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In pursuit of causes for the greatest mass extinction: the Permo-Triassic Boundary in the Southern Hemisphere – part I

Fishing for fossils in 260 million years old sedimentary rocks of a former epicontinental sea in southern Brazil

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Abstract

Various catastrophic and/or episodic events have been suggested to have caused the end-Permian mass extinction close to the Permo-Triassic Boundary (PTB). However, the theories and extinction-scenarios are predominantly based on the sedimentary record and fossil record of the Northern Hemisphere, the Southern Hemisphere and in particular the fossil fish record being least well explored. In this first of four contributions, we briefly review existing theories, introduce to the current discussion around the greatest extinction event ever and comment on the palaeontological and geochemical potential of fish fossils particularly from near the PTB in Brazil. As an example, new Late Permian fishes from the Corumbataí Formation in southern Brazil are discussed; although fragmentary in preservation, fishes with surprisingly primitive affinities may be discovered.

Auf der Suche nach Ursachen für das grösste Massenaussterbe-Ereignis: die Perm-Trias-Grenze der Südhemisphäre – Teil 1
Das Fischen nach Fossilien in 260 Millionen Jahre alten Sedimentgesteinen eines ehemaligen epikontinentalen Meeres in Südbrasilien

Verschiedene katastrophenhafte und/oder episodische Ereignisse sind als Ursachen für das Massenaussterbe-Ereignis am Ende des Perms in der Nähe der Perm-Trias-Grenze (PTB) vorgeschlagen worden. Die Theorien und Aussterbe-Szenarien gründen allerdings mehrheitlich auf dem Sediment- und Fossilbeleg der Nordhemisphäre, während die Südhemisphäre und speziell der fossile Fisch-Beleg am wenigsten weit erforscht sind. In diesem ersten von vier Beiträgen rekapitulieren wir kurz bestehende Theorien, führen in die gegenwärtige Diskussion um das allergrösste Aussterbe-Ereignis ein und kommentieren das paläontologische und geochemische Potential fossiler Fischreste insbesondere aus PTB-Nähe in Brasilien. Am Beispiel spätpermischer Fischfossilien aus der Corumbataí-Formation in Südbrasilien zeigen wir, dass aus diesen Schichten fragmentarisch erhaltene Fische mit überraschend primitiven Merkmalen gefunden werden können.

Key words: Brazil – fossil fishes – geochemistry – mass extinction – palaeontology – Permian – Permo-Triassic Boundary – Southern Hemisphere – Corumbataí Formation

1 INTRODUCTION

About 260 million years ago, at the end of the Permian period, the continents of the Northern Hemisphere (Laurasia) and the continents of the Southern Hemisphere (Gondwana) were joined together into a single super-continent called Pangaea, enclosing the ancestral ocean Tethys (Fig. 1). Two enormous seas existed; the Tethys, largely enclosed by Pangaea, and Panthalassa, an enormous ocean that surrounded the supercontinent. Extraordinary fossil records of that time frame teach us that nearly all life in seawater, and also a high percentage of fauna and flora living in freshwater and on land – estimates frequently range from 70–95% of all species – disappeared in a geologically short time, presumably a few ten thousands of years (ERWIN, 1993; BOWRING et al., 1999). At a higher taxonomic level, for instance at the family level, five major extinction events can be made out in a generalized diversity curve across the entire Phanerozoic (spanning about 550 million years), and in which the end-Permian event clearly stands out as the most severe one (Fig. 1). But the string of events leading to the great mass extinction, its causes and effects, are still unknown and vividly debated.

During the Late Permian, the interior, large seas and lakes of the Southern Hemisphere's super-continent Gondwana had become more and more shallow, and the climate increasingly arid. The usually «more productive» marine (platform) sequences such as those found in the Tethys

