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The phylogeny of varanoid lizards and the affinities of snakes

MICHAEL S. Y. LEE

Zoology Building A08, School of Biological Sciences, University of Sydney, N.S.W. 2006, Australia

CONTENTS

SUMMARY

Evidence that platynotan squamates (living varanoid lizards, snakes and their fossil relatives) are monophyletic is presented. Evolutionary relationships within this group are then ascertained through a cladistic analysis of 144 osteological characters. Mosasauroids (aigialosaurs and mosasaurs), a group of large marine lizards, are identified as the nearest relatives of snakes, thus resolving the long-standing problem of snake affinities. The mosasauroid–snake clade (Pythonomorpha) is corroborated by 40 derived characters, including recumbent replacement teeth, thecodonty, four or fewer premaxillary teeth, supratemporal–prootic contact, free mandibular tips, crista circumfenestralis, straight vertical splenio-angular joint, loss of posterior ramus of the coronoid, reduced basipterygoid processes, reduced interpterygoid vacuity, zygosphene–zygantral articulations, and absence of epiphyses on the axial skeleton and skull. After mosasauroids, the next closest relatives of snakes are varanids (*Varanus*, *Saniwa* and *Saniwides*) and lanthanotids (*Lanthanotus* and *Cherminotus*). Derived features uniting varanids and lanthanotids include nine cervical vertebrae and three or fewer pairs of sternal ribs. The varanid–lanthanotid–pythonomorph clade, here termed Thecoglossa, is supported by features such as the

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anteriorly positioned basal tubera, and the loss of the second epibranchial. Successive outgroups to thecoglossans are *Telmasaurus*, an unresolved polytomy (*Estesia*, Gobidermatidae and Helodermatidae), *Paravaranus* and *Proplatynota*. The 'necrosaurs' are demonstrated to be an artificial (polyphyletic) assemblage of primitive platynotans that are not particularly closely related to each other.

Snakes are presumed to have evolved from small, limbless, burrowing lizards. The inability of previous analyses to resolve the affinities of snakes has been attributed to extensive convergence among the numerous lineages of such lizards. The present study contradicts this claim, demonstrating that the problem is due instead to omission of critical fossil taxa. No modern phylogenetic analysis of squamate relationships has simultaneously included *both* mosasauroids and snakes: previous studies have therefore failed to identify the mosasauroid–snake association and the suite of derived characters supporting it. Mosasauroids are large aquatic animals with well-developed appendages, and none of the derived characters uniting mosasauroids and snakes is obviously correlated with miniaturization, limb reduction or fossoriality. Recognition that mosasauroids, followed by varanids and lanthanotids, are the nearest relatives of snakes will also facilitate studies of relationships within snakes, which until now have been hampered by uncertainty over the most appropriate (closely related) lizard outgroups.

1. INTRODUCTION

It has long been known that snakes are somehow related to 'lizards' (e.g. Daudin 1803). However, the exact nature of this relationship, namely which 'lizards' are most closely related to snakes, has been difficult to determine more precisely (e.g. Bellairs 1972; Arnold 1984; Rage 1982, 1987; Estes *et al*. 1988; Rieppel 1988; Greer 1990; Cundall *et al*. 1993). As detailed in a recent review (Rieppel 1988), many disparate groups of squamates have been proposed to be snake ancestors, e.g. scincomorphs, varanids, mosasauroids and amphisbaenians, but the evidence for each of these hypotheses has been inconclusive. The only comprehensive analysis of squamate interrelationships performed to date (Estes *et al*. 1988) could only conclude that snakes were 'Scleroglossa *incertae sedis*', i.e. snakes belong somewhere within a large clade composed of all squamates except iguanians. This absence of an adequate phylogenetic perspective has made it extremely difficult to evaluate conflicting ideas about the evolutionary biology of snake origins: for instance, whether they arose in an aquatic (Nopcsa 1908, 1923), fossorial (Walls 1942; Underwood 1957*a*, 1970), or sheltering (Bellairs 1972; Shine 1986) habitat. Thus, as recently as 1987, Rage concluded that 'both the origin of snakes and the relationships between snakes and lizards at this time remains unknown' (p. 53).

Previous attempts to resolve the affinities of snakes within squamates have either considered a limited number of taxa, or a limited number of characters. For instance, Estes *et al*. (1988) identified many phylogenetically informative characters but only coded them for extant squamates, largely excluding fossil forms from their analysis. Many of these fossil squamates have been previously proposed to be related to snakes (e.g. Cope 1869, 1878). Similarly, Pregill *et al*. (1986) and Rieppel (1980*a*) identified many taxonomically significant characters in Anguimorpha – the group of squamates often considered to contain snakes (e.g. McDowell & Bogert 1954; Schwenk 1988) – but did not include snakes in their analysis. Conversely, Rieppel (1988) discussed a large number of living and fossil squamate taxa, but only considered 19 characters, rejecting many of these traits as uninformative.

It should be emphasized that the scope of the problem and state of knowledge at the time forced the above studies to be incomplete. For instance, Estes *et al*. (1988) attempted the first comprehensive cladistic analysis of all the squamate families, and relationships within Squamata at the time were so poorly known that including fossil, as well as recent taxa, would have been prohibitively difficult. Although, as a result of the problems just discussed, previous studies failed to resolve the affinities of snakes, in identifying many potentially useful characters, and in providing a broad (if tentative) outline of squamate interrelationships, they laid vital groundwork for the present study.

Here, I summarize the evidence that indicates that snakes are part of Platynota (the clade consisting of living varanoids and their fossil relatives). I then undertake a comprehensive phylogenetic analysis of this clade, including all recent and important fossil taxa. Relevant traits used in previous studies have been re-evaluated and, if considered valid, included. However, the distribution of these characters has been reinterpreted by scoring them for taxa not considered in those analyses. Also, examination of specimens has indicated that previous studies have wrongly interpreted the distribution of some of these characters: they have been modified accordingly. More importantly, however, many new characters were identified during the course of this study. This is partly because the inclusion of a larger number of relevant taxa increases the number of potentially informative characters. For example, previous studies excluded fossil taxa (e.g. Estes *et al*. 1988; Rieppel 1980*a*), and interpreted many characters as autapomorphies of snakes, and thus, uninformative with respect to their position within squamates. In the present study, however, fossil forms are included. Many of these snake 'autapomorphies' can now be identified in some of these fossil forms, and are now potential synapomorphies uniting snakes and one or more squamate taxa. In addition, during the course of this study I have attempted to identify as many phylogenetically informative osteological characters as possible, rather than rely purely

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on the characters used in other studies. As has been shown elsewhere, the latter approach can severely bias phylogenetic analyses (Lee 1995).

My reasons for limiting the present study to osteological characters are as follows: (i) most of the taxa in this analysis are extinct, and thus are known from osteology alone; (ii) the distribution of many soft anatomical characters is poorly known, even in living taxa; (iii) osteological characters usually form the bulk of the characters in morphological data sets (e.g. 130 out of the 148 characters in Estes *et al.* 1988). Of course, osteological characters represent only a subset of the total amount of phylogenetic information available, albeit a fairly large subset. It is hoped that the conclusions of this analysis will be supplemented and tested in the future by the addition of information derived from similarly comprehensive studies of soft anatomy, behaviour and molecular sequences from living forms.

The present analysis, therefore, attempts to resolve the affinities of snakes by considering a more complete set of taxa, and a larger number of characters, than previous studies. As will become clear, this enlarged data set reveals that there is very strong evidence indicating that snakes are related to marine varanoids (aigialosaurs and mosasaurs). Although this arrangement was suggested long ago by Cope (1869, 1878), recent workers using modern phylogenetic methods have not been able to find much support for it, or for any other theory of snake affinities. This paper therefore presents a well-corroborated hypothesis of ophidian relationships presented within a modern (cladistic) framework. These phylogenetic conclusions should pave the way for a much more fruitful discussion of the evolutionary biology of snake origins than has hitherto been possible.

2. MONOPHYLY OF THE INGROUP (PLATYNOTA)

Helodermatids, *Lanthanotus* and *Varanus*, and all other (fossil) taxa more closely related to these forms than to other extant anguimorphs (xenosaurids and anguids), form the ingroup used in this analysis (see section 4). The taxon name Platynota is here applied to this group, and Varanoidea is used to refer to crown-clade platynotans (Pregill *et al.* 1986). As there is considerable evidence that snakes are part of Platynota (see below), snakes have also been included in the ingroup. Pregill *et al.* (1986) and Estes *et al.* (1988) listed numerous synapomorphies uniting extant platynotans (*Heloderma*, *Lanthanotus* and *Varanus*). Of these synapomorphies, the following can be confirmed to be present also in the fossil taxa included in this analysis, and in snakes, and thus support the monophyly of the ingroup (Platynota).

1. Frontals with descending processes located in their middle and anterior region (present, but poorly-developed, in *Paravaranus*: Borsuk-Bialynicka 1984 p. 15).
2. Maxilla does not reach posterior region of orbit.
3. Hypoglossal and vagal foramina located very close to jugular foramen.
4. Marginal teeth pointed, recurved and widely spaced.
5. Replacement teeth erupt posterolingual to functional teeth ('varanid'-type tooth replacement).
6. Premaxillary teeth smaller than maxillary teeth (convergent in some lacertoid scincomorphs).
7. Absence of resorption pits at the base of teeth (the resorption pit in mosasaurs is confined to the pedicel and does not encroach onto the tooth base).
8. Loose splenial-dentary contact, with much intervening connective tissue.
9. Cranial osteoderms highly fragmented or absent.

In addition, I have been able to identify another character supporting platynotan (i.e. ingroup) monophyly.

10. Extensive medial exposure of angular.

There are also several characters supporting monophyly of a clade consisting of extant platynotans (*Heloderma*, *Lanthanotus*, *Varanus* and snakes). However, these cannot be scored in many or all fossil taxa, either because of poor preservation or because they are soft anatomical or behavioural traits.

11. Loss of carotid duct (Estes *et al.* 1988; Greer 1990).
12. Free part of tongue notched at least 20–40% (Estes *et al.* 1988).
13. Loss of caudal autotomy septa within caudal vertebrae (Estes *et al.* 1988; Greer 1990). 'Pseudautotomy' has been reported in some snakes (Slowinski & Savage 1995), but these taxa lack distinct autotomy septa and tail regenerative abilities.
14. Clavicles rod-like, i.e. not expanded proximally (not determinable in snakes).
15. Shortened anterior process of interclavicle (not determinable in snakes).
16. Male combat dance (Greer 1990).
17. Absence of short-term colour change ability (Greer 1990).

Although snakes have been tentatively included in the ingroup, two problematical limb-reduced squamate taxa, amphisbaenians and dibamids, have been excluded. The platynotan affinities of snakes have been suggested repeatedly (e.g. Cope 1869; Camp 1923; Nopcsa 1923; McDowell & Bogert 1954; McDowell 1972; Bellairs 1972). Recent cladistic analyses of squamate phylogeny have supported this view. Based on morphological data, Schwenk (1988), and, more tentatively, Estes *et al.* (1988), agreed that the best hypothesis of snake relationships is that they have anguimorph affinities, most probably lying within Platynota. Forstner *et al.* (1995) reached similar conclusions based on molecular data. However, unlike snakes, the inclusion of amphisbaenians and dibamids within Platynota is highly unlikely, and the current consensus is that both are scincomorphs. Schwenk (1988) and Wu *et al.* (1995) found evidence uniting amphisbaenians and scincomorphs. Estes *et al.* (1988) could not resolve the position of amphisbaenians, but noted that there was little evidence allying them with anguimorphs. Similarly, Estes *et al.* (1988), Schwenk (1988), and Rieppel (1984) all agreed with the long-

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held view that the most likely position of dibamids is within Scincomorpha. Greer (1985) concluded that dibamids shared the largest number of derived traits with amphisbaenians, although he emphasized that many other arrangements had almost as much support. Given that amphisbaenians are probably scincomorphs, the hypothesis of dibamid–amphisbaenian relationships is not necessarily inconsistent with the traditional, dibamid–scincomorph pairing. As discussed above, snakes have all the diagnostic traits of platynotans, while evidence for alternative relationships (reviewed in Rieppel 1988) is not particularly strong. In contrast, amphisbaenians have only four or five (1, 2, 5, 7 and in *Bipes* only, 14), and dibamids have only two (1 and 2), while stronger evidence places both taxa within Scincomorpha. Thus, snakes have been included in the ingroup, but amphisbaenians and dibamids have been excluded.

Bainguis was suggested by Borsuk-Bialynicka (1984) to belong to the ingroup (Platynota). It is known from a badly damaged skull, in which many sutures are invisible due to osteodermal encrustation and/or poor preservation. Some postcranial fragments from another individual have been assigned to this taxon on the basis of osteodermal similarities. A smaller skull has also been assigned (dubiously) to this taxon because it exhibits similar proportions. Thus, it is not certain that the three specimens really belong to the same species. Furthermore, even if the specimens are correctly associated, whether *Bainguis* belongs to the ingroup or outgroup cannot be ascertained: it has been described as exhibiting both scincomorph and anguimorph traits (Borsuk-Bialynicka 1984). As it is so imperfectly known, its inclusion or exclusion from the analysis is unlikely to influence the topology of the resultant tree. I have also been unable to examine the material first-hand. *Bainguis* has therefore not been included in the analysis at this stage.

Parviraptor was recently described by Evans (1995) as a probable basal platynotan. However, only a few elements (fragments of the palate and skull roof and vertebrae) have been identified for this genus. Because it is so imperfectly known, and its identity as an anguimorph is not beyond doubt (Evans 1995 p. 48), I have also not included this taxon in the analysis at this time. Further study of the material of this taxon in the British Museum, University College London, U.K., and Freie Universität, Berlin, Germany, is required before its relationships can be comprehensively ascertained.

Dolichosaurs – long-necked, marine varanoid-like squamates – might also be part of the ingroup. However, existing descriptions are old, very brief and probably inaccurate in many respects (e.g. Owen 1851). Furthermore, the material is currently being restudied by Dr Gordon Bell and Michael Polcyn (South Dakota School of Mines, U.S.A.) and Dr Michael Caldwell (Field Museum, Chicago, U.S.A.). For these reasons, I have not included dolichosaurs in the current analysis, but will await forthcoming descriptions, which should allow further testing of the conclusions of this study.

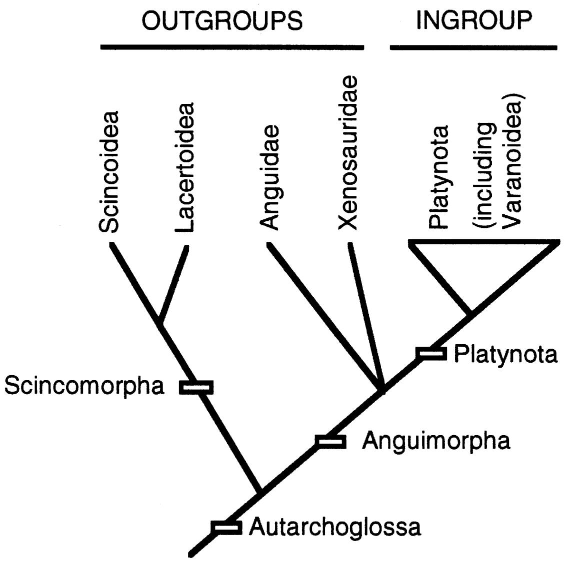

Figure 1. The higher level phylogenetic assumptions of this study, after Estes *et al.* (1988). The nearest relatives of the ingroup (Platynota) are xenosaurids and anguids. Scincomorphs are the next closest outgroup. Platynota, Xenosauridae and Anguidae form an unresolved trichotomy, with Scincomorpha being the sister group to all three taxa.

3. POLARITY AND OUTGROUPS

In order to ascertain the polarity of characters within Platynota, I have adopted the outgroup arrangement suggested by the analysis of Estes *et al.* (1988) (see figure 1). Thus, the nearest outgroups to the Platynota are the Anguidae and Xenosauridae. However, these three taxa form an unresolved trichotomy. The next outgroup is the Scincomorpha, consisting of the Lacertoidea and Scincoidea. The characters supporting this higher-level arrangement are listed in Estes *et al.* (1988). As table 1 shows, for most of the characters, the same character state is present in all outgroups, and thus, polarity is unequivocal. In other characters, one character state is present in all anguids, xenosaurids, and at least some scincoids and some lacertoids: these characters could also tentatively be polarized. The primitive state in all these characters is scored as 0. Characters 14, 23, 41, 52, 62, 84, 85, 101, 132 and 143, however, were so variable in the outgroups that the primitive state for the ingroup could not be determined.

4. TERMINAL TAXA

The outgroup and ingroup terminal taxa used in this analysis are briefly discussed below. All are monophyletic, with the exception of Aigialosauridae, which is a metataxon, there being no evidence for either monophyly or paraphyly (Archibald 1994). The relationships within each terminal taxon are summarized, as this information is relevant for determining the primitive state of characters polymorphic within terminal taxa. Serpentes (snakes) consists of two highly divergent sister taxa, the worm-like scolecophidians

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Table 1. *The character–taxon matrix compiled in this study. The 144 characters are numbered as in the main text. The four outgroup taxa were used to infer the primitive state in the ingroup. The 'root' taxon was coded for all primitive states and used to root the tree in the parsimony analysis. A question mark denotes that the character state is not yet known in the taxon, whereas N means the character is not applicable in that taxon (e.g. many limb characters for snakes). Where intra-taxon polymorphism exists, but the primitive state can be reasonably inferred, the taxon has been coded for that state. Only if the primitive state is uncertain has a taxon been coded as polymorphic. A means either state 0 or 1 is primitive for a taxon, B means either state 1 or 2 is primitive, C means any of states 0, 1 and 2 might be primitive*

	Characters																													
Taxa	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
Outgroups																														
Lacertoidea	0	0	0	0	0	0	0	0	0	0	0	0	0	A	0	0	0	0	0	0	A	0	A	0	0	0	0	0	0	0
Scincoidea	0	0	0	0	0	0	0	0	0	0	0	0	0	A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Anguidae	0	0	0	0	0	0	0	0	0	0	0	0	0	A	0	0	0	0	0	0	0	A	0	A	0	0	0	A	0	0
Xenosauridae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
'Root'	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0
Ingroups																														
Proplatynota	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	?	0	?	0	0	?
Paravaranus	0	0	1	0	?	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	?	0	?	0	1	0
Helodermatidae	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	1	1	1	0	0	1	0	0	0	0
Gobidermatidae	0	0	0	0	0	0	0	0	1	0	0	0	0	A	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Estesia	0	0	0	1	0	0	0	0	1	0	0	1	1	1	0	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0
Telmasaurus	?	?	?	?	0	?	?	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	A	0	0	1	0	0	?	0
Saniwa	?	?	?	1	?	0	0	1	1	0	1	0	0	?	?	?	0	0	0	0	0	0	0	0	0	?	?	0	0	0
Saniwides	0	0	0	?	?	0	0	1	1	0	?	0	0	1	0	?	0	0	0	0	0	0	1	0	0	?	0	0	0	0
Varanus	0	0	A	2	0	0	0	1	1	0	1	0	0	1	1	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0
Cherminotus	0	0	0	1	0	0	0	?	1	0	?	0	0	1	0	?	0	0	0	0	0	1	0	0	0	?	0	0	0	0
Lanthanotus	0	0	1	1	0	0	0	1	1	0	1	0	1	1	0	0	0	0	0	0	1	1	1	0	0	1	0	0	0	0
Aigialosauridae	1	1	0	2	0	1	0	1	1	0	?	1	0	0	?	0	0	?	0	0	0	0	1	0	1	1	?	0	1	1
Mosasauridae	1	1	0	2	0	1	0	1	1	0	2	1	0	0	0	0	0	1	0	0	0	0	1	0	1	1	1	0	1	1
Scolecophidia	0	0	A	1	1	0	1	0	1	1	N	0	N	1	2	1	1	1	1	1	1	1	N	1	1	0	1	1	N	0
Alethinophidia	0	0	0	1	1	0	1	0	A	1	2	0	0	1	2	1	1	1	1	1	1	1	0	1	1	1	1	1	0	0

	Characters																													
Taxa	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60
Outgroups																														
Lacertoidea	0	0	0	A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Scincoidea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Anguidae	A	0	0	0	0	A	0	A	0	0	A	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0
Xenosauridae	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
'Root'	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0
Ingroups																														
Proplatynota	?	?	0	0	0	?	?	?	?	0	0	?	0	?	?	?	?	?	?	0	1	?	0	0	0	0	0	0	0	0
Paravaranus	?	?	0	0	0	?	0	0	0	0	0	?	0	0	?	0	0	0	0	?	1	?	0	0	0	0	1	0	0	0
Helodermatidae	0	0	0	1	0	N	0	1	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0
Gobidermatidae	0	0	0	0	0	?	0	0	0	0	0	?	0	0	?	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0
Estesia	0	0	0	0	0	0	0	0	0	0	0	?	0	0	?	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0
Telmasaurus	1	0	0	0	0	?	?	?	0	0	0	?	0	0	?	0	0	0	0	?	?	?	0	0	0	?	1	0	0	0
Saniwa	1	0	0	0	0	?	?	?	1	0	?	?	?	?	?	?	?	0	?	?	1	?	0	0	0	0	1	0	0	0
Saniwides	1	0	0	0	0	0	?	?	1	0	0	?	0	0	?	0	1	0	0	?	1	?	0	0	0	1	1	0	0	1
Varanus	1	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	1	0	1	0	1	2	0	0	0	1	1	0	0	1
Cherminotus	1	0	0	0	0	?	0	0	1	0	0	?	0	0	?	0	1	0	1	0	1	?	0	0	0	0	1	0	0	0
Lanthanotus	1	0	0	0	0	N	0	0	1	0	0	1	0	0	1	0	1	0	2	0	0	2	0	0	0	0	1	0	0	0
Aigialosauridae	0	1	1	1	1	1	?	?	?	0	?	?	?	?	?	?	?	?	?	?	1	?	?	?	?	?	?	?	?	?
Mosasauridae	0	1	1	1	1	1	1	1	1	0	0	1	0	1	1	0	0	0	2	0	1	0	0	0	0	0	1	1	0	0
Scolecophidia	2	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	2	1	1	3	1	1	1	N	A	1	1	N
Alethinophidia	2	0	1	1	1	1	N	1	1	1	1	1	1	1	1	1	0	1	2	1	A	3	1	1	1	0	0	1	1	A

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Table 1 (*cont*.)

