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Re-assessment of varanid evolution based on new data from *Saniwa ensidens* Leidy, 1870 (Squamata, Reptilia)

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ABSTRACT

Saniwa ensidens is a pivotal taxon for understanding varanid evolution. A complete specimen of *Saniwa ensidens* was recently described, offering important new insights into the morphology of this taxon. We apply these new data to a broader-scale study of squamate relationships in order to understand the phylogenetic position of *Saniwa ensidens* and of varanids more generally. Among the other fossils included in our analysis were the Eocene taxon “*Saniwa*” *feisti*, the Miocene *Varanus rusingensis*, and the giant Pleistocene varanid *Megalanía prisca*. We compare the phylogenetic hypothesis from our analysis of morphology with a recent molecular-based hypothesis and find numerous differences in the phylogenetic relationships within *Varanus*. We constrained our morphological data set to the phylogenetic pattern presented by the molecular data to further analyze the possible phylogenetic relationships of the fossil taxa. Our analyses show that *Saniwa ensidens* is the sister taxon to crown-group *Varanus* and that “*Saniwa*” *feisti* is a basal member of the varanid lineage, not closely related to *Saniwa ensidens*. Both *Varanus rusingensis* and *Megalanía prisca* are members of the crown radiations of *Varanus*.

INTRODUCTION

Monitor lizards and their fossil relatives compose a speciose squamate clade with a deep fossil record. *Saniwa ensidens* is an Eocene squamate universally regarded as having some affinity with modern monitor

lizards (Varanidae) (fig. 1). Rieppel and Grande (2007) recently described an exceptionally well-preserved specimen of *Saniwa ensidens* from “Locality H” within the Eocene deposits of Fossil Lake, Wyoming (see Grande and Buchheim, 1994). This new specimen offers insights that improve the understanding

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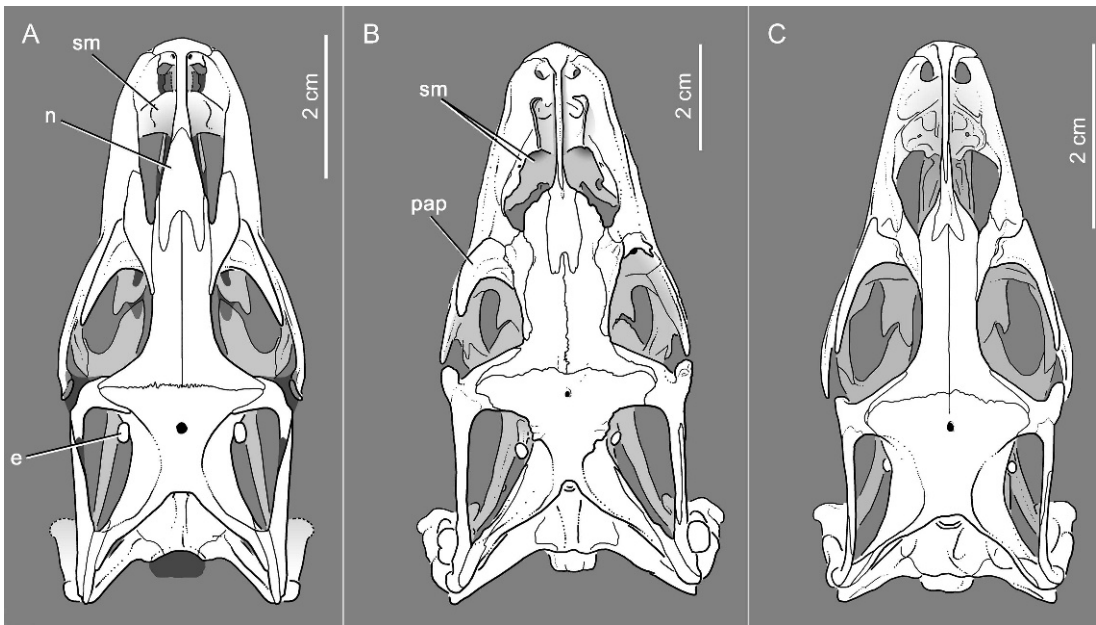


Fig. 1. Skulls of three varanines in dorsal view: (A) *Saniwa ensidens* (reconstructed based on FMNH PR 2378), (B) *Varanus albigularis* (AMNH R 47726), and (C) *Varanus gouldii* (drawn after Maisano, 2001b). Note the general conservation of features between the three taxa. *Saniwa ensidens* possesses a greater contribution of the prefrontal to the dorsal skull roof and that the maxillae extend further dorsomedially (Rieppel and Grande, 2007). Reconstructed portions *Saniwa ensidens* are shown as semi-opaque shadows to minimize the morphology they hide. Note that the right palpebral has been removed from *Varanus albigularis* and that this taxon has a large and elaborate septomaxilla. Abbreviations: e, epipterygoid; n, nasal; pap, palpebral; sm, septomaxilla.

of the placement of *Saniwa ensidens* among varanoids. Additionally, incorporation of new morphological data may help to resolve the interrelationships of other fossil varanoids and within the genus *Varanus* through a better understanding of character polarities and character evolution.

Many fossil squamates have been suggested as being close relatives of modern varanids (e.g., *Megalanias prisca*, *Saniwides mongoliensis*, *Telmasaurus grangeri*), but with only limited cladistic analysis of these relationships. Conrad (2008) recently provided an extensive morphological data matrix addressing global squamate relationships. Norell et al. (2008) further expanded on this analysis, adding several additional varanid species and morphological characters.

