphragms. (**h**) K 4552, *Arthropitys isoramis* (Neregato *et al.* 2015), longitudinal view showing branch scars. (**i**) TOF 187, *Arthropitys isoramis* (Neregato *et al.* 2015), lowermost stem portion showing the root system. (**j**) K 6040, *Sphenophyllum* sp. (Neregato *et al.* 2017). Specimens in (a)–(h) & (j) stored at the Museum für Naturkunde Chemnitz, Germany; specimen in (i) is at the Museu de Paleontologia e Estratigrafia Professor Dr Paulo Milton Barbosa Landim, UNESP – Rio Claro, Brazil. Scale bars: (a) Scale bar = 10 cm; (b) scale bar = 1 cm; (c) scale bar = 30 mm; (d) scale bar = 250 µm; (e) scale bar = 5 cm; (f) scale bar = 1 cm; (g) scale bar = 2.5 cm; (h) scale bar = 2 cm; (i) scale bar = 5 cm; (j) scale bar = 1 mm.

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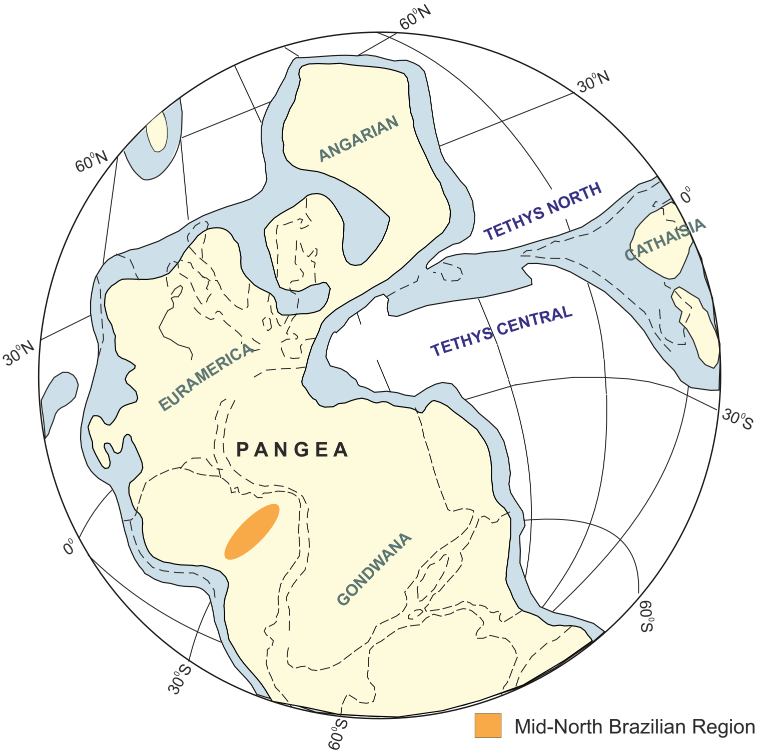

Fig. 8. The supercontinent Pangaea during the Cisuralian, showing the intermediate geographical position of the 'Mid-North Brazilian Region' between the Euramerican and Gondwanan floristic provinces. Neregato *et al.* (2017) recently proposed this phytogeographical unit based on the high endemism of the Permian petrified floras from the Parnaíba Basin.

basins. At the same time, it is important to emphasize that palaeobiogeographical interpretations based on comparisons of palaeoxylofloras must be undertaken with caution because fossil wood taxonomy is highly artificial for gymnosperms and ferns as well. The discovery of reproductive structures or fructifications would help to refine our picture of the botanical affinities of taxa established on the basis of vegetative portions. To date, only a few fertile pinnules attached to the stems of the tree-fern *Tietea* and unpublished fragments of callipterid sporangia have been identified among the plant fossils collections from the Parnaíba Basin. Therefore, further collecting and research are needed to determine whether the endemism of the Parnaíba Basin palaeoflora is a real signal or an artefact of collection effort.

