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The Origin of *Varanus*: When Fossils, Morphology, and Molecules Alone Are Never Enough

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Abstract: One of the many interesting questions in evolutionary studies of varanid lizards is the origin of the genus *Varanus*. The fossil record indicates the earliest emergence of this genus on Gondwana, although the remains of early varanid lizards have been discovered in Laurasia. The relationships among extant *Varanus* can generally be inferred using molecular phylogenetic techniques, although several attempts to generate a phylogeny of *Varanus* have used morphological characters. We identify two key-regions of global dispersal for varanid lizards that may be used to test hypotheses on the origin of this genus in a phylogeographic framework. The landmass currently connecting Africa and Asia as well as the Lesser Sunda Islands in southern Wallacea may have facilitated intercontinental radiation of varanid lizards, which are distributed in Africa, Asia, and Australia. We consider that an integrated approach such as phylogeography might better explain the origin of this charismatic lizard group than any single analytical method.

Introduction

Current views on the evolution of varanids oppose a Gondwanan to a Laurasian origin. On one hand, the lineages of varanid lizards were thought to have diversified in Australia, a fragment of Gondwana, and dispersed through Southeast Asia to their current distribution. On the other hand, varanids were thought by others to have originated in Asia, a fragment of Laurasia, and dispersed to Australia via the Indonesian Archipelago. Here we review morphological and molecular studies and propose two key routes for inter-continental dispersal. Present land connection between Asia and Africa as well as the Lesser Sunda Islands are two critical regions for deducing the origins of global varanid radiation. In spite of resolved phylogenetic relationships among almost

all extant varanid species, an approach describing the pattern of lineage distribution over geographic space is still needed to deduce the dispersals of extant species.

Two prevailing scenarios on the origin and radiation of varanid lizards are hypothesized based upon two different bases. A Gondwanan hypothesis is based on species diversity, whereas a Laurasian hypothesis is based on the fossil record. We review these two hypotheses by taking into account selected published phylogenetic studies based on morphological and molecular datasets and discuss them in light of paleontological data. The two scenarios for the origin of *Varanus* are presented below.

Laurasian origin: central Asia

Based on the fossil record, Estes (1983) postulated a radiation of varanid lizards from an ancestral source in Asia. Having radiated from what is now Mongolia during the Late Cretaceous to Early Cenozoic (80-50 Ma), early varanid lizards dispersed to almost all major fragments of Laurasia and Gondwana, including North America, Europe, Africa, and Australia. Extant Asian varanids are descendants of the Mongolian lineages, while those that dispersed to North America and Europe (30-45 Ma, Oligocene-Eocene) are now extinct. So far, we know from fossils that modern varanids reached some Gondwanan fragments i.e., Africa, India, and Australia, and might have failed to reach others i.e., Antarctica, Madagascar, and South America. To date, no fossil monitor lizards have been found in South America or Madagascar. The absence of varanids in South America is presumably due to the disappearance of connections between Africa and South America about 100 Ma. Varanids seem to be also lacking in Madagascar, probably because this island has been separated from Africa since about 155 Ma (Rabinowitz *et al.*, 1983; Torsvik *et al.*, 1998; Wells, 2003; Ali & Aitchison, 2008). Similarly, no fossil varanid has been reported from Antarctica. This view of Laurasian origin is supported by morphological (e.g., Sprackland, 1991) and molecular data (e.g., Fuller *et al.*, 1998). On the other hand, varanids seem to first appear on Gondwanaland much later in Africa. A fossil of *Varanus* stem-clade was recovered from the Early Oligocene Egypt (Smith *et al.*, 2008). The oldest evidence of varanid lizards on all Gondwanan fragments is recently reported as a *Varanus* from the Late Eocene (37 Ma) of Egypt, which is also thought as an indication of the emergence of this genus in Africa (Holmes *et al.*, 2010). Therefore, varanids in general are likely to have emerged first in Laurasia, while the genus *Varanus*, in particular, may have evolved during a later period on Gondwana. Nonetheless, overall records of fossil varanids so far found on Gondwanan fragments i.e., Africa and Australia are much younger than those found in central Asia, with the oldest Laurasian and Gondwanan varanid fossils differ by about 40 Ma.