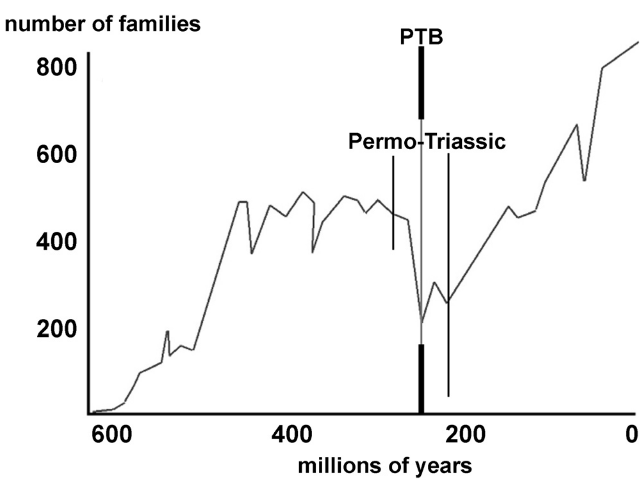

Fig. 1. An estimate of change in organismic diversity at the family level over the course of 600 million years (simplified from SEPKOSKI, 1984). There are several periods showing decline in diversity but note the abrupt drop in diversity (about 260 million years ago) before the Permo-Triassic Boundary (vertical line, which is also the boundary between the Palaeozoic and the Mesozoic, currently dated 252.4 million years before present). Fine lines delineate the lower boundary of the Permian and the upper boundary of the Triassic.

Abb. 1. Eine Annäherung der Veränderung organismischer Diversität auf Familienebene im Verlaufe von 600 Millionen Jahren (vereinfacht nach SEPKOSKI, 1984). Es sind mehrere Perioden des Diversitätniedergangs feststellbar, aber man beachte den abrupten Abfall der Diversität (vor etwa 260 Millionen Jahren) vor der Perm-Trias-Grenze (vertikale Linie, welche auch die Grenze zwischen dem Palaeozoikum und dem Mesozoikum darstellt, zurzeit mit 252,4 Millionen Jahren datiert). Die dünnen Linien markieren die untere Grenze des Perms und die obere Grenze der Trias.

province are absent from this part of the world. Instead, the shallow water deposits of the epeiric (epicontinental) seas were frequently reworked by huge storms – evidence of these storm deposits are the abundant «hammocky cross stratifications» and lots of bone beds as typical storm wave deposits. As a corollary of this sedimentary depositional pattern, articulated, well-preserved vertebrate fossils of Late Permian age are a relative rarity in South America. Besides, the endemic character of most genera and species of Gondwanan basins hinders one to one comparisons with the better-known faunas from the Northern Hemisphere.

The end-Permian mass extinction is also called the «Mother of Mass Extinctions» (ERWIN, 1993). As can be depicted from Fig. 1, the eradication of species was far more drastic than during the famous end-Cretaceous mass extinction (the K-T event) that led to the disappearance of about 75% of species including dinosaurs and allowing mammals to further rise and diversify (e.g. SLOAN et al., 1986). The duration and, in particular the geographic extent of the end-Permian extinction, however, are still a matter of much controversy. Some researchers argue that continental life (PITRAT, 1973) was less severely hit by the Permo-Triassic Boundary (PTB) extinction event or that fishes (excluded from earlier analyses) show no such extinction pattern at the family level (SCHAEFFER, 1973). Other authors (e.g. ANGIELCSZYK and KURKIN, 2003) claim, that poor understanding of the real systematic affinities between allegedly cosmopolitan taxa may be leading to spurious conclusions.

The freshwater realm close to the Paleozoic-Mesozoic Boundary is the most difficult to assess of all continental palaeo-habitats, because these realms are often less fossiliferous or yield less complete remains of ancient creatures. Fragmentary fish remains in particular are notoriously difficult to identify. For this reason, PITRAT (1973) in his pioneer study – on the assessment of the extinction of vertebrates near the PTB – decided not to include the relatively scarce fish record available at that time. However, once a taxonomic framework is in place, these ubiquitous fish fossils yield extremely valuable supplementary information on changes in diversity and palaeoenvironment.

Although biological extinction events before the Permo-Triassic Boundary are not understood in detail, we now know that catastrophic events whose effects were powerful and global enough must have taken place to speed up the pace of species extinction at an unprecedented rate. For instance, large-scale and extensive volcanism (RACKI, 2004) as evidenced by the «Siberian traps» (RENNE et al., 1995); sudden and global sea level drop (WIGNALL and HALLAM, 1992); substantial methane gas releases at continental margins (PAULL et al., 1992); oceanic anoxia, stagnation and turnover (HALLAM, 1989; KNOLL et al., 1996); and finally asteroid or meteorite impacts (BOWRING et al., 1999) have all been discussed as possible cause-effect scenarios. Combinations of one or more of possible causes or, a series of subsequent events are also conceivable. For instance, extensive vulcanism can sometimes be linked with asteroid impact(s) (KAIHO et al., 2001; overview in ERWIN, 2006).