	Characters																													
Taxa	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90
Outgroups																														
Lacertoidea	0	0	0	0	0	A	0	0	A	A	0	0	0	0	0	0	A	0	0	0	0	0	0	1	0	0	0	0	0	0
Scincoidea	0	0	0	0	0	0	0	0	0	A	0	0	0	0	0	0	A	0	0	0	0	0	0	1	0	0	0	0	0	0
Anguidae	0	A	0	0	0	A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Xenosauridae	0	A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
‘Root’	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	0	0	0	0	0
Ingroups																														
Proplatynota	?	?	0	0	0	?	0	?	0	?	0	0	0	0	0	0	1	0	0	0	0	?	?	0	?	0	0	0	1	0
Paravaranus	0	0	0	0	?	0	1	?	0	0	?	0	0	?	0	?	?	?	0	0	?	?	?	0	?	0	0	0	1	?
Helodermatidae	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1	1	0
Gobidermatidae	0	?	0	?	0	?	1	?	0	0	0	0	0	0	0	0	1	0	0	0	0	?	?	0	?	0	1	1	1	0
Estesia	0	0	0	0	0	1	1	0	0	0	0	?	?	0	0	0	1	0	0	0	0	?	?	0	?	0	1	1	1	?
Telmasaurus	?	0	0	0	?	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	1	1	?	?
Saniwa	0	0	0	1	?	0	1	?	?	0	0	?	0	0	0	?	1	?	0	0	0	?	?	0	1	0	1	1	1	?
Saniwides	?	0	0	1	0	1	1	?	0	0	0	0	0	0	0	0	1	0	0	0	0	?	?	0	0	0	?	1	1	?
Varanus	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	1	1	1	0
Cherminotus	0	?	1	0	0	1	1	?	0	0	0	0	0	0	0	?	1	0	0	0	0	?	?	0	0	0	?	?	1	?
Lanthanotus	0	0	1	0	0	1	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0	1	1	0	0	0	1	1	1	0
Aigialosauridae	0	?	?	?	0	?	?	1	1	1	1	1	1	1	?	0	1	1	1	1	1	1	1	1	1	?	1	1	2	?
Mosasauridae	0	1	0	0	0	0	N	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	2	1
Scolecophidia	1	1	N	0	1	0	N	1	1	1	0	A	1	A	A	1	A	N	1	1	2	0	2	0	0	2	1	0	1	1
Alethinophidia	1	1	N	0	1	0	N	1	1	1	0	1	1	A	1	1	0	1	1	1	2	0	2	0	0	2	1	0	1	1

	Characters																													
	91	92	93	94	95	96	97	98	99	100	101	102	103	104	105	106	107	108	109	110	111	112	113	114	115	116	117	118	119	120
Outgroups																														
Lacertoidea	0	0	0	A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Scincoidea	0	0	0	A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Anguidae	0	0	0	0	0	0	0	0	0	0	A	0	0	0	A	0	0	0	0	0	0	0	0	0	0	A	0	0	A	0
Xenosauridae	0	0	0	0	0	0	0	0	0	0	A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
‘Root’	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ingroups																														
Proplatynota	0	0	1	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Paravaranus	?	0	1	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Helodermatidae	0	1	1	A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Gobidermatidae	0	1	?	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Estesia	0	1	1	0	0	0	0	0	0	?	?	0	?	?	0	?	?	?	0	0	?	?	?	?	?	?	?	?	?	?
Telmasaurus	?	?	1	0	0	0	1	0	0	?	?	0	?	?	?	?	?	?	0	0	?	0	?	?	?	?	?	?	?	?
Saniwa	0	0	1	0	0	1	1	0	1	0	0	0	1	1	1	0	0	?	0	0	?	0	0	0	0	0	1	?	0	0
Saniwides	0	1	1	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Varanus	0	1	0	1	N	1	0	0	1	0	0	0	1	1	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0
Cherminotus	?	1	?	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Lanthanotus	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0
Aigialosauridae	1	0	?	?	?	0	2	0	0	0	1	0	0	0	1	?	1	0	1	?	0	0	0	1	1	1	1	A	0	0
Mosasauridae	1	0	0	0	1	0	2	1	0	0	1	0	0	0	1	1	1	0	1	1	0	0	1	1	1	1	1	?	0	1
Scolecophidia	1	2	0	1	N	0	2	0	0	1	1	1	0	N	0	1	0	N	0	1	1	1	1	0	0	0	N	1	1	N
Alethinophidia	1	C	1	A	1	0	2	1	0	1	1	1	0	N	1	1	0	N	0	1	1	1	A	0	0	0	N	1	1	N

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Table 1 (*cont.*)

Taxa	Characters 121	122	123	124	125	126	127	128	129	130	131	132	133	134	135	136	137	138	139	140	141	142	143	144
Outgroups																								
Lacertoidea	0	0	0	0	0	A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	A	0	0
Scincoidea	0	0	0	0	0	0	0	0	0	0	0	A	0	0	0	0	0	0	0	0	0	A	0	0
Anguidae	0	0	0	0	0	A	0	0	0	0	0	A	0	0	0	0	0	0	0	0	0	0	A	0
Xenosauridae	0	0	0	0	0	0	0	0	0	0	0	A	0	0	0	0	0	0	0	0	0	0	1	0
‘Root’	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	?	0
Ingroups																								
Proplatynota	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Paravaranus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?
Helodermatidae	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	1	0	0
Gobidermatidae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?
Estesia	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Telmasaurus	?	?	?	?	?	?	0	0	0	1	0	0	0	0	0	0	?	0	0	0	?	?	?	0
Saniwa	?	?	?	0	1	0	?	0	1	0	0	0	0	0	0	1	0	?	0	?	?	?	0	
Saniwides	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?
Varanus	0	1	0	0	1	1	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	1	A
Cherminotus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?
Lanthanotus	0	1	0	0	0	1	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	1	1	0
Aigialosauridae	0	0	1	0	0	0	0	1	0	2	0	1	1	0	1	1	0	0	1	1	?	?	?	1
Mosasauridae	0	0	1	0	0	0	0	1	0	2	1	1	1	0	1	1	0	1	1	1	0	1	?	1
Scolecophidia	1	N	N	1	N	N	1	N	1	2	1	1	N	1	1	N	N	1	N	1	1	N	1	1
Alethinophidia	1	N	N	1	N	N	1	N	1	2	1	1	N	1	1	N	N	1	N	1	1	N	1	1

and the more typically snake-like alethinophidians. Scolecophidians and alethinophidians possess different character states for many characters, making the primitive condition in snakes difficult to determine. Accordingly, Serpentes has been subdivided into two terminal taxa, Scolecophidia and Alethinophidia, and these taxa have been coded with their respective character states.

Terminal taxa with no living representatives are marked with an asterisk. Autapomorphies of all terminal ingroup taxa are listed, because, with the addition of fossil taxa in the ingroup, many of the autapomorphies for *Heloderma*, *Lanthanotus* and *Varanus* proposed in Estes *et al.* (1988) occur in other (fossil) taxa and are thus not diagnostic of these genera.

(*a*) *Outgroup taxa*

(i) *Scincoidea*

The Scincoidea consists of three taxa, Scincidae, Cordylidae and Gerrhosauridae. Characters supporting scincoid monophyly are listed in Estes *et al.* (1988). It should be noted, however, that another analysis (Presch 1988) concluded that the three scincoid taxa do not form a monophlyetic group: however, that analysis considered fewer characters and taxa, and was emphasized by that worker to be preliminary. Estes *et al.* (1988) and Lang (1991) tentatively suggest that cordylids and gerrhosaurids are most closely related, together forming the sister group of scincids.

(ii) *Lacertoidea*

The Lacertoidea is a large clade consisting of four monophyletic families: Xantusiidae, Lacertidae, Teiidae and Gymnophthalmidae (= Microteiidae). Estes *et al.* (1988) list several characters corroborating the monophyly of lacertoids. As discussed above, although Presch (1988) reached different conclusions, the hypothesis of relationships proposed by Estes *et al.* (1988) appears to be better supported (Arnold 1989): xantusiids (lacertids (teiids, gymnophthalmids)).

(iii) *Anguidae*

The anguidae consists of the limbed diploglossines, gerrhonotines and (extinct) glyptosaurs, and the limbless anniellines and anguines. Anguid monophyly is well corroborated, despite some suggestions to the contrary (Rieppel 1980*a*). Characters diagnosing this group are discussed in Gauthier (1982) and Estes *et al.* (1988). The most recent comprehensive phylogenetic analyses of this group is by Gauthier (1982) who proposed the following scheme: anniellines (anguines (glyptosaurs (gerrhonotines, diploglossines))). Good (1987*a*) also concurred that anniellines were the sister group to all other anguids.

(iv) *Xenosauridae*

This clade consists of two very disparate sister taxa, *Xenosaurus* and *Shinisaurus*. Diagnostic characters are discussed in Rieppel (1980*a*), Gauthier (1982) and Estes *et al.* (1988).

(*b*) *Ingroup taxa*

(i) *Proplatynotia**

Examination of Borsuk-Bialynicka’s (1984) description suggests that this taxon has the following autapomorphies.

1. Anteroposteriorly elongated suborbital fenestra.

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2. Long, narrow interptergyoid vacuity.
3. Very large, circular premaxillary foramen.
4. Internal naris extends posteriorly well beyond posterior tip of vomer.

(ii) *Paravaranus**

Examination of Borsuk-Bialynicka's (1984) description suggests that this taxon has the following autapomorphies.

1. Nasals with median crest.
2. W-shaped frontoparietal suture.
3. Parietal foramen on frontoparietal suture (convergent in iguanians and teiids).
4. Pterygoids almost contact vomers (Borsuk-Bialynicak 1984).
5. Parabasiphenoid with median fontanelle on the ventral surface, near the suture with the basioccipital.

Paravaranus was excluded from the Anguimorpha by Borsuk-Bialynicka on the basis of the lack of three proposed synapomorphies of anguimorphs: a long and narrow alar process of the prootic, a narrow distal end of the paroccipital process and a trapezoidal sphenoccipital suture. The latter two traits are problematical, as I can detect no clear-cut differences between anguimorphs and non-anguimorphs in the relevant areas. The long narrow alar process of the prootic is not found in some basal anguimorphs (e.g. *Xenosaurus*) and, furthermore, also occurs in many non-anguimorph squamates. Thus, none of these traits proposed to exclude *Paravaranus* from the Anguimorpha is valid.

Conversely, *Paravaranus* exhibits the following platynotan synapomorphies: long, sharp, recurved, widely-spaced teeth, descending processes of the frontals (weakly developed only) and maxilla not reaching posterior region of orbit. It cannot be scored for the other platynotan traits. Based on this, it is included in the present analysis.

(iii) *Helodermatidae*

The following osteological autapomorphies diagnose the two extant species of *Heloderma*, *H. suspectum* (the Gila monster) and *H. horridus* (the Beaded Lizard).

1. Steep nasal process of maxilla (Pregill *et al.* 1986; Estes *et al.* 1988).
2. Maxillary dental shelf curved medially (Pregill *et al.* 1986; Estes *et al.* 1988).
3. Large anterior process of ectopterygoid, covering palatine in ventral view.
4. Dentary teeth with venom grooves (Pregill *et al.* 1986; Estes *et al.* 1988).
5. Hypapophyses lost from third and subsequent cervical vertebrae (Pregill *et al.* 1986; Estes *et al.* 1988).
6. Neural spines narrow and tall (Pregill *et al.* 1986; Estes *et al.* 1988).
7. Short tail, 25–40 caudal vertebrae (Pregill *et al.* 1986; Estes *et al.* 1988).
8. Thick, hexagonal osteoderms covering head and body (Pregill *et al.* 1986; Estes *et al.* 1988).

The two studies cited above list many other osteological autapomorphies, but noted that they were equivocal.

(iv) *Gobidermatidae** (Parviderma *and* Gobiderma)

These two taxa are both known from only skulls. Based on the descriptions and figures in Borsuk-Bialynicka (1984), I can seen no major differences between them except for a size difference. Borsuk-Bialynicka noted that the dentary is much more curved dorsoventrally in the larger animal, *Gobiderma*. However, the curvature of the dentary increases in size and age in extant varanids, such as *Varanus niloticus*. The coronoids were also claimed to be very different in shape, but they appear to be almost identical (see Borsuk-Bialynicka 1984, figure 9, plates 5, 7 and 13). The two taxa share a distinctive (autapomorphic) pattern of tubercular osteoderms concentrated in a circular zone centred around the frontoparietal suture. The two taxa are also identical in all characters for which they can be scored in the following cladistic analysis: the only difference is that the frontals are fused in *Parviderma* but separate in some (but not all) *Gobiderma*. Furthermore, both taxa were found in the same locality and horizon. For these reasons, in this analysis I have provisionally treated the two genera as a clade and thus, a single terminal taxon (here called Gobidermatidae, based on the better–known included genus).

(v) *Estesia**

This taxon exhibits the following autapomorphies.

1. 'An extensive convex surface medial to the posterior ridge on the posterior surface of the quadrate' (Norell *et al.* 1992).
2. Small supratemporal fenestra.
3. Paroccipital process projects posterolaterally (rather than approximately laterally).
4. Ectopterygoid projects ventrally below pterygoid.
5. Basal tubera extended into long lateral process.

(vi) *Telmasaurus**

This taxon is diagnosed by a median crest extending along the frontals and anterior end of the parietals (Borsuk-Bialynicka 1984). Borsuk-Bialynicka (1984) proposed two other features: the 'waist' in the parietal is located posteriorly, and the quadrate articulates well away from the posterolateral arm of the parietal. However, in both these features, *Telmasaurus* does not appear to differ from other anguimorphs such as *Varanus*.

(vii) *Saniwa**

This taxon exhibits the following autapomorphies.

1. Proportionately large cranium.
2. Distal portion of the paroccipital process expanded ventrally.
3. Entepicondyle rectangular in shape, ectepicondylar ridge reduced distally.

(viii) *Saniwides**

Examination of Borsuk-Bialynicka's (1984) description suggests that this taxon has the following autapomorphies.

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1. Anterior end of snout greatly compressed dorsoventrally.
2. Squamosal very long (extending almost to orbit).

(ix) *Varanus*

The following osteological autapomorphies diagnose the extant genus *Varanus*, to the exclusion of putative fossil relatives identified in this cladistic analysis (figure 15), *Saniwa* and *Saniwides*.

1. Jugal very slender.
2. Long, forked palatal process of premaxilla (Rieppel 1980*a*).
3. Jugal fails to contact postorbitofrontal (Estes *et al*. 1988).
4. Palatal shelf on posterior portion of maxilla reduced (i.e. narrow).

Many other proposed autapomorphies of *Varanus* cannot be scored for *Saniwides* (characters 3 and 5 below) or for both *Saniwa* and *Saniwides* (all other characters below), and thus might transpire to diagnose a larger group.

1. Dorsal process of epipterygoid articulates with alar process of prootic (Estes *et al*. 1988) (might also be present in mosasaurs: Russell 1967).
2. Fifteen scleral ossicles (Estes *et al*. 1988).
3. Ribs absent on first five cervical vertebrae (Hoffstetter & Gasc 1968). Ribs present on the fifth and subsequent cervicals in *Saniwa*, not yet determined in *Saniwides*.
4. Very long lateral arms of the interclavicle.
5. Posterior coracoid emargination present (Estes *et al*. 1988). Absent in *Saniwa*, not yet determined in *Saniwides*.
6. Short pubis, with short, ventrally-directed symphyseal process and distally placed pubic tubercle (Estes *et al*. 1988).
7. Carpal intermedium lost (Renous-Lecuru 1973).
8. Proximal articulations of the fifth metatarsal reduced (Robinson 1975).
9. Median ridge on ventral surface of the vomers, between the openings for Jacobsen's organ.
10. Presence of a depression on the dorsal surface of the palatal shelf of the maxilla, immediately in front of the septomaxilla (termed the 'maxillary recess' by DeBraga & Carroll 1993).

Estes *et al*. (1988) list some other traits, but these were either acknowledged by these authors to be equivocal, or are shown in this study to diagnose a larger grouping including *Varanus* and its fossil relatives.

No real consensus, or even well-corroborated hypothesis, exists regarding the relationships between the species groups (subgenera) of the forty-two or so species within *Varanus*: e.g. compare Sprackland (1991) with King *et al*. (1991). Relationships within the group are currently under study by A. Kluge (Michigan, U.S.A.) and W. Böhme (Bonn, Germany).

(x) *Cherminotus**

Based on the description of Borsuk-Bialynicka (1984), I can only find one possible autapomorphy of this taxon, the greatly reduced number of marginal teeth. There are only five teeth on the maxilla, and eight on the dentary. Because both known specimens are small, this might be an ontogenetic feature. However, this taxon is clearly distinct from all other taxa included in this analysis, as it exhibits a unique combination of character states (see table 1).

(xi) *Lanthanotus*

This taxon consists of a single living species, *Lanthanotus borneensis* (the earless monitor). Osteological autapomorphies diagnostic of this taxon, excluding *Cherminotus*, identified in this cladistic analysis as its nearest relative (see figure 15), are as follows.

1. Broad palatal shelf of maxilla (Pregill *et al*. 1986). The crenulated medial edge of this shelf almost meets the vomer.
2. Orbital rims form prominent bulges on the side of the skull in dorsal view, projecting laterally well beyond the level of the snout and cheek.
3. Groove on palatine leading anteriorly from suborbital foramen.
4. Ectopterygoid with distinct notch on lateral margin.
5. Internal naris very narrow and slit-like.

As well, the following characters are unique to *Lanthanotus* but cannot yet be scored for *Cherminotus* (its presumed nearest relative, based on the results of the current analysis).

1. Six scleral ossicles (Estes *et al*. 1988).
2. Descending processes of frontals positioned near the posterior end of the frontals.
3. Second sacral rib with robust shaft (almost as robust as first sacral).
4. Sternum with only two pairs of ribs (Estes *et al*. 1988).
5. Sternum short and triangular, rather than diamond-shaped.
6. Two anterior processes on interclavicle.
7. Reduced phalangeal counts. Four phalanges on fourth digit of manus and pes, three phalanges on fifth digit of pes. The last trait also occurs in a few mosasaurs (Russell 1967).
8. Lateral plantar tubercle of fifth metatarsal situated very distally (Rieppel 1980*b*).

The other osteological traits listed in Estes *et al*. (1988) were acknowledged by these authors to be equivocal.

(xii) *Aigialosauridae**

The Aigialosauridae consists of *Aigialosaurus*, *Opetiosaurus* and *Carsosaurus*, all medium-sized lizards with incipient aquatic specializations. There is uncertainty whether *Aigialosaurus* and *Opetiosaurus* are synonymous (Caldwell *et al*. 1995; Bell 1994). Monophyly of the group is uncertain. Aigialosaurs are all very similar, but this is because they are all at approximately the same evolutionary grade, having acquired many of the cranial specializations of mosasaurs but retaining most of the generalized postcranial features typical of

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terrestrial platynotans (Carroll & DeBraga 1992). Caldwell *et al*. (1995) present weak evidence for aigialosaur monophyly, while Carroll & DeBraga (1992) present evidence, which they also acknowledged as equivocal, that the group is paraphyletic with respect to mosasaurs. In the most recent analysis (Caldwell 1996), aigialosaurs formed an unresolved polytomy with respect to mosasaurs. Accordingly, aigialosaurs are here treated as a metataxon.

(xiii) *Mosasauridae**

Mosasaurs consist of the basal genus *Halisaurus*, and three major clades, the Mosasaurinae, Tylosaurinae and Plioplatecarpinae. All are large, marine forms. The most recent phylogenetic analyses of the group (DeBraga & Carroll 1993; Caldwell 1996) have resulted in the following arrangement: *Halisaurus* (Mosasaurinae (Tylosaurinae, Plioplatecarpinae)). Characters supporting the monophyly of the Mosasauridae, extracted from a larger list in DeBraga & Carroll (1993), are as follows.

1. Posterior dorsal ribs reduced in length.
2. Glenoid posteriorly oriented.
3. Shaft of humerus short and compressed, humerus less than 2.3 times the length of the trunk centra.
4. Ulna short and articulating with 'intermedium'.
5. Carpal ossification reduced.
6. Metacarpal 5 elongated.
7. Digits flattened, limbs paddle-like.
8. Tibia and fibula short and dorsoventrally flattened.
9. Astragalus and calcaneum not attached to one another.