Importantly, the interrelationships within *Varanus* have not been directly addressed in an analysis also analyzing the phylogenetic placement of *Saniwa ensidens*. Recent analyses

of *Varanus* have been based on molecular data (Fuller et al., 1998; Ast, 2001, 2002b; Pepin, 2001), which cannot address the position of fossil taxa. The fossil taxa *Megalanias prisca* and *Varanus rusingensis* have never been included in a cladistic analysis focusing on relationships and interrelationships of *Varanus*. Additionally, various fossils too incomplete to be included here have been referred to the Varanidae. Noteworthy is the Middle Miocene *Iberovaranus* (Hoffstetter, 1969; Estes, 1983), which could be an early occurrence of *Varanus* or proximal outgroup, but whose position cannot be analyzed without the discovery of more complete remains.

Varanus contains 68 extant species according to Uetz (2008) with a size range rivaling that between rats and elephants (Pianka, 1995). Although many aspects of the osteology of *Varanus* are conservative, some details are variable between species (see Mertens, 1942c) (fig. 1B, C). Given such diversity, it is

problematic that most morphology-based analyses code *Varanus* as a single terminal taxon without reference to a particular species or phylogenetic hypothesis of *Varanus* interrelationships. *Lanthanotus borneensis*, the extant sister group to *Varanus* (Pregill et al., 1986; Estes et al., 1988; Wu et al., 1996; Evans and Barbadillo, 1998, 1999; Gao and Norell, 1998; Lee, 1998; Evans et al., 2005; Conrad, 2008; but see Northcutt, 1978 and Caldwell, 1999), does not help much in reconstructing the basal *Varanus* morphology because it is very derived when compared with primitive varanoids, monstersaurs, and fossils previously allied with varanids. A better understanding of the interrelationships of *Varanus* species and *Lanthanotus* in the context of their fossil relatives could offer new insights into character polarities within Varanidae and its stem lineage, and help in accurately identifying the basal character states among the species of *Varanus*.

Here, we will add to recent analyses in order to further elucidate the phylogenetic placement of *Saniwa ensidens*, the phylogenetic interrelationships of other proximal varanid outgroups, and the interrelationships of *Varanus* species.

MATERIALS AND METHODS

DATA MATRIX: A number of studies have investigated the relationships of varanids and the interrelationships of Varanoidea over the last five decades (McDowell and Bogert, 1954; Rieppel, 1980a; Branch, 1982; Borsuk-Bialynicka, 1983, 1984; Pregill et al., 1986; Estes et al., 1988; Norell et al., 1992; Pianka, 1995; Caldwell, 1996; Dal Sasso and Pinna, 1997; Lee, 1997; Caldwell, 2000; Lee and Caldwell, 2000; Nydam, 2000; Rieppel and Zaher, 2000a; Pepin, 2001; Rieppel et al., 2006; Conrad, 2008; Norell et al., 2008). Most recently, Conrad (2008) presented an extensive morphological analysis of squamate relationships. Norell et al. (2008) augmented this analysis by adding 29 taxa (including the basal varanine *Ovoo gurvel*) and nine new characters. To this matrix of 251 taxa and 373 characters we have now added four more *Varanus* species (*Varanus albogularis*, *Varanus gilleni*, *Varanus rudicollis*, and *Varanus salvator*) and coded

Saniwa ensidens based on the complete skeleton (FMNH PR 2378) and a cast of a partial skull (FMNH PR 2380) recently described by Rieppel and Grande (2007).

ANALYSIS 1: We analyzed these data using the computer program T.N.T. (Goloboff et al., 2003) using the New Technology Search (1000 replicates) and three subsequent ratchet runs (each of 1000 replicates). Our analysis recovered 2373 equally short trees, each with a length of 3846 steps and a retention index of 0.7138.

We report both the strict and Adams consensus trees for taxa of interest (fig. 2), the latter as reconstructed by the computer program PAUP* (Swofford, 2001). Adams consensus trees are reported rather than majority-rule trees. Adams consensus collapses problematic/volatile taxa to their most basal supported position and retains branches that are supported in all of the principle trees, regardless of the position of volatile taxa.

ANALYSIS 2: To further test the position of *Saniwa ensidens* and other fossil varanids, such as *Megalanina prisca* and *Varanus rusingensis*, we created a subset of the data containing only “*Saniwa*” *feisti*, *Necrosaurus cayluxi*, *Saniwides mongoliensis*, *Telmasaurus grangeri*, *Aiolosaurus oriens*, *Lanthanotus borneensis*, *Cherminotus longifrons*, *Ovoo gurvel*, *Saniwa ensidens*, *Megalanina prisca*, and all of the *Varanus* species present in the global analysis described above (reduced matrix A). These data were then analyzed in the same manner as the global data (see above). Because the results of this analysis were very similar to those of the global analysis (see below), the RMA was used for further tests that would have been prohibitively time-consuming or impossible given the global data matrix.

ANALYSIS 3: We ran a third analysis in which only extant taxa were included for comparison with a recent molecular phylogeny of varanids (Ast, 2001, 2002a). Ast’s (2001) study was chosen for comparison because it is one of the most taxonomically inclusive and one of the most recent molecular-based studies of extant varanoid interrelationships. Fuller et al. (1998) and King et al. (1999) have also recently analyzed varanid interrelationships using molecular data and produced a phylogenetic hypothesis that is generally similar to