Gondwanan origin: Australia

Hutchinson & Donnellan (1993) argued that varanids could have originated in Gondwanaland. Several lines of evidence support the hypothesis that ancestral forms of varanids may have gone through a major diversification in Australia and radiated to Southeast Asia. First, the

primitive subgenus *Varanus* is distributed in Australia. Second, immunological data show a deep divergence within Australian varanids (Baverstock *et al.*, 1993). Third, twenty-four out of fifty-eight recognized species currently occur in Australia (Böhme, 2003). Thus, more than a third of the total currently described varanid species are distributed in Australia alone. This hypothesis of a Gondwanan origin assumes a dispersal route from Australia to the Indonesian Archipelago. Active dispersal from Australia into Asia should have occurred relatively recently i.e., during or after the Miocene, when Australia was closer to Southeast Asia. Otherwise, varanids might have reached Asia by vicariance during the Early Eocene, after India drifted and collided with Eurasia (~57 Ma), eventually raising the Himalayan Mountains and Tibetan Plateau by 35 Ma (Ali & Aitchison, 2005, 2008). The latter scenario assumes the occurrence of ancestral monitor lizards on the Indian fragment of Gondwanaland following the break-up of this supercontinent during the Middle Jurassic. Thus, early varanids are assumed to have occurred on Gondwana before it broke into two fragments about 170 Ma. One fragment included India, Madagascar, the Seychelles, Australia, and Antarctica, whereas the other included Africa and South America (Ali & Aitchison, 2008).

Morphology of varanids

Varanid lizards are relatively conservative in their morphology, despite the high interspecific variation in body size (Pianka, 1994). External morphological characters are conventionally used to describe monitor lizard species and are categorized into meristic and morphometric features. Meristic characters are those that can be quantified using numbers or counts (e.g., number of scales around mid-body), whereas morphometric characters are quantified by measurements (e.g., distance between nostril and eye). Robert Mertens (1942) based his classification of 24 species of *Varanus* on external morphology and cranial structure, and assigned them to eight subgenera. He grouped these characters into four categories i.e., body form, nostril shape and its relative location on the head, scalation and the coloration of scales, as well as the shape of the skull and dentition. Based on this observation, Mertens considered monitor lizards to have originally evolved within Asia, and then radiated from there to their present distributions, including in Australia and Africa. He argued that South Asia and the Indonesian Archipelago together are the focal points of monitor lizard evolution, because seven out of eight subgenera prevail within this region.

Mertens pointed out that only two out of eight subgenera succeeded in Australia, while the number of species in Australia was similar to that in Asia. Furthermore, he regarded the morphological characters of African species as derived from those of Asian varanids. A later approach to characterize species was through the use of internal morphological characters. Hemipenes morphology (Branch, 1982; Böhme, 1988) and lung morphology (Becker *et al.*, 1989) have been used to reconstruct the phylogeny of some representative species distributed in Africa, Asia, and Australia. A general agreement between hemipenal and lung studies implies a varanid radiation out of Australia to Asia and Africa. Both studies placed *V. griseus* basal in the African radiation, signifying this species was an intermediate form between African and Asian species.

Sprackland (1991) examined 23 varanid species using a total of 57 characters. Although most of these characters were morphological, molecular and ecological characters were also included. Groups based upon hemipenal structure (Böhme, 1988) were incorporated as distinguishing characters along with groups defined using karyotype morphology (King & King, 1975; King *et al.*, 1991) and protein electrophoresis (Holmes *et al.*, 1975). Sprackland's study was aimed at clarifying relationships of the *V. prasinus* group, which was hypothesized as being derived from *V. indicus* stock. In his study, Sprackland postulated west-to-east clinal evolution and implied that the ancestors of *Odatria* (small Australian varanids) were of Asian origin. Additionally, Sprackland's phylogeny showed that *V. komodoensis* was the sister to *V. varius*, both of which formed a lineage that, in turn, is the sister to *Odatria*. It is important to note, that in this Asian radiation scenario, *V. gouldii* was believed to have arisen from an Asian ancestor and evolved later into *V. priscus*, which is now extinct. However, a relatively close affinity of *V. gouldii* with an extant or extinct Asian *Varanus* may still have to be determined to support this west-to-east theory. On the other hand, the Asian *V. salvator* has been suggested to have a close relationship with three Australian species, i.e. *V. komodoensis*, *V. priscus*, and *V. varius* based on skull morphology (Head *et al.*, 2009).

Molecular phylogeny of varanids

The rapidly growing molecular systematic techniques have allowed hypotheses of varanid lizards phylogenies based on DNA sequences. Ast (2001) performed a phylogenetic analysis involving 40 living species of all varanid subgenera and designated three varanoid

species as outgroups. She confirmed the monophyly of the superfamily Varanoidea and the family Varanidae, and proposed that the African clade is basal within the family. Asian and Australian species were described as sister groups, which was reflected in the split between Indo-Asian and Indo-Australian clades. The Indo-Asian clade gave rise to two subclades, each of which has a separate geographic range. The subclade Indo-Asian A encompassed all Asian species distributed in the Indonesian Archipelago to Sulawesi, which lies on the western part of Wallacea. The subclade Indo-Asian B nested those species distributed to the east of Sulawesi through to the Pacific islands off of New Guinea. The Indo-Australian clade separated large- and small-bodied *Varanus* into *gouldii* group and *Odatria*, respectively.

To date, the phylogeny of Ast (2001) is probably the most comprehensive and reliable study inferring relationships among extant varanid lizards, because it is well sampled across the taxonomic classification and geographic distribution. Three major clades in this phylogeny are monophyletic, and they seem to be concordant with a pattern of geographic distribution. The African clade consists of species distributed in Africa and western Asia, whereas the large Asian clade consists of species distributed in Asia. The Australian clade contains all species occurring in Australia, as well as the New Guinean *V. salvadorii* and *V. komodoensis*, which occurs only in the Lesser Sundas. The relationship among *V. varius*, *V. komodoensis*, and *V. salvadorii* in this phylogeny is determined monophyletic. The clade containing these three species that are distributed in Australia, Asia, and New Guinea is basal in the larger Australian clade, and may suggest Australia as the origin of varanid radiation to Asia and New Guinea. However, a Gondwanan source of varanid radiation is rejected based on mitochondrial gene re-arrangement data (Amer & Kumazawa, 2008).

The role of phylogeography

Present distribution of varanids is limited to three continents, namely Africa, Asia, and Australia, where the climate can be relatively warm. The discovery of fossil varanids beyond the range of the living forms generally suggests a larger historical distribution for these lizards. In turn, the broader distribution of varanids in the past may reflect a wider distribution of a warmer zone on Earth. Indeed, it has been suggested that Cretaceous greenhouse warming effectively raised temperatures at high latitudes while reducing equator-to-pole temperature gradients (Ufnar *et al.*, 2004). Given the

wider distribution of varanids in areas of warmer climate in the past, we may be able to infer the diversification processes for varanids. The extent of genetic divergence among populations of closely related species in the present geographic range can be estimated from DNA sequences, in order to assess patterns of lineage distribution. In turn, an association between geographic distribution of lineages and the level of differentiation among populations of various varanid species may be used to formulate a scenario about varanid radiation in light of the past geological processes that have formed today's geography.

The extent of the geographic distribution of a species, their phylogenetic relationships, and their dispersal ability is discussed in phylogeography. Studies in phylogeography often integrate at least three components to elucidate present geographic distribution of a species i.e., genealogical relationship (intraspecific phylogeny) based on molecular data, dispersal ability, and geography. Intraspecific phylogeny is used to infer relationships among haplotypes that may correlate with geographic distance and show population structure. Dispersal ability is an important factor in the distribution of species that involves active movement of individuals, which may be influenced by geography e.g., water barriers to strictly terrestrial species. Phylogeography may be a powerful tool to demonstrate population structuring as well as speciation processes, for example, to clarify the relationships among populations of member species within the *V. indicus* spp. complex. Within the last decade, a number of new species have been recognized from this varanid group by re-evaluations of described species as well as a result of discoveries from remote islands (Böhme, 2003). Given the distribution of these cryptic species on islands, a hypothesis of speciation through isolation may be tested in a phylogeographic study for this species complex. A hypothesis of speciation through isolation may also be tested for some other varanids, for example *V. togianus*, which is distributed in a limited range and shows a high degree of endemism. This species was formerly recognized as a subspecies of the widespread *V. salvator* (Koch *et al.*, 2007).

Key-regions of varanid intercontinental radiation

We identify two key-regions across the present-day varanid distribution range that may be useful in helping to clarify the intercontinental radiation of *Varanus*. These two regions are: 1) the land connection between Africa and Asia that lies in the Middle East, and 2) the Lesser Sunda Islands, which coincide with southern Wallacea.

Varanids might have radiated through these regions independently and this hypothesis can be a highlight in phylogeographic studies. Phylogeny alone would not be sufficient to show species radiation, because it does not take into account dispersal and geographic factors that are indispensable to shedding light on population-level divergence. We explore two hypotheses of varanid radiation through these two regions below.

Varanus griseus is distributed along the landmass connecting Africa and Asia. This area is mostly dry and may have allowed the unique adaptive evolution of this monitor lizard to such an extreme habitat. In Africa, the distribution of *V. griseus* includes the northern regions of the Saharan Desert (Bayless, 2002), whereas the populations in Asia are distributed in Central Asia, the Arabian Peninsula, and southwestern Asia to northwestern India (Böhme, 2003). The relationships among regional populations in Africa and Asia may be determined by analyzing the population structure across its range in conjunction with morphological data. Further analyses investigating the relationships between *V. griseus* and its closely related species might eventually reveal a pattern of species radiation across the region. Two closely related species that overlap in their distribution with *V. griseus* are *V. niloticus* in northern Africa, and *V. bengalensis* in northwestern Asia. Interestingly, an hypothesis on the relationship between African and Asian varanids has come from several phylogenetic studies which placed Asia as a possible source of radiation to Africa (e.g., Böhme, 1988; Baverstock *et al.*, 1993; Amer & Kumazawa, 2008). An investigation on the morphological characters of *V. griseus* is currently running at ZFMK in Bonn, Germany. Results of this study may be applicable for a future phylogeographic analyses among populations of *V. griseus* in Africa and Asia, which is central in the varanid evolutionary history studies.

The Lesser Sunda Islands lie in southern Wallacea. This region coincides with the margins of the Eurasian and Indian-Australian plates (Hall, 2002), which is characterized by the presence of small islands clustered in chains. The presence of small islands in this region seems to confound scenarios of varanid radiation between Asia and Australia that are essentially the contradictory hypotheses of the Laurasian versus Gondwanan origin of varanids. It is thanks to the shallow (~200 m) water barrier between Australia and New Guinea (Hall, 2002) and the Pleistocene Glacial Maxima (Kuhle, 1988) that the distribution of varanid lizards on the nearby Sahul Shelf may be understandable. The presence of *V. panoptes*, *V. indicus*, and *V. prasinus* populations in

southern New Guinea and northern Australia has been the source of a hypothetical scenario of varanid radiation in this region, which was based upon their recent divergence in the Late Pleistocene about 20,000 years ago. During that time, the land bridge between New Guinea and Australia disappeared due to increased sea levels and the populations on New Guinea and Australia started to diverge (Baverstock *et al.*, 1993). Nevertheless, the divergence between Asian and Australian varanids is still subject to a detailed assessment. Information from phylogeny alone is not sufficient to infer the patterns of intra- and interspecific divergences at population level, which are among the important features in understanding their evolutionary history. Additionally, it is interesting to note, that some ecological factors such as predation by mammalian species could prevent the diversification of small varanids in the Lesser Sunda Islands and also Wallacea in general (Sweet & Pianka, 2007). Thus, a bias for large-size species may be expected in the distribution of varanids in this joint periphery of Asia and Australia.

The complex zoogeography of Wallacea seems to be generally influenced by the geological evolution of this region (Hall, 1998). During the formation of islands in Wallacea, animal species evolved through processes of vicariance and dispersal. Plate tectonics seem to affect the distribution of both Asian and Australian species particularly in the Lesser Sundas, which is situated in the southern part of Wallacea. The current distribution of *V. komodoensis* in the Lesser Sundas is an intriguing fact in the biogeography of *Varanus*. Phylogenies for extant varanids suggest *V. varius*, of eastern Australia, as the sister species to *V. komodoensis* (e.g., Ast, 2001). On the other hand, the extinct *V. priscus* of central Australia is also considered a sister species to *V. komodoensis* (Head *et al.*, 2009). Thus, based on its relationships with both extant and extinct varanids, *V. komodoensis* is suggested to have a close affinity with Australian species. It is possible, that the island of Timor in the Lesser Sundas might have been a stepping-stone in the dispersal of ancestral *V. komodoensis* from Australia to the Lesser Sundas. However, this hypothesis should also be tested in a phylogeographic context, because information from phylogenies and fossil is not adequate to explain processes that operate at population level, such as dispersal. The fossil *V. bolkayi* found on Java and two varanid vertebrae from western Timor were presumed to represent a subspecies of *V. komodoensis* (Hooijer, 1972), suggesting a wider distribution for *V. komodoensis* from Timor to Java. If dispersal occurred from Australia to the Lesser Sundas, it should have occurred relatively recently. Timor lies on the Indian-Australian Plate and

was relatively distant from the Lesser Sundas. Only in the Late Miocene, about 5 Ma (Hall, 2002), the Indian-Australian Plate moved northward, bringing Timor closer to the Lesser Sundas. Thus, *V. komodoensis* might have dispersed from Australia to the Lesser Sundas not more than 5 million years ago. Indeed, fossils of *V. komodoensis* from Pliocene Australia suggest an origin of this species in Australia at least 3.8 Ma (Hocknull *et al.*, 2009). Nevertheless, fossil *V. komodoensis* might also be found in Southeast Asian sites such as the Southeast Asian savanna corridor, which spanned between mainland Southeast Asia and Australia during the last glaciation period (Bird *et al.*, 2005). Savanna is one of the occupied habitats for *V. komodoensis* in the Lesser Sunda Islands besides monsoon forest and grassland (Auffenberg, 1981). However, no reliable fossil is currently recorded from Asia, presumably because this savanna corridor is now submerged under the sea.

Conclusion

We acknowledge that the origin of varanid lizards of the genus *Varanus* still remains debatable, despite the advances in phylogenetic studies for this lizard group. Fossils are reliable evidence of ancestral species and their historical distribution. However, fossils are relatively scarce and may be underrepresented in some parts of the world. As phylogeny and fossils may be still insufficient to substantiate either view on the origin of varanids in general, one may expect to seek hints from the relationships among populations of extant species within the two key-routes of intercontinental dispersal. These two regions include the landmass connecting Asia and Africa, as well as the Lesser Sunda Islands in southern Wallacea. The latter coincides with the margin of the Eurasian and Indian-Australian plates, for which the complex geology may reflect current distribution patterns of fauna in this region. An approach to solving this riddle is the application of phylogeographic methods, which makes possible an identification of the population structure with regard to their phylogenetic relationships and dispersal processes. This approach also seems to be useful for making inferences about the historical dispersal of *V. komodoensis*, for which the extant populations only occur on several islands within the Lesser Sundas. However, support from paleogeographic and geological data as well as multiple fossil records from both sides bordering this island group is needed to make a robust hypothesis about the evolutionary processes that gave rise to the restricted *V. komodoensis* populations. Eventually, patterns for varanid radiation between Asia

and Australia could also be well-corroborated by using similar approaches. The application of phylogeography may be extended to unravel relationships among African and Asian species with regard to the direction of the geographic radiation of *V. griseus*.

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Fig. 1. The evolution and dispersal route of varanid lizards. Laurasian hypothesis is based on fossil records (Estes, 1983) and indicated by grey arrows, whereas Gondwanan hypothesis is based on species diversity (Hutchinson & Donellan, 1993) and indicated by white arrows. Map shows Late Cretaceous-Tertiary transition (~65 Ma), redrawn after a paleogeographic map available at <http://jan.ucc.nau.edu/~rcb7/globaltext2.html> by Ron Blakey, Geology Department, Northern Arizona University. Laurasian and Gondwanan fragments are indicated in this map with the letters “L” and “G”, respectively.

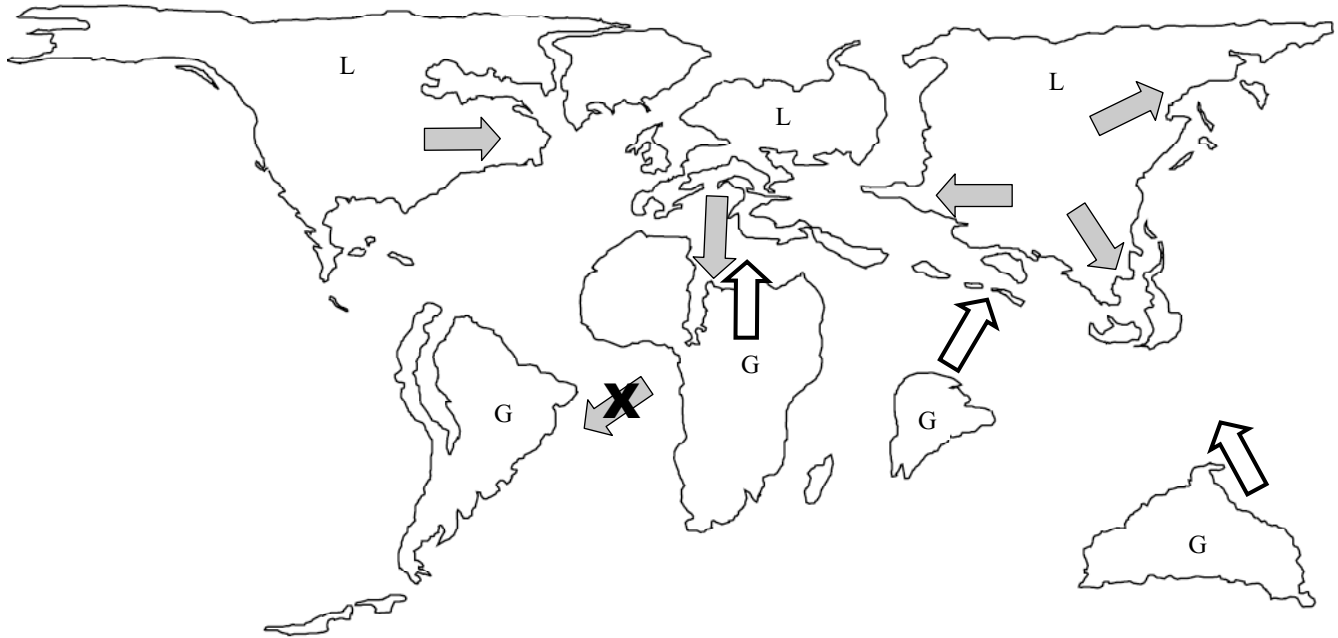


Fig. 2. Hypothetical dispersal of ancestral varanids from Asia as illustrated in Estes (1983). Varanid lizards are thought to have originated in central Asia during the Cretaceous (~80 Ma) based on fossils found in Mongolia, whereas the genus *Varanus* is thought to have emerged in Africa sometime in the Eocene, more than 37 Ma (Holmes, 2010).