(xiv) *Scolecophidia*

The small, worm-like scolecophidians are often considered to be the most primitive living snakes. Although it has often been doubted that typhlopids, leptotyphlopids and anomalepids form a monophyletic Scolecophidia (e.g. McDowell & Bogert 1954; Heise *et al*. 1995), this hypothesis appears to be well corroborated by the following synapomorphies.

1. Dentary short, less than 35% of the skull length (McDowell 1987; Cundall *et al*. 1993).
2. Absence of lacrimal foramen (McDowell 1987).
3. Pterygoid does not approach jaw joint (List 1966; Cundall *et al*. 1993).
4. Quadrate slants very sharply anteroventrally, so that the element is almost horizontal and the jaw condyle is far anterior to the cephalic condyle.
5. Quadrate tendon of *adductor mandibulae externus pars profundus* reduced or absent (Cundall *et al*. 1993).
6. Optic foramen entirely enclosed within frontal.
7. Third type of fundic gland (Rieppel 1988).
8. Multilobed liver (Underwood 1967; Groombridge 1979; Rieppel 1988).
9. Retina composed of rods only (Underwood 1967; Rieppel 1988).
10. Presence of *musculus geniomucosalis* (Groombridge 1979; Rieppel 1988).

Relationships between the three scolecophidian families are uncertain: Kluge (1991) suggested that typhlopids and leptotyphlopids were most closely related, while Rieppel (1988) concluded that typhlopids and anomalepids were most closely related.

(xv) *Alethinophidia* (*including* Dinilysia*)

The monophyly of alethinophidians ('advanced snakes', here including the fossil form *Dinilysia*) is supported, albeit weakly, by three characters.

1. Subvomerine process of palatine (see Cundall *et al*. 1993).
2. Vertical quadrate shaft (Rieppel 1988).
3. Enclosure of optic foramen between parietal and frontal (Rieppel 1988).

Additionally, many characters corroborate a more restricted clade consisting of all alethinophidians except *Dinilysia*.

1. 'Laterosphenoid' element separating exits for V2 and V3 in the trigeminal foramen (Rieppel 1979*a*; McDowell 1987).
2. Median pillars of frontal, separating olfactory nerves (Underwood 1967; McDowell 1987; Cundall *et al*. 1993).
3. Mobile nasofrontal joint (Rieppel 1978*b*).
4. Teeth on anterior process of palatine (Rieppel 1988).
5. Supraorbital process of parietal, which extends anteriorly along the dorsal margin of the orbit (Cundall *et al*. 1993)

Thus, *Dinilysia* appears to be the sister group to all other alethinophidians, as suggested by Rieppel (1988) and Kluge (1991). Many derived characters found in recent alethinophidians have not yet been confirmed in *Dinilysia*. These might corroborate the grouping of all alethinophidians (including *Dinilysia*) or the more restricted clade of alethinophidians excluding *Dinilysia*.

1. 'Complex' articulation between vomer and medial (choanal) process of palatine (Cundall *et al*. 1993).
2. Coronoid covered laterally by dorsal process of the compound (postdentary) element (McDowell 1987; Cundall *et al*. 1993).
3. First branchial arch element absent (Cundall *et al*. 1993).
4. *Adductor mandibulae externus pars superficialis* inserts partly on dorsal edge of *adductor externus profundus* (Cundall *et al*. 1993).
5. Absence of *intermandibularis posterior*, *pars posterior*. (Cundall *et al*. 1993).
6. Multisegmented *musculus multifidus* (Rieppel 1988).

Although there seems to be agreement that the most basal alethinophidians are those families informally known as 'henophidians', no real consensus exists regarding relationships between these groups (e.g. Cadle *et al*. 1990; Rieppel 1988; Kluge 1991; Cundall *et al*. 1993). The only area of agreement concerns the position of *Dinilysia* as the sister taxon to all other alethinophidians. In interpreting the primitive condition for alethinophidians, I have focused on the basal groups: *Dinilysia*, *Anomochilus*, aniliids, cylindrophids, uropeltids and xenopeltids.

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5. POLYMORPHISM WITHIN TERMINAL TAXA

Many of the terminal taxa are rather diverse, and are hence polymorphic for certain characters. Where more than one character state is present in a taxon, I have attempted to infer the primitive state by optimizing the character on the best-supported phylogenetic hypothesis of relationships within the taxon (see Section 4). For some terminal taxa, however, well-corroborated phylogenies did not exist. If, however, after attempts at optimization, the primitive character state within the taxon is still uncertain, I have coded the group as polymorphic (possessing the character states that optimization suggests could be primitive). It should be emphasized, therefore, that if a taxon is variable for a character but that the primitive state can be confidently established, the taxon has been coded as possessing that primitive state, rather than as polymorphic.

6. TRANSFORMATION SERIES

Nearly all the characters (133 out of 144) are binary. For the few multistate characters, transformation series are derived that minimize the amount of evolutionary change between character states. Based on this criterion, the multistate characters 4, 49, 72, 92 and 130 can be ordered into linear morphoclines. The extremes in a morphocline were coded as being derivable from each other only via intermediate stages (i.e. the transformation from 0 to 2 entails two steps, 0 → 1 and then 1 → 2). These characters were thus coded as ordered or additive. Arguments in favour of this approach are presented in Wilkinson (1992) and Slowinski (1993). Characters forming bifurcating transformation series when polarized were recoded into two characters (98 and 99, 122 and 123) (see Wiley *et al.* 1991). Multistate characters 11, 52, 81, 83, 86, 89 and 97 cannot be arranged into any clear morphocline, all character states appearing to be approximately equidistant from each other: these characters were therefore treated as unordered. Only in such special cases should a multistate character be treated as 'unordered'. More complex transition series are obviously possible, but none were applicable to the multistate characters in this study.

7. CHARACTERS

In the following character list, the character most common in the outgroups is coded as 0. In most cases, the same character state is present uniformly in all four outgroups, making the polarity obvious. However, for characters that are highly variable in the outgroups, polarity could not be determined (see section 3 and table 1). Although many of the characters in this study are new (i.e. have not been used in a formal cladistic analysis before), characters used in previous studies (Rieppel 1980*a*; Pregill *et al.* 1986; Estes *et al.* 1988; DeBraga & Carroll 1993) have also been reassessed and, if considered valid, included in the current analysis. The latter characters are annotated thus: R, previously used by Rieppel; P, Pregill *et al.*; E, Estes *et al.*; D, DeBraga & Carroll. The distribution of character states across the ingroup and outgroup taxa is shown in table 1. Some interpretations of character states in certain taxa are not straightforward, however. These are discussed in the character analysis. Most characters are illustrated: in the descriptions of these characters, the description of each character state is followed by a listing of a figure showing that particular character state.

(*a*) *Skull roof*

1. *Dorsal process of premaxilla*. Does not contact frontal, 0 (figure 2*a*). Contacts frontal, 1 (figure 2*d*). Anguids primitively exhibit state 0, although the derived condition occurs in some gerrhonotines (*Abronia* and *Barisia*). D

2. *Nasals*. Large, 0 (figure 2*a*). Vestigial or absent, 1 (figure 2*d*). D

3. *Nasals*. Separate, paired, 0 (figure 2*a*). Fused, single, 1 (figure 2*c*). Both conditions are widespread in scolecophidians. This character is variable within *Varanus*: most species have fused nasals, however, many small forms (subgenus *Odatria*) have paired nasals. Borsuk-Bialynicka (1984 p. 62) has stated that the poorly preserved nasals of *Cherminotus* were 'probably not fused', and it has therefore been tentatively coded with state 0. Nasals are absent from most mosasaurs: however, when present, they are paired (Russell 1967). Scincoids primitively retain paired nasals, although feylinine scincids have fused nasals (Greer 1970). R P E

4. *External naris*. 'Not retracted', i.e. prefrontal and frontal both excluded from posterior narial margin by nasal and maxilla, 0. 'Slightly retracted', i.e. prefrontal (but not frontal) enters posterior narial margin, 1 (figure 2*c*). 'Greatly retracted', i.e. prefrontal and frontal enter posterior narial margin, 2 (figure 2*b*). The three states form a clear morphocline, 0–1–2, and this character has been ordered. Although dried skulls of *Heloderma* often appear to exhibit states 1 or 2 (e.g. figure 2*a*), this is due to desiccation and shrinkage, and the posterior 'narial margin' is consequently irregular: fresh material exhibits state 0 (Pregill *et al.* 1986). In fossil taxa coded with states 1 or 2, the posterior narial margin is smooth and finished, and is thus unlikely to be the result of postmortem changes. R P E D

5. *Lateral wall of septomaxilla*. Small ridge, does not closely approach nasal, 0 (figure 2*a*). Large vertical flange, closely approaching nasal, 1 (figure 2*f*). The ridge in *Lanthanotus*, discussed by McDowell & Bogert (1954), is not much larger than in other lizards (Rieppel 1983). Lacertoids primitively lack the flange, although teiids (e.g. *Ameiva* AUSM R73364) have a large flange.

6. *Snout length*. Antorbital length of skull < 50% of total skull length, 0 (figure 2*a*). Antorbital length of skull > 50% of total skull length, 1 (figure 2*d*). D

7. *Maxilla-premaxilla contact*. Sutural contact, 0 (figure 2*a*). Abutting, non-sutural contact, 1 (figure 2*f*). Scolecophidians have state 1, even though in leptotyphlopids the maxilla and premaxilla abut (e.g. Brock 1932).

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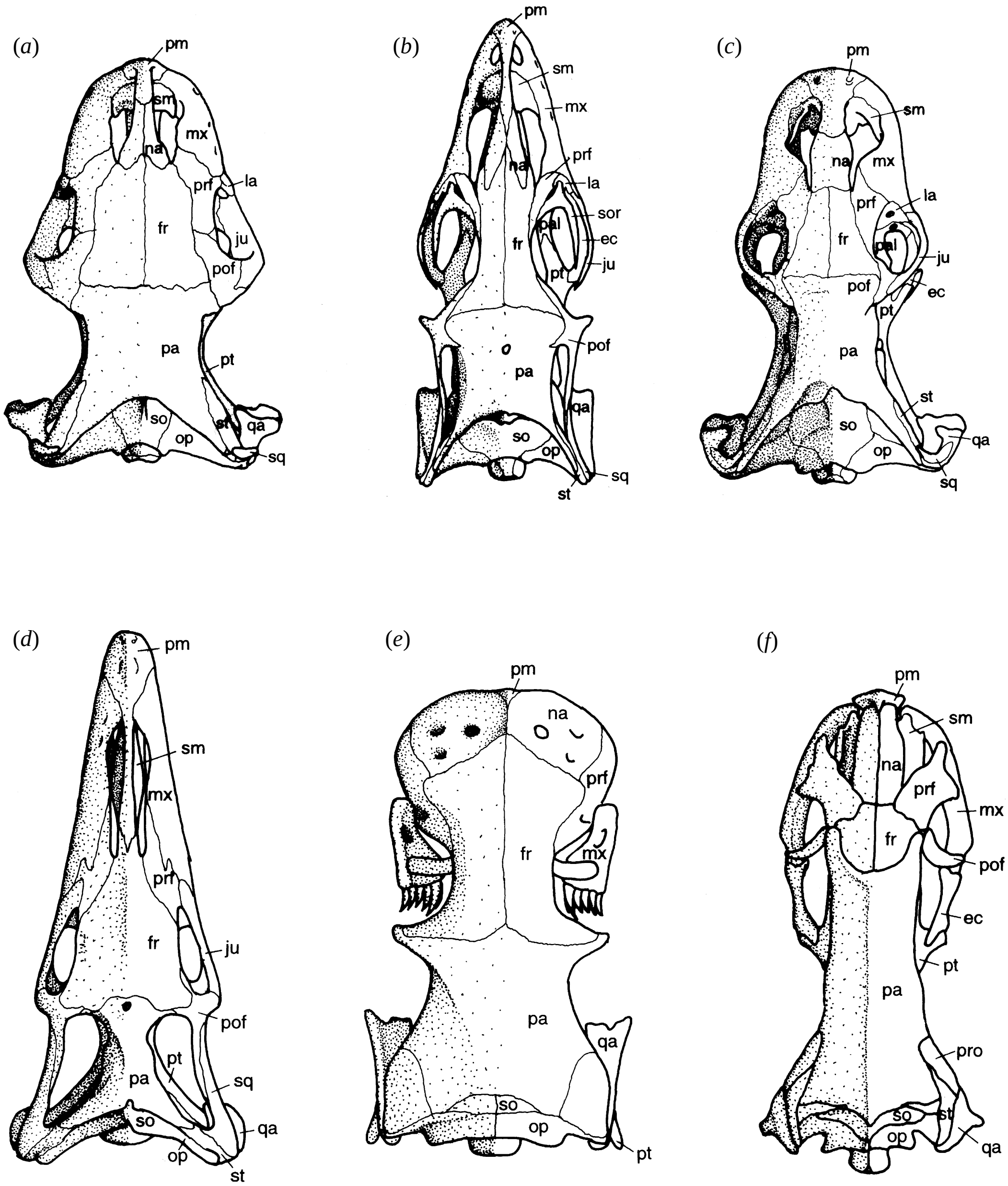

Figure 2. Skulls of varanoids in dorsal view. (*a*) *Heloderma*, (*b*) *Varanus*, (*c*) *Lanthanotus*, (*d*) *Platecarpus* (Mosasauridae), (*e*) *Ramphotyphlops* (Scolecophidia), (*f*) *Cylindrophis* (Alethinophidia). (*a*) after AMNH 109521, 66998, (*b*) after AMS R138712, (*c*) Rieppel 1980*a*, (*d*) after Williston (1898), (*e*) after AMS R19116, (*f*) after Rieppel 1983.

8. *Nasal* (*dorsal*) *process of maxilla*. On middle of maxilla, 0 (figure 3*a*). On posterior end of maxilla, 1 (figure 3*c*). This character is at least partially correlated with the next: however, following Pregill *et al.* (1986), I have coded them as separate traits. This character cannot be coded in many scolecophidians, where the maxilla is so highly modified that the dorsal process cannot be identified. However, *Leptotyphlops* has a less modified maxilla, and shows state (0). P

9. *Posterior end of maxilla*. Extends posteriorly to the centre of the orbit, or beyond, 0 (figure 3*a*). Posterior end does not reach middle of orbit, 1 (figure 3*b*). This trait is highly variable in basal alethinophians, and the primitive state is thus uncertain: e.g. *Dinilysia*, aniliids and cylindrophids exhibit state 0, uropeltids and *Anomochilus* exhibit state 1. Although *Paravaranus* appears to exhibit state 1 in lateral view, there is a posterior flange of the maxilla (visible only in palatal view) that extends to the middle of the orbit (Borsuk-Bialynicka 1984). P E D

10. *Lacrimal*. Present, 0 (figure 3*a*). Absent, 1 (figure 3*f*). The lacrimal is present, though rarely preserved, in mosasaurs (e.g. Lingham-Soliar 1995). Lang (1991) suggests that either state might be primitive for scincoids: however, state 0 is found in basal scincids, gerrhosaurids and cordylids and can be inferred to be primitive for Scincoidea (G. Shea personal communication). E

11. *Posterior lacrimal foramen*. Single, enclosed by prefrontal and lacrimal (or, in taxa without a lacrimal, the corresponding portion of the maxilla), 0. Double, enclosed by prefrontal and lacrimal/maxilla, 1. Single, enclosed entirely by prefrontal, 2. The three states do not form a clear morphocline, and this character is

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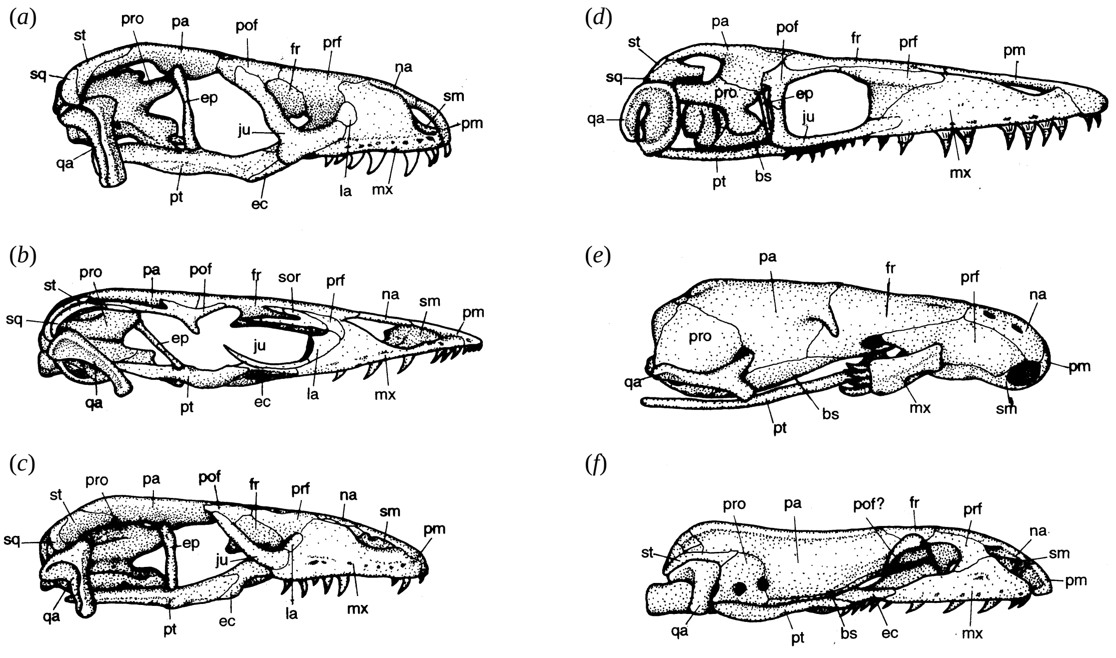

Figure 3. Skulls of varanoids in right lateral view. (*a*) *Heloderma*, (*b*) *Varanus*, (*c*) *Lanthanotus*, (*d*) *Platecarpus* (Mosasauridae), with upper temporal arch omitted to show parietal–prootic contact, (*e*) *Ramphotyphlops* (Scolecophidia), (*f*) *Cylindrophis* (Alethinophidia). (*a*) after AMNH 109521, 66998, (*b*) after AMS R138712, (*c*) 1980*a*, (*d*) after Russell 1967, (*e*) after AMS R19116, (*f*) after Rieppel 1983.

unordered. Mosasaurs (e.g. *Clidastes* AMNH 192, *Platecarpus* AMNH 1820 and 14788) appear to have state 2. Scolecophidians have lost the lacrimal foramen and cannot be scored. Although the situation in *Dinilysia* is uncertain, all adequately known alethinophidians have state 2 (see McDowell 1987). R P E

12. *Prefrontal*. Without antorbital ridge, 0 (figure 3*a*). With antorbital ridge extending from anterodorsal margin of orbit towards external naris, 1 (figure 3*d*). D

13. *Prefrontal*. Does not contact postfrontal, 0 (figure 2*b*). Contacts postfrontal, 1 (figure 2*a*). Scolecophidians and basal alethinophidians have lost the postfrontal, and cannot be scored. It should be noted, though, that anomalepid scolecophidians have 'orbital' bones of uncertain homology in this region (List 1966). Although *Anniella* has state 1, primitive anniellines (*Apodosauriscus*) and all other anguids have state 0. The primitive state in mosasaurs is 0 (e.g. *Halisaurus*, *Clidastes*, *Platecarpus* and *Prognathodon*), even though *Plotosaurus* has state 1. Most basal alethinophidians have lost the postorbital and cannot be coded: however, *Dinilysia* exhibits state 0. R P E D

14. *Frontals*. Fused into a single median element, 0 (figure 2*d*). Unfused, paired elements, 1 (figure 2*a*). Both conditions are widespread within anguids (e.g. gerrhonotines and diploglossines, 0; anniellines and anguines, 1), gobidermatids (*Parviderma*, 0; most *Gobiderma*, 1), lacertoids (Estes *et al*. 1988; Arnold 1989) and scincoids (Greer 1970; Lang 1991). R E D

15. *Descending* (*subolfactory*) *processes of frontals*. Not meeting one another in midline, 0 (figure 4*c*). Meeting in midline, 1 (figure 4*a*). Meeting lateral edges of parasphenoid, 2 (figure 3*e*, *f*). R P E D

16. *Frontoparietal contact* (*axis of mesokinetic joint*). Mobile, 0 (figure 2*b*). Immobile, 1 (figure 2*e*).

17. *Descending process of parietal*. Does not contact basisphenoid, 0 (figure 3*b*). Contacts basisphenoid, 1 (figure 3*e*).

18. *Descending processes of parietal*. Weak, not sutured to prootic, 0 (figure 3*c*). Large, sutured to prootic, 1 (figure 2*d*).

19. *Parietal skull table*. Wide, jaw adductors confined to ventral surface, and lateral edge dorsal surface, of parietal, 0 (figure 2*a*). Reduced to narrow sagittal crest, jaw adductors inserting on entire dorsal surface of parietal, 1 (figure 2*f*). Most *Varanus* have state 0, although some very large old individuals approach state 1 (e.g. Mertens 1942*c*).