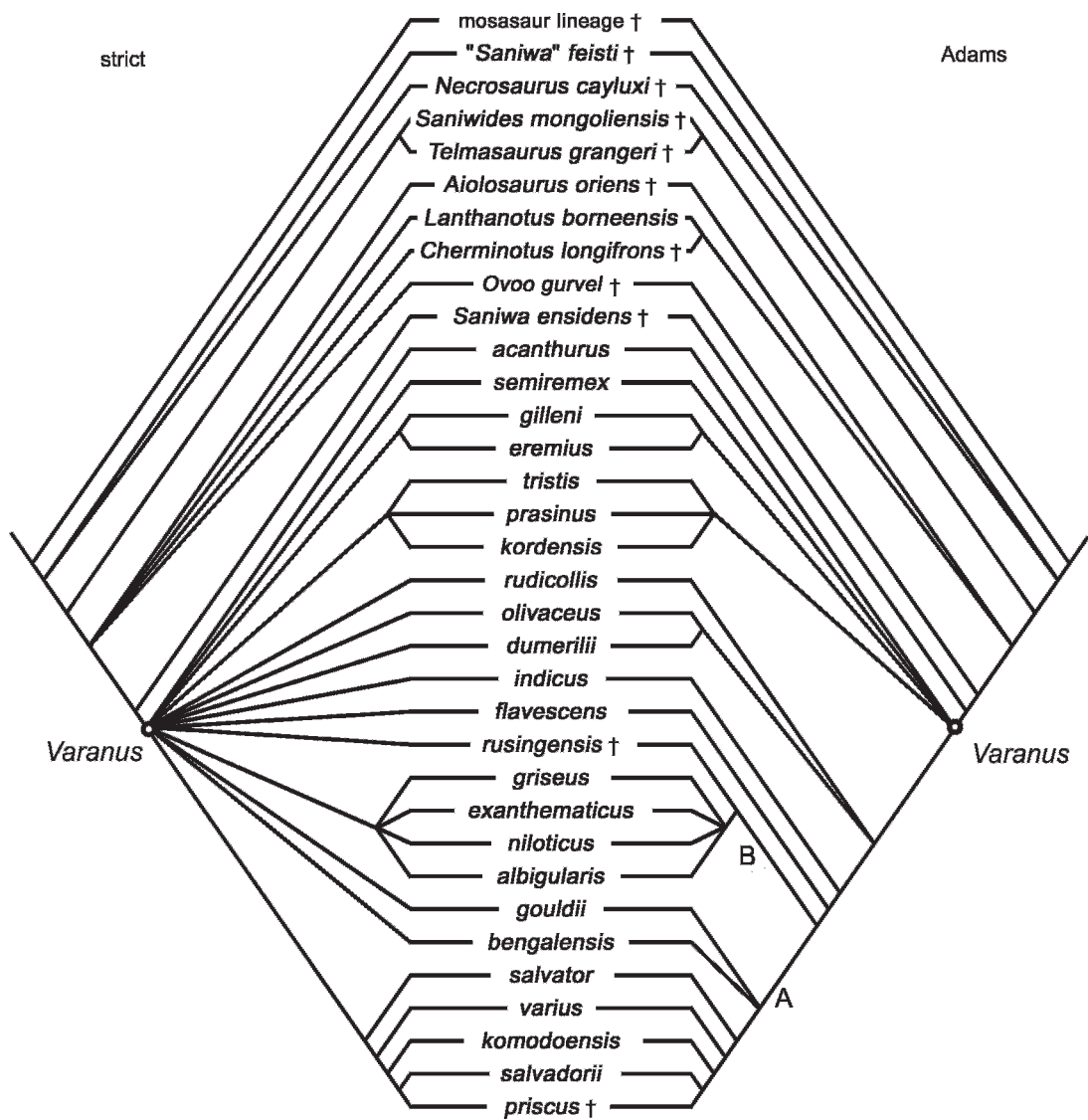


Fig. 2. Strict (left) and Adams rule (right) consensus cladograms representing areas of interest from the global analysis of squamate relationships described in the text (note, non-varaniform taxa omitted). Extinct taxa are denoted by daggers (†). Groups A and B (from the text) are identified here and referred to again in figure 4.

that of Ast (2001), but the latter was slightly more taxonomically inclusive. Pianka (1995) recovered a slightly different result, using different techniques. Fitch et al. (2006) analyzed relationships among a subset of *Varanus*, and their results generally agree with those of Ast (2001).

ANALYSIS 4: Finally, we constructed a constraint tree for reduced matrix A (RMA) in which the extant taxa common both to it

and the analysis of Ast (2001) were forced into the topology of the latter study. This constraint tree was treated as a “backbone” constraint in PAUP* so that nonoverlapping taxa were could be placed within the constraint tree.

DATA ACQUISITION: Morphological data were acquired through direct observations of specimens (appendix 1) and published data. Published data were used to supplement the

codings for some extant *Varanus* (Mertens, 1942a, c, b; Bellairs, 1949; McDowell and Bogert, 1954; Rieppel, 1980a; Jenkins and Goslow, 1983; Landsmeer, 1983; Rieppel, 1993; Pianka, 1995; Zaher and Rieppel, 1999a; Rieppel and Zaher, 2000b; Maisano, 2001b; Pepin, 2001; Rieppel and Grande, 2007; Uetz, 2007), *Lanthanotus* (McDowell and Bogert, 1954; Rieppel, 1980a, b, 1983; Zaher and Rieppel, 1999b, a; Maisano, 2001a; Rieppel and Zaher, 2000b; Maisano et al., 2002), the included Gobi taxa (Gilmore, 1943; Borsuk-Bialynicka, 1983; Estes, 1983; Borsuk-Bialynicka, 1984; Gao and Hou, 1996; Gao and Norell, 1998, 2000), *Saniwa ensidens* (Gilmore, 1928; Estes, 1983; Caldwell, 2003; Rieppel and Grande, 2007), *Megalanina prisca* (Hecht, 1975; Molnar, 1990, 2004; Lee, 1995; Erickson et al., 2003), and *Varanus rusingensis* (Clos, 1995).

MONOSPECIFIC TAXA: Note that *Aiolosaurus oriens*, *Cherminotus longifrons*, *Lanthanotus borneensis*, *Saniwides mongoliensis*, *Telmasaurus grangeri* are each monospecific and may, hereafter, be referred to by their generic names only.