There are three possible extraterrestrial impact sites of alleged PTB age that have been reported to date (DIETZ and FRENCH, 1973; BECKER et al., 2004; VON FRESE et al., 2006) as possible triggers for the Permo-Triassic mass extinction. The only accessible crater on land, and which is reliably dated around 250 million years, is the 40 km wide «Araguainha Dome», situated in the bordering region between the states of Goiás and Mato Grosso in central-western Brazil (THEILEN-WILLIGE, 1982; CRÓSTA, 1987, 1999). We are currently also investigating sedimentary rocks and their fossil remains around the «impacted area» in search for clues to the effect of this event on the biota at that time (MUTTER et al., in prep.).

Two more impact structures have recently been detected off the west coast of Australia, whose exact age is unknown but their possible age ranges overlap with the PTB as well (UYSAL et al., 2001; IASKY and GLIKSON, 2005).

During the Late Permian, the shallow seas covering large areas of Brazil were periodically affected by huge storms. Gigantic waves affected the bottom of the water bodies and picked up the skeletal remains of animals that had lived in these areas. Subsequently, highly turbulent waters and windstorm areas discharged their load of accumulated bones, teeth, shells, sand and mud in stratified deposits. After sedimentation more or less thorough consolidation into rock took place over a geological time span, and one is left with sandstones, mudstones, shell beds and bone beds. The latter yield localized but abundant teeth and scales of extinct sharks and bony fishes (see below), but also remains of many other organisms. These fossils tell us an exciting and compelling story about ancient fish life and their palaeoenvironments.

2 FISHING IN THE ROCKS

Fishes are pioneer settlers among vertebrates in all types of aquatic habitats and react very sensitively to changes in their environment. It is reasonable to assume that these characteristics also can be applied to Permo-Triassic fishes – making these organisms excellent indicators for sudden palaeoenvironmental changes. Palaeoichthyological and geochemical signals derived from their teeth and scales can provide evidence about the different types of water bodies, especially the original salinity and even temperature. Combined with information about contemporary terrestrial life, fish fossils ideally complement palaeobiogeographic patterns of land tetrapod faunas – abundantly present in the Permo-Triassic of Gondwana (Fig. 2).

With respect to our knowledge of Gondwanan vertebrate life during this crucial time frame, the most complete sedimentary sequences are in the South African Karoo Basin, which comprises almost continuous successions of Carboniferous to Jurassic rocks (overview in RUBIDGE, 2005). Amphibians and mammal-like reptiles are very well known and used in biostratigraphy, whereas Permo-Triassic fishes (reported from 6 of 8 currently accepted vertebrate biozones) – still require more field work and comparative studies to be extended to a global context.

The best-preserved Late Permian fishes come from the Lower Beaufort Group and were described by BENDER (2000, 2001, 2002). Yet there are also Early Mesozoic freshwater assemblages that can be brought into context with other faunas and faunal assemblages of eastern Gondwana, in particular the Middle Triassic Bekker's Kraal fauna (BROUGH, 1931, 1934; HUTCHINSON, 1973, 1975, 1978; JUBB and GARDINER, 1975) and other penecontemporaneous assemblages in the Karoo (BENDER and HANCOX, 2003); the three Australian faunas from the Sydney-Bowen Basin (HUTCHINSON, 1973, 1975) and possibly, the poorly known fossils of the Parnaíba Basin (Fig. 2). HUTCHINSON (1973, 1975) accomplished very successful studies comparing Early Mesozoic fishes from South Africa and Australia. Both Brazil and South Africa yield very localized records of fishes of that time but their study is in the initial stage. Upon closer examination, the Late Permian fish assemblages of the Karoo Basin and the Paraná Basin may or may not show great similarity in composition or diversity.

Nevertheless, a lot of fossil material and all the necessary methods are now in place in order to unlock the palaeoichthyological and geochemical signals and reconstruct the palaeoenvironmental conditions around the PTB.