20. *Posterolateral process* (*suspensorial ramus*) *of parietal*. Long, 0 (figure 2*a*). Short, 1 (figure 2*f*). E

21. *Parietal foramen*. Present, 0. Absent, 1. R P E

22. *Upper temporal arcade*. Present, postorbital and squamosal large, 0 (figure 3*b*). Absent, postorbital and squamosal reduced or absent, 1 (figure 3*a*). The primitive condition in anguids is uncertain: the arcade is absent in anniellines but present in other forms. In *Proplatynota*, the posterior portion of the arcade is broken off: however, the robustness of the preserved anterior (postorbital) portion suggests that the arcade was complete. R P E

23. *Postorbital and postfrontal*. Separate ossifications, 0. Single ('postorbitofrontal') element, 1 (figure 3*b*). Anguids primitively exhibit state 0 (e.g. gerrhonotines, anguines, anniellines), although state 1 has evolved within diploglossines. Both conditions occur in *Telmasaurus* (Gilmore 1943; Borsuk-Bialynicka 1984), and are widespread within lacertoids (e.g. Arnold 1973, 1983, 1989; Estes *et al*. 1988). Although both conditions occur in scincids (e.g. Greer 1970), gerrhosaurids and cordylids have state 0, which can therefore be assumed to be primitive for Scincoidea. Scolecophidians and most basal alethinophidians have lost these elements,

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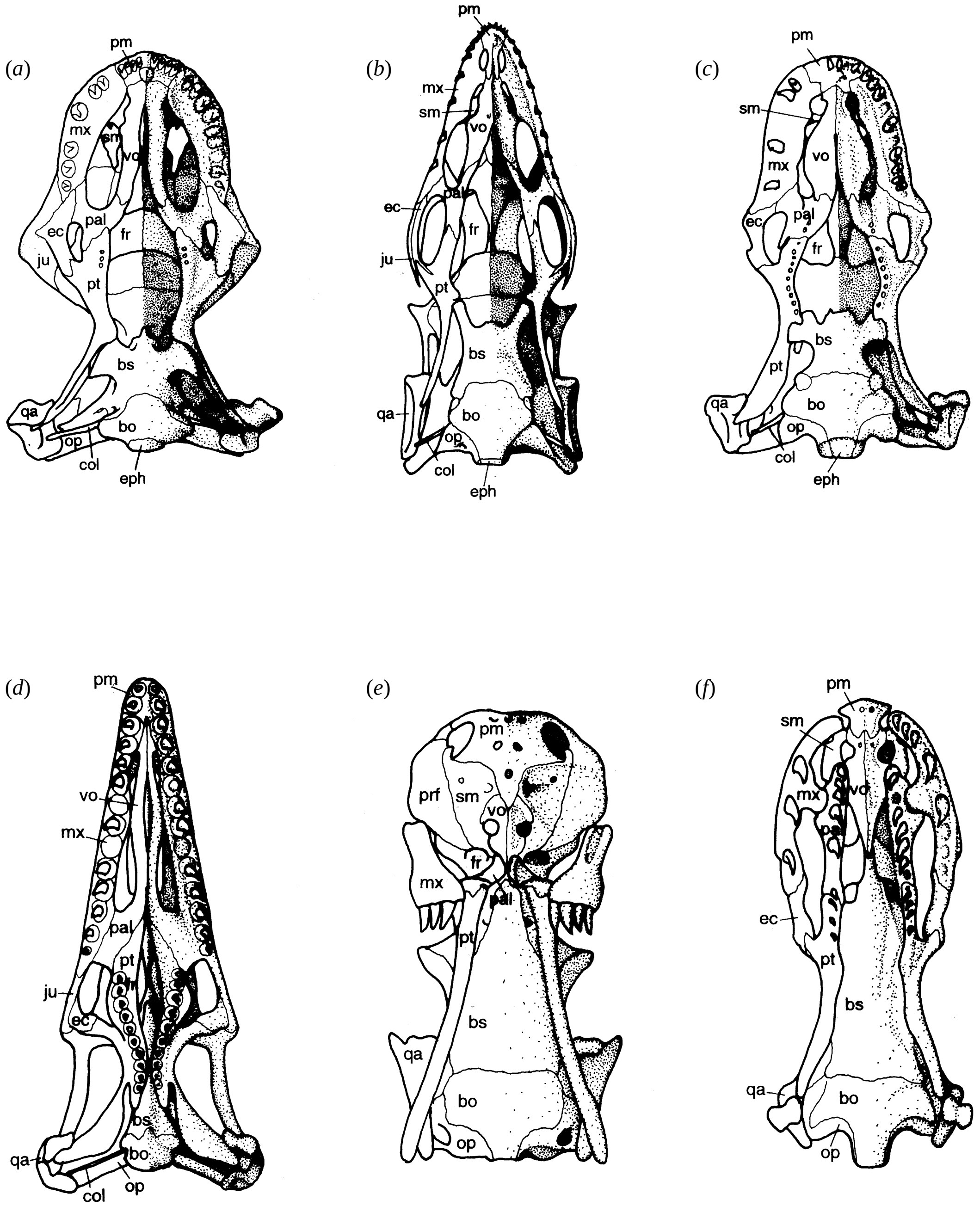

Figure 4. Skulls of varanoids in ventral view. (*a*) *Heloderma*, (*b*) *Varanus*, (*c*) *Lanthanotus*, (*d*) *Platecarpus* (Mosasauridae), (*e*) *Ramphotyphlops* (Scolecophidia), (*f*) *Cylindrophis* (Alethinophidia). (*a*) after AMNH 109521, 66998, (*b*) after AMS R138712, (*c*) Rieppel 1980*a*, (*d*) after Williston (1898), (*e*) after AMS R19116, (*f*) after Rieppel 1983.

and cannot be scored. However, the basal alethinophidian *Dinilysia* has been described as having separate postorbitals and postfrontals (Estes *et al*. 1970). R P E

24. *Posterior margin of orbit*. Complete, jugal meets postorbital, 0 (figure 3*c*). Incomplete, jugal reduced and does not meet postorbital, or jugal absent altogether, 1 (figure 3*b*). The primitive condition in anguids cannot be determined: anniellines have an incomplete arch, all other anguids have a complete arch. R E

25. *Supratemporal*. Does not contact prootic, 0 (figure 5*a*). Extends medially along the anterior margin of the paroccipital process to contact prootic, 1 (figure 5*b*). In those scolecophidians which retain a vestigial supratemporal, i.e. anomalepids (Haas 1964, 1968) and leptotyphlopids (Brock 1932), the element (often misidentified as a tabular) is pressed tightly against the prootic.

26. *Supratemporal*. Small, total length less than half the maximum width of the skull, 0. Large, total length at least half the maximum width of the skull, 1 (figure 2*a*). Width of skull, rather than length of skull, or length of the suspensorial ramus of the parietal, has been chosen for the baseline measurement in order to avoid correlation with other characters (in particular, characters 6 and 20). The primitive state in lacertoids is state 0, which characterizes xanthusiids, lacertids and some teiids. New material (see appendix 1) of the aigialosaur *Opetiosaurus* reveals that this group has state 1. Mosasaurs also have a large supratemporal: how-

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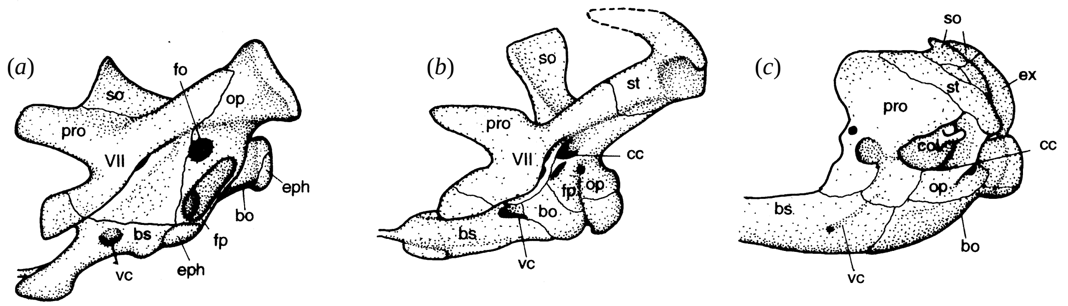

Figure 5. Braincases of varanoids in left lateral view. (*a*) *Varanus*, (*b*) *Platecarpus* (Mosasauridae), (*c*) *Anomochilus* (Alethinophidia). (*a*) after CSIRO REPS86, (*b*) after Russell 1967 and AMNH 1820, (*c*) after Cundall & Rossman (1993).

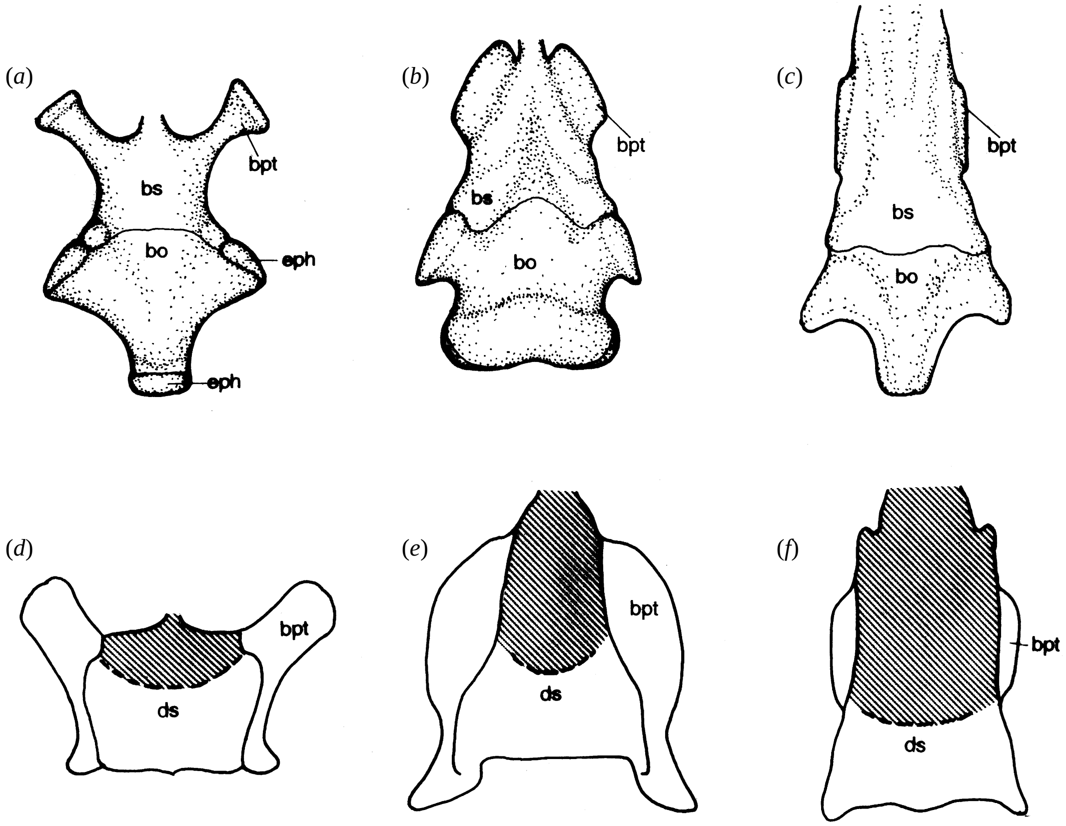

Figure 6. Basisphenoid–basioccipital complex of varanoids in ventral view. (*a*) *Varanus*, (*b*) *Platecarpus* (Mosasauridae), (*c*) *Cylindrophis* (Alethinophidia). Basisphenoid of varanoids in dorsal view: area in front of dorsum sella is shaded. (*d*) *Varanus*, (*e*) *Platecarpus* (Mosasauridae), (*f*) *Anilius* (Alethinophidia). (*a*) after CSIRO REPS86, (*b*) after AMNH 1820, (*c*) after Rieppel 1983 and BMNH 1930.5.8.47, (*d*) after CSIRO REPS86, (*e*) after Russell 1967, (*f*) after Rieppel (1979*b*).

ever, as much of it is hidden beneath the parietal, the element appears small in many reconstructions. Most basal alethinophidians (e.g. aniliids, cylindrophids, *Dinilysia*, *Anomochilus*) exhibit state 1, but uropeltids exhibit state 0. Alethinophidians have been tentatively coded with state 1. In *Proplatynota*, the supratemporal is not preserved: however, the morphology of the suspensorial ramus of the parietal indicates that the supratemporal was small. Borsuk-Bialynicka's (1984) description of *Cherminotus* is ambiguous: the dorsal view shows the animal with state 0, the lateral view, with state 1. P

27. *Supratemporal*. Confined to skull roof, does not form part of braincase, 0 (figure 5*a*). Forms part of posterior portion of braincase, 1 (figure 5*b*). Most alethinophidians clearly exhibit state 1. In some basal alethinophidians, the supratemporal is vestigial and this character is difficult to determine: however, inspection of the relevant material shows that such forms also have state 1 (e.g. uropeltids, BMNH 1930.5.8.75). In scolecophidians which retain a vestigial supratemporal (often misinterpreted as a tabular), the element lies against the braincase, very close to the quadrate, or even between the quadrate and braincase (Brock 1932; Haas 1964; List 1966). Scolecophidians have been interpreted as having state 1.

28. *Squamosal*. Present, 0 (figure 2*b*). Absent, 1 (figure 2*f*). The primitive condition in anguids is uncertain: anniellines lack a squamosal, all other anguids possess one. E

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29. *Jugal*. Does not extend anteriorly past orbital rim, 0 (figure 3*a*). With a horizontal process that extends anteriorly past the orbital rim, and projects under the lacrimal, 1 (figure 3*d*). This is not applicable in scolecophidians, which lack a jugal. The jugal is absent in almost all alethinophidians: it might be present in *Dinilysia*, although the element in question might be a postorbital (G. Underwood, personal communication in Rieppel 1988), or, most likely, the anterior portion of the ectopteryoid (personal observation). The element, if it is a jugal, exhibits state 0.

30. *Quadrate*. 'Normal', i.e. without elaborated suprastapedial process, 0 (figure 3*a*). 'Circular' in lateral view, i.e. with enlarged, curved, posteroventrally directed suprastapedial process, 1 (figure 3*d*). D

31. *Quadrate*. Tympanic recess present, outer conch (tympanic crest) is a high wall which projects laterally, 0 (figure 4*a*). Tympanic recess reduced, outer conch reduced to a low ridge but still projects laterally 1 (figure 4*b*). Tympanic recess absent, outer conch reduced and directed anterolaterally, external surface of quadrate only weakly concave, 2 (figure 3*e*, *f*). The primitive condition in anguids is uncertain: e.g. diploglossines and gerrhonotines have state 0, anniellines and *Ophisaurus* have state 1. This character forms a morphocline 0 ↔ 1 ↔ 2, and has been ordered. R P D

32. *Tympanic membrane*. Not ossified, 0. Ossified, 1. State 1 is present in mosasaurs (e.g. Vaughn & Dawson 1956) and has recently been described in aigialosaurs (Carroll & DeBraga 1992). D

(*b*) **Braincase**

33. *Basipterygoid processes*. Long (i.e. projecting far anterolaterally beyond the body of the basisphenoid), 0 (figure 6*a*). Short (i.e. not projecting very far beyond the body of the basisphenoid), 1 (figure 6*b*). D

34. *Articulatory facet for pterygoid, at distal end of basipterygoid process*. Limited: small sub-circular area, 0 (figure 6*a*). Extensive: anteroposteriorly elongated area, 1 (figure 6*b*). State 1 might be correlated with a soft anatomical feature, the reduction or loss of the eustachian passage (McDowell & Bogert 1954). Both states are widespread within lacertoids (e.g. see Estes *et al*. 1988). Both states also occur within scincids. However, as gerrhosaurids and cordylids have state 0 (e.g. Lang 1991), this can be been assumed to be primitive for Scincoidea.

35. *Anterior portion of basisphenoid* ('*parasphenoid*'). Tapers abruptly immediately anterior to the dorsum sella, extending rostrally as a narrow cultriform process, 0 (figure 6*d*). Extends anteriorly as a wide plate for a considerable distance in front of dorsum sella before narrowing into a cultriform process, 1 (figure 6*e*).

36. *Cultriform process*. Curved (concave edge facing dorsally) in lateral view; lies ventral to the level of the dorsum sella, 0. Straight and horizontal in lateral view, lies on the same level as the dorsum sella, 1. The primitive condition in anguids cannot be ascertained; aniellines have state 1 but other anguids have state 0. Character cannot be scored in scincoids or helodermatids, which have an extremely short cultriform process.

37. *Vidian canal*. Completely enclosed within basisphenoid, 0. Anterior portion is an open groove on lateral surface of basisphenoid, 1. Scolecophidians (McDowell 1967*a*; Rieppel 1979*a*, 1988) and mosasaurs (e.g. Russell 1967, figure 9; *Platecarpus* USNM 18274) have state 1. Alethinophidians have a highly autapomorphic condition and cannot be coded objectively: the vidian canal is an open groove on the *internal* surface of the basisphenoid (Rieppel 1988).

38. *Rear opening of vidian canal*. Situated anteriorly, well away from the basisphenoid–basioccipital suture, 0 (figure 5*a*). Situated posteriorly, near the basisphenoid–basioccipital suture, 1 (figure 5*b*). The primitive condition in anguids is uncertain: state 1 occurs in anniellines and anguines, state 0 in all other anguids.

39. *Basal tubera*. Posteriorly located: positioned closer to occipital condyle than to basipterygoid process, 0 (figure 4*a*). Anteriorly located: positioned mid-way between occipital condyle and basipterygoid process, 1 (figure 4*c*). Although Borsuk-Bialynicka (1984) reconstructs *Saniwides* and *Cherminotus* with state 0, the photographs in that paper indicate that both have state 1.

40. *Optic foramen* (*II*). Open, not fully enclosed in bone, 0. Fully enclosed in bone, 1. The foramen is enclosed entirely by the frontal in scolecophidians, and (primitively) by the frontal and parietal in alethinophidians.

41. *Prootic crest* (ridge on lateral surface of the prootic, overhanging foramen pro nervi facialis – see next character). Well-developed flange, 0 (figure 5*b*). Weak ridge, 1 (figure 5*c*). The primitive condition in anguids is uncertain: the crest is poorly developed in anniellines and anguines but well-developed in other anguids. R

42. *Foramen pro nervi facialis* (lateral exit on prootic for hyomandibular branch of the facial, VII, nerve). Single, 0. Double, 1. R

43. *Trigeminal foramen*. Not enclosed in bone, 0 (figure 3*a*). Enclosed between prootic and descending flange of parietal, 1 (figure 3*f*).

44. *Footplate of stapes*. Not surrounded by ridges projecting from the lateral surface of the braincase elements, 0 (figure 5*a*). Surrounded by flanges from prootic and opisthotic, 1 (figure 5*c*). In mosasaurs, these flanges only encircle the stapedial footplate. In scolecophidians and alethinophidians, they are greatly elaborated into the crista circumfenestralis and also surround the fenestra perilymphatica (see character 46). Although Estes *et al*. (1970) suggested that the crista was absent in the basal alethinophidian *Dinilysia*, the crista is present (Rage 1984; Rieppel 1988), as in all other alethinophidians. Mosasaurs also have state 1 (e.g. *Platecarpus* USNM 18274).

45. *Internal process of extracolumella* (distal extension of stapes). Only distal tip contacts quadrate, contact weak, 0. Extensive and firm contact with the posterior region of the cephalic condyle of the quadrate, 1. Mosasaurs (Camp 1942; Russell 1967) and *Lanthanotus* (McDowell 1967*b*) both have state 1. State 1 is also found in scolecophidians and all basal alethinophidians

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(Rieppel 1980*c*). In higher alethinophidians (booids and caenophidians), however, the articulation has shifted ventrally and lies on the quadrate shaft rather than on the cephalic condyle.

46. *Fenestra perilymphatica*. Perilymphatic duct exits directly onto the lateral surface of the braincase, 0 (figure 5*b*). Perilymphatic duct exits into (large) juxtastapedial recess, formed by the crista circumfenestralis, 1 (figure 5*c*).

47. *Opisthotic*. With weak horizontal flange extending between basal tubera and paroccipital process; proximal portion of the stapes exposed in ventral view, 0 (figure 4*a*). With strong horizontal flange extending posterolaterally from basal tubera to paroccipital process, obscuring proximal portion of the stapes in ventral view, 1 (figure 4*b*).

48. *Exoccipitals*. Does not meet one another dorsal to foramen magnum, supraoccipital enters dorsal margin of opening, 0. Meeting one another dorsal to foramen magnum to exclude supraoccipital from the opening, 1.

49. *Supraoccipital*. Does not contact parietal, large unossified gap persists between elements, 0. Abuts parietal: two elements meet but contact is non-sutural, and a tiny gap might remain between the two elements along part of the dorsal edge of the supraoccipital, 1. Sutural contact with parietal, entire dorsal edge of supraoccipital contacts parietal, 2. The three states form a clear morphocline, 0–1–2, and this character has been ordered. R P D

(*c*) *Palate*

50. *Maxilla*. Sutures with vomer anterior to opening for Jacobsen's organ, 0 (figure 4*a*). Does not suture with vomer anterior to opening for Jacobsen's organ, 1 (figure 4*f*).