PREVIOUS ANALYSES

Saniwa ensidens has a long history of systematic association with varanids (see, for example, Camp, 1923, Gilmore, 1928, and McDowell and Bogert, 1954) and resembles extant varanids in cranial morphology. Other fossil taxa such as *Aiolosaurus oriens*, *Cherminotus longifrons*, *Proplatynotia longirostrata*, *Saniwides mongoliensis*, and *Telmasaurus grangeri* are also similar to Varanidae (Gilmore, 1943; Borsuk-Bialynicka, 1984; Lee, 1997; Gao and Norell, 2000), and many of these taxa have been referred to Varanidae in the past.

Four recent studies have addressed many of these taxa. Lee (1997) presents a phylogenetic hypothesis in which *Proplatynotia longirostrata* and *Paravaranus angustifrons* are the sister taxa to the extant varanoids, *Telmasaurus* is the sister taxon to a clade containing varanids, mosasauroids, and snakes, and *Saniwa ensidens* and *Saniwides* are successively closer sister taxa to the extant *Varanus*. Pepin (1999) presents a very similar analysis, but resolves the interrelationships more fully,

recovering the mosasauroid clade as intermediate between “gobidermatids” and crown-group Varanoidea. Norell and Gao (1997) point out that one of the weaknesses of Lee’s (1997) (and, by extension, Pepin’s 1999) study is that it assumes the monophyly of a clade containing *Gobiderma pulchrum* and *Parviderma inexacta*, even though there is no evidence to suggest such a relationship. Indeed, Gao and Norell (1998) offer evidence suggesting that *Gobiderma pulchrum* is a monstrosaur (closer to *Heloderma* than to *Varanus*) and *Parviderma inexacta* may be more closely related to varanids. Other weaknesses of the Lee (1997) study are its constraint of snakes as platynotans and the selection/construction of some of the morphological characters (see Zaher and Rieppel, 1999b, a). Gao and Norell (1998) offer a different hypothesis of relationships, based on a broader sampling of fossil and extant taxa, but including neither snakes nor mosasauroids. Conrad (2008) suggests that snakes are not closely related to anguimorphs, but that they are scincoids.

RESULTS

SEARCH RESULTS

ANALYSIS 1: Our global analysis recovered 2373 equally short trees, each with a length of 3846 steps and a retention index of 0.7138. Both strict and Abrams consensus are illustrated (fig. 2).

ANALYSIS 2: Our analysis of reduced matrix A (RMA) recovered 144 equally short trees, each with a length of 288 steps and a retention index of 0.5621. Only the Adams consensus of this search is illustrated (fig. 3).

ANALYSIS 3: The analysis limited to extant taxa recovered three equally short trees, each with a length of 204 steps and a retention index of 0.4729. The strict and Adams consensus for this analysis are identical (see fig. 4).

ANALYSIS 4: The analysis run with a backbone constraint for extant varanids recovered 70 equally short trees, each with a length of 308 steps and a retention index of 0.5056. The results of this analysis are described more fully below.

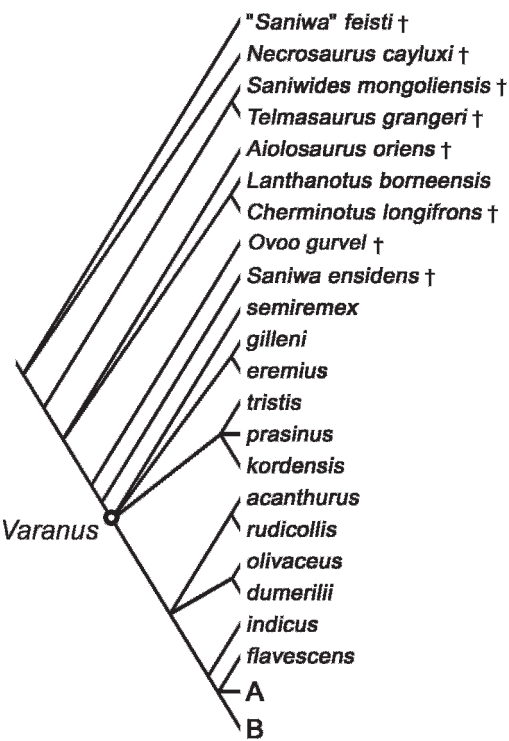


Fig. 3. Analysis from reduced matrix A (RMA) analysis. See the text for details. Groups A and B are identical in their topology to those denoted in figure 2.

SYSTEMATIC RESULTS

CHARACTER LIST: The complete list of characters and character states are found in Conrad (2008) and Norell et al. (2008). Both of these papers are available for free in pdf format from <http://digitallibrary.amnh.org/dspace>. The data are presented in a format that allows them to be copied and pasted to a new document in nexus format, T.N.T. (Goloboff et al., 2003) format, etc.

CLADE DIAGNOSES: According to the current study, “*Saniwa*” *feisti*, *Necrosaurus cayluxi*, *Saniwides*, *Telmasaurus*, and crown-group Varanidae form a clade based on five unambiguous synapomorphies. These are 58(0) straight (linear) interorbital frontal margins, 61(1) subolfactory processes of the frontals partly surrounding the olfactory tracts of the brain, 65(1) presence of an external maxillofrontal contact, 115(2) presence of a single line of palatine teeth, and

