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Lepidosaurs from Gondwana: An Introduction

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ABSTRACT.—**Lepidosaurian reptiles (squamates and rhynchocephalians) comprise one of the world's most diverse groups of tetrapods, with most of that diversity found in regions of the world that once formed the supercontinent of Gondwana. In this special section of the *Journal of Herpetology*, we present both review and original studies on the evolution of lepidosaurs from Gondwana. In this contribution, we provide a brief introduction to those studies and also present metadata collected from the Web of Science on the progress of the study of lepidosaurian evolution. The latter indicate a substantial increase of research interest in multiple aspects of lepidosaur evolution worldwide, with special increase for lepidosaurs from Gondwanan continents. We conclude by setting some of the main goals we hope to achieve in the study of lepidosaurs from Gondwana in the near future.**

RESUMO.—**Os lepidossauros (escamados e rincocéfalos) representam um dos grupos de tetrápodes mais diversos no mundo, com grande parte dessa diversidade ocorrendo em regiões do planeta que no passado formavam parte do supercontinente de Gonduana. Nessa seção especial do *Journal of Herpetology* são apresentados estudos originais e de revisão acerca da evolução dos lepidossauros em Gonduana. Na presente contribuição, é provida uma breve introdução a tais estudos e também apresentamos metadados obtidos através da Web of Science sobre o progresso recente no estudo da evolução dos lepidossauros. Estes últimos indicam um aumento substancial do interesse acadêmico sobre múltiplos aspectos da evolução desse grupo em todo o mundo, com especial aumento na pesquisa acerca dos lepidossauros em continentes de origem gonduânica. Por fim, indicamos novos objetivos e metas a serem atingidas no estudo dos lepidossauros de Gonduana no futuro próximo.**

Lepidosaurian reptiles comprise a substantial portion of extant terrestrial vertebrate life on Earth with more than 10,000 species of squamates, plus *Sphenodon* as the sole living taxon of the clade Rhynchocephalia (Uetz and Hošek, 2017). A large portion of this diversity occurs in parts of the world that once formed the southern supercontinent of Gondwana. During the Middle Jurassic (~175 million years ago), Gondwana started to break apart into multiple landmasses that eventually formed present-day South America, Africa, Madagascar, India, Antarctica, Oceania, the Arabian Peninsula, and other smaller additional portions of the Middle East (Smith et al., 1994; Blakey, 2008). Even when excluding areas that used to be part of peri-Gondwanan terranes during the Mesozoic, Gondwanan continents currently house about 60% of the world's species of lepidosaurs with over 6,100 species (Uetz and Hošek, 2017), including *Sphenodon punctatus* in New Zealand. This corresponds to 60% more species of lepidosaurs than currently found in Laurasian areas (~3,600 species); the difference may be even greater if southern Europe is counted as a peri-Gondwanan terrane (Blakey, 2008). Therefore, investigating the patterns and processes that molded the 230 million years of lepidosaurian evolution (Jones et al., 2013) and the $\geq$ 210 million years of lepidosaur evolution in Gondwana (Hsiou et al., 2015) is fundamental to a broad understanding of how the tremendous modern diversity came to exist.

Numerous lines of investigation have been explored to understand lepidosaurian evolution in Gondwana. Biogeographic and phylogenetic studies using extant organisms as a model allow multiple inferences of deep-time evolutionary patterns. They also benefit from larger sample sizes and the availability of molecular data. Complementary to this, studies that use fossil organisms or integrate them with extant taxa data have the benefit of having direct evidence of organismal morphology and distribution in deep time and space. In September 2015, to assess the major recent advances in the study of lepidosaurian evolution in Gondwana, we assembled a group of specialists from all parts of the world for the Second Lepidosaurs of Gondwana symposium during the Fifth Latin American Congress of Vertebrate Paleontology, in Colonia del Sacramento, Uruguay (Fig. 1). Numerous recent findings and broad reviews were presented during the meeting that took place 10 yr after the first Lepidosaur Symposium in Rio de Janeiro, Brazil. Some of those findings and additional others are presented as articles in the present issue, accompanied by additional contributions relevant to this topic.