51. *Vomer*. Main portion (i.e. excluding the anterior end, which forms the margin of the opening to Jacobsen's organ) plate-like, 0 (figure 4*c*). Main portion rod-like, 1 (figure 4*a*). This trait is variable within basal alethinophidians (*Anomochilus*, uropeltids and aniliids, 0; *Dinilysia*, cylindrophids and xenopeltids, 1). R P

52. *Opening of Jacobsen's organ* (fenestra vomeronasalis externa). Continuous with choana, 0. Separated from choana, enclosed by septomaxilla, maxilla and vomer, 1 (figure 4*a*). Separated from choana, enclosed by maxilla and vomer only, 2 (figure 4*b*). Closed by septomaxilla and vomer only, 3 (figure 4*f*). The primitive condition in anguids appears to be 2, as anniellines, anguines and diploglossines have state 2. However, gerrhonotines (*Abronia*, *Elgaria*, *Gerrhonotus*) have state 1. In many taxa (e.g. helodermatids), superficial examination would suggest that the opening was closed by the maxilla and vomer alone (state 2). However, closer inspection reveals that the opening is primarily formed by the septomaxilla and vomer, the maxilla sending a medial flange that hides the septomaxilla portion of the rim (state 1). This character is unordered, as the four states do not form a clear morphocline. Also, variability in the outgroups means that polarity is uncertain.

53. *Vomers*. Anterior to palatines, 0 (figure 4*a*). Medial to palatines, 1 (figure 4*f*).

54. *Palatine*. Sutures anteriorly with vomer, 0 (figure 4*a*). Palatine and vomer with mobile contact, 1 (figure 4*f*).

55. *Palatine*. Sutures laterally with maxilla, 0 (figure 4*b*). Palatine and maxilla with mobile contact, 1 (figure 4*f*).

56. *Palatine*. With choanal groove (depression on ventral surface extending posteriorly from choana), 0 (figure 4*c*). Without choanal groove, 1 (figure 4*b*). The palatines are so reduced and modified in scolecophidians that this character cannot be scored objectively. Mosasaurs retain state 0 (e.g. *Platecarpus*, AMNH 14788, 14800, 1820). *Dinilysia* (Estes *et al.* 1970) and other basal alethinophidians possess a groove, but this is lost in higher snakes. R

57. *Palatine*. Long (as long as vomer), 0. Short (half as long as vomer), 1. Scolecophidians are variable for this trait: leptotyphlopids have state 0, typhlopids and anomalepids have state 1. P

58. *Palatines*. Widely separated from each other by large interpterygoid vacuity, 0. Approach each other closely, interpterygoid vacuity reduced, 1.

59. *Palatine*. Without distinct medially-directed process, 0 (figure 4*a*). With rectangular process projecting medially from the middle portion of the palatine towards the skull midline, 1 (figure 4*f*).

60. *Pterygoids*. With groove on ventral surface, extending from suborbital foramen towards basicranial articulation, 0 (figure 4*a*). This groove is triangular, being widest anteriorly. Without such groove, 1 (figure 4*b*). This character cannot be coded in scolecophidians, where the pterygoid is reduced to a thin rod, nor in some basal althenophidians (e.g. aniliids, xenopeltids), where the pterygoid is also highly modified. Even in basal alethinophidians which retain a generalized pterygoid, the trait is variable (e.g. uropeltids, 1; cylindrophids, 0; *Anomochilus* seems to have an intermediate condition of a weak groove).

61. *Epipterygoid*. Present, 0. Absent, 1. The epipterygoid is present, but very small, in anniellines. Although the element is not preserved in *Paravaranus*, a facet for it on the pterygoid suggests that it was present (Borsuk-Bialynicka 1984).

62. *Pterygoid*. Anterior (palatine) process merges gradually (in a gentle curve) with the lateral (ectopterygoid) process, 0 (figure 4*b*). Anterior process distinctly set off from lateral process, the two portions meeting at a distinct angle, 1 (figure 4*f*). This trait is variable within xenosaurids (*Xenosaurus*, 0; *Shinisaurus*, 1) and within anguids (e.g. anguines, gerrhonotines, diploglossines, 0; anniellines, 1).

63. *Ectopterygoid*. In dorsal view, medial to ventral margin of orbit (formed by jugal), 0 (figure 4*a*). Directly under ventral margin of orbit, 1 (figure 4*c*). This trait cannot be scored in scolecophidians or alethinophidians, where the jugal is absent.

64. *Ectopterygoid*. Ventral surface horizontal, or faces ventromedially, 0 (figure 4*a*). Ventral surface faces ventrolaterally, 1 (figure 4*b*). Among scolecophidians, leptotyphlopids (which retain a discrete ectopterygoid) have state 0. Other scolecophidians have lost the

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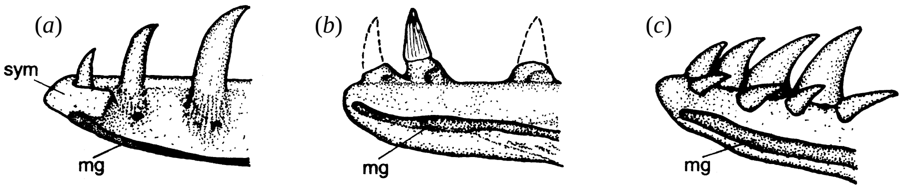

Figure 7. Anterior (symphyseal) area of mandibles of varanoids in medial view. (*a*) *Varanus*, (*b*) *Platecarpus* (Mosasauridae), (*c*) *Cylindrophis* (Alethinophidia). (*a*) after AMS R138712, (*b*) after Russell 1967 and AMNH 1820, (*c*) after AMS R131356.

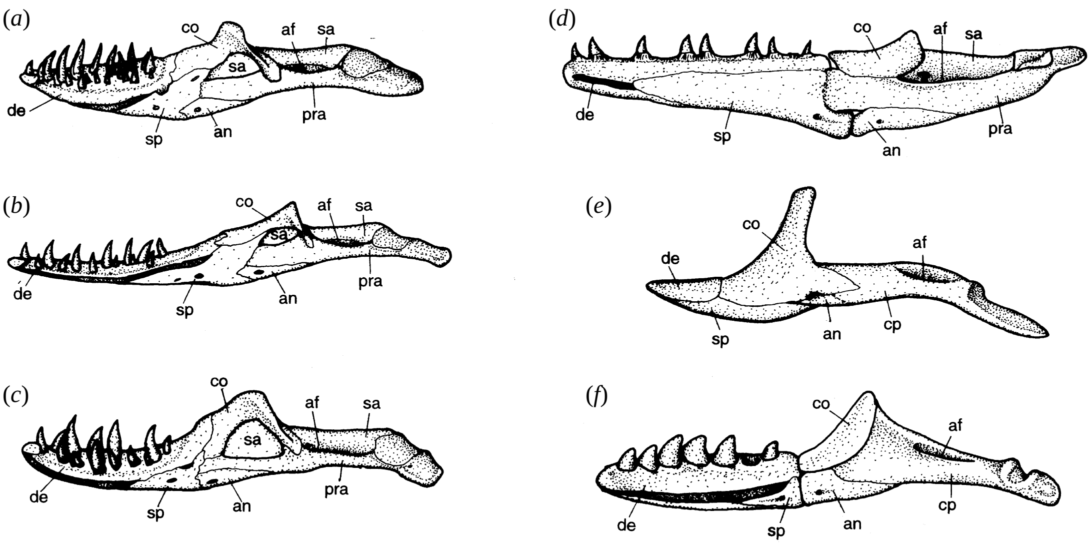

Figure 8. Right lower jaws of varanoids in medial view. (*a*) *Heloderma*, (*b*) *Varanus*, (*c*) *Lanthanotus*, (*d*) *Platecarpus* (Mosasauridae), (*e*) *Ramphotyplops* (Scolecophidia), (*f*) *Anomochilus* (Alethinophidia). (*a–c*) after Rieppel (1980*a*), (*d*) after Russell 1967 and AMNH 1820, (*e*) after AMS R19116, (*f*) reconstructed from both rami illustrated in Cundall & Rossman (1993).

ectopterygoid, or have had it reduced to a thin rod, and cannot be coded (e.g. List 1966).

65. *Maxilla–septomaxilla contact*. Rigid, septomaxilla with extensively sutured to the dorsal surface of the palatal flange of the maxilla, 0. Mobile, septomaxilla with small, non-sutural contact with maxilla, 1.

66. *Maxilla*. Enters suborbital foramen, 0 (figure 4*f*).Excluded from suborbital foramen by palatine and ectopterygoid, 1 (figure 4*a*). The primitive condition in anguids is uncertain: anniellines have state 1, other anguids, state 0. Most basal alethinophidians (e.g. *Dinilysia*, cylindrophids, aniliids, xenopeltids, *Anomochilus*) have state 0, and this is assumed to be primitive for alethinophidians, even though uropeltids have state 1. Both states are widespread in lacertoids (e.g. Presch 1980). R P E

(*d*) *Lower jaw*

67. *Subdental shelf medial to teeth*. Present, 0. Absent, 1. The subdental shelf is a ridge lying medial to the groove containing pleurodont teeth. This character therefore cannot be ascertained in taxa with discrete tooth sockets (mosasaurs, scolecophidians and alethinophidians). The shelf is present, but weakly developed, in anguids (Estes *et al*. 1988). E

68. *Mandibular symphysis*. Rigid, anterior tips of dentary with a discrete flat symphyseal area, 0 (figure 7*a*). Mobile, anterior tips of dentary smoothly rounded (i.e. without flat symphyseal area), 1 (figure 7*b*).

69. *Meckelian groove*. Exposed ventrally, extends along the ventromedial edge of the lower jaw, 0 (figure 7*a*). Not exposed ventrally, confined entirely to the medial surface of the lower jaw, 1 (figure 7*b*). This character cannot be coded in some scolecophidians, which lack the groove (typhlopids). However, scolecophidians which retain the groove (leptotyphlopids and anomalepids) have state 1. Both states are widespread in lacertoids (Lang 1990; Estes *et al*. 1988). E

70. *Anterior tip of splenial*. On ventral edge of dentary, 0 (figure 8*a*). On medial surface of dentary, 1 (figure 8*d*). Both states occur within scincoids and within lacertoids (e.g. Lang 1990; Estes *et al*. 1988). *Proplatynota* has been interpreted as having state 1, but this condition might be a result of post-mortem displacement of the dentary.

71. *Dentary*. Curved in lateral or medial view, with concave dorsal (tooth-bearing) edge, 0 (figure 8*b*). Completely straight in lateral view, 1 (figure 8*d*). This character cannot be coded in scolecophidians with a highly modified dentary (leptotyphlopids). However, scolecophidians which retain a more normal dentary (anomolepids and typhlopids) have state 1.

72. *Posterior end of splenial*. In line with, or behind, coronoid process, 0. Anterior to coronoid process, 1 (figure 8*a*). Scolecophidians are highly variable for this

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trait, e.g. typhlopids have state 0 (Haas 1964), leptotyphlopids have state 1 (Brock 1932). R P E D

73. *Splenial–angular contact*, in medial view. Overlapping, irregular and with limited movement possible, 0 (figure 8*a*). Abutting, straight (vertical) and highly mobile, 1 (figure 8*d*). R D

74. *Splenial–angular contact.* Not exposed in lateral view, 0. Exposed extensively in lateral view, 1. This character is variable both within scolecophidians (e.g. List 1966) and basal alethinophidians (*Dinilysia*, *Anomochilus*, aniliids 0; uropeltids, cylindrophids, 1).

75. *Coronoid.* Extends anteroventrally on medial surface of lower jaw, to suture with splenial, 0 (figure 8*a*). Does not reach splenial, 1 (figure 8*d*). This trait is variable within scolecophidians (typhlopids and anomalepids, 0; leptotyphlopids, 1). Although the coronoid may closely approach the splenial in mosasaurs, a true sutural contact is not present (e.g. Lingham-Soliar 1995). P D

76. *Mental foramina on lateral surface of dentary*. More than two, 0. Two or fewer, 1.

77. *Coronoid.* Without large anterior extension, 0. With long horizontal anterior extension overlapping dentary laterally, 1. Both states are widespread in scincoids and lacertoids (see Lang 1990; Estes *et al.* 1988). Scolecophidians are also polymorphic for this trait: typhlopids (e.g. List 1966) and some anomalepids (e.g. Dunn 1941) have state 1; leptotyphlopids have state 0 (e.g. List 1966). Estes *et al.* (1988) coded this character as two correlated traits: presence of large anterolateral flange of coronoid, and extensive lateral overlap of coronoid and dentary. P E

78. *Posterior ramus of coronoid*, forming anteromedial margin of adductor fossa. Present, coronoid shaped like an inverted V in medial view, 0 (figure 8*a*). Absent, coronoid rod-shaped in medial view, 1 (figure 8*d*). The condition in scolecophidians is difficult to interpret: the coronoid is modified into a triangular plate (e.g. Haas 1964), an autapomorphy of this group. D

79. *Subcoronoid fenestra on medial surface of the mandible* (exposing surangular in medial view). Fenestra present, large gap between coronoid and prearticular, 0 (figure 8*a*). Fenestra absent, prearticular expands dorsally and contacts the entire ventral edge of the coronoid, 1 (figure 8*d*). Although state 1 occurs in some scincids (e.g. Nash & Tanner 1970; Estes *et al.* 1988), state 0 occurs in other scincids, and in gerrhosaurids and cordylids (Lang 1991), and is primitive for Scincoidea. D

80. *Adductor fossa.* Faces medially, 0 (figure 8*c*). Faces dorsally, 1 (figure 8*f*).

81. *Surangular.* Does not enter articular cotyle, 0. Enters and forms half the articular cotyle, 1. Fused with articular, contribution to articular cotyle cannot be determined, 2. The three states do not form a clear morphocline, and this character is unordered. Although state 2 occurs in some anguids, state 0 appears to be primitive for the group (see Rieppel 1980*a*). D R

82. *Disarticulated surangular.* With pointed anterior end, 0. With flat anterior end, 1. The surangular does not exist as a discrete element in scolecophidians or alethinophidians. However, the 'surangular portion' of the compound bone in these taxa is pointed anteriorly. R P E

83. *Surangular.* With long anterior projection that is overlapped laterally by dentary, dentary moderately notched posteriorly, 0. Does not project far into dentary, dentary not notched posteriorly, 1. With long anterior projection that projects into a deep notch in the dentary, 2. The three states do not form a clear morphocline and this character is unordered. R P E

84. *Ventral margin of lower jaw.* Smoothly curved, 0. With a distinct ventral lump in the region of the splenio-angular joint, 1.

85. *Retroarticular process.* Simple, without medial flange, 0. With medial flange, 1. State 1 occurs in almost all anguids and appears to be primitive for this group, even though *Abronia* has state 0. E D

(*e*) **Dentition**

86. *Implantation of marginal teeth.* Pleurodont, without discrete alveoli under each tooth, 0. Thecodont, teeth implanted in sockets, 1. 'Modified thecodont', teeth ankylosed to the margins of sockets, 2. This character does not form a clear morphocline and is thus unordered. See Lee (1996*a*) for further discussion. E D

87. *Marginal teeth.* Without carinae, 0. With carinae on the anterior and posterior edges, 1. Scolecophidians have been coded with state 1: leptotyphlopids have anterior and posterior carinae, and typhlopids have weak posterior carinae. The condition in basal alethinophidians is difficult to score, they have carinae but these are positioned on the labial and lingual surfaces (e.g. aniliids, uropeltids, cylindrophids, xenopeltids, *Anomochilus*). Such carinae are also found in many caenophidians (Vaeth *et al.* 1985). D

88. *Plicidentine* (infoldings of dentine at the base of teeth, forming striations). Absent or very weak, 0. Strong, 1. All basal alethinophidians lack plicidentine, although it occurs in some acrochordids and colubrids (see Vaeth *et al.* 1985). P E

89. *Resorption pits at base of tooth crown.* Present, 0. Absent, 1. Tooth crown situated on high pedestal, resorption pit at base of pedestal (but does not encroach upon crown), 2. The three states do not form a clear morphocline, and this character is unordered. P E

90. *Replacement marginal teeth.* Erupt upright, growing straight upwards into functional position, 0 (figure 9*a*). Erupt horizontally, and then rotate through ninety degrees about the base, into functional position, 1 (figure 9*b*). Scolecophidians have been asserted to have state 0 (McDowell & Bogert 1954): however, they have state 1, as do mosasaurs (Lee 1996*a*).

91. *Premaxillary teeth.* Five or more teeth in total, 0 (figure 4*a*). Four or fewer teeth, 1 (figure 4*d*). Even though teeth are not preserved, the morphology of the premaxilla in aigialosaurs suggests that only four teeth were present (Carroll & DeBraga 1992). D

92. *Maxillary teeth.* Thirteen or more, 0 (figure 2*d*). Between twelve and nine, 1 (figure 2*a*). Eight or fewer, 2 (figure 2*e*). The three states form a clear morphocline, 0–1–2 and this character has been ordered. Although *Anniella* has state 2, the most primitive annielline (*Apodosauriscus*) appears to have state 0, as do other

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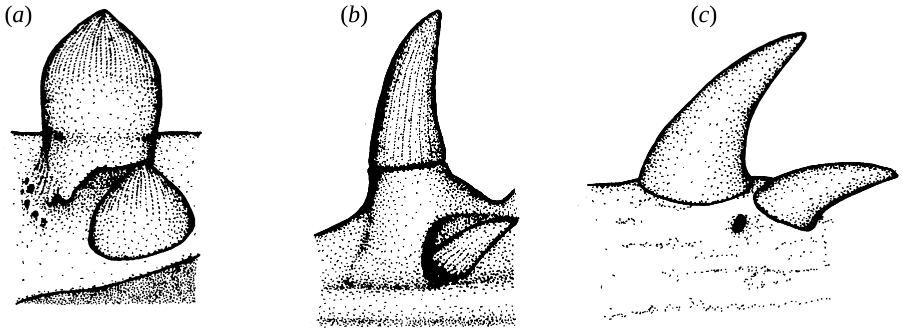

Figure 9. Tooth replacement in varanoids. (*a*) Dentary tooth of *Varanus*. (*b*) *Maxillary tooth of Platecarpus* (Mosasauridae), illustrated inverted for comparative purposes. (*c*) Dentary tooth of *Cylindrophis* (Alethinophidia). (*a*) after BMNH 1983.1132, (*b*) after AMNH 1820, (*c*) AMS R131356.

anguids. Although not all of the teeth are preserved in *Paravaranus*, the length of the maxilla and the spacing of the teeth suggests that there were at least 13 teeth. Alethinophidians are highly variable: *Dinilysia*, 0; cylindrophids, 1; *Anomochilus*, uropeltids and aniliids, 2. P D

93. *Palatine*. Edentulous, 0 (figure 4*b*). Toothed, 1 (figure 4*c*). State 1 is tentatively interpreted as primitive for helodermatids: the basal fossil form *Heloderma texanum*, and most *H. horridus* have this state, but most *H. suspectum* have state 0. State 0 is primitive for anguids, although anguines such as *Ophisaurus* have state 1. In *Paravaranus*, the limits of the palatine are uncertain, as palatine–pterygoid suture is indeterminate. However, the area occupied by the palatine in other varanoids bears small denticles. Even though illustrations of *Lanthanotus* depict it with an edentulous palatine (e.g. Rieppel 1980*a*, 1983), teeth are present (e.g. Estes *et al*. 1970; Borsuk-Bialynicka 1984). R P E D

94. *Pterygoid*. Toothed, 0 (figure 4*c*). Edentulous, 1 (figure 4*b*). This character is highly variable within basal alethinophidians (e.g. *Dinilysia*, aniliids, cylindrophids, xenopeltids, 0; uropeltids and *Anomochilus*, 1), lacertoids (Arnold 1973, 1989; Estes *et al*. 1988) and scincoids (Greer 1970; Estes *et al*. 1988). R P E D

95. *Pterygoid teeth*. Small, closely spaced denticles, 0 (figure 4*c*). Long, widely-spaced, recurved teeth, 1 (figure 4*d*). This character is not applicable in taxa which lack pterygoid teeth (see previous character). Alethinophidians with pterygoid teeth always have state 1, with the possible exception of *Dinilysia*, where these teeth are not preserved but the empty alveoli are small (Estes *et al*. 1970). R P E D

(*f*) ***Axial skeleton***

96. *Precondylar constriction on centrum*. Absent or weak, 0 (figure 10*d*). Pronounced, 1 (figure 10*e*). E

97. *Zygosphenes and zygantra*. Absent, 0 (figure 10*g*). Present, articular surface of zygosphene faces dorsally, 1 (figure 10*h*). Present, articular surface of zygosphene faces ventolaterally, 2 (figure 10*i*). The three states do not form a clear morphocline. Although zygosphenes and zygantra are 'present' in states 1 and 2, their morphology differs so greatly that homology cannot be assumed but should be tested by congruence with other characters. This character is therefore unordered. Mosasaurs primitively have zygosphenes and zygantra (morphology as described for state 2) throughout the presacral column: however, the zygosphene–zygantral articulations are reduced in the posterior dorsals of derived forms such as *Mosasaurus* (Lingham-Soliar 1991*a*, 1995). E D

98 *and* 99. *Vertebral condyles in trunk region*. A bifurcating character recoded as two binary characters. Character 98: primitive, condyles facing dorsally (none of the condylar surface is exposed in ventral view) (figure 10*e*) or slightly dorsally (only the ventral edge of the condylar surface is visible in ventral view) (figure 10*d*), 0; derived, condyles facing posteriorly (much of the condylar surface is visible in ventral view) (figure 10*f*), 1. Character 99: primitive, condyles facing posteriorly or slightly dorsally, 0; derived, condyles facing dorsally, 1. The inferred morphocline is: condyles face posteriorly (98–1, 99–0) ← condyles face posterodorsally (98–0, 99–0) → condyles face dorsally (98–0, 99–1). The primitive condition of this character in alethinophidians appears to be 98–1, 99–0: *Dinilysia*, uropeltids, aniliids and xenopeltids all have posteriorly facing condyles. However, cylindrophids have dorsoposteriorly facing condyles. E D

100. *Neural spines*. High spinous projection, 0. Reduced to low ridge, 1. All basal alethinophidians have low neural spines.