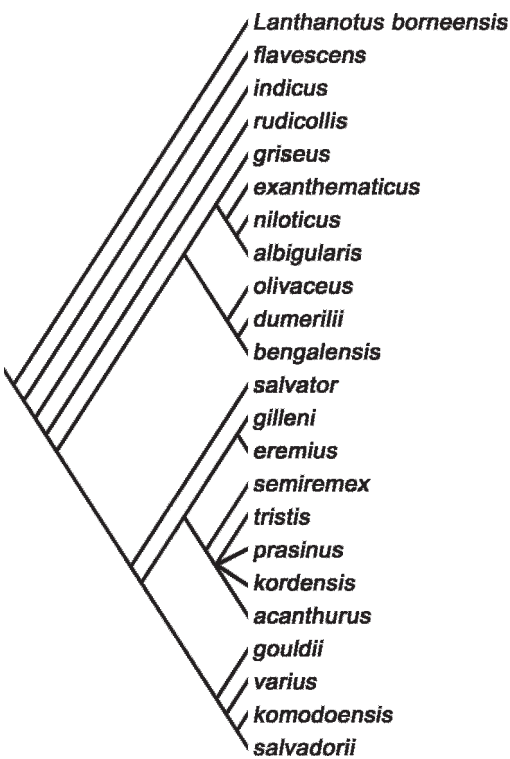


Fig. 4. Phylogenetic hypothesis generated by analysis of the RMA when all fossil taxa are deleted. Note that this topology shows similarities with the morphological analyses in figures 2 and 3, and also with that of the molecular analysis of Ast (2001) (fig. 5).

233(1) presence of at least weak precondylar vertebral constriction. “*Saniwa*” *feisti* and *Necrosaurus cayluxi* form a polytomy at the base of this clade. This and other polytomies within the results of this analysis may be present, in part, because of the inclusion of incomplete specimens. *Saniwides*, *Telmasaurus*, and crown-group varanids form a clade based on 55(0) presence of separate (unfused) frontals in adults, 70(0) presence of a U-shaped frontoparietal suture, 124(1) presence of an ectopterygoid-palatine contact anterior to the suborbital fenestra, and 183(1) dorsal dentary contribution to the anterior inferior alveolar foramen. Within this clade, *Telmasaurus* and *Saniwides* form an exclusive clade diagnosed by 115(0) presence of palatine tooth patches, and 118(0) pterygoid teeth arranged in multiple rows/patches.

Varanidae is typically considered to include extant *Varanus*, *Lanthanotus*, and all descendants of their last common ancestor (Pregill et al., 1986; Estes et al., 1988; Pianka, 1995; Lee, 1998; Bernstein, 1999; Conrad, 2004, 2008). The current analysis recovers five unambiguous synapomorphies for Varanidae including *Aiolosaurus*. *Aiolosaurus* forms a polytomy with lanthanotines and varanines in this analysis (for a review on the phylogenetic placement of *Aiolosaurus*, see Norell et al., 2008). The five character states supporting Varanidae are 3(1) presence of a blunt and rounded snout, 65(0) absence of an external maxillo-frontal contact, 149(1) presence of a broad crista tuberalis that incorporates the paroccipital processes, 151(1) an anteriorly placed speno-occipital tubercle, and 178(0) a ventrally arched dentary. The *Cherminotus-Lanthanotus* clade is supported by 32(1) presence of a medial palatine flange on the maxilla, 83(1) presence of a nuchal fossa at the posterior margin of the parietal, and 107(0) presence of a rod-shaped vomer.

Varaninae (sensu Pregill et al., 1986 as modified by Conrad, 2008; all taxa sharing a more recent common ancestor with *Varanus varius* than *Lanthanotus borneensis*) is here diagnosed by 27(1) presence of a midline contact of the maxillae posterior to the premaxillary nasal process, 51(1) absence of a jugal-postorbital contact, and 62(1) midline contact of the subolfactory processes on the frontals. *Saniwa ensidens* is found to be the sister taxon to crown-group *Varanus* in all the principle trees in this analysis. The six unambiguous synapomorphies uniting this clade are 3(0) presence of a tapering snout (fig. 1) (reversed in some *Varanus*), 10(1) presence of dermal sculpturing on the frontal and parietal, 42(1) presence of a posterolateral lacrimal flange, 43(1) a double lacrimal foramen, 44(1) an enlarged primary lacrimal foramen, and 111(0) palatine longer than wide. The species of *Varanus* are united to the exclusion of *Saniwa ensidens* based on the following synapomorphies: 52(2) Jugal lying mostly posterior to the maxilla, with little or no overlap, 69(1) presence of parietal tabs on the frontal, 74(1) frontal tabs present on the parietal, 115(1) absence of palatine teeth, and 118(2) absence of pterygoid teeth.

Varanus rusingensis and *Megalanina prisca* (hereafter *Varanus prisca*) are both nested within the extant *Varanus* radiation according to this analysis. *Varanus prisca* is the sister taxon to *Varanus salvadorii*, sharing with it 69(0) absence of parietal tabs on the frontal. *Varanus komodoensis* forms a clade with *Varanus prisca* and *Varanus salvadorii* based on 32(1) presence of a medial palatine flange on the maxilla and 111(0) palatine longer than wide. *Varanus varius* is the next most proximal sister taxon and shares with the other species listed 3(1) a blunt, rounded snout and 372(0) distal placement of the fleshy external nares. *Varanus salvator* shares with these other taxa three unambiguous synapomorphies, including 72(1) broad and squared lateral flange of the parietal at the frontoparietal suture, 138(1) reduced crista prootica without a distinct ventral extension, and 189(1) splenial extending for less than one-half the dentary length. *Varanus gouldii* and *Varanus bengalensis* form a polytomy with the *salvator-varius-komodoensis-salvadorii-prisca* group in a clade hereafter referred to as “group A”. Group A is diagnosed by 1(3) an extremely elongate antorbital snout (constituting more than half the craniobasal length) and 233(2) vertebrae with strong precondylar constriction.

Group A forms a polytomy with *Varanus flavescens* and a clade containing the mostly African taxa *Varanus albigularis*, *Varanus exanthematicus*, *Varanus griseus*, *Varanus niloticus*, and *Varanus rusingensis*; hereafter referred to as “group B”. Group B is united by a single unambiguous synapomorphy, which is 212(5) presence of globidont posterior teeth. All of group B besides the Miocene *Varanus rusingensis* form an unresolved clade united by 292(0) presence of a separate astragalus and calcaneum.