3 GATHERING SLIPPERY CLUES

For obvious reasons, palaeoichthyologists would rather rely on examining the most complete fish fossils discovered, but even those rarily show any signs of preservation

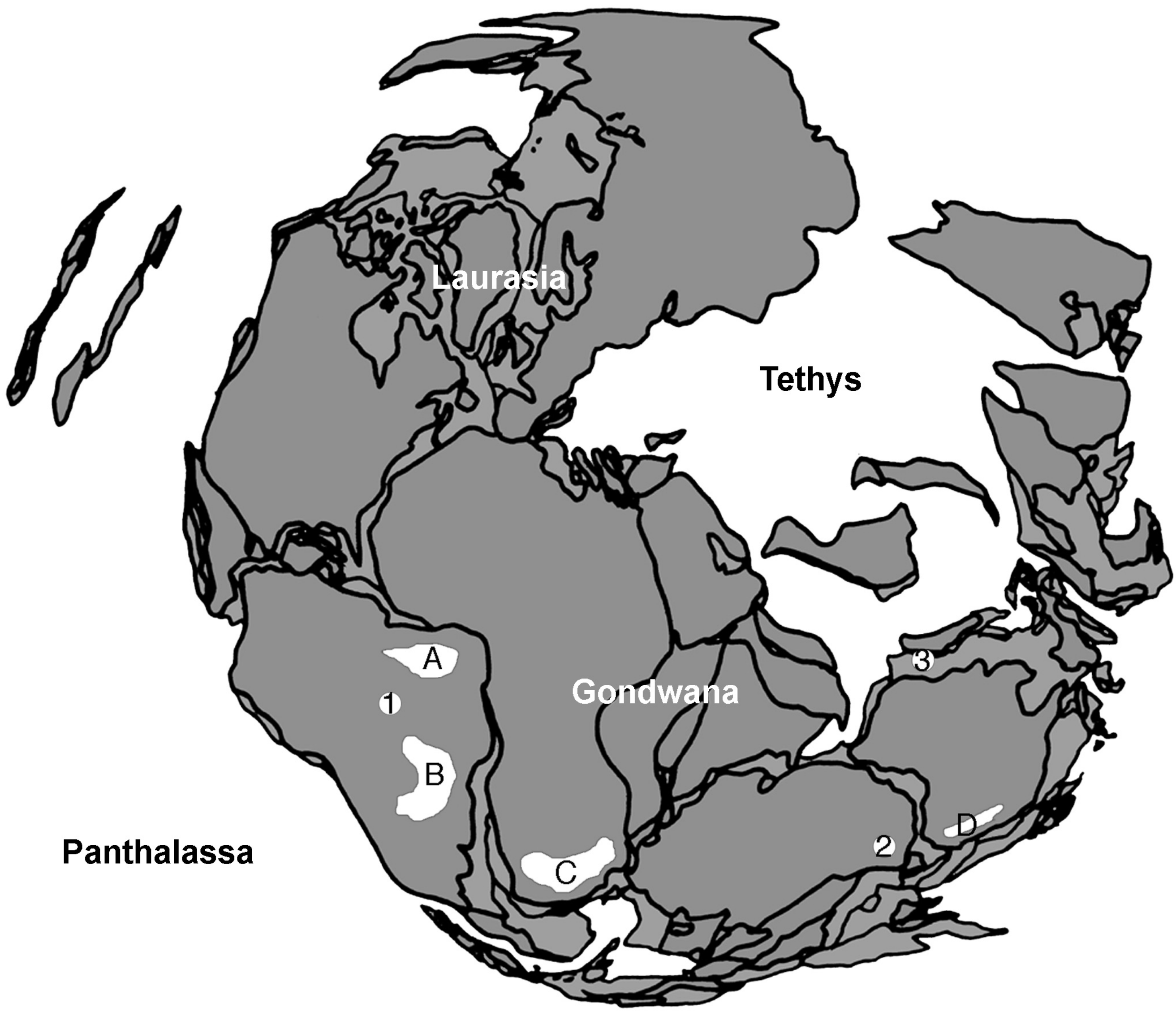

Fig. 2. Snapshot of the palaeogeography of continents around the PTB (modified from GOLONKA and FORD, 2000) showing continents of the Northern Hemisphere (Laurasia) and the Southern Hemisphere (Gondwana) joined together in the supercontinent Pangaea. Circles indicate suggested PTB impact craters (1, «Araguainha Dome» in Brazil; 2, «Wilkes Land» below Antarctica ice shield; 3, «Bedout High» off the north west coast of Australia). Irregular areas indicate Southern Hemisphere Late Permian and Early Triassic basins yielding relevant Gondwana fish assemblages (A, «Parnaíba Basin» in Brazil; B, «Paraná Basin» in Brazil; C, «Karoo Basin» in South Africa; D, «Sydney-Bowen Basin» in Australia).