Among the invited contributions presented in this volume are some review papers that amalgamate long term and also recent developments in the evolution of lepidosaurs in Gondwana. Among these, papers on the Mesozoic fossil record of lizards from Brazil (including the oldest known squamate species from South America) and the fossil record of snakes from Brazil provide valuable insights into early squamate evolution in Brazil and South America in general. Additionally, a study on the mosasaurs from Gondwana provides a broad view of the distribution and taxonomy of these aquatic lizards during the Late Cretaceous in the southern hemisphere. A final review includes the identification of the conspicuous tooth implantation patterns in the Rhynchocephalia ("tuataras"). Original contributions include a case study on the patterns of intraspecific osteological variation within the Australian agamid *Ctenophorus*, the morphological evolution of geckos from the southernmost areas of South America, a redescription of the extinct species *Callopistes bicuspidatus*, and a geometric morphometrics assessment of patterns of change in the morphospace of fossil lizards.

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FIG. 1. Participants of the Fifth Latin American Congress of Vertebrate Paleontology, in Colonia del Sacramento, Uruguay. From right to left: Sebastián Apesteguía (Argentina), Annie Schmaltz Hsiou (Brazil), Santiago Brizuela (Argentina), Hongyu Yi (China), Tiago R. Simões (Brazil), Dirley Y. Cortéz Parra (Colombia), Michael Caldwell (Canada), Fernando Garberoglio (Argentina), Randall L. Nydam (USA), Christopher J. Bell (USA), Juan D. Daza (Colombia), Nicholas Longrich (USA), Fábio Veiga (Brazil), Paulo Rosario Romo de Vivar Martínez (Mexico), John L. Pereira (Brazil), Luísa Menezes (Brazil), Núbia Galvez (Brazil). Not in the picture the elusive Reina Harding (USA) and Natalia Triviño (Argentina).

The amount of interest in this topic has been increasing worldwide in recent years and the volume of published research reflects the intensified interest on this topic. To quantitatively evaluate the changes in the volume of research on lepidosaurs from Gondwanan regions of the planet, we searched for scholarly articles in the Web of Science core database. We investigated the number of papers published during the 10 yr between the two meetings on lepidosaurs from Gondwana and the 10 yr preceding the first meeting. We looked for all published papers mentioning lepidosaurs (keywords: Lepidosauria, Squamata, Rhynchocephalia, *Sphenodon*, lizards, snakes, and amphisbaenians) carried out in the particular areas of our interest herein (Gondwanan vs. Laurasian regions) and mentioning keywords related to evolutionary research (e.g., evolution, biogeography, macroevolution, phylogeny, and fossils). We subsequently filtered the evolutionary research papers for those that focused on the study of fossil organisms, only to assess how many of those were produced with the aid of paleontological data.

The results (Table 1) indicate general studies on the evolution of lepidosaurs in Gondwana dramatically increased between 2006 and 2015 compared to the preceding 10 yr. Although evolutionary studies on lepidosaurs from Laurasian regions increased by 298%, there was an increase of 340% on lepidosaurs from Gondwana. Of these, there was an increase of 432% of research papers on lepidosaurs that used or mentioned fossil specimens from Gondwana between 2006 and 2015 compared to the 10 previous years, whereas there was an increase of 312% of equivalent papers from Laurasian regions. Therefore, there was a substantial increase in the study of lepidosaurs worldwide (mostly on squamates) between 2006 and 2015, marked mostly by an increase in the study on lepidosaurs from Gondwanan regions. This increase was even more substantial in studies using fossil lepidosaurs from Gondwana.

Among potential factors explaining these increases in published work were the global spread of the internet and online resources that sped up publication times and access to literature (Clack, 2012) and also facilitated collaborative work. On top of that was an increase in the number of research laboratories and graduate students in countries from the Southern Hemisphere since 2000. India and Australia are among some of the countries with the largest increase in the number of PhD students since 1998 (Cyranoski et al., 2011). Although South American countries, in general, did not see an equivalent overall increase in the number of PhD students during the same time frame, some particular areas of research benefited from an increase in the number of students and funds. For instance, there was a substantial increase of government funds, students, and published papers in paleontology in Brazil and Argentina between 2000 and 2015 (Fernández et al. 2014; Kellner, 2015) that contributed to an increase in the known number of fossil organisms (including deep-time studies on lepidosaurs) from South America.