Group A, group B, and *Varanus flavescens* form a clade with *Varanus indicus*; united by 141(1) presence of a double facial foramen and 312(0) absence of keeled scales on the body. This clade, in turn, forms a polytomy with *Varanus rudicollis* and a clade composed of *Varanus dumerillii* and *Varanus olivaceus*. This clade is diagnosed by 20(1) fused nasals and 111(1) palatine subequal in length and width, and forms a polytomy with other *Varanus* (fig. 2).

Comparisons with molecular studies: The analysis above differs significantly from the phylogenetic hypothesis of the interrelationships of *Varanus* proposed by Ast (2001), although there are several points of congruence (compare figs. 2, 3, and 5). Notably, both analyses recover a clade containing the large-bodied taxa *Varanus komodoensis*, *Varanus salvadorii*, and *Varanus varius* and a clade containing the African taxa *Varanus exanthematicus*, *Varanus griseus*, and *Varanus niloticus*. In contrast to Ast (2001), we find no support for major Indo-Asian clades. Instead these clades are found to be paraphyletic or polyphyletic with respect to African and Indo-Australian clades. The Indo-Australian group (as identified by Ast, 2001) is not monophyletic. *Varanus bengalensis* and *Varanus salvator* are found to belong to the otherwise mostly Indo-Australian clade termed group A above. Ast (2001) found *Varanus bengalensis* and *Varanus salvator* to be nested members of the Indo-Asian A clade in her study. Most of the other members of Ast's (2001) Indo-Asian clades included in our global analysis form a paraphyletic assemblage representing proximal sister taxa to the clade including groups A and B.

Taxonomic inclusiveness is a key consideration when comparing and contrasting these analyses. Ast's (2001) analysis is more taxonomically inclusive amongst extant taxa, and she included multiple "subspecies" and/or specimens from multiple localities for many species. By contrast, our morphological analyses (above and below) benefit from the inclusion of fossil taxa (e.g., *Saniwa ensidens*) that may, in some cases, offer a clearer understanding of the primitive morphology for some nodes and certainly help to polarize characters throughout the tree. We will further investigate these considerations below.

RESULTS OF COMPARATIVE ANALYSES

ANALYSIS 2 (RMA analysis): Analysis of RMA reveals a very similar Adams consensus tree to that of the global analysis (compare figs. 2 and 3). Clades A and B were identical between the two analyses. Adams consensus of the RMA analysis was unable to resolve the relative position of *Varanus flavescens* with

respect to clades A and B, but resolved the position of *Varanus acanthurus* as a sister-taxon to *Varanus rudicollis*. All of the more basal taxa on the varanid lineage remained in the same position as with the global analysis. The RMA is used in the following analyses.

ANALYSIS 3 (extant-only analysis) (fig. 4): We re-analyzed RMA with all fossil taxa deleted, in part, to test the importance of fossils in our analysis and to isolate possible similarities in the signal between the molecular data and our morphological data.

When all fossil taxa are deleted from the RMA, we recover an Indo-Asian monitor clade consisting of the taxa *Varanus olivaceus*, *Varanus bengalensis*, and *Varanus dumerilii*. The interrelationships of these three taxa is that revealed by Ast's (2001) analysis, but with several other taxa removed; that is, some of the Indo-Asian taxa common to both analyses (see the right side of fig. 5) fall outside of the Indo-Asian clade recovered in our extant-only analysis. Ast (2001) finds *Varanus flavescens* and a clade composed of *Varanus rudicollis* and *Varanus salvator* to be successively more remote sister taxa to her *Varanus bengalensis*–*Varanus dumerilii* clade. She also finds *Varanus prasinus* and *Varanus indicus* to be nested members of a clade including *Varanus olivaceus* (Ast, 2001). In the current analysis of extant taxa, *Varanus flavescens*, *Varanus indicus*, and *Varanus rudicollis* are suggested to be basal *Varanus* species. *Varanus salvator* is recovered as the sister taxon to a mostly Indo-Australian clade including taxa typically assigned to the clade *Odatria* (e.g., *Varanus acanthurus*) and some large-bodied varanids (e.g., *Varanus gouldii* and *Varanus komodoensis*); *Varanus prasinus* is nested within our Indo-Australian clade. Our extant-only analysis recovered *Varanus gouldii* as a basal member of the clade containing *Varanus varius*, *Varanus komodoensis*, and *Varanus salvadorii*, whereas Ast (2001) recovered it as more closely related to the Indo-Asian clades (but see Ast, 2002b).

Thus, similarities between the extant-only analysis performed here and the molecular analysis (Ast, 2001) not present in analyses 1 or 2 above include the recovery of an Indo-Asian clade and consolidation of Indo-Australian taxa into a single clade (figs. 2, 3,