101. *Ribs*. Begin from fourth cervical vertebra, 0. Begin from third cervical vertebra, 1. The primitive condition in anguids is uncertain, since both conditions are widespread in the group (Hoffstetter & Gasc 1969). The primitive condition in xenosaurids is similarly uncertain: *Xenosaurus* has state 1 (Hoffstetter & Gasc 1968), *Shinisaurus* has state 0 (Hecht & Costelli 1969). The holotype of the aigialosaur *Aigialosaurus dalmaticus* clearly shows ribs on the third cervical (Carroll & DeBraga 1992).

102. *Precloacal vertebrae*. Fewer than 100 precloacal vertebrae, 0. More than 120 precloacal vertebrae, 1.

103. *Cervical vertebrae*. Not longer than dorsal vertebrae, and with anteroposteriorly narrow neural arch, 0 (figure 10*a*). Elongated, longer than dorsal vertebrae and with anteroposteriorly broadened neural arch, 1 (figure 10*b*).

104. *Cervical neural spines*. Inclined slightly postero-

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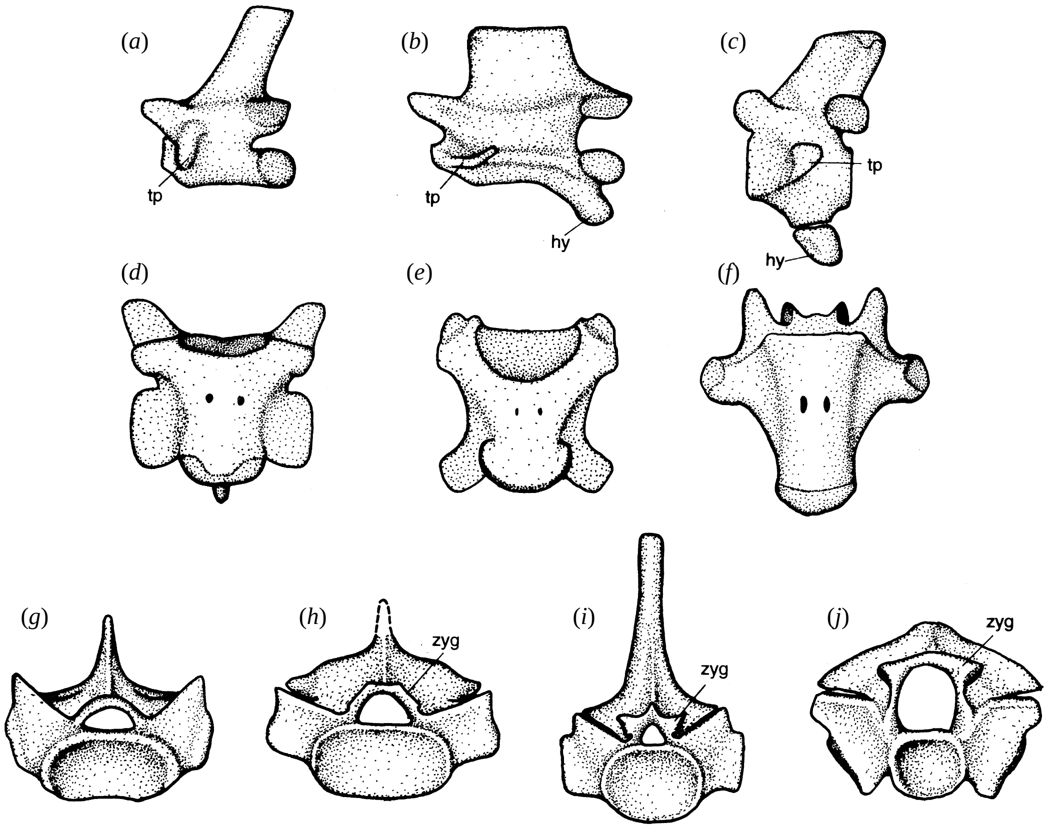

Figure 10. Cervical vertebrae of varanoids in left lateral view. (*a*) *Heloderma*, (*b*) *Varanus*, (*c*) *Platecarpus* (Mosasauridae). Dorsal vertebrae of varanoids in ventral view. (*d*) *Heloderma*, (*e*) *Varanus*, (*f*) *Clidastes* (Mosasauridae). Dorsal vertebrae of varanoids in anterior view. (*g*) *Varanus*, (*h*) *Saniwa*, (*i*) *Clidastes* (Mosasauridae), (*j*) *Eoanilius* (Alethinophidia). (*a*) after AMNH 109521, (*b*) after CSIRO REPS17, (*c*) after Russell 1967, (*d*) after AMNH 109521, (*e*) after CSIRO REPS17, (*f*) after AMNH 1548, (*g*) after CSIRO REPS17, (*h*) after AMNH 1020A, (*i*) after AMNH 1548, (*j*) after Rage (1974).

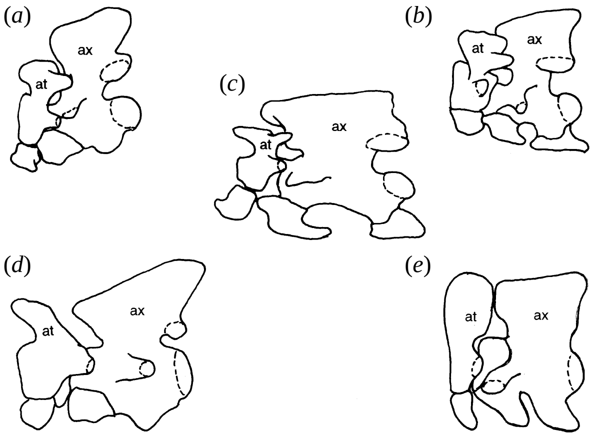

Figure 11. Atlas– axis complexes of varanoids, in left lateral view. (*a*) *Heloderma*, (*b*) *Lanthanotus*, (*c*) *Varanus*, (*d*) *Clidastes* (Mosasauridae), (e) Typhlops (Scolecophidia). (*a–c*) after Rieppel (1980*a*), (*d*) after Russell (1967), (*e*) after List (1966).

dorsally, 0 (figure 10*a*). Exactly vertical, 1 (figure 10*b*). This trait cannot be scored for scolecophidians or basal alethinophidians, which have very low neural spines in this region (see character 100).

105. *Cervical hypapophyses*. Only extending from first cervical to fifth cervical (at most), 0. Extending from first to sixth cervical (or more), 1. The primitive condition in anguids is uncertain: anniellines and anguines have state 1, other anguids have state 0.

106. *Dorsoposterior process on atlas neural arch*, overlying axis neural arch. Present, 0 (figure 11*a*). Absent, 1 (figure 11*d*). The primitive condition in alethinophidians is state 1 (uropeltids, aniliids, cylindrophids), even though many higher forms (e.g. xenopeltids) have state 0. The dorsoposterior process is absent in mosasaurs, e.g. *Mosasaurus* (Lingham–Soliar 1995).

107. *Posterior hypapophyses on axis (and other cervical) vertebra*. Sutured with centrum, 0 (figure 11*a*). Separate from centrum, 1 (figure 11*d*). *Lanthanotus* has state 0 (Rieppel 1983), even though it has been reconstructed with state 1 (Hoffstetter 1968).

108. *Number of cervical vertebrae*. Eight or fewer, 0. Nine or more, 1. This character cannot be determined in scolecophidians, alethinophidians or annielline anguids, which have lost the shoulder girdle and forelimbs. Mosasaurs primitively have seven cervicals, although certain derived forms such as *Hainosaurus* have up to ten (DeBraga & Carroll 1993). P E D

109. *Transverse processes on third and subsequent cervicals*. Near anterior edge of the lateral surface of the centrum, 0 (figure 10*a*). In the middle of the lateral surface of the centrum, 1 (figure 10*c*).

110. *Shape of condyles and cotyles in mid-dorsal vertebrae*. Oval, horizontal (mediolateral) dimension wider than vertical (dorsoventral) dimension, 0. Circular, 1. Some

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scolecophidians have been illustrated with oval condyles (e.g. *Typhlops*, Rage 1984): however, examination of specimens (e.g. USNM 32074) shows that the condyles are round. D

111. *Lymphapophyses* (*forked 'sacral' ribs*). Absent, 0 (figure 13*d*). Present, 1 (figure 13*e*).

112. *Tail*. Long, at least 40% of the length of presacral (precloacal) region, 0. Short, less than 40% of the length of precloacal region, 1. D

113. *Pygals* (anterior caudal vertebrae lacking chevrons). Four or fewer, 0. Five or more, 1. The primitive condition in alethinophidians is uncertain since both conditions occur (e.g. uropeltids and xenopeltids, 0; aniliids, 1). Scolecophidians lack chevrons on all caudal vertebrae (1). D

114. *Caudal zygapophyses*. Present on all caudal vertebrae, 0. Absent in distal caudal vertebrae, 1. D

115. *Caudal transverse processes*. Present on all caudal vertebrae, 0. Absent in distal caudal vertebrae, 1. D

116. *Caudal neural spines*. Not taller than dorsal neural spines, tail not dorsoventrally expanded, 0. Taller than dorsal neural spines, tail dorsoventrally expanded, 1.

117. *Peduncles on caudal vertebrae for chevrons*. Weakly developed, barely raised above the surface of the centrum, 0. Prominent raised tubercles, 1. This character cannot be scored in scolecophidians (which lack chevrons) or alethinophidians, (where the chevrons are completely fused to the vertebrae). It also cannot be scored in many mosasaurs (which also have fused chevrons): however, where the chevrons are separate, the articulatory peduncles are prominent. P

(*g*) *Shoulder girdle and forelimb*

118. *Clavicles*. Present, 0. Absent, 1. The primitive condition in anguids uncertain. Anniellines lack the clavicle, while all other anguids possess one. The rudimentary bone in the shoulder region of anniellines is most probably a scapulocoracoid (Underwood 1976). The primitive condition in aigialosaurs is uncertain: clavicles were not found in all the (articulated) specimens described by Carroll & DeBraga (1992), but are definitely present in *Carsosaurus* (Caldwell *et al.* 1995 and personal observation). The primitive condition in mosasaurs is also uncertain: although clavicles are only known to be present in one form (*Plotosaurus*), facets on the interclavicle suggest that clavicles were present in many other taxa (Russell 1967). E

119. *Interclavicles*. Present, 0. Absent, 1. The primitive condition in anguids is uncertain. Anniellines lack the interclavicle (e.g. Underwood 1976) but other anguids retain it. E

120. *Lateral* (*clavicular*) *process of interclavicle*. Present, 0. Absent, 1. *Lanthanotus* exhibits state 0 (Estes *et al.* 1988; *contra* Rieppel 1980*b*). E D

121. *Ossified sternum*. Present, 0. Absent, 1. Among anguids, anniellines lack a sternum, but most other anguids possess them. For reasons outlined under character 127, I will tentatively assume that a sternum was primitively present in anguids but lost in anniellines.

122 *and* 123. *Sternal ribs*. A bifurcating character recoded as two binary characters. 122: four pairs or more, 0; three pairs or fewer, 1. 123: four pairs or fewer, 0; Five pairs or more, 1. Cannot be scored in taxa which lack a sternum. The morphocline is: three pairs or fewer (122–1, 123–0) ← four pairs (122–0, 123–0) → five pairs or more (122–0, 123–1). Cannot be scored in taxa which lack a sternum. P E D

124. *Scapulocoracoid*. Present, 0. Absent, 1. The rudimentary element in the shoulder region of anniellines appears to be a scapulocoracoid (Underwood 1976). All other anguids also retain a scapulocoracoid.

125. *Ventral portion of glenoid rim*. Flush with posterior edge of coracoid, 0 (figure 12*a*). Projects posteriorly beyond posterior edge of coracoid, 1 (figure 12*b*).

126. *Posterior coracoid foramen*. Absent, 0 (figure 12*a*). Present, 1 (figure 12*b*). The primitive condition in anguids is uncertain, e.g. *Barisia* has the foramen, *Mesaspis* lacks it, while in *Elgaria* and *Gerrhonotus* the region is very weakly ossified! P E

127. *Forelimbs*. Large, 0. Greatly reduced or absent, 1. Among anguids, anniellines lack forelimbs, but most other anguids possess them. If only the distribution of character states is considered, the primitive condition in anguids is uncertain. However, it appears implausible that the anniellne condition was primitive for anguids and that the remaining anguids re-evolved a perfectly normal forelimb: thus, I will tentatively assume that a well-developed forelimb was primitively present in anguids, though lost in anniellines. The same arguments apply to other *complex* structures such as the sternum, pelvis and hindlimb which are absent or vestigial in anniellines but present (and of normal morphology) in other anguids. However, it is dangerous to make such assumptions regarding the direction of evolution of simpler structures. Such structures have indeed been shown to have disappeared and reappeared, e.g. the simple, rod-like clavicles of dinosaurs were lost in theropods, but some derived forms have re-evolved a similar structure (Bryant & Russell 1993).

128. *Olecranon process of ulna*. Large pointed projection, 0. Small, rounded knob, 1. This is not applicable in taxa with reduced forelimbs (see preceding character). D

(*h*) *Pelvis and hindlimb*

129. *Pelvis*. Well developed, 0. Minute or absent, 1. The pelvis is rudimentary in anniellines, but normal in most other anguids. For reasons outlined under character 127, I will assume that a well-developed pelvis was primitive for anguids but reduced in anniellines.

130. *Pelvic elements* (*ilium*, *ischium*, *pubis*). Co-ossified into an innominate bone, 0. Distinct elements but strongly sutured together, 1 (figure 13*b*). Distinct elements, weakly united, 2 (figure 13*c*). The three states form a clear morphocline, 0–1–2, and this character has been ordered. Scolecophidians and alethinophidians which retain pelvic rudiments (and thus can be coded for this character) exhibit state 2.

131. *Ilium*. Dorsal portion articulates with distal end

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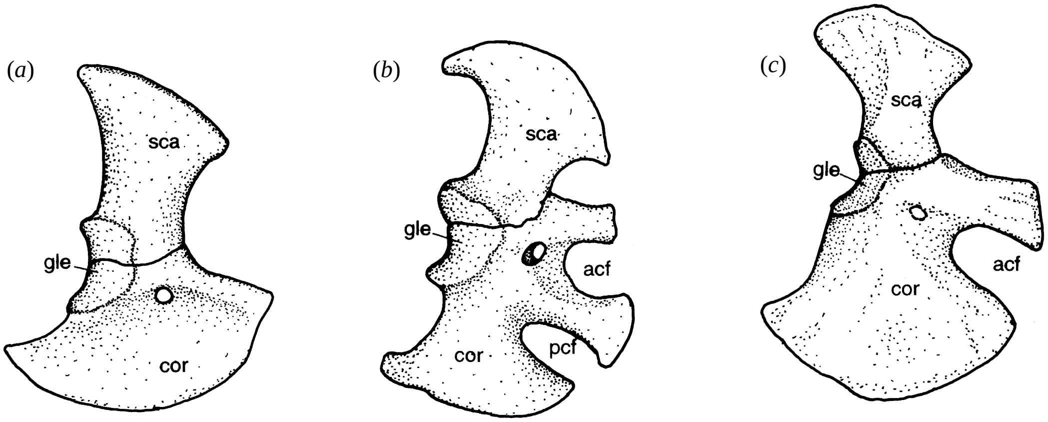

Figure 12. Scapulocoracoids of varanoids in right lateral view. (*a*) *Heloderma*, (*b*) *Varanus*, (*c*) *Halisaurus* (Mosasauridae). (*a*) after AMNH 109521, (*b*) after Lecuru 1968, (*c*) after DeBraga & Carroll (1993).

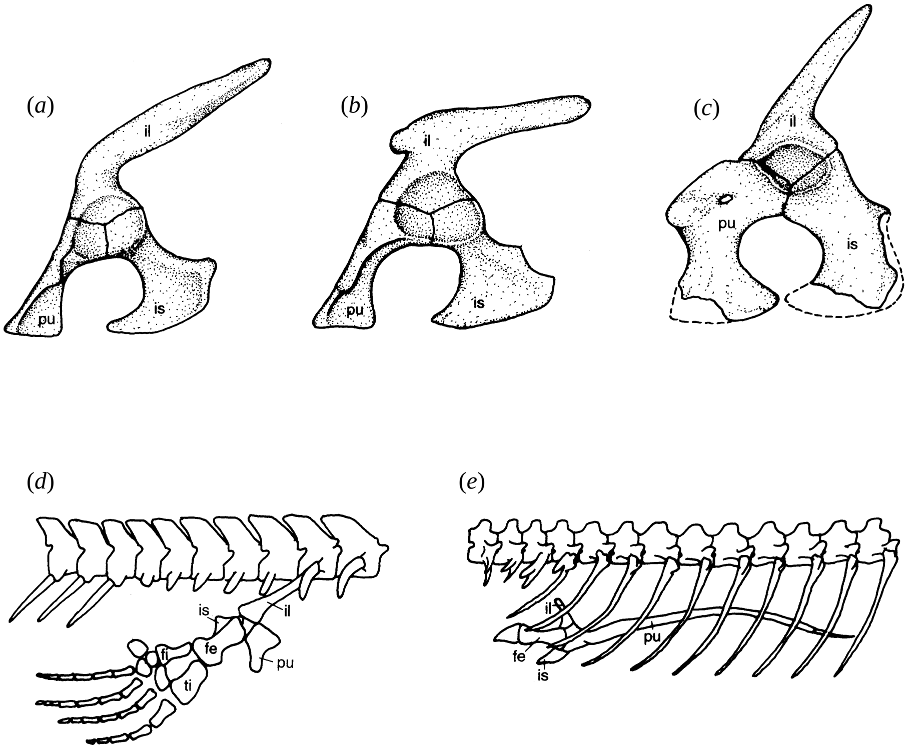

Figure 13. Pelves of varanoids, in left lateral view. (*a*) *Heloderma*, (*b*) *Varanus*, (*c*) *Halisaurus* (Mosasauridae). Pelvic regions of (*d*) *Clidastes* (Mosasauridae) and (*e*) *Python* (Alethinophidia), showing the position of the ilium medial to the sacral ribs. (*a*) after AMNH 109521, (*b*) after UMZC R9586, (*c*) after DeBraga & Carroll (1993), (*d*) after Russell (1967) and Dobie *et al*. (1986), (*e*) after Renous *et al*. (1976).

of sacral ribs, 0. Dorsal portion lies medial to distal end of 'sacral' ribs, 1. In scolecophidians and alethinophidians, true sacral ribs are absent. However, the ilium in these taxa lies medial to the ribs in the 'sacral' region. Mosasaurs also have state 1 (figure 13*d*; Dobie *et al*. 1986), contrary to earlier reconstructions (e.g. Williston 1898; Russell 1967).

132. *Sacral blade of ilium*. With anterior process, 0 (figure 13*b*). Without anterior process, 1 (figure 13*a*). The primitive condition in xenosaurids is uncertain: *Xenosaurus* has the anterior process, *Shinisaurus* lacks it. The same applies to anguids (anniellines and anguines, 1; other anguids, 0) and scincoids (scincids, 1; cordylids and gerrhosaurids, 0). Outgroup variability means this character cannot be polarized.

133. *Pubis*. Curved plate, with a transversely oriented 'lip' near acetabulum, 0 (figure 13*a*). Flat plate, entire surface faces laterally, 1 (figure 13*c*). In scolecophidians and alethinophidians, the pubis is vestigial or absent, and this character cannot be scored. D

134. *Hindlimbs*. Well developed, 0. Minute or absent, 1. Hindlimbs are absent in anniellines, but present in most other anguids. For reasons discussed under

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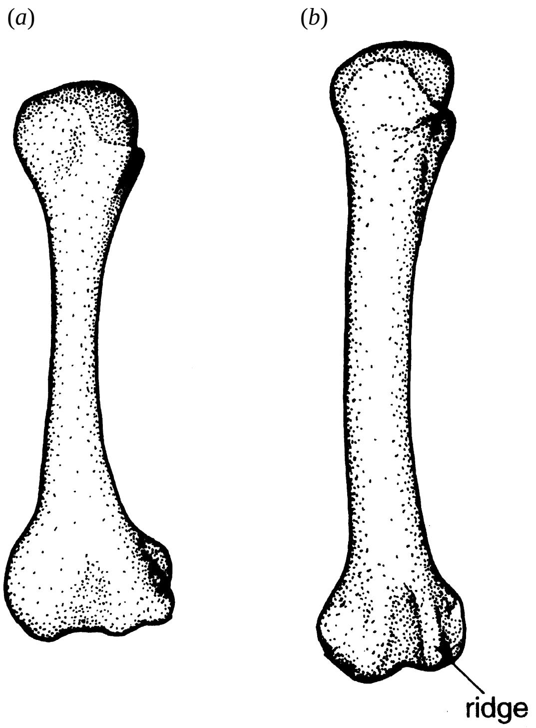

Figure 14. Right femora of varanoids, in dorsal view. (*a*) *Heloderma*, (*b*) *Varanus*. (*a*) after AMNH 109521, (*b*) after UMZC R9586.

character 127, I will assume that well-developed hindlimbs were primitive for anguids but lost in anniellines.