Abb. 2. Momentaufnahme der Paläogeografie der Kontinente um die PTB (abgeändert nach GOLONKA und FORD, 2000), in welcher die Kontinente der Nordhemisphäre (Laurasia) und die der Südhemisphäre (Gondwana) zum Superkontinent Pangäa zusammengefügt waren. Die Kreise bezeichnen mögliche PTB-Einschlagkrater (1, «Araguainha Dome» in Brasilien; 2, «Wilkes Land» unterhalb der Antarktis; 3, «Bedout High» vor der Nordwestküste Australiens). Irreguläre Flächen symbolisieren relevante oberpermische und untertriassische Becken Gondwanas, aus denen Fossilreste geborgen werden (A, «Parnaíba-Becken» in Brasilien; B, «Paraná-Becken» in Brasilien; C, «Karoo-Becken» in Südafrika; D, «Sydney-Bowen-Becken» in Australien).

of soft tissues like skin and muscles. More often than not and most localities around the world only yield fragmentary and disarticulated skeletal remains. While the identification of species belonging to these faunal assemblages may often be dubious, there is considerable value in using the relatively abundant fish teeth and scales as material for morphological and systematic comparisons. Analyses of certain stable isotopes – assumingly incorporated during lifetime — in bone and in particular in enamel allow interpretations with regard to their original habitat. Even time control and environmental clues can be derived from comparisons of excursions of isotope curves based on data from skeletal tissues as they can be derived from sedimentary rocks (HOFFMAN et al., 1998; STEMMERIK et al., 2001; HEIMHOFER et al., 2003). The great majority of Late Palaeozoic and Early Mesozoic fish teeth, scales and dermal bones possess an enamel-like – hypermineralized – cover that is ideal for geochemical studies, because this tissue is generally less prone to or more selective towards diagenetic alterations than bone, dentine or calcified cartilage – the other frequently preserved hard tissues of fossil vertebrates. Most importantly, scales are frequently one of the most characteristic features of the best preserved specimens, and therefore detached scales can sometimes be identified and ascribed to known genera and species.

Recent studies on fossil bivalve shell types show that there are considerable differences in the potential of apparent diagenetic change among different families of bivalves (MOLLÁ et al., 2006a, b). The structure of the hard tissues along with their degree of original mineralization is pivotal for the outcome of palaeoenvironmental interpretations.

The data normally available to palaeontologists is therefore highly heterogeneous and requires collating information using distinctive and sophisticated methods. Although scientists normally strive for quantitative (and hence, less subjective) assessment of phenomena, it can be easily shown that the fossil evidence around the Permo-Triassic Boundary is highly variable in quality of preservation and rarely suitable for a quantitative approach (MUTTER et al., subm.). Although it is possible to chose certain localities in order to use quantitative methods and analyse the Late Palaeozoic/Early Mesozoic record of fossils, it is necessary to critically review the results in the light of total evidence (MUTTER, subm.).

4 THE MIDDLE-LATE PERMIAN FISHES OF BRAZIL

The uppermost Permian sedimentary rocks of Brazil (Passa Dois Group) possibly straddle the PTB and have been further subdivided into several geological units: the basal Iratí, Serra Alta, Teresina and the youngest Rio do Rasto formations, with the Corumbataí Formation being considered the equivalent of the Teresina Formation (the formations above the Iratí Formation are sometimes called Estrada Nova) in the State of São Paulo (MILANI and ZALÁN, 1999; SANTOS et al., 2006; SOUZA, 2006). The absolute age of these formations, however, is unsettled (MUTTER and RICHTER, 2007). Previous finds include among many other vertebrate groups; fin spines, teeth and scales of selachians (ancient sharks), petalodont tooth plates (Holocephali; «chimaeroids») complete and fragmentary actinopterygians (ray-finned fishes), tooth plates of ceratodontids (lungfishes) and surprisingly, also scales and fin spines of acanthodians (somewhat shark-like fishes with lots of spines near their fins) (RICHTER and LANGER, 1998; MUTTER and RICHTER, 2007).