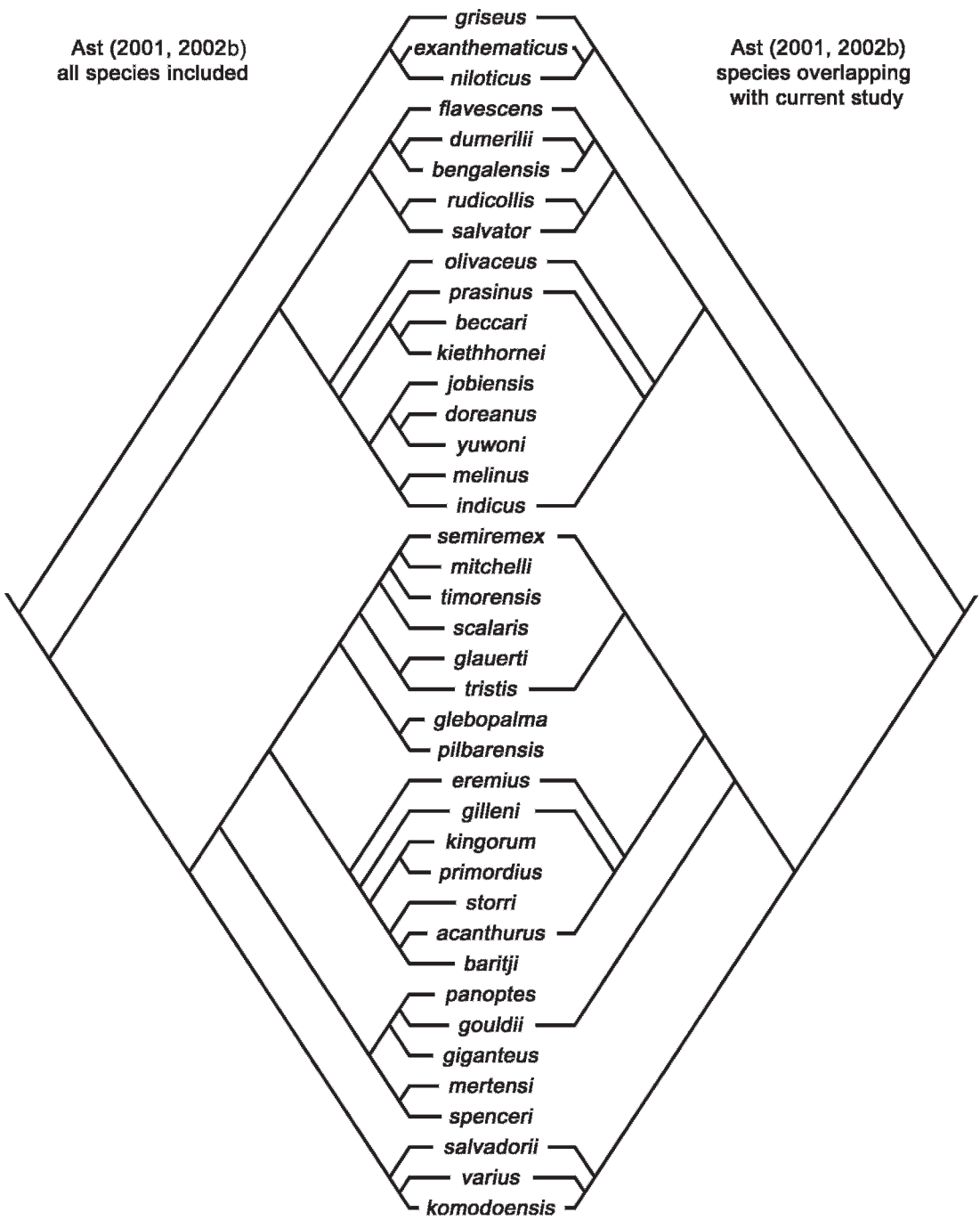


Fig. 5. Phylogenetic hypothesis for the extant *Varanus* species as presented by Ast (2001, 2002a). The left side shows all of the species included in her analysis. The right side is a cladogram of the same topology, but with only the species included in both Ast (2001, 2002a) and the current morphological analysis.

5). This result raises the possibility that the absence of historical morphological data provided by fossils may be a factor in the recovery of those clades by molecular analyses. Inclusion of fossil outgroups to *Varanus* (e.g., *Saniwa ensidens*) and fossil *Varanus* (e.g., *Varanus rusingensis*) apparently repolarize character states such that the attraction of some Indo-Asian taxa and the two main clades of Indo-Australian taxa is reduced. However, the possibility remains that there also may be undetected morphological tendencies associated with becoming large, leading to convergence between *Varanus salvator*, *Varanus gouldii*, and the large-bodied Indo-Australian taxa within morphological phylogenetic analyses. Molecular data may be less susceptible to this bias, and the problem of subjectivity present in morphological character formulation.

ANALYSIS 4 (constrained tree analysis): Our constrained tree analysis was designed to test the placement of fossil taxa given the context of the molecular phylogeny presented for *Varanus* by molecular evidence.

Saniwa ensidens was found to be the sister taxon to *Varanus* in all of the principle trees recovered in this analysis. *Varanus rusingensis* was somewhat variable in its placement. It was variably recovered as the sister taxon to all of other *Varanus*, to *Varanus olivaceus*, or to *Varanus flavescens*. *Varanus prisca* was consistently recovered in a nested position within the extant *Varanus* radiation. It was variably found to be the sister taxon to *Varanus salvadorii*, the sister taxon to *Varanus varius*, the sister taxon to a clade containing *Varanus varius* and *Varanus komodoensis*, or the outgroup to a clade containing *Varanus komodoensis*, *Varanus salvadorii*, and *Varanus varius*.

DISCUSSION

FOSSIL VARANIDAE CONCLUSIONS: *Saniwa ensidens* is a pivotal taxon for understanding the evolution of the varanid lineage because of its placement and the completeness of the known remains. Our analyses confirm the placement of *Saniwa ensidens* as the sister taxon to *Varanus* within Varaninae (fig. 2). *Saniwa ensidens* differs from *Varanus* mainly

in possessing a more anteriorly extensive jugal, a simpler frontoparietal suture, and in the plesiomorphic retention of palatal teeth. The overall appearance of the skull roof of *Saniwa ensidens* is similar to that of extant *Varanus*, especially given the diversity present in the latter (see fig. 1 and Mertens, 1942a, b, c, 1942c).

Some other taxa sometimes considered close relatives of *Varanus* are actually outgroups to the crown-group Varanidae. *Saniwides mongoliensis* and *Telmasaurus grangeri* form a clade that is one of the proximal outgroups to Varanidae in our analysis. This conclusion contrasts with those of some earlier studies (e.g., Lee, 1997 and Pepin, 1999), which suggested *Saniwides* formed a clade with *Varanus* exclusive of *Saniwa ensidens*. The recently described specimens of *Saniwa ensidens* have clarified similarities between that taxon and *Varanus*.