135. *Femur*. Gracile, 0. Stout, 1. Scolecophidians and alethinophidians which retain limbs exhibit state 1.

136. *Femur*. Curved in dorsoventral plane, 0. Not curved, 1. In scolecophidians and alethinophidians this character cannot be coded; the femur is either absent, or so short that the curvature cannot be determined. D

137. *Distal condyles of femur*. Dorsal surface of preaxial condyle smooth, 0 (figure 14*a*). Dorsal surface of preaxial condyle with sharp ridge extending along long axis of femur, 1 (figure 14*b*).

138. *Limb epiphyses*. Present, 0. Absent, 1. In scolecophidians and alethinophidians, epiphyses are absent in the rudimentary hindlimbs.

139. *Astragalus and calcaneum*. Co-ossified into single bone, 0. Distinct elements, either suturally united or separate from one another, 1. This character cannot be determined in scolecophidians or alethinophidians, where the astragalus and calcaneum cannot be identified. D

(*i*) *Other characters*

140. *Epiphyses* on skull (e.g. on basal tubera) and axial skeleton (ventral edge of transverse processes). Present, 0. Absent, 1. Snakes have lost the cranial and axial epiphyses (Haines 1969). These structures are also absent in mosasaurs and aigialosaurs, although epiphyses are present in the limbs (only) of aigialosaurs (e.g. Caldwell *et al*. 1995).

141. *Scleral ossicles*. Present, 0. Absent, 1.

142. *Scleral ossicles*. Fourteen or more, 0. Thirteen or fewer, 1. Both states are widespread within lacertoids and scincoids (Estes *et al*. 1988). This character cannot be scored in those taxa lacking scleral ossicles. P E

143. *Second epibranchial*. Present, 0. Absent, 1. P E

144. *Osteoderms over skull and body*. Present, 0. Absent, 1. Both conditions are present in *Varanus* (McDowell & Bogert 1954). Because osteoderms are frequently not preserved in fossil forms, I have been conservative and only coded fossil taxa as lacking osteoderms when numerous skeletons are known and all lack osteoderms. However, when only a single individual of a fossil taxon is known and associated osteoderms are identified, osteoderms can be assumed to be present. E

8. PARSIMONY ANALYSIS AND RESULTS

The above data were analysed using the branch and bound function in PAUP, version 3.1.1 (Swofford 1993). The tree was rooted with an ancestral taxon exhibiting the inferred primitive states for all characters (see section 3). Characters that could not be polarized were coded as unknown in this ancestral taxon.

The random trees function revealed that the distribution of tree lengths was highly skewed, with very few shortest trees, consistent with (e.g. Hillis 1991), but not proof of (Kallersjö *et al*. 1992), a strong phylogenetic signal in the data. Four most-parsimonious trees were found, each 214 steps long and with a consistency index (c.i.) of 0.73. However, the expected value of this index is highly data dependent: having fewer taxa, or characters with derived states that are not widely distributed, reduces the expected amount of character conflict (Sanderson & Donoghue 1989). For example, an analysis which includes only two taxa, or only autapomorphies, will always have a c.i. of 1. The retention index (r.i.) corrects for these factors (Farris 1989). In this analysis, the r.i. is 0.79, a reflection of the large number of taxa and the fact that many of the derived states are widely distributed.

The strict component consensus tree (see Wilkinson 1994) is shown in figure 15. The phylogeny is highly asymmetrical, with dichotomies tending to occur on one side of the phylogeny (the side leading to snakes). However, the number of taxa was too small for the pattern to be significantly different from random. For example, according to the model in Slowinski & Guyer (1989), the probability of 15 taxa having a basal dichotomy yielding sister groups of 1 and 14 taxa – as happened in the present study – is 0.142.

The degree of support for each grouping in the analysis was ascertained by the Bremer index – the minimum number of extra steps required to break up a clade found on the most parsimonious tree (Bremer 1988). These indices are not as burdened by assumptions as bootstrapping values, but have the obvious drawback of not being expressible in statistical terms. For example, to say that Pythonomorpha (the mosasaur–aigialosaur–scolecophidian–alethinophidian clade) has a support index of 18 means that the shortest tree in which these four taxa do not form a clade is 18 steps longer than the most-parsimonious tree. In order

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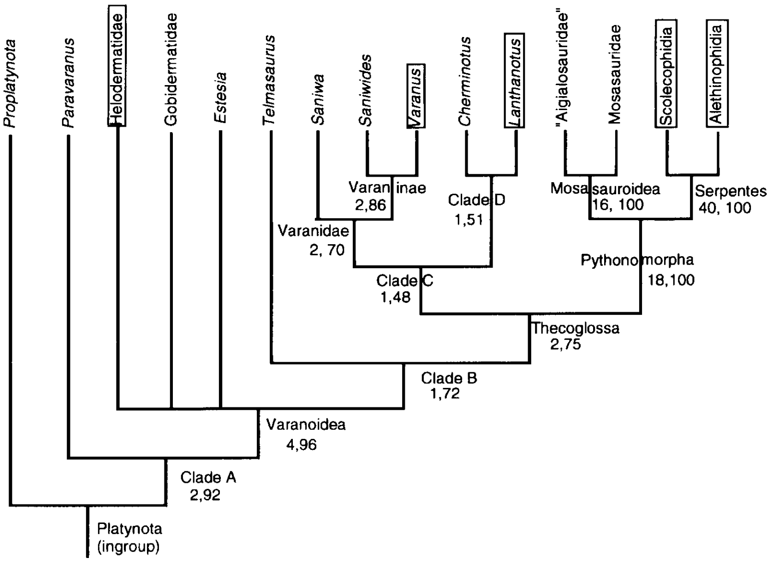

Figure 15. The phylogenetic relationships of platynotan squamates, as indicated by the present phylogenetic analysis. This is the strict consensus of the four most parsimonious trees. The Bremer index of each clade is shown first, followed by the bootstrapping frequency.

to obtain this index, a constraint tree is entered into PAUP: in this constraint tree, the four pythonomorph taxa form a clade, but relationships within this clade, and between the pythonomorph clade and all other ingroup taxa, are unresolved. PAUP is then instructed to find the most parsimonious tree which is *not* consistent with this constraint tree. The difference between the length of this tree (232), and the length of the most parsimonious unconstrained tree (214), is the support index. This procedure is repeated for each clade represented in the most-parsimonious tree. The support index for each clade thus obtained is shown in figure 15. It is clear that, while Mosasauroidea, Serpentes and Pythonomorpha are comparatively well supported, many of the other clades are only weakly corroborated. This, however, is due, not to character incongruence, but to missing data. Many of the fossil platynotan taxa are very poorly known: because they can only be coded for a few characters, they can 'fit' into numerous different positions in the cladogram with little loss in parsimony (Wilkinson 1995; Wilkinson & Benton 1995). As a result, the support indices for clades that contain them are usually rather weak.

The bootstrapping function in PAUP (200 iterations, branch and bound) was also used to assess the statistical significance of the various groupings found in the analysis. The support or confidence level (Felsenstein 1985) for each clade is also shown in figure 15.

Characters were optimized onto the cladogram using the delayed transformation (DELTRAN) function in PAUP, which assumes that changes in character states occur at the latest time consistent with the phylogeny. This is the approach adopted in most studies (e.g. Gauthier *et al.*, 1988; Bryant & Russell, 1992). However, this has the consequence that, for ambiguous characters, delayed optimization favours convergence over reversal. Ambiguous characters are those which can optimize equally parsimoniously in two or more pathways, e.g. a single acquisition and then a reversal, or as two convergent acquisitions. There is little evidence, however, that convergence is more prevalent than reversal (Kluge 1989).

9. TAXONOMIC IMPLICATIONS

In the following section, a new indented monophyletic taxonomy of platynotans is proposed. Categorical ranks are eschewed. Only well-corroborated clades are named, and these taxon names are given ancestry-based (rather than character–based) definitions (see DeQueiroz & Gauthier 1992). Predictably, the two snake taxa (scolecophidians and alethinophidians) are united by a large suite of characters. Surprisingly, however, the next most robust clade is a grouping containing mosasauroids and snakes.

The major taxonomic proposals elaborated below are as follows: the well-known name Varanoidea is restricted to the crown clade bounded by *Heloderma*, *Lanthanotus* and *Varanus*, while the less common name Platynota is used to refer to the more inclusive clade consisting of the crown clade and all stem (fossil) taxa that lie outside the extant crown clade. The phylogenetic conclusions of this study mean that snakes (Serpentes) must be included within both Varanoidea and Platynota. The name Necrosauridae is discarded. This name is firmly entrenched in the literature to refer to a heterogenous (and non-monophyletic) assemblage of fossil taxa, including *Proplatynota* and gobidermatids (e.g. Estes 1983; Borsuk-Bialynicka 1984). Attempting a monophyletic redefinition would only lead to confusion, and I have chosen instead to discard it. Finally, the name Pythonomorpha is resurrected and used in much the same spirit as Cope (1869) proposed it: to emphasize the affinities between mosasaurs and snakes.

The diagnostic changes for each clade under delayed transformation (see §8) are listed here. Characters which diagnose other (more or less inclusive) clades under accelerated transformation are indicated with

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an asterisk. All other characters are optimization independent.

(*a*) ***Platynota***

Definition. *Heloderma*, *Lanthanotus* and *Varanus*, and all taxa more closely related to these forms than to other anguimorphs. A stem-based definition (see DeQueiroz & Gauthier 1992).

Diagnosis. In addition to the characters listed under 'ingroup monophyly', the following characters diagnose the ingroup, but are secondarily absent in some taxa.

1. Vomer rod-like. Reverses in *Lanthanotus* (character 51: 0 → 1, c.i. = 0.5).
2. Coronoid with horizontal anterior extension. Reverses in alethinophidians (77: 0 → 1, c.i. = 0.5).
3. Resorption pits absent. Further modified in mosasauroids (89: 0 → 1, c.i. = 1).
4. Palatine toothed. Reverses (teeth lost) in *Varanus*, mosasaurs and scolecophidians (93: 0 → 1 c.i. = 0.25).

Comments. Borsuk-Bialynicka (1984), Pregill *et al*. (1986) and Evans (1995) have all applied the taxon name Platynota (Baur 1890) to living varanoids and their fossil relatives. Platynota is here given a phylogenetic definition most consistent with the existing definition. Pregill *et al*. (1986) and Evans (1995) included all ingroup taxa in Platynota. All ingroup taxa, except *Proplatynota*, were included in Platynota by Borsuk-Bialynicka (1984). *Proplatynota* was excluded from Platynota because it was interpreted as lacking the 'defining' characters. However, the preceding phylogenetic analysis demonstrates that *Proplatynota* possesses the diagnostic characters of platynotans (see section 2).

Unnamed clade A (*all platynotans except Proplatynota*)

Diagnosis.

1. Palatine short, half as long as vomer. Reverses in alethinophidians (57: 0 → 1, c.i. = 0.5).
2. Subdental shelf absent (67: 0 → 1, c.i. = 1).

Comment. Although bootstrapping suggests that this clade is well-corroborated, it has not been named as it is unlikely to be regularly discussed.

(*b*) ***Varanoidea***

Definition. The most recent common ancestor of *Heloderma*, *Lanthanotus* and *Varanus*, and all its descendants. A node-based, crown-clade definition (see DeQueiroz & Gauthier 1992; Lee 1996*b*). Depending on their true phylogenetic position (at present unresolved), gobidermatids and *Estesia* might or might not be part of this group.

Diagnosis.

1. Posterior end of maxilla does not reach middle of orbit. Reverses in *Heloderma* (9: 0 → 1, c.i. = 0.5).
2. Supratemporal large. Reverses in scolecophidians (26: 0 → 1, c.i. = 0.5).
3. Maxilla enters suborbital foramen. Reverses in *Saniwa* and pythonomorphs (66: 0 → 1, c.i. = 0.33).

*4. Surangular, when disarticulated, with flat anterior end. Reverses in snakes (82: 0 → 1, c.i. = 0.5).

5. Marginal teeth with carinae (87: 0 → 1, c.i. = 0.5). Reverses in *Heloderma* (87: 0 → 1, c.i. = 0.5).
6. Plicidentine present. Lost in snakes (88: 0 → 1, c.i. = 0.5).
7. Less than 13 maxillary teeth. Reverses in mosasauroids (92: 0 → 1, c.i. = 0.5).

*8. Pelvic elements separate, not co-ossified into single innominate bone. (130: 0 → 1, c.i. = 1).

*9. Thirteen or fewer scleral ossicles. Reverses in *Varanus* (142: 0 → 1, c.i. = 0.5).

Comments. Although most of the characters diagnosing this clade are equivocal (being secondarily absent in some members), the Bremer index, and bootstrapping values, indicate that the grouping is robust. I have followed Pregill *et al*. (1986) and Estes *et al*. (1988) in applying the taxon name Varanoidea (Camp 1923).

Unnamed clade B (Telmasaurus *and thecoglossans*)

Diagnosis.

1. Lacrimal foramen double. Condition in pythonomorphs difficult to score (11: 0 → 1, c.i. = 1).
2. Quadrate with reduced tympanic conch. Reverses in mosasauroids (31: 0 → 1, c.i. = 0.67).

(*c*) ***Thecoglossa***

Definition. The most recent common ancestor of varanids and pythonomorphs, and all its descendants. A node-based definition (see DeQueiroz & Gauthier 1992).

Diagnosis. Because of the amount of missing data in *Telmasaurus*, many of these traits (*) might diagnose the previous, more inclusive clade.

*1. External naris slightly retracted. Convergent in *Estesia* (4: 0 → 1, c.i. = 0.5).

2. Basal tubera anteriorly located (39: 0 → 1, c.i. = 1).

*3. Foramen pro nervi facialis double (42: 0 → 1, c.i. = 1).

4. Supraoccipital contacts parietal. Further elaborated, convergently, in *Lanthanotus* and pythonomorphs (49: 0 → 1, c.i. = 0.5).

*5. Surangular does not project far into dentary (83: 0 → 1, c.i. = 1).

*6. Cervical hypapophyses extending at least to sixth cervical. Reverses in scolecophidians (105: 0 → 1, c.i. = 1).

*7. Prominent peduncles on caudal centra for chevrons (117: 0 → 1, c.i. = 1).

*8. Second epibranchial absent (143: 0 → 1, c.i. = 1).

Comments. *Varanus*, *Lanthanotus*, snakes and related fossil taxa form a robust clade. I here apply the taxon name Thecoglossa (Cope 1900) to this clade. This seems appropriate because *Varanus*, *Lanthanotus* and snakes share derived similarities of the tongue (McDowell 1972; Schwenk 1988), although the tongue sheath of *Varanus* and snakes (to which the name Thecoglossa refers) does not appear to be present in *Lanthanotus*.

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Unnamed clade C

Diagnosis.

1. Dorsal maxillary process positioned near posterior end of maxilla. Convergent in *Paravaranus*, reversed in snakes (8: 0→1, c.i. = 0.33).
2. Opisthotic with horizontal flange partially flooring middle ear (47: 0→1, c.i. = 1).
3. Opening of Jacobsen's organ not bordered by septomaxilla (52: 1→2, c.i. = 1).
4. Nine cervical vertebrae (108: 0→1, c.i. = 1).
5. Three or fewer pairs of sternal ribs (122: 0→1, c.i. = 1).

(*d*) *Varanidae*

Definition. *Varanus* and all taxa more closely related to *Varanus* than to *Lanthanotus*. A stem-based definition (see DeQueiroz & Gauthier 1992).

Diagnosis.

1. Ventral surface of ectopterygoid faces ventrolaterally (64: 0→1, c.i. = 1).
2. Precondylar constriction on centrum (96: 0→1, c.i. = 1).
3. Vertebral condyles face dorsally (99: 0→1, c.i. = 1).
4. Cervical vertebrae elongated (103: 0→1, c.i. = 1).
5. Cervical neural spines vertical (104: 0→1, c.i. = 1).
6. Ventral portion of glenoid rim projects beyond posterior edge of coracoid (125: 0→1, c.i. = 1).
7. Sacral blade of ilium with anterior process. Convergent in *Telmasaurus* (132:1→0, c.i. = 0.5).
8. Distal condyle of femur with dorsal ridge (137: 0→1, c.i. = 1).

Comments. Varanidae (Gray 1827), as here defined, includes *Saniwa*, *Saniwides* and *Varanus* but not *Lanthanotus* and *Cherminotus*.

(*e*) *Varaninae*

Definition. The most recent ancestor of *Varanus* and *Saniwides* and all its descendants. A node-based definition (see DeQueiroz & Gauthier 1992).

Diagnosis.

*1. Postorbital and postfrontal fused (23: 0→1, c.i. = 0.2).

2. Palatines without choanal groove (56: 0→1, c.i. = 1).
3. Pterygoids without ventral groove (60: 0→1, c.i. = 1).

Comments. Bootstrapping and the Bremer index both suggest that this clade is rather robust. The name Varaninae (Camp 1923) is here applied to this group. The ending reflects the nesting of this group within Varanidae.

Unnamed clade D

Diagnosis.

1. Upper temporal arcade incomplete. Convergent in helodermatids and snakes (22: 0→1, c.i. = 0.33).
2. Ectopteryoid laterally placed (63: 0→1, c.i. = 1).

Comments. Should this clade become more highly corroborated in the future, I suggest applying the name Lanthanotidae to it. Lanthanotidae (Steindachner 1878) was originally erected to contain only *Lanthanotus*, and was thus redundant.

(*f*) *Pythonomorpha*

Definition. The most recent common ancestor of mosasauroids and snakes, and all its descendants. A node-based definition (see DeQueiroz & Gauthier 1992).

Diagnosis.

1. Lacrimal foramen enclosed entirely by prefrontal (11: 1→2, c.i. = 1).
2. Parietal with large descending flange, sutured to prootic (18: 0→1, c.i. = 1).
3. Supratemporal contacts prootic (25: 0→1, c.i. = 1).
4. Supratemporal intercalated between quadrate and braincase (27: 0→1, c.i. = 1).
5. Basipterygoid processes do not project far beyond body of basisphenoid (33: 0→1, c.i. = 1).
6. Basipterygoid articulation elongated anteroposteriorly. Convergent in helodermatids (34: 0→1, c.i. = 0.5).
7. Body of basisphenoid extends far anteriorly beyond dorsum sellae (35: 0→1, c.i. = 1).
8. Cultriform process straight in lateral view (36: 0→1, c.i. = 1).
9. Vidian canal is an open groove anteriorly. Present in scolecophidians, but further modified in alethinophidians (37: 0→1, c.i. = 1).
10. Rear opening of vidian canal situated far posteriorly. Convergent in helodermatids (38: 0→1, c.i. = 0.5).
11. Crista circumfenestralis present (44: 0→1, c.i. = 1).

*12. Extracolumella with extensive contact with quadrate. Convergent in *Lanthanotus* (45: 0→1, c.i. = 0.5).

13. Supraoccipital sutures extensively with parietals. Convergent in *Lanthanotus* (49:1→2, c.i. = 0.5).
14. Palatine with long anterior process (58: 0→1, c.i. = 1).
15. Anterior process of pterygoid distinct from lateral process (62: 0→1, c.i. = 1).
16. Maxilla enters suborbital foramen. Reversal (66: 1→0, c.i. = 0.33).
17. Mandibular symphysis highly mobile (68: 0→1, c.i. = 1).
18. Meckelian groove confined to medial surface of lower jaw (69: 0→1, c.i. = 1).
19. Anterior tip of splenial on medial surface of lower jaw (70: 0→1, c.i. = 1).
20. Posterior end of splenial does not overlap coronoid. Convergent in *Lanthanotus* (72:1→2, c.i. = 0.67).
21. Splenial–angular contact, in medial view, is

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straight, vertical and highly mobile (73: 0 → 1, c.i. = 1).

22. Coronoid does not contact splenial. This character is partly correlated with character 72 (75: 0 → 1, c.i. = 1).

23. Posterior ramus of coronoid reduced or absent (78: 0 → 1, c.i. = 1).

24. Subcoronoid fossa obliterated (79: 0 → 1, c.i. = 1).

25. Adductor fossa faces dorsally (80: 0 → 1, c.i. = 1).

27. Replacement teeth erupt horizontally (90: 0 → 1, c.i. = 1).

28. Four or fewer premaxillary teeth (91: 0 → 1, c.i. = 1).

29. Pterygoid teeth large and recurved. Not applicable in scolecophidians (95: 0 → 1, c.i. = 1).

30. Zygosphenes and zygantra present, articular surface of zygosphene faces ventrolaterally. Very different accessory vertebral articulations occur in *Telmasaurus* and *Saniwa* (97: 0 → 2, c.i. = 0.67).

