

“Mesozoic and Cenozoic lissamphibian and squamate assemblages of Laurasia”—introduction to the special issue

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Lissamphibia (frogs, salamanders, caecilians, and albanerpetontids) and Squamata (lizards, snakes, and amphisbaenians) have been persistent components of many non-marine ecosystems on Earth since the early part of the Mesozoic. Both clades have extant and fossil occurrences on every modern continent, except Antarctica. The three Northern Hemisphere continents of Europe, Asia, and North America, which owe their origins largely to the mid-Mesozoic break-up of the former supercontinent Laurasia, have yielded the lion's share of fossils for both groups. Consequently, the Laurasian fossil record has been critical for shaping our ideas about the diversities and evolutionary histories of lissamphibians and squamates.

The earliest collections and descriptions of fossil lissamphibians and squamates from the former Laurasian continents date back to the early 1800s in Europe, followed decades later by discoveries in North America (western USA) in the 1870s and in Asia (Mongolia) in the 1920s (e.g. see historical summaries by Caldwell 2007; Estes 1981, 1983; Sanchiz 1998). Until the middle part of the twentieth century, descriptive work on fossil lissamphibians and squamates tended to focus on articulated skeletons, such as those of Oligo–Miocene anurans from Central Europe (e.g. von Meyer 1860; Wolterstorff 1885) and of Early Cretaceous

lizards and of what is now regarded as an albanerpetontid from Italy (e.g. Costa 1864). Although generally of less interest, isolated and articulated bones recovered by quarrying, surface collecting, or dry screening also merited some attention; to cite two examples, a mandible from the late Oligocene of France became the holotype of the earliest named fossil lizard, *Dracaenosaurus crozeti* Gervais 1848–1852, and the dozen or so fossil lissamphibians and squamates named by Cope and Marsh in the late 1800s from the Late Jurassic and latest Cretaceous of the western USA were described on isolated bones (e.g. Cope 1876; Marsh 1872, 1887, 1892). Even after more than a century of work, by the middle part of the twentieth century our understanding of fossil lissamphibians and squamates was limited to a small number of taxa known mostly from Europe and western North America, and largely from the Cenozoic. Aside from scattered and intriguing Mesozoic occurrences, little was known about either group from that era and much of the entire Asian fossil record remained a blank.

Two developments in the latter part of the twentieth century dramatically improved our access to the lissamphibian and squamate fossil records. The first development was the widespread adoption in the 1950s of screen washing (McKenna 1962) as a method to bulk process fossiliferous matrix by washing it through fine screens in order to recover small bones, teeth, and scales preserved in the rock. Screen washing was pioneered by palaeomammalogists and is still widely used by them as a way to recover mammalian teeth and jaws, particularly from fossil localities that are not suitable for hand quarrying and as a way to salvage fossils from the rubble left behind after quarrying. The “by-catch” of non-mammalian fossils caught in the screens often includes jaws, vertebrae, and other bones of lissamphibians and squamates. Estes' (1964) monograph, “Fossil vertebrates from the Late Cretaceous Lance Formation, eastern Wyoming” demonstrated that screen washing could provide large enough samples to

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enable the small-bodied component of fossil vertebrate ecosystems to be documented and interpreted in more detail than had previously been possible. Among the approximately 75 vertebrate species that Estes (1964) recognised, there were 8 species of lissamphibians and 15 species of squamates, with about one-third of those being new. Screen washing continues to be an important way to amass large samples of small vertebrate fossils and, in regions like western North America, it has been responsible for the vast majority of lissamphibian and squamate fossils collected and described from there since the 1960s. The other significant development has been fieldwork programs that have targeted poorly sampled stratigraphic intervals, geographic regions, or both. Notable findings stemming from such fieldwork in the Northern Hemisphere over the past few decades include: (1) dramatically improved samples of lissamphibians and squamates of Cenomanian–Santonian age in western North America (e.g. see reviews by Gardner and DeMar 2013, this issue; Nydam 2013a [this issue], 2013b) and the first records of Late Cretaceous lissamphibians and squamates in the eastern USA (e.g. Crane 2011; Denton and O’Neill 1998); (2) discoveries of diverse lissamphibian and squamate assemblages in microsites of Late Cretaceous age in Uzbekistan and neighboring Asian countries (e.g. Nessov 1981, 1988; Roček and Nessov 1993; Skutschas 2013, this issue) and in Western and Central Europe (e.g. Folie and Codrea 2005; Rage 2013, this issue; Szentesi et al. 2013; Vasile et al. 2013); (3) discoveries of well-preserved lissamphibian and squamate body fossils of Late Jurassic–Early Cretaceous age in China (e.g. Chang et al. 2003; Evans et al. 2007; Gao et al. 2013; Wang et al. 2010) and of Early Cretaceous age in Spain (e.g. Báez 2013; Báez and Sanchiz 2007; Evans and Barbadillo 1998; Evans and Milner 1996); and (4) discoveries of lizards, frogs, and salamanders of Early Cretaceous age in Japan (e.g. Evans and Manabe 2008; Evans et al. 1998, 2006).

