Anatomy, phylogeny and palaeobiology of early archosaurs and their kin

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Archosauria include two extant clades, crocodylians and avians. However, the diversification of the avian and crocodylian crown groups are relatively recent events that began during the Late Cretaceous (Brochu 2001, 2003; Clarke *et al.* 2005), less than 100 Ma ago. These crown diversifications are shallow in time compared to the much deeper divergence of the crocodylian and avian stem lineages in the Triassic, approximately 250 Ma ago (Butler *et al.* 2011; Nesbitt 2011; Nesbitt *et al.* 2011). The early archosaurian diversification began in the wake of the devastating end-Permian mass extinction, and the divergence of both lineages and disparate body forms was rapid, occurring less than 10 Ma after the first archosaur (Nesbitt *et al.* 2010). This initial diversification was severely affected by the end-Triassic mass extinction approximately 50 Ma later, and only three major archosaur clades – pterosaurs, dinosaurs and crocodylomorphs – survived to diversify during the rest of the Mesozoic.

Since the cladistic revolution first affected studies of archosaur phylogeny nearly 30 years ago (e.g. Benton 1985; Clark 1986; Gauthier 1986; Sereno 1986; Benton & Clark 1988), many workers attempted to elucidate the early evolutionary history of archosaurs during the late 1980s and early 1990s (e.g. Benton & Clark 1988; Sereno 1991; Parrish 1993; Juul 1994). Whereas the pace of phylogenetic study for pterosaurs, dinosaurs and crocodylomorphs continued unabated through to the present day, early archosaur work reached little consensus (Gower & Wilkinson 1996), and novel phylogenetic datasets attempting to resolve the interrelationships of the major early clades were comparatively rare after the mid-1990s. Nonetheless, discoveries of new taxa and specimens continued throughout the 1990s and 2000s.

With these new discoveries, interest in the evolutionary history of early archosaurs and their close relatives has accelerated in the past 10 years, as evidenced by the vast number of recent studies concentrating on these diapsid reptiles. Since 2000, a minimum of 48 new taxa of early archosauriforms (Table 1) has been named, and nearly all of these are Triassic in age. The combination of the discovery of new species in existing collections and the re-evaluation of previously described specimens has had a major impact on our understanding of the evolutionary history of these groups.

Yet, the accelerated pace of discovery and disparate worldwide locations of these new fossils, as well as early archosaur researchers themselves, has impeded consensus in the field. Therefore, in September 2011, two of the co-editors (S.J. Nesbitt and J.B. Desojo) convened the first symposium of early archosaur evolution at the IV Congreso Latinoamericano de Paleontología de Vertebrados in San Juan, Argentina. It focused on recent advances in the study of early archosaurs and their relatives in order to coalesce researchers from across the globe to present, discuss and synthesize current research on early archosauriform evolution. During that meeting, researchers from Poland, Russia, Brazil, Germany, China, the USA, Argentina and the UK (Table 2) gave 30 presentations over 2 days addressing new and redescribed specimens, new phylogenetic hypotheses, functional morphology and macroevolutionary patterns.

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Table 1. *New taxa of early archosauriforms described since 2000*

Non-archosaurian archosauriforms
Archeopelta arborensis Desojo *et al.* (2011)
Chanaresuchus ischigualastensis Trotteyn *et al.* (2012)
Koilamasuchus gonzalezdiazi Ezcurra *et al.* (2010)
Osmolskina czatkowicensis Borsuk-Białynicka & Evans (2003)
Yonghesuchus sangbiensis Wu *et al.* (2001)
Doswellia sixmilensis Heckert *et al.* (2012)
Phytosaurs
Mystriosuchus westphali Hungerbühler & Hunt (2000)
Nicrosaurus meyeri Hungerbühler & Hunt (2000)
Machaeroprosopus jablonskiae Parker & Irmis (2006)
Pravusuchus hortus Stocker (2010)
Protome batalaria Stocker (2012)
Aetosaurs
Apachesuchus heckerti Spielmann & Lucas (2012)
Adamanasuchus eisenhardtae Lucas *et al.* (2007)
Aetobarbakinoides brasiliensis Desojo *et al.* (2012)
Desmatosuchus smalli Parker (2005)
Redondasuchus rineharti Spielmann *et al.* (2006)
Rioarribosuchus chamaensis Lucas *et al.* (2006)
Sierritasuchus macalpini Parker *et al.* (2008)
Stagonolepis olenkae Sulej (2010)
Stenomyti huangae Small & Martz (2013)
Tecovasuchus chatterjeei Martz & Small (2006)
Typothorax antiquum Lucas *et al.* (2002)
'Rauisuchians'
Arganasuchus dutuiti Jalil & Peyer (2007)
Bystrowisuchus flerovi Sennikov (2012)
Decuriasuchus quartacolonia França *et al.* (2011)
Diandongosuchus fuyuanensis Li *et al.* (2012)
Effigia okeeffeae Nesbitt & Norell (2006)
Hypselorhachis mirabilis Butler *et al.* (2009)
Polonosuchus silesiacus Sulej (2005)
Postosuchus alisonae Peyer *et al.* (2008)
Qianosuchus mixtus Li *et al.* (2006)
Yarasuchus deccanensis Sen (2005)
Non-crocodyliform crocodylomorphs
Dromicosuchus grallator Sues *et al.* (2003)
Junggarsuchus sloani Clark *et al.* (2004)
Kayentasuchus walkeri Clark & Sues (2002)
Litargosuchus leptorhynchus Clark & Sues (2002)
Phyllodontosuchus lufengensis Harris *et al.* (2000)
Redondavenator quayi Nesbitt *et al.* (2005)
Triassic pterosaurs
Austridactylus cristatus Dalla Vecchia *et al.* (2002)
Caviramus schesaplanensis Fröbisch & Fröbisch (2006)
Eudimorphodon cromptonellus Jenkins *et al.* (2001)
Raeticodactylus filisurensis Stecher (2008)
Non-dinosaurian dinosauromorphs
Agnosphitys cromhallensis Fraser *et al.* (2002)
Asilisaurus kongwe Nesbitt *et al.* (2010)
Diodorus scytobrachion Kammerer *et al.* (2012)
Dromomeron gregorii Nesbitt *et al.* (2009)
Dromomeron romeri Irmis *et al.* (2007)
Sacisaurus agudoensis Ferigolo & Langer (2007)
Silesaurus opolensis Dzik (2003)

