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GONDWANAN PERSPECTIVES: TRIASSIC ECOSYSTEMS. PALEOBIOLOGICAL ASPECTS AND THE CONTEXT OF RECOVERY FROM THE GREAT EXTINCTION

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TERATOLOGICALTRIASSIC PALYNOMORPHS

Aberrant miospores from the Ladinian Quebrada de los Fósiles Formation, Puesto Viejo Group, San Rafael Basin.

NEW LATE TRIASSIC NANNOFOSSILS FROM MENDOZA

Calcareous nannofossils from the Late Triassic Arroyo Malo Formation have global biostratigraphic implications.

FISH SCALES FROM TRIASSIC LACUSTRINE DEPOSITS

Macro- and micromorphological scale study of endemic actinopterygian family (Pseudobeaconiidae), Cuyana Basin.

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SOUTH AMERICAN TRIASSIC EXPOSURES have been well-known for several decades since the main regional maps of the continent were made by European geologists at the beginning of the 20th century. Triassic fossils have appeared almost since the early years of exploration. With time, they have shown to be particularly abundant and diverse, especially in some areas in the South of Brazil and the West of Argentina (Fig. 1). Triassic South American fossils, including vertebrates, invertebrates, and plants, are well-known worldwide. Particularly famous is an excellent extension of outcrops in to one region in Argentina, the Talampaya National Park and Ischigualasto Provincial Park in La Rioja and San Juan provinces. These are two huge, protected areas of the Triassic Ischigualasto-Villa Unión Basin that were nominated jointly from the 2005 as a Human Heritage site by UNESCO because of their extraordinary fossil and natural content (*e.g.*, Rogers *et al.*, 1993, 2001; Arcucci *et al.*, 2004; Martínez *et al.*, 2011, 2013; Césari & Colombi, 2016; Mancuso *et al.*, 2020, 2022; Pedernera *et al.*, 2020; Desojo *et al.*, 2020). Associated with the same rift system, the Marayes Basin host a very diverse biota that has recovered in recent years (*e.g.*, Spalletti *et al.*, 2011; Martínez *et al.*, 2015; Morel *et al.*, 2015). Other Triassic basins, like Cuyana Basin and San Rafael Block in Mendoza province, also offer extensive exposures of continental sediments at the foot of the Andes (*e.g.*, Marsicano & Barredo, 2004; Brea *et al.*, 2009; López-Arbarello *et al.*, 2010; Pedernera *et al.*, 2021a). All these Triassic outcrops are available to researchers to continue all sorts of geological and paleontological studies. Their colorful and scenic landscapes are enjoyed by tourists worldwide, attracted by their natural and scientific value.

During the Triassic Period (~252–201 million years ago), triggered fault systems in Western Gondwana produced deep rift valleys. After the end-Permian mass extinction, these basins hosted important continental ecosystems documenting the origin and early diversification of the Mesozoic biota in Gondwana. Gondwana is particularly useful for studies on land environments because it possesses many rich Triassic fossil assemblages preserved in sedimentary diverse non-marine strata that span most of the Triassic Period. South American basins are particularly well-studied, with abundant geochronological age constraints. The recent advances in radioisotopic dating and magnetostratigraphy supplied a new view of biostratigraphic schemes, which were imprecise because key index taxa present different first and last appearances across geographic space (*e.g.*, Rogers *et al.*, 1993; Ávila *et al.*, 2006; Spalletti *et al.*, 2008; Kent *et al.*, 2014; Ottone *et al.*, 2014; Marsicano *et al.*, 2016; Desojo *et al.*, 2020; Mancuso *et al.*, 2020; Colombi *et al.*, 2021). Therefore, new radioisotopic and magnetostratigraphic age constraints from fossiliferous sequences in South America have allowed the revision of absolute ages and relative correlation of key Gondwanan biota (Irmis *et al.*, 2022).

The Triassic in South America is crucial for the evolutionary history of several groups of vertebrates. It is widely known that, in this period in South America, the first representatives of several key groups of vertebrates (Fig. 2), like carnivore and herbivore basal dinosaurs and dinosauriforms are recorded, as well as some of the more ancient turtles

and crocodylomorphs (*e.g.*, Sereno *et al.*, 1993; Rougier *et al.*, 1995; Martínez *et al.*, 2011; Abdala *et al.*, 2020; Leardi *et al.*, 2020; Novas *et al.*, 2021; Marsicano *et al.*, 2022). It is also essential for mammal history because the more derived cynodonts and the closest ancestors to mammals are present in these units. On the other hand, it is also important for the evolution of plants. The *Dicroidium* flora (Fig. 2) is abundant and diverse in many sites and localities of Triassic basins (*e.g.*, Morel *et al.*, 2015; Bodnar *et al.*, 2020; Pedernera *et al.*, 2022). They were the first seed plants to appear. The palynomorphs at this level have a long history of studies during the 20th century, being the only way to assess possible ages and correlations between units (*e.g.*, Zavattieri & Batten, 1996). Although less known to the public, many groups of freshwater arthropods like ostracods and conchostracans (Spinicaudata) and insects (Fig. 2), both terrestrial and aquatic, are also very well represented by eloquent and abundant fossils sometimes for the first time in these levels and are the base of many recent studies on arthropod evolutionary history (*e.g.*, Gallego, 2010; Lara *et al.*, 2017, 2021). Ichnites have also been studied for a long time in these Triassic basins. Their presence supports paleobiological interpretations in geological units that do not preserve body fossils, allowing the record of "ghost paleofaunas" otherwise hidden (*e.g.*, Marsicano & Barredo, 2004; Marsicano *et al.*, 2004).

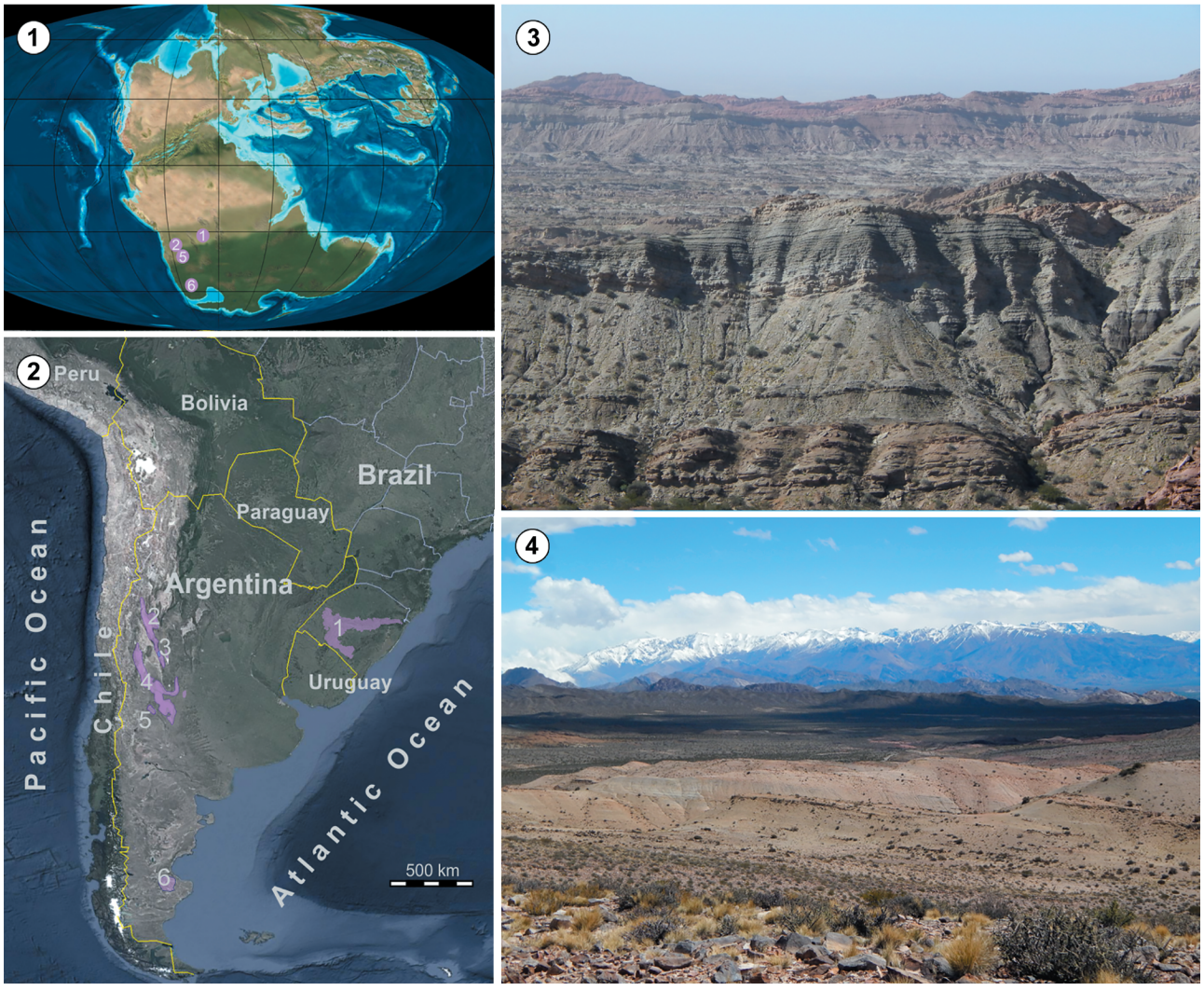

Figure 1. 1, Paleogeographic map for the Triassic (modified from https://deeptimemaps.com/), with the paleolatitudes location of the South American basins, with 95% confidence intervals (data from van Hinsbergen *et al.*, 2015). **2,** Location of South American Triassic basins. 1. Paraná Basin. 2. Ischigualasto-Villa Unión Basin. 3.Marayes-Carrizal Basin. 4. Cuyana Basin. 5. San Rafael Basin 6. El Tranquilo Basin. **3,** Panoramic photo of the Ischigualasto-Villa Unión Basin outcrops. **4,** Panoramic photo of the Cuyana Basin outcrops from the Paramillos subbasin.

After the early discoveries of F. von Huene in Brazil (*e.g.*, Huene, 1935) and decades later by A. Romer and J. Bonaparte in Argentina concerning vertebrates (*e.g.*, Romer 1966, 1970; Bonaparte, 1997), we witnessed during the last decades a significant acceleration of discoveries in many animal and plant groups. Also, new types of studies started developing, using new technology and theoretical frameworks. Today we found several groups of researchers in different regions and institutions of Argentina and Brazil actively working and producing new data on many aspects of Triassic paleofaunas and paleofloras, developing research in particular groups, in their phylogenetic relationships, detailed anatomy and paleobiology and trying to reconstruct Triassic paleoenvironments and paleoclimate. The recent flourishing of Triassic studies was in part promoted by the organization, at the turn of the century, of several scientific meetings called "*Reuniones del Triásico del Cono Sur*" by a group of celebrated Argentinian scholars such as L. A. Spalletti, R. Herbst, and A. Artabe (Fig. 3) that spread their enthusiasm for this geological period to many young paleontologists that are today leaders in these studies and help to edit the volume called "*El Sistema Triásico en la Argentina*" in 2001, published by the Fundación Museo de La Plata (Artabe *et al.*, 2001). At the same time, in 2002, P. N. Stipanicic and C. A. Marsicano (Fig. 3) edited the *Léxico Estratigráfico de la Argentina Volumen VIII* dedicated exclusively to the Triassic that clarified the nomenclature and stratigraphic status of many geological units (Stipanicic & Marsicano, 2002).

More than 10 years ago in the Congreso Argentino de Paleontología organized by the Asociación Paleontológica Argentina at La Plata in 2010, we proposed the first Symposium called *"Ecosistemas triasicos: su paleobiología y el contexto de recuperación de la gran extinción".* This meeting was a necessary update 10 years after the mentioned books. The result was that the symposium showed a lot of new possibilities in the Triassic studies and the necessity to assess the chronostratigraphic control of Triassic levels in South American basins. A second symposium was held in the same paleontological congress at General Roca, Rio Negro, in 2016. New localities in Argentina and new absolute ages were communicated for different Triassic basins. Finally, in 2021, after the global pandemic, the first virtual Congreso de la Asociación Paleontológica Argentina was organized. We proposed to continue communicating new and impor-

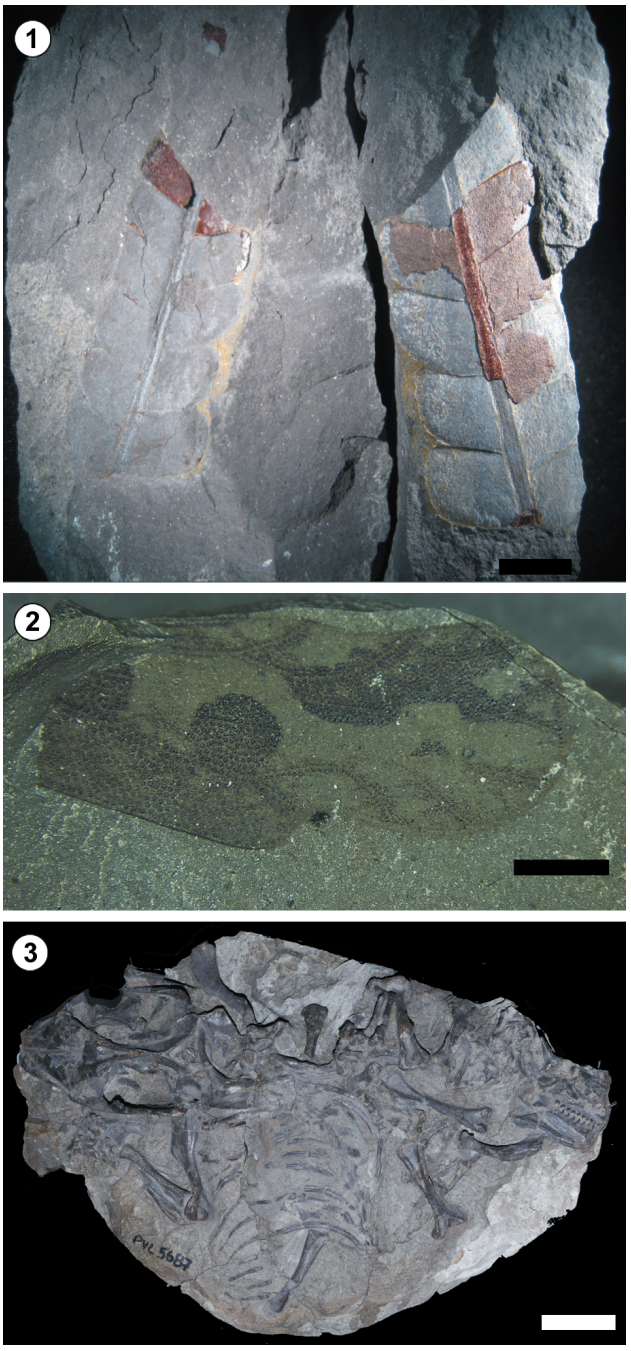

Figure 2. Examples of the Triassic biota. **1,** ***Zuberia fesimantellii*** (Johnston) Frenguelli (IANIGLA-PB-810, IANIGLA-PB-814) from the Cacheuta Formation (Cuyana Basin, Mendoza, Argentina). Pteridosperms (seed ferns), an extinct group of plants, more specifically to the Order Umkomasiales. This group of plants dominated the terrestrial ecosystems of Gondwana during the Triassic. Modified from Pedernera *et al.* (2021b). Scale bar, 1 cm. **2,** ***Dysmorphoptiloides losrastrosensis*** sp. nov. (Dysmorphoptilidae Handlirsch), holotype PULR-I N° 350a/b from the Los Rastros Formation (Ischigualasto-Villa Unión Basin, La Rioja Province, Argentina). Modified from Lara *et al.* (2021). Scale bar, 2 mm. **3,** ***Massetognathus pascuali*** is the most common tetrapod found in the Chañares Formation (Ischigualasto-Villa Unión Basin, La Rioja Province, Argentina). Modified from Mancuso *et al.* (2014). Scale bar, 4 cm.

tant scientific knowledge generated by new researchers contributing to the Triassic ecosystems and paleoenvironments. This volume is then the result of an invitation from editors of *Ameghiniana* to edit some of the contributions of this last symposium in the form of articles.

The four articles included in this volume show a wide range of subjects and reveal, in our opinion, the diversity of themes, tools, and techniques that researchers have nowadays to answer essential questions about Triassic ecosystems.

Pérez Panera *et al.* (this issue) significantly contributes to our knowledge of Upper Triassic nannofossils in the southern hemisphere, a type of fossil not addressed usually

Figure 3. Enthusiastic colleagues who promoted new works on the Triassic period of Argentina. **1,** Analia Artabe (Professor at Universidad Nacional de La Plata, Principal Investigator at CONICET) during a field trip at Mendoza Argentina. **2,** Rafael Herbst (1936-2017) (former Professor at Universidad Nacional del Nordeste, Investigator at CONICET) during VIII Congreso Argentino de Paleontología y Bioestratigrafía, Corrientes, Argentina. **3,** Luis A. Spalletti (Professor at Universidad Nacional de La Plata, Superior Investigator at CONICET) and Claudia A. Marsicano (Professor at Universidad Nacional de Buenos Aires, Principal Investigator at CONICET) during a field trip at Arroyo Lapa, Neuquen, Argentina. **4,** Claudia A. Marsicano (Professor at Universidad Nacional de Buenos Aires, Principal Investigator at CONICET) and Pedro Stipanicic (1921-2008) (former Investigator at CONICET) at the Asociación Geológica Argentina.

for this period. It includes a new biostratigraphic scheme for these Upper Triassic calcareous nannofossils, discussing their origin and geographic spreading.

Zavattieri and Gutierrez (this issue) present the first occurrence of synchronous teratologies across multiple plants and algal lineages within a single site coinciding with nearby repeated explosive volcanism. Moreover, they have shown how explosive volcanoes can directly cause developmental disturbances felt throughout entire plant communities in the deep past.

Giordano *et al.* (this issue) is a very attractive and valuable contribution dealing with the macro and microanatomy of scales of the endemic actinopterygian family Pseudobeaconiidae. They have taken a first step in an intriguing field, which could inspire future detailed work of the same kind.

Escobar *et al.* (this issue) provide new insights into the poorly known anatomy of the lower jaw in *Dinodontosaurus*, focusing on new and historical specimens from Argentina. The new material is very eloquent, representing the best material of *D. brevirostris* collected since the 1970s. A study with such detail gives attention to specific parts of the anatomy and considers its taxonomic and phylogenetic significance.

Until this point of this text, we present to the reader the past and present of the studies of the Triassic Period in South America, their paleontological and evolutionary importance, and their relevance for global research. Moreover, the local communities where these outcrops became tourist attractions of economic interest. However, no less important is the future of these studies. There are several poorly explored basins yet and many known fossiliferous sites rich enough to continue to visit and interpret in the following decades. Although scarce, even the marine Triassic localities still need to be revised. The interpretation of the climate and paleoenvironments where all these paleofauna and paleoflora developed is still in its preliminary stage; the geochronology is far to be concluded in the Triassic sequence and the correlation with Brazilian basins still needs to be clarified. We expect to encourage modestly with this special issue of Ameghiniana to explore and study by the new generations of paleontologists the incredible diversity of Triassic ecosystems.

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