Over the past few decades, there has been a substantial increase in the number of fossil localities and specimens, improved stratigraphic and geographic sampling, and the recognition of numerous new taxa (not all formally named) of fossil lissamphibians and squamates in the Northern Hemisphere. Similar progress has also been made in the Southern Hemisphere, but for a variety of reasons (e.g. less research focus, geopolitical instability, more limited exposures of sedimentary rocks of appropriate age and depositional environments, transportation challenges), there the results have been more modest. Nevertheless, the former Gondwanan continents clearly preserve significant lissamphibian and squamate fossils, including some intriguing occurrences for both clades, such as: a moderately diverse assemblage of neobatrachian anurans in the Early Cretaceous of Brazil (Báez et al. 2009); Late Cretaceous putative salamanders in Africa and South America (Evans et al. 1996; Martill et al. 2013; Rage et al. 1993); and a surprisingly diverse snake assemblage of reportedly early Late

Cretaceous age in Sudan (Werner and Rage 1994). We can expect the Gondwanan lissamphibian and squamate records to improve as fieldwork and research continues in the Southern Hemisphere and, consequently, to provide new perspectives into the evolutionary histories of both clades.

The continued importance of the Northern Hemisphere as our primary source of direct information about the fossil record, past diversities, and evolutionary histories of lissamphibians and squamates was evident during the “Insights from the Fossil Record into the Evolution of Extant Amphibians and Reptiles” symposium during the Seventh World Congress of Herpetology held in August 2012 in Vancouver, Canada. During that symposium, about 20 scientists presented talks and posters focused on particular taxonomic groups, often with emphasis on fossil records from certain times and geographic regions (Fig. 1).

Although an early proposal to produce a comprehensive symposium volume was met with almost universal silence, there was enough interest from a minority of participants and some colleagues who were unable to attend the Congress to proceed with two collections of more thematically-focused papers, both scheduled to be published in late 2013. One of those, “Recent Advances in Morphology and Evolution of Living and Extinct Squamates” contains 14 papers and will appear as an upcoming special issue edited by Daza and Miller (in press) of *The Anatomical Record*. The other collection is this one—“Mesozoic and Cenozoic Lissamphibian and Squamate Assemblages of Laurasia”—and features five papers by six authors. Our original intention with this issue was to have a collection of papers that thoroughly covered the Mesozoic and Cenozoic lissamphibian and squamate records for all of Europe, Asia, and North America. As often happens with these kinds of edited collections, the comprehensive taxonomic, temporal, and geographic coverage that we had hoped for was not fully realised. Obvious gaps in the collection of papers presented here are: no coverage post-Palaeocene for lissamphibians or squamates in North America; no salamander or albanerpetontid coverage for Europe; and no coverage for Asian squamates or for salamanders and albanerpetontids from that continent outside of Siberia, Kazakhstan, and Middle Asia. Despite these limitations, the collection of papers constituting this Special Issue provides up-to-date reviews and, in some cases, preliminary and previously unpublished information on the remaining portions of the lissamphibian and squamate records in the Northern Hemisphere. These papers complement and update earlier treatments that are more global in coverage (i.e. anurans by Sanchiz 1998; non-anuran lissamphibians by Estes 1981; albanerpetontids by Gardner and Böhme 2008; lizards and amphisbaenians by Estes 1983; snakes by Rage 1984) and those that are more geographically and/or temporally constrained (e.g. North American Mesozoic and Tertiary snakes, anurans, and salamanders and albanerpetontids by Holman 2000, 2003, 2006, respectively;



Fig. 1 Most of the key participants of the “Insights from the Fossil Record into the Evolution of Extant Amphibians and Reptiles” symposium, held during the Seventh World Congress of Herpetology, August 2012 in Vancouver, Canada. *Back row* (left to right): Dave DeMar Jr., Pavel Skutschas, and Krister Smith. *Middle row* (left to right): Randall

Nydam, Jim Gardner, Michael Caldwell, Christopher Brochu, and Walter Joyce. *Front row* (left to right): Susan Evans, Jason Anderson, Marc Jones, Johannes Müller, Alessandro Palci, and Yuan Wang. Missing from the photo is the elusive Juan Daza. Photo by Dong Liping and courtesy of Pavel Skutschas

Chinese Mesozoic and Tertiary lissamphibians and squamates by Wang et al. 2008 and Wang and Li 2008, respectively; Mesozoic lissamphibians from Mongolia and the Central Asiatic Republics by Shishkin 2000; Cretaceous lizards from Mongolia by Alifanov 2000; and Jurassic and Early Cretaceous lizards and amphisbaenians worldwide by Evans 2003). Our expectation is that the wealth of information compiled and the ideas presented in the five papers constituting this Special Issue will serve as a foundation for future work on the fossil records and evolutionary histories of lissamphibians and squamates, both in the Northern Hemisphere and globally.