In addition to the unique character of the Parnaíba Basin Permian fossil wood assemblage described by Neregato *et al.* (2017), it is noteworthy that no glossopterids have been identified to date, which argues against the inclusion of the assemblage in the Gondwanan Floral Province. Although there are some links to the Euramerican Floral Province, the overall composition of the flora seems best interpreted as a distinct phytogeographical unit instead of simply being a transitional assemblage between the Euramerican and Gondwanan realms. The palaeogeographical position (*c.* 30°S in north-central Gondwana), and climatic (tropical summerwet) and sedimentary (braided fluvial systems and playa lakes associated with evaporitic and gypsum deposits) data support this conclusion, indicating a set of biotic and abiotic features exclusive to this region of the South American continent. In this context, the evolution of a diverse flora adapted to these unique conditions is not surprising. Neregato *et al.* (2017) proposed a new formal phytogeographical unit, the 'Mid-North Brazilian Region' (MNBR), on the basis of the Parnaíba Basin palaeoflora, representing the plant community that existed in tropical summerwet climates in the southern low latitudes of northern Gondwana during the Cisuralian. We endorse this conclusion, and propose that the links with the Euramerican Floral Province could indicate that the MNBR diverged from the southernmost part of the former province, in the tropical portion of Gondwana.

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As with the palaeoflora, the PFF tetrapod assemblage has highly significant biogeographical implications because it represents a unique snapshot of tropical Gondwanan terrestrial ecosystems during the early Permian (Cisuralian). Nearly all other Cisuralian tetrapod assemblages are found in a narrow equatorial band stretching from SW USA, through maritime Canada and into Western Europe (e.g. Anderson & Cruickshank 1978; Berman *et al.* 1997; Lucas 2006). The presence of the early-diverging dvinosaur *Timonya*, the trimerorhachid dvinosaur *Procuhy* and the captorhinid reptile *Captorhinikos* in the PFF parallels contemporary North American communities, which include the dvinosaurs *Trimerorhachis* (Milner & Schoch 2013), *Isodectes* (Sequeira 1998) and *Slaugenhopia* (Milner & Sequeira 2004), as well as *Captorhinikos* and several other captorhinid species. This similarity suggests that the equatorial tetrapod assemblage best known from the Cisuralian of North America extended into the Gondwanan tropics, lending credence to Sidor *et al.*'s (2005) hypothesis that the anachronistic faunal assemblage from late Permian (Lopingian) Moradi Formation of Niger is, in part, a relict of a formerly more widespread tetrapod community type (see also Bernardi *et al.* 2017). However, given their diversity and abundance in the Cisuralian of North America (e.g. Romer & Price 1940; Reisz 1986; Brocklehurst *et al.* 2013), non-mammalian synapsids are conspicuous by their absence from the PFF. It is unclear whether this is a real absence, perhaps driven by unfavourable environmental conditions or unsuitable habitat types, or an artefact resulting from the comparatively minor amount of collecting effort that has been expended on the PFF.

The occurrence of rhinesuchid temnospondyls in the PFF represents both the oldest and most northerly record of the clade, which is otherwise known from middle Permian to Early Triassic higher latitude assemblages in southern Gondwana (e.g. Schoch & Milner 2000; Marsicano *et al.* 2017). When combined with the fact that early-diverging dvinosaurs, such as *Trimerorhachis*, *Procuhy*, *Slaugenhopia* and *Timonya*, are known from the early Permian tropics, but more derived taxa such as *Dvinosaurus*, *Thabanchuia* and *Tupilakosaurus* are found in higher latitude areas in Greenland, Russia and southern Africa, it is tempting to suggest that the early Permian tropics served as an important cradle for temnospondyl diversity. Additional discoveries will be needed to determine whether this is a real biogeographical pattern or simply an artefact of poor sampling. Nevertheless, this intriguing possibility emphasizes the growing importance of the PFF for our understanding of Permian tetrapod evolution, and the continued need for palaeontological exploration in traditionally poorly studied geographical areas.

Final remarks

Although the Permian PFF and MF have produced a well-studied fossil record that is of growing scientific importance, there is still much to be discovered about the palaeontology of these units. This is particularly true when considering the outcrop area that remains unexplored, especially in the southern parts of the states of Piauí and Maranhão, and the western part of Tocantins. Nevertheless, the data obtained so far allow the following conclusions:

- The ages suggested by the fossils of the PFF and MF fall within the Cisuralian, particularly in the Artinskian–Kungurian interval. In spite of the recent efforts to discover rocks that could be radiometrically dated, no radiometric age has been obtained so far. This supports the hypothesis that the high concentration of silica found in these formations results from syndepositional and/or early-diagenetic processes (Matysová *et al.* 2010), not volcanic events as suggested by some authors (Faria & Truckenbrodt 1980*a*). We encourage further study of the microfossil record of the PFF and MF because of the potential such work holds for refining relative age estimates for the formations. Besides the traditional sporomorphs, we recommend searching for other microfossils that can be employed for biostratigraphy, such as conodonts in sediments of supposedly marine origin (black shales) that are concentrated in the SW portion of the basin.
- There are multiple fossiliferous horizons in the PFF and MF. Composite sections compiled from exposures along the eastern and SE margins of the basin (i.e. near the municipalities of Timón, Monsenhor Gil, Pastos Bons and Nova Iorque) show a clear fossiliferous succession. From bottom up, this succession is composed of animal remains (fishes and amphibians), often associated with ichnofossils, followed by occurrences of stromatolites or algal/microbial mats in association with silicified plant remains in the upper portion of the rocky packages. These sequences seem to corroborate the existence of complete transgressive–regressive sequences in the formations, but it is still unclear is whether there is more than one of these sequences distributed throughout the basin. Based on the tripartite division of the PFF and the occurrence of petrified plant fossils in at least two well-defined intervals within the Permian rocks (in the Basal Silex Member of the PFF and in the lowermost MF), it appears likely that there are at least two of these sedimentary sequences. Whereas the basal strata crop out in the eastern and SE parts of the basin, the highest strata are best exposed in the SW region. However, the exact durations and

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temporal distribution of these sequences is not yet known. They could be concentrated in a short time span, or they could extend through much of the Artinskian–Kungurian time interval.

- Although sedimentologists have repeatedly mentioned the occurrence of marine deposits in the PFF (Faria & Truckenbrodt 1980*a*; Pinto & Sad 1986), the fossils collected from the formation do not clearly demonstrate the existence of typical marine environments. Instead, the fossils are related to continental environments, which supported communities comprised of terrestrial (plants) and freshwater (fishes and amphibians) organisms; marine invertebrates and vertebrates are conspicuously absent. Sharks and closely related forms are present, but the ability of Paleozoic chondrichthyans to live in freshwater and brackish conditions in inland water bodies is well known. Their occurrence, therefore, does not necessarily indicate a marine depositional environment for vertebrate-bearing horizons. Stromatolites are also ambiguous environmental indicators because they can be found either in the margins of freshwater and brackish water bodies, or in nearshore marine environments. Rößler (2006) reported stromatolites encrusting plant axes, which points to their formation in terrestrial conditions (e.g. lake shorelines, ponds) in the PFF. Among the fossils discovered to date, only undescribed, high-diversity ichnological assemblages found in Pastos Bons suggest salinity levels close to marine conditions. Geochemical and microfossil analyses of black shales and calcareous rocks of putative marine origin, which are distributed in the SW portion of the basin (Tocantins and Maranhão states), are highly recommended because of their potential to confirm the existence of higher-salinity environments. The high diversity of chondrichthyans signals that at some point there was a connection between the Parnaíba Basin and other surrounding basins which allowed the dispersal of taxa that gave rise to the endemic species mentioned here (Table 2). This implies that at least one transgressive event must have occurred. The transgression may have come from the SW, where it is potentially indicated by the presence of carbonates and carbonaceous shales. The supposedly marine facies become thinner to the east, and seem to disappear entirely near the ENE rim of the basin. This transgression might be related to the event that generated the carbonaceous platform deposits of the early Permian Copacabana Formation of Bolivia (di Pasquo *et al.* 2014), located to the SW in the Peru–Bolivia Basin, whereas in the Brazilian basin of Amazonas, to the NW, only terrestrial sediments were depositied at this time (Andirá Formation: Cunha *et al.* 2007). Alternatively, it is possible that this transgressive event is related to the deposition of the carbonates and black shales of the Irati Formation in the Paraná Basin (Holz *et al.* 2010). This would fit with the possible Kungurian age we posit for the PFF, and the presence of shared taxa such as *Itapyrodus punctatus* and *Tietea* spp. However, the connection between the basins would necessarily pass through parts of either the Parecis Basin or by the São Francisco Basin, where deposits of probable Permian age are present but have not been studied (Silva *et al.* 2003). A final possibility is that a connection existed to the north, which is suggested by the presence of taxa such as *Glikmanius* andxenacanth sharks that are shared with Euramerica.
- The palaeogeographical position of the Parnaíba Basin (*c.* 30°S), climatic modelling (tropical warm semi-arid) and sedimentary indicators (evaporitic and gypsum deposits, flash-type fluvial systems) support a seasonally dry climate for the basin during Permian times. Although the fossil plants display a number of structures related to withstanding dry conditions, they also present features that favour sufficient water availability to support the continuous growth of arborescent pteridophytes (tree-ferns and calamitaleans) and large gymnosperms over multiple years. The majority of fossil vertebrates known from the PFF would require permanent bodies of water as well as the gigant amphibian *Prionosuchus plummeri*. This argues against a semi-arid climate and favours the existence of milder conditions with rather humid summers, more consistent with a 'tropical summerwet climate' (Neregato *et al.* 2017). Although the basin was located in the Permian desertic belt, evidence of wetter environmental conditions can be explained by the local climatic effects of an epireic sea or a large lake system in the basin, or the presence of dense riparian vegetation along major river courses. There is also the possibility that there were highland areas adjacent to the coastal plains and shorelines where sedimentation was taking place. This hypothesis is especially relevant for the plant record of the MF, where tree-ferns such as *Tietea* predominate. The combination of large water bodies and mountainous topography can result in wetter local–regional climates due to the effects of mountains on atmospheric circulation, as in modern orobiomes (Cox & Moore 2005).
- Palaeogeographically, the Parnaíba Basin was positioned in the southern limit for low latitudes of the southern hemisphere, between the Euramerican Floristic Province situated in the palaeotropical belt to the north and the Gondwanan Floristic Province to the south, in temperate to cold higher latitudes. This intermediate position allowed the region to function as a dispersal corridor or