Table 2. *List of the Participants of the Early Archosaurs and Their Kin Symposium 2011*

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The current Special Publication arose from this symposium, containing synthetic reviews of the major early archosauriform clades, along with additional contributions of new research on a variety of topics. The 11 syntheses cover most of Triassic archosauriform diversity, and these summaries provide the most up-to-date information on each clade provided by experts currently studying these groups. In each of these chapters, authors provide a consensus view of the evolutionary importance of the clade, phylogenetic definition(s), its fossil record both in time and space, a brief description of the anatomy, the most up-to-date hypotheses of phylogenetic relationships (within the group and among other archosauriforms), available palaeobiological inferences and future perspectives. What is particularly noticeable among all these summaries is the renewed attention to resolving early archosauriform and archosaur phylogeny.

The remaining contributions reflect the diversity of new work on the early archosauriform fossil record. Large advances in our understanding of the evolution of early archosauriforms have been gained by new fieldwork and the re-analysis of previously collected specimens. These discoveries are reflected in the wealth of new anatomical data presented here (e.g. *Prestosuchus* braincase, **Mastrantonio *et al.* 2013**; Brazilian *Chanaresuchus*, **Raugust *et al.* 2013**; *Decuriasuchus* skull, **De França *et al*. 2013**; new Colorado aetosaur, **Small & Martz 2013**; *Postosuchus* postcrania, **Weinbaum 2013**; new *Poposaurus* cranial material, **Parker & Nesbitt 2013**; and *Sacisaurus* full description, **Langer & Ferigolo 2013**), particularly with respect to a blossoming of South American work. These data, in turn, help to provide new information that advance phylogenetic hypotheses (Early–Middle Triassic tracks, **Niedźwiedzki *et al.* 2013**; new *Poposaurus* cranial material, **Parker & Nesbitt 2013**; and *Sacisaurus* full description, **Langer & Ferigolo 2013**). With all the focus on new taxa and their phylogenetic implications, higher-order palaeobiological study of early archosauriforms has not always kept pace but new work is remedying this situation. Emerging insights into functional morphology (mandibular joint evolution, **Holliday & Nesbitt 2013**; *Prestosuchus* leg muscles, **Liparini *et al.* 2013**), growth and ontogeny (new Colorado aetosaur, **Small & Martz 2013**; aetosaur osteoderm histology, **Taborda *et al.* 2013**), and macroevolutionary patterns (body size evolution, **Turner & Nesbitt 2013**) are enriching our understanding of this Triassic radiation.

The dramatic recent increase in our knowledge of early archosaurs and their relatives has advanced what major research questions we can ask. Fortunately, the number and geographical distribution of early archosaur researchers has expanded, especially among early-career scientists. As a community, we are revisiting the alpha taxonomy and osteology of older nominal taxa using apomorphy-based identifications in order to avoid chimeric holotypes (a problem in previous taxonomic studies that mixed 'rauisuchian' with dinosaur material, and aetosaur with phytosaur material) and the potential circularity of conflating stratigraphical/geographical attribution with appropriate morphologically-based diagnoses. At the same time, new fieldwork globally has targeted areas that have the potential to fill in gaps in our understanding of archosaur phylogeny and palaeobiology. Morphological studies are taking into consideration the ongoing need to revise and discover additional characters using new types of data (e.g. functional, histological) for use in future systematic analyses. Similarly, technological advances have played their part, from the use of digital photography and 3D surface imaging to greatly enhance the speed and accuracy of recording information on specimens that are too numerous and large to be loaned between national and international collections, to the application of computed tomography to non-destructively examine internal structures of bones. These approaches have ultimately led to advances in understanding the palaeobiology of the early relatives of archosaurs. For example, our understanding of early archosaur locomotion, diet, ontogeny and behaviour have all improved.

One of the important accomplishments of this synthesis is that most of the specialists of the world achieved a sufficient consensus to write several overviews of early archosaurs on the present book, given the diversity of opinion, language and culture. Therefore, this Special Publication serves as a true synoptic 'state-of-the-art' view of our understanding of early archosaurs and their relatives. We hope it serves as a benchmark for current knowledge and highlights future research avenues.

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