Roček (2013, this issue) draws on his career-long experience studying fossil and extant anurans to provide an updated account of Mesozoic and Tertiary anurans from Europe, Asia (including India, which prior to its collision in the Late Cretaceous was part of the former Gondwanan landmass), and North America. The first part of his paper briefly summarises the most notable discoveries and taxa, whereas the latter part is an encyclopedic-style set of concise taxonomic accounts. His paper builds on similar, but now somewhat outdated, treatments for anurans by Sanchiz (1998), Roček (2000), and Roček and Rage (2000). (*Palaeobio Palaeoenv* 93(4). Doi: [10.1007/s12549-013-0131-y](https://doi.org/10.1007/s12549-013-0131-y)).

Skutschas (2013, this issue) provides an informative and up-to-date summary of the Mesozoic salamander and albanerpetontid record from Siberia, Kazakhstan, and

Middle Asia (i.e. Kyrgyzstan, Tajikistan, Turkmenistan, and Uzbekistan) based on work by others and his ongoing research program to collect and describe lissamphibian fossils and taxa from the former USSR. His paper is especially useful for compiling a wealth of previously published information (much of which was in Russian) and new findings, and for placing the relevant fossils and taxa into stratigraphic and geographic context. Although somewhat overshadowed by the spectacular body fossils emerging from the Jehol Biota and similar deposits in China (e.g. Gao et al. 2013; Wang 2004), the more western and northern portions of the Asian Mesozoic salamander record are notable for containing a number of Jurassic age stem salamanders and for having Cretaceous crown salamander assemblages that, although comparable in age and depositional setting to those from the North American Western Interior, are dissimilar in their taxonomic compositions. For reasons unknown, albanerpetontids are virtually unknown from the Late Cretaceous of Asia (where they are documented by just half dozen bones from the Late Cretaceous of Uzbekistan), whereas they are abundantly represented in deposits of comparable age in Europe and North America. (*Palaeobio Palaeoenv* 93(4). Doi: [10.1007/s12549-013-0126-8](https://doi.org/10.1007/s12549-013-0126-8)).

Gardner and DeMar (2013, this issue) present a comprehensive chronological review of North American Mesozoic and Palaeocene lissamphibian assemblages, based on

published and unpublished occurrences from over 60 geological formations. Their review is complemented by locality maps and time scales showing the geographic and stratigraphic distributions of localities and by faunal lists in which the relative reliability of taxonomic identifications are reported. A series of on-line appendices provide detailed information (e.g. citations and specimen numbers) and justifications for the taxonomic identifications included in their faunal lists. Using the occurrence data compiled for their paper, the authors present the first species richness curve for Mesozoic and Palaeocene lissamphibians restricted to North America. Not surprisingly, the peaks and troughs in that curve closely match the amount of research focus that has been expended on fossils and taxa from the different time intervals. (*Palaeobio Palaeoenv* 93(4). Doi: [10.1007/s12549-013-0130-z](https://doi.org/10.1007/s12549-013-0130-z)).

Rage (2013, this issue) brings decades of firsthand experience to his review of Mesozoic and Cenozoic squamates from Europe. The European continent is blessed with an extensive and well-studied squamate record, much of which Rage has helped document. As such, he is able to provide an authoritative, yet highly readable, chronological account of the evolutionary and palaeobiogeographic histories for European fossil squamates. He also discusses how squamate groups reacted to various environmental stresses through time, such as the terminal Cretaceous extinction and climatic changes during the Cenozoic. (*Palaeobio Palaeoenv* 93(4). Doi: [10.1007/s12549-013-0124-x](https://doi.org/10.1007/s12549-013-0124-x)).

Nydam (2013a, this issue) presents an overview of the distribution and diversity of North American squamates from the Late Jurassic through the early–mid-Palaeocene, based on published accounts and new, largely unpublished findings.¹ Distributional patterns of major groups of squamates are illustrated using a series of locality maps and time scales. Much of this work is a summary of his nearly two decades' worth of investigation into the North American squamate fauna, its changes over time, and palaeobiogeographical patterns. (*Palaeobio Palaeoenv* 93(4). Doi: [10.1007/s12549-013-0129-5](https://doi.org/10.1007/s12549-013-0129-5))

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memento of that symposium. Finally, we thank Peter Königshof and Sinje Weber for supporting our proposal to publish this collection of papers as a Special Issue of *Palaeobiodiversity and Palaeoenvironments* and for their help in all subsequent phases of this project.

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¹ Due to uncertainties in the nearly simultaneous publication dates Nydam (2013a, this issue) left unnamed many of the “new taxa” that are presented in Nydam (2013b).

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