31. Ribs begin from third cervical (101: 0 → 1, c.i. = 1).

32. Dorsoposterior process on atlas neural arch absent (106: 0 → 1, c.i. = 1).

33. Condyles on centra circular in shape (110: 0 → 1, c.i. = 1).

34. Five or more pygals (113: 0 → 1, c.i. = 1).

35. Pelvic elements not suturally united (130: 1 → 2, c.i. = 1).

36. Femur stout (135: 0 → 1, c.i. = 1).

37. Cranial and axial epiphyses absent (140: 0 → 1, c.i. = 1).

38. Osteoderms lost. Also characterizes most, but not all, species of *Varanus* (144: 0 → 1, c.i. = 1).

Comments. Perhaps the most surprising result of this phylogenetic analysis is the robust grouping of mosasauroids with snakes. The characters corroborating this arrangement come from all areas of the skeleton, and many are unique among squamates. Cope (1869) argued that mosasaurs were related to snakes (see Discussion), and originally erected the taxon name Pythonomorpha for all the mosasaur taxa then known. As Cope's original definition of Pythonomorpha is now redundant with Mosasauridae, I here suggest reapplying it to designate the larger grouping identified by Cope, namely mosasauroids and snakes. Thus, although the content of Pythonomorpha has been altered, the spirit in which Cope used the name has been retained, namely, to emphasize affinities between mosasaurs and snakes.

(*g*) ***Mosasauroidea***

Definition. The most recent common ancestor of 'aigialosaurs' and mosasaurs, and all its descendants. A node-based definition (see DeQueiroz & Gauthier 1992).

Diagnosis.

1. Dorsal process of premaxilla contacts frontal (1: 0 → 1, c.i. = 1).

2. Nasals greatly reduced (2: 0 → 1, c.i. = 1).

3. External naris greatly retracted. Convergent in *Varanus* (4: 1 → 2, c.i. = 0.67).

4. Snout elongated (6: 0 → 1, c.i. = 1).

*5. Dorsal maxillary process on posterior end of maxilla. Convergent in varanids and *Paravaranus* (8: 0 → 1, c.i. = 0.33).

6. Prefrontal with horizontal antorbital ridge. Convergent in *Estesia* and *Telmasaurus* (12: 0 → 1, c.i. = 0.33).

7. Frontals fused. Also occurs in *Paravaranus* and *Telmasaurus* (14: 1 → 0, c.i. = 0.33).

*8. Postfrontal and postorbital fused. Also in helodermatids, *Estesia*, *Lanthanotus* and within varanines (23: 0 → 1, c.i. = 0.2).

9. Jugal extends anteriorly past orbital rim (29: 0 → 1, c.i. = 0.05).

10. Quadrate with large curved suprastapedial process (30: 0 → 1, c.i. = 1).

11. Quadrate with large outer (tympanic) conch. Reversal of condition diagnostic of *Telmasaurus* and thecoglossans (31: 1 → 0,, c.i. = 0.67).

12. Tympanic membrane ossified (32: 0 → 1, c.i. = 1).

13. Dentary with straight dorsal edge (71: 0 → 1, c.i. = 1).

*14. Splenial–angular contact greatly exposed in lateral view (74: 0 → 1, c.i. = 1).

*15. Surangular enters articular condyle (81: 0 → 1, c.i. = 1).

16. Ventral margin of lower jaw with ventral lump (84: 0 → 1, c.i. = 1).

17. Retroarticular process with medial flange. Also occurs in *Saniwa* (85: 0 → 1, c.i. = 0.5).

18. Marginal teeth with high pedestals, resorption pits confined to pedestals (89: 1 → 2, c.i. = 1).

19. More than thirteen maxillary teeth. Reversal of varanoid condition (92: 1 → 0, c.i. = 0.5).

*20. Vertebral condyles face posteriorly. Convergent in alethinophidians (98: 0 → 1, c.i. = 0.5).

21. Posterior hypapophysis on atlas not sutured to centrum (107: 0 → 1, c.i. = 1).

22. Transverse processes on posterior cervicals situated on middle of lateral surface of centra (109: 0 → 1, c.i. = 1).

23. Zygapophyses absent in distal caudals (114: 0 → 1, c.i. = 1).

24. Transverse processes absent in distal caudals (115: 0 → 1, c.i. = 1).

*25. Sternum with five or more pairs of sternal ribs (123: 0 → 1, c.i. = 1).

*26. Olecranon process of ulna greatly reduced (128: 0 → 1, c.i. = 1).

*27. Pubis faces laterally, no anterior 'lip' (133: 0 → 1, c.i. = 1).

*28. Femur straight, not curved in dorsoventral plane (136: 0 → 1, c.i. = 1).

*29. Astragalus and calcaneum distinct (139: 0 → 1, c.i. = 1).

Comments. Mosasaurs and aigialosaurs are united by a large suite of characters, and form a robust clade, as proposed by McDowell & Bogert (1954), Russell (1967) and DeBraga & Carroll (1993). Camp (1923)

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originally erected Mosasauroidea to include only Mosasauridae. Mosasauroidea as originally conceived was therefore a redundant taxon name. However, I have followed recent workers (e.g. Bell 1994; Caldwell *et al*. 1995) and removed this redundancy by using the name Mosasauroidea to apply a more inclusive clade consisting of mosasaurs and their nearest relatives, 'aigialosaurs'.

(*h*) *Serpentes*

Definition. The most recent common ancestor of scolecophidians and alethinophidians, and all its descendants. A node-based, crown-clade definition (see DeQueiroz & Gauthier 1992; Lee 1996*b*).

Diagnosis.

1. High lateral wall of septomaxilla (5: 0 → 1, c.i. = 1).
2. Maxilla–premaxilla contact mobile, non-sutural (7: 0 → 1, c.i. = 1).
3. Lacrimal absent (10: 0 → 1, c.i. = 1).
4. Descending (subolfactory) processes of frontals meeting parasphenoid (15: 0 → 1, c.i. = 0.5).
5. Frontoparietal joint immobile (16: 0 → 1, c.i. = 1).
7. Descending processes of frontal and parietal contact basisphenoid (17: 0 → 1, c.i. = 1).
8. External jaw adductors insert on dorsal surface of parietal (19: 0 → 1, c.i. = 1).
9. Posterolateral processes of parietal absent (20: 0 → 1, c.i. = 1).
10. Parietal foramen absent. Convergent in helodermatids, *Estesia*, and *Lanthanotus* (21: 0 → 1, c.i. = 0.25).
11. Upper temporal arcade absent. Convergent in helodermatids and *Lanthanotus* (22: 0 → 1, c.i. = 0.33).
12. Posterior orbital margin incomplete. Convergent in *Varanus* (24: 0 → 1, c.i. = 0.5).
13. Squamosal absent (28: 0 → 1, c.i. = 1).
14. Tympanic recess absent (31: 1 → 2, c.i. = 0.67).
15. Optic (II) foramen enclosed in bone (40: : 0 → 1, c.i. = 1).
16. Prootic crest reduced to weak ridge. Convergent in helodermatids (41: 0 → 1, c.i. = 0.5).
17. Trigeminal (V) foramen enclosed between parietal and prootic (43: 0 → 1, c.i. = 1).
18. Perilymphatic duct exits into juxtastapedial recess (46: 0 → 1, c.i. = 1).
19. Exoccipitals meet above foramen magnum (48: 0 → 1, c.i. = 1).
20. Maxilla does not suture with vomer (50: 0 → 1, c.i. = 1).
21. Opening of Jacobsen's organ enclosed by septomaxilla and vomer (52: 0 → 2, c.i. = 1).
22. Vomers medial to palatines (53: 0 → 1, c.i. = 1).
23. Palatine and vomer with mobile (non-sutural) contact (54: 0 → 1, c.i. = 1).
24. Palatine and maxilla with mobile (non-sutural) contact (55: 0 → 1, c.i. = 1).
25. Palatine with medial process (59: 0 → 1, c.i. = 1).
26. Epipterygoid absent (61: 0 → 1, c.i. = 1).
27. Mobile maxilla–septomaxilla contact (65: 0 → 1, c.i. = 1).
28. Two or fewer mental foramina on dentary (76: 0 → 1, c.i. = 1).
29. Surangular completely fused with articular (81: 0 → 2, c.i. = 1).
30. Disarticulated surangular with pointed anterior end. Reversal of varanoid condition (82: 1 → 0, c.i. = 0.5).
31. Surangular with large anterior projection that projects into a notch in the dentary (83: 1 → 2, c.i. = 1).
32. Marginal teeth ankylosed to rims of alveoli (86: 0 → 2, c.i. = 1).
33. Plicidentine absent. Reversal of varanoid condition (88: 1 → 0, c.i. = 0.5).
34. Neural spines greatly reduced (100: 0 → 1, c.i. = 1).
35. More than 120 precloacal vertebrae (102: 0 → 1, c.i. = 1).
36. Lymphapophyses present (111: 0 → 1, c.i. = 1).
37. Tail short, less than 40% the length of the precloacal region (112: 0 → 1, c.i. = 1).

*38. Clavicles absent (118: 0 → 1, c.i. = 1).

39. Interclavicles absent (119: 0 → 1, c.i. = 1).
40. Sternum absent (121: 0 → 1, c.i. = 1).
41. Scapulocoracoid absent (124: 0 → 1, c.i. = 1).
42. Forelimbs absent (127: 0 → 1, c.i. = 1).
43. Pelvis vestigial or absent (129: 0 → 1, c.i. = 1).

*44. Ilium medial to ribs. Convergent in mosasaurs (131: 0 → 1, c.i. = 0.5).

45. Hindlimbs vestigial or absent (134: 0 → 1, c.i. = 1).

*46. Limb epiphyses absent. Convergent in mosasaurs (138: 0 → 1, c.i. = 0.5).

47. Scleral ossicles absent (141: 0 → 1, c.i. = 1).

Comments. As expected, the two groups of snakes are united by a large suite of characters, and I have followed Estes *et al*. (1988) in applying the taxon name Serpentes (Linnaeus 1766) to a crown group. The monophyly of snakes has never really been in doubt, and many of the above diagnostic characters have been identified in previous studies (e.g. Underwood 1967; Bellairs 1972; Rieppel 1988; Estes *et al*. 1988; Cundall *et al*. 1993). McDowell & Bogert's (1954) suggestion that typhlopids were not closely related to other snakes (including other scolecophidians) was shown by Underwood (1957*a*, 1967) to be unsupported. Typhlopids have all the snake synapomorphies listed above for which they can be coded.

10. DISCUSSION: THE PLATYNOTAN AFFINITIES OF SNAKES AND MOSASAUROIDS

As expected, the current analysis supports the widely held view that among living varanoid 'lizards', *Lanthanotus* and *Varanus* are sister taxa, *Heloderma* being more distantly related (e.g. Rieppel 1980*a*; Pregill *et al*. 1986; Estes *et al*. 1988). In addition, however, the analysis clarifies the phylogenetic position of many poorly studied fossil squamate taxa that have long been suspected to have varanoid affinities. Many of these

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fossil forms fall along the stem lineages leading to highly derived living groups, helping to fill in large morphological gaps separating extant anguimorphs. Such taxa have been shown to provide crucial information in phylogenetic reconstruction by 'breaking up' otherwise long branches of a cladogram (e.g. Gauthier *et al*. 1988). For example, *Proplatynota* and *Paravaranus* are very primitive relatives of varanoids, while *Telmasaurus* falls between helodermatids and higher varanoids (*Lanthanotus*, *Varanus*, snakes and related fossil taxa).

The affinities of marine platynotans (mosasauroids) have also been uncertain. Regardless of the position of snakes (see below), most recent studies have assumed mosasauroids are closely related to terrestrial varanoids, based partly on general (but poorly specified) similarities in the skull (e.g. McDowell & Bogert 1954; Russell 1967; Rieppel 1980; Pregill *et al*. 1986). However, none of the these studies provided clear evidence for this arrangement: the first two were not performed within a cladistic framework, while the latter two cladistic studies of platynotans only mentioned mosasauroids briefly, and did not include them in the actual analysis. The only two phylogenetic analyses of the platynotan affinities of mosasauroids are Carroll & DeBraga (1992) (see also DeBraga & Carroll 1993) and Caldwell *et al*. (1995). Carroll and DeBraga's conclusion that mosasauroids are the sister group of the *Varanus–Lanthanotus* clade (among living taxa), is very similar to the present arrangement. However, two of the four characters they listed as supporting a mosasauroid–*Varanus–Lanthanotus* clade are equivocal. The transverse pterygopalatine suture is not present in any of the three taxa (figure 4*b–d*), while the narrow supratemporal process of the parietal is difficult to define: e.g. the process in mosasauroids and *Lanthanotus* does not appear to be narrower than in *Heloderma* – that in *Lanthanotus* superficially appears to be narrower because it is longer (figure 2) The other two characters (firm supraoccipital–parietal contact; dentary not notched posteriorly laterally for surangular) appear to be valid (see characters 49 and 83).

In contrast, Caldwell *et al*. (1995) differed from the present study, by uniting all living platynotans (*Heloderma*, *Lanthanotus*, *Varanus*), to the exclusion of mosasauroids, on the basis of eight characters. Two of these appear to be valid: fewer than twelve maxillary teeth (their character 9, my character 92); and ectopterygoid contacting palatine to exclude maxilla from suborbital foramen (their 42, my 66). The remaining characters are not compelling. Premaxillary teeth smaller than maxillary teeth (their character 2) are found in all platynotans, including mosasaurs (Russell 1967), and are here interpreted as supporting platynotan monophyly. Paired frontals (their 12, my 14) are not unique to *Heloderma*, *Lanthanotus* and *Varanus*, but are also found in many anguids and scincomorphs. The short palatine (their 39, my 57) is not applicable to mosasaurs, where the palatine and vomer are not distinct from one another (M. W. Caldwell, personal communication). Mosasaurs and living varanoids do not appear to differ clearly with respect to their character 46 (basisphenoid participation in sphenoccipital tubercle; see figure 4). The angular with greater medial than lateral exposure (their 51) is not characteristic of *Heloderma*, but occurs in some anguids (Rieppel 1980*a*). The remaining character (their 43) is difficult to assess as it is rather briefly defined: proximal head of ectopterygoid 'long and contacts body of pterygoid'. Thus, their study, which they emphasized was preliminary, did not resolve conclusively the relationships between mosasauroids and terrestrial varanoid lizards.

The present study has considered all the valid characters identified in the above studies, along with a large sample of other characters. This study demonstrates that consideration of all (osteological) evidence indicates that mosasaurs are the sister group of the *Varanus–Lanthanotus* clade among terrestrial platynotan lizards.

More important than the resolution of affinities between mosasauroids and other 'lizards', however, is the recognition that mosasauroids are the nearest relatives of snakes. Cope (1869) proposed long ago that snakes and mosasauroids (then known only from mosasaurs) were related. He listed ten characters (p. 253) supporting this arrangement. While seven of the characters have distributions that render them invalid as snake–mosasauroid synapomorphies, the remaining three were correctly identified as synapomorphies: the free mandibular symphysis, mobile splenial–angular joint, and well-developed zygosphenes. In response to criticism by Owen (1877), Cope (1878) proposed a further seven snake–mosasauroid characters, of which only one is a valid synapomorphy: the firm parietal–prootic suture. More recently, Bellairs & Underwood (1951) acknowledged that mosasauroids had some ophidian characters such as a free mandibular symphysis, and well-developed zygosphenes, but noted that various cranial specializations of mosasauroids, and their relatively late stratigraphic occurrence, precluded them from being snake ancestors. However, these observations are still consistent with mosasauroids being the sister group of snakes, a possibility not explored by Bellairs & Underwood. Shortly afterwards, McDowell & Bogert (1954 p. 62) suggested that a *Lanthanotus*–mosasauroid grouping was closely related to snakes, based on the common possession of a highly mobile splenial–angular contact, reduced limbs and loss of the fifth phalanx in the fourth pedal digit. However, the highly mobile splenial–angular contact is really confined to mosasauroids and snakes – the contact in *Lanthanotus* is only slightly less firm than in typical platynotans. Limb reduction occurs repeatedly within anguimorphs, and mosasauroids retain five phalanges in the fourth toe (Carroll & DeBraga 1992). Thus, McDowell & Bogert failed to provide compelling evidence in support of their views, which never became widely accepted. Since then, no other workers have seriously investigated Cope's hypothesis, and thus, no further evidence supporting this scheme came to light.

The cladistic evidence uniting mosasauroids and snakes is substantial, and affinities between these two groups have been suggested repeatedly in the past. It is therefore surprising that no modern studies have identified these characters or proposed this grouping.

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However, the reasons for this are fairly clear: no recent phylogenetic analysis of squamate relationships has included both mosasauroids and snakes. For instance, Pregill *et al*. (1986) and Rieppel (1980) included neither taxon in their analyses of anguimorph relationships. Carroll & DeBraga (1992) (DeBraga & Carroll 1993) and Caldwell *et al*. (1995) attempted to determine the position of mosasauroids within squamates, but did not consider snakes in their analyses. Conversely, Estes *et al*. (1988) compiled exhaustive lists of phylogenetically informative characters in squamates, but restricted their study to extant taxa. They therefore considered snakes, but not mosasauroids. Since mosasauroids were omitted from their analysis, the derived characters uniting in mosasauroids and snakes would have been overlooked, being interpreted as unique features of snakes (and thus, uninformative with respect to the position of snakes within Squamata). Thus, some of the characters listed in Estes *et al* (1988) as unique, or at least definitely autapomorphic, in snakes are actually synapomorphies uniting mosasauroids and snakes: the anteriorly open vidian canal, mobile mandibular symphysis, crista circumfenestralis (weakly developed, but present, in mosasauroids), and well–developed zygosphene–zygantral articulations.

Because of the perceived paucity of informative characters bearing on snake affinities, many studies have suggested that the relationships of snakes with other squamates is unresolved (e.g. Bellairs & Underwood 1951; Rage 1987; Estes *et al*. 1988; Rieppel 1988). Rieppel (1988) has recently published a detailed historical review of the literature on snake relationships, and thus, this topic will not be discussed at length again here. He noted that previous studies have at best been able to advance tentative and unconvincing evidence supporting various hypotheses of snake affinities, and suggested that the problem was intractable largely because of 'the high degree of character incongruence' caused by several lineages of squamates, including snakes, independently evolving limblessness, small size and fossoriality (p. 37). Other workers have reached similar conclusions (e.g. Greer 1985). However, the above analysis demonstrates that the failure to resolve snake relationships is probably due, not to messy data caused by high levels of convergence, but to the failure of previous studies to include pivotal taxa. It should be emphasized that none of the characters uniting mosasauroids and snakes are correlated with limblessness, small size or fossoriality. Mosasauroids primitively retain well-developed limbs, and are relatively large (at least 1 m long) for squamates (e.g. Carroll & DeBraga 1992). In contrast, snakes are limbless, and primitively, small (e.g. see Cundall *et al*. 1993). As well, mosasauroids and snakes are highly divergent ecologically. All mosasauroids, even the most primitive forms, possess aquatic specializations, such as high, laterally compressed tails with reduced zygapophyseal articulations (Bellairs & Underwood 1951; DeBraga & Carroll 1993; Caldwell *et al*. 1995). Most basal snakes are partly or entirely fossorial (Bellairs & Underwood 1951; Cundall *et al*. 1993). Many of their characteristics have been demonstrated to be related to such habits: limblessness and elongated bodies, short caudal region, reduced eyes and orbital cartilages, absence of the tympanic membrane and cavity, hearing mechanism designed to transmit ground-borne vibrations, low neural spines, consolidated braincase and fused, immobile metakinetic 'joint' (e.g. Bellairs & Underwood 1951; Gans 1975). Additionally, the derived characters uniting mosasauroids and snakes come from all areas of the body and do not form any obvious functional complexes. All these observations suggest that these similarities are highly unlikely to be related to convergent adaptation to similar ecological milieus (e.g. Arnold 1990). It is notable that the difficulties resolving the affinities of two other limb-reduced squamate taxa, dibamids and amphisbaenians, have also been attributed to high levels of convergent evolution among burrowing squamates: there is the distinct possibility that their affinities are proving difficult to resolve because of failure to consider crucial fossil evidence. The importance of including all relevant taxa, fossil and living, in phylogenetic analysis has been well demonstrated (e.g. Gauthier *et al*. 1988; Lee 1995).

The position of snakes within Squamata as a whole has been problematical because snakes are so highly modified that many characters used in squamate systematics cannot be objectively assessed in them. For example, most characters of the appendicular skeleton cannot be coded in snakes, which have lost the forelimbs and shoulder girdle, and have (at most) vestigial hindlimbs and pelvic elements. Similarly, the number of scleral ossicles and cervical vertebrae cannot be determined, since snakes lack scleral ossicles and a distinct neck region. An inspection of table 1 will show that scolecophidians and alethinophidians are coded as 'not applicable' for many characters. However, realization that mosasauroids are the nearest relatives of snakes sheds light on the wider relationships of snakes within Squamata, since mosasauroids *can* be coded for many of these characters. In particular, as discussed above, the present study shows that mosasaurs have many traits that place them, successively, within Platynota, and within Varanoidea (as the sister group to *Varanus* and *Lanthanotus*). The fact that mosasaurs also share many characters uniquely with snakes therefore 'anchors' snakes within Platynota and Varanoidea, even though snakes are so highly modified that they cannot be coded for some characters diagnostic of Platynota or Varanoidea. Not all the evidence in this analysis is congruent with this arrangement: snakes definitely lack two of the synapomorphies of varanoids – plicidentine and a surangular with a blunt