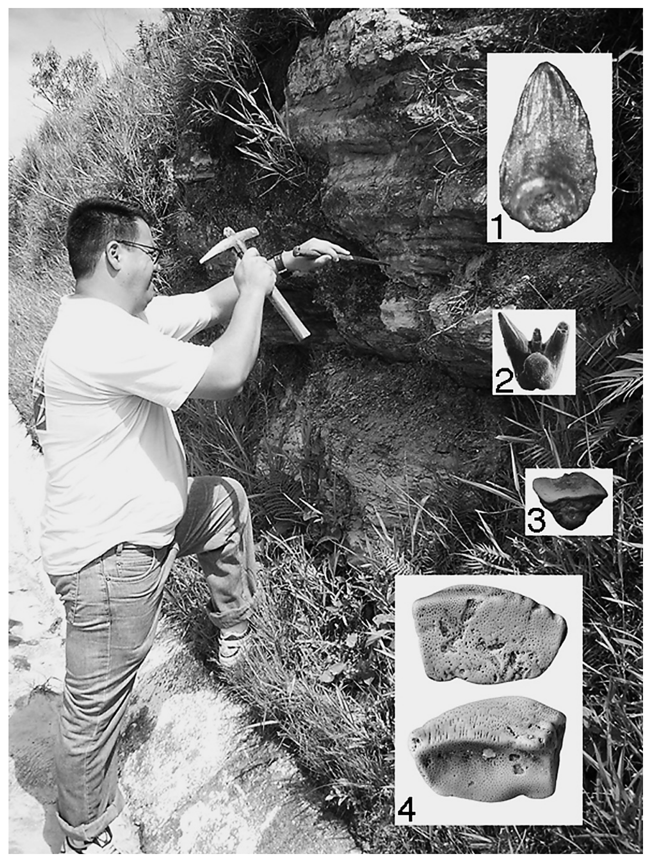

Fig. 3. A roadcut of the Upper Permian Corumbataí Formation in southern Brazil (State of São Paulo) with outcropping fossiliferous horizons. The insets show typical Middle-Late Permian fish remains from Brazil. 1, a dermal denticle («scale») of an ancient shark; 2, a xenacanth shark tooth (*Xenacanthus sp.*); 3, an acanthodian scale (cf. *Acanthodes*); 4, a chimaeroid tooth.

Abb. 3. Ein Strassenaufschluss der oberpermischen Corumbataí-Formation in Südbrasilien (im Staat São Paulo) mit fossilführenden Schichten. 1, ein Dermaldentikel (eine «Schuppe») eines altertümlichen Haifisches; 2, ein xenacanthiformer Haifisch-Zahn (*Xenacanthus* sp.); 3, eine Acanthodier-Schuppe (cf. *Acanthodes*); 4, Zahn eines Chimären-Artigen.

Such incomplete yet abundant fish remains have for instance been recovered from bone beds of the Late Permian Corumbataí Formation of the Paraná Basin in southern Brazil (Fig. 3). The occurrence of xenacanth shark teeth, lungfish teeth and actinopterygian remains come as no surprise, because these sharks have been reported as increasingly abundant across the PTB and bony fishes (lungfishes, coelacanths and ray-finned fishes) are widespread at that time. Two members of archaic fish groups, however, Paleozoic sharks and the assemblage of *Acanthodes*-like scales represent puzzling occurrences unprecedented by any PTB-vicinity deposits anywhere in the world (MUTTER and RICHTER, 2007). Despite the fragmentary nature of all these remains, there is considerable significance in their discovery, because the entire group of acanthodians was believed to have gone extinct in the Early Permian (BENTON, 1993) but may now be considered to have survived to possibly swim within paddling distance of the PTB (MUTTER and RICHTER, 2007). Furthermore, shark teeth comparable to «*Protacrodus*» were only known from strata older than Permian (JAEKEL, 1925; GINTER, 2002).

The great majority of fish remains from the Middle-Late Palaeozoic of Brazil are to some extent unique, reminiscent of classic Palaeozoic fish assemblages and they do not directly relate to any known Early Triassic assemblages.

Actinopterygian (ray-finned fishes) teeth and scales are abundantly present in Brazilian Permian rocks, but in their majority, they cannot be assigned to a specific species at present. Nevertheless, this kind of remains, recovered from selected horizons, will still yield supplementary information to help interpret the palaeoenvironment.

By studying fish assemblages like the ones occurring in the State of São Paulo, as well as elsewhere in Brazil and in other parts of the Southern Hemisphere, we hope to be able to extract at first, qualitative «survival rates» of fishes across the PTB and later, place them into context with contemporaneous records of the Northern Hemisphere. This should produce a crisper picture of the severity of the conditions witnessed by the fish faunas around the PTB and should yield a more realistic extinction/survival scenario for some of these creatures across this Boundary in the Southern Hemisphere.

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