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landscape linkage (Beier & Loe 1992) between the tropics and northern Gondwana. Such corridors or linkages are regions of connectivity that facilitate the movement of multiple species and maintain ecological processes between two or more significant habitat areas (Beier *et al.* 2008). The linkage allowed taxa from the tropics, such as *Psaronius*, callipterid pteridosperms, trimerorhachid temnospondyls and captorhinid reptiles, to reach northern Gondwana (Tables 1 & 2), and probably took the form of a moisture corridor that crossed NE Africa and connected the basin to the tropics of SE North America and Western Europe (UK, France and Germany). According to updated palaeogeographical reconstructions for the Permian (Blakey 2008), the orogeny resulting from the collision of Gondwana (NW Africa) and Laurentia (eastern North America) could have generated a moisture corridor by diverting moisture-laden easterly atmospheric circulation towards the continent. The tectonic processes involved in the final stages of uplift may also have given rise to a system of potentially interconnected epeiric seas or large lakes that facilitated the dispersal of plants and animals, especially amphibians, towards the Parnaíba Basin. A similar corridor is expected to the south, connecting the Parnaíba and Paraná basins and explaining therefore, the occurrence of shared taxa (see Tables 1 & 2). Nevertheless, similarity analyses have underscored the high degree of endemism of the Parnaíba Basin biota (Neregato *et al.* 2017) (Tables 1 & 2). These data have been used to distinguish this area from other biogeographical regions, justifying Neregato *et al.*'s (2017) recent naming of the 'Mid-North Brazilian Region' as a new phytogeographical unit. Depending on the exact age of the Permian fossils, the Parnaíba Basin was likely to have been not only a dispersal corridor for animals and plants, but also a centre of origin for some of the taxa such as rhinesuchid temnospondyls (Cisneros *et al.* 2015) or tree-fern *Tietea*.

The fossil record of terrestrial ecosystems from northern Gondwana has long been very poorly known, creating a significant gap in our knowledge of Permian biogeography. In this contribution, we emphasize how recent work in the Parnaíba Basin is helping to close this gap. Through the collaboration of researchers at institutions located within the basin with other Brazilian and international colleagues, a new picture is emerging of a highly distinctive biota with broad evolutionary significance. Nevertheless, further stratigraphic, sedimentological and palaeontological studies are needed to solve persistent problems and test hypotheses related to the geochronology, palaeoenvironment, palaeoclimate and palaeobiogeography of the Parnaíba Basin.

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