Varanus rusingensis is probably the oldest known member of the extant *Varanus* radiation. The only doubt about this hypothesis is raised by a small subset of the trees generated from the constrained analysis described above (analysis 4). This taxon demonstrates that the *Varanus* clades had diversified by and reached Africa no later than the Early Miocene (Clos, 1995). “*Megalanina*” *prisca* is confirmed to fall within the extant radiation of *Varanus*.

INCLUSION OF INCOMPLETE FOSSILS: As is often the case, inclusion of fossils in this analysis also means the inclusion of taxa that cannot be scored for every character state. Indeed, many of the extant taxa were coded from incomplete specimens or species for which specific knowledge of some character systems (e.g., some soft characters) could not be scored. Inclusion of these additional data will benefit future iterations of this analysis pending fuller description of specific taxa and/or discovery of more complete fossils.

CONCLUSIONS ABOUT CLADES OF *VARANUS*: The interrelationships of the *Varanus* clades have been approached both using molecular and morphological data. Ast’s (2001) relatively inclusive analysis of extant *Varanus* produced a result that differs significantly from our morphology-based global analysis, which included numerous nonvaranids, fossil varanids, and several extant *Varanus*. Taxon

sampling is at least partly responsible for this disparity in results; the morphological analysis includes fewer extant taxa and the molecular study includes no fossils. However, the specific limitations of each approach also must be further investigated. A combined analysis of morphological and molecular data may offer a way of further investigating this problem in the future. Further discoveries of complete specimens of fossil taxa (like the recently described *Saniwa ensidens*), more complete descriptions of fossil and extant taxa, and increased sampling of molecular data for extant taxa will also further improve future studies of varanid systematics.

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APPENDIX 1

COMPARATIVE MATERIAL OF VARANID-LINEAGE MATERIAL, SUPPLEMENTARY TO CONRAD (2008).

Institutional abbreviations: AMNH, American Museum of Natural History; FMNH, Field Museum of Natural History; IGM, Institute of Geology, Mongolian Academy of Sciences, Ulaanbaatar, Mongolia

Aiolosaurus oriens IGM 3/171; fossil varanoid *Ovoogurvel*; *Saniwa ensidens* FMNH PR 2378, FMNH PR 2380; *Telmasaurus grangeri* AMNH FR6643; *Varanus albigularis* AMNH R-47726, AMNH R47725, FMNH 17142, FMNH 22354; *Varanus prisca* AMNH FR-1968, AMNH FR-6302, AMNH FR-6303, AMNH FR-6304; *Varanus rudicollis* AMNH R-141071; *Varanus salvator* AMNH R142471, FMNH 31358

APPENDIX 2

ADDITIONAL VARANID CODINGS

Here we offer the codings for *Saniwa ensidens* and the species of *Varanus* added here to the matrix compiled by Conrad (2008) and Norell et al. (2008). Note that both these components of the data matrix may be cut from the pdf available (free) from <http://library.amnh.org>.

Saniwa ensidens

1100?10001	110?000001	?130?1?110
?100000?0	1111001100	?1?1002000
????0?001	0110010?00	0100000110
00110?1001	10?-101110	0100201110
0001010?00	?0000020??	?010???0?0
?01?????1?	?00?0?001	1?????0000
01????00??	?1?011??01	000-101101
1202001100	2??000???1	2012021-01
12110?0?00	0211001000	111?002???
0?0200000-	1001??0000	00???0????
0?0?0-0-0-	0?????????	???????????
???????????	???????????	???????????
???3???????	??0	

Varanus albigularis

2100010001	1200001001	0130010110
1010000-00	1111001100	11-1002100
110-000011	0211010000	0100000110
0011021001	100-101111	1100101210
0001010100	00000020-1	1010001010
1010000011	2100000001	1010000000
01020-0001	0110110001	000-101101
1512001100	2010001101	2012021-01
1211010000	0211001000	1110002000
000200000-	1001100000	00000?1-1
0000?0?00?	00000?????	0?????????
???????????	???????????	???????????
???5000010	220	

Varanus gilleni

1100010001	120000100?	??30011100
1010000-?0	111100110-	12-1002000
110-000011	0?11010000	0000020110
0011021001	100-101110	1100101210
0001010?00	0000002?0?	?0?00?1010
1010000011	?100000001	1010000000
01120-0011	0110110001	000-100101
1202001100	201000???1	20?2021-??
?2?10100?0	021100?000	11?002000
0??200000-	100???0000	??0000?1-1
0000?0?00?	00000?????	0?????????
???????????	???????????	???????????
???90000?0	?10	

Varanus rudicollis

3100010001	1100001001	0130011110
1010000-00	1111001100	12-1002000
110-000011	0211010000	0010020110
0011021001	100-101110	1100101210
0001010000	0000002001	0010001010
1010000011	2000000001	1010000000
01120-0001	0110110001	000-100101
1202001100	2010001101	2022021-11
1211010000	0211001000	1111002000
001200000-	1001110000	01?000?1-1
0000?0?000	01000?????	0?????????
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???{89}000010	?10	

Varanus salvator

2100010001	1200001001	1130011110
1010000-00	111100110-	12-1002000
110-000011	0111010000	0110000110
0011021001	100-101110	1100101210
0001010000	00000021-1	1000001010
10100???11	2000000001	1000000000
01120-0011	0110110001	000-100101
1202001100	201000???1	2022021-01
1211010000	0211001000	1110002000
010200000-	100???0000	010000?1-1
0000?0?00?	00000?????	0?????????
???????????	???????2???	???????????
???80000?0	?10	

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