We expect and hope the next 10 yr will be as increasingly productive as was the last decade on the study of lepidosaurs, not just from Gondwanan regions but worldwide. In fact, given the recent trend, we likely will need to host a meeting of researchers focused on lepidosaurs from Gondwana more frequently than every 10 yr. We also hope future meetings may integrate paleontologists and neontologists to boost the exchange of ideas and methods between these areas and to achieve the greater goal of a holistic understanding of lepidosaur evolution. Such integration occurred during the 7th World Congress of Herpetology in Vancouver, Canada, and contributed to a greater exchange of ideas and collaborations between paleo- and neo-herpetologists (Gardner and Nydam, 2013; Jones and Pearson, 2013; Daza, 2014). Although the benefits of integrating data from fossils and extant taxa are not new to the study of lepidosaurs, there could be substantial improvements on the exchange of ideas and integration of research programs. Finally, our major research goals for the next 10 yr include: 1) reducing the major sampling gap in the fossil record of lizards between Laurasia and Gondwana (Evans, 2003; Gardner and Nydam, 2013; Simões et al., 2015); 2) expanding the knowledge of madstoid snakes and their role in early snake evolution; and 3) providing greater integration of recent methodological advances toward the study of large-scale evolutionary patterns in lepidosaurs (e.g., phylogenetic comparative methods, finite element analyses), as already performed for other vertebrates, such as mammals and birds.

TABLE 1. Record of studies on lepidosaurian reptiles extracted from the Web of Science database.

	[a]Le+La	Le+La+Evo	Le+La+Pal	Le+Go	Le+Go+Evo	Le+Go+Pal
1995–2005	1,083	300	51	1,131	301	28
2006–2015	2,458	893	159	2,653	1,025	121

[a] Le+La = Studies on lepidosaurs from Laurasian derived regions; Le+Go = studies on lepidosaurs from Gondwanan derived regions; Pal = studies focused on fossils; Evo = studies focused on multiple areas of evolutionary biology.

Literature Cited

Blakey, R. C. 2008. Gondwana paleogeography from assembly to breakup—A 500 m.y. odyssey. Geological Society of America Special Papers 441:1–28.

Clack, J. A. 2012. Gaining Ground: The Origin and Evolution of Tetrapods. Indiana University Press, USA.

Cyranoski, D., N. Gilbert, H. Ledford, A. Nayar, and M. Yahia. 2011. The PhD factory. Nature News 472:276–279.

Daza, J. D. 2014. What's so special about squamates? Anatomical Record 297:341–343.

Evans, S. E. 2003. At the feet of the dinosaurs: the early history and radiation of lizards. Biological Reviews 78:513–551.

Fernández, D. E., L. Luci, C. S. Cataldo, and D. E. Pérez. 2014. Paleontology in Argentina: history, heritage, funding, and education from a southern perspective. Palaeontologia Electronica 17.3.6E:1–18.

Gardner, J. D., and R. L. Nydam. 2013. Mesozoic and Cenozoic lissamphibian and squamate assemblages of Laurasia—introduction to the special issue. Palaeobiodiversity and Palaeoenvironments 93: 391–395.

Hsiou, A. S., M. A. G. De França, and J. Ferigolo. 2015. New data on the Clevosaurus (Sphenodontia: Clevosauridae) from the Upper Triassic of southern Brazil. PLoS ONE 10:e0137523.

Jones, M. E., C. L. Anderson, C. A. Hipsley, J. Müller, S. E. Evans, and R. R. Schoch. 2013. Integration of molecules and new fossils supports a Triassic origin for Lepidosauria (lizards, snakes, and tuatara). BMC Evolutionary Biology 13. Available online: 10.1186/1471-2148-1113-1208.

Jones, M. E. H., and M. Pearson. 2013. 7th World Congress of Herpetology (meeting report). Palaeontological Association Newsletter 83:64–68.

Kellner, A. W. A. 2015. Apresentação: para onde caminha a paleontologia brasileira? Ciência e Cultura 67:20–24.

Simões, T. R., E. Wilner, M. W. Caldwell, L. C. Weinschütz, and A. W. A. Kellner. 2015. A stem acrodontan lizard in the Cretaceous of Brazil revises early lizard evolution in Gondwana. Nature Communications 6. doi: 10.1038/ncomms9149.

Smith, A. G., D. G. Smith, and B. M. Funnell. 1994. Atlas of Mesozoic and Cenozoic Coastlines. Cambridge University Press, England.

Uetz, P., and J. Hošek. 2017. The reptile database [Internet]. Available from: http://www.reptile-database.org. Accessed 3 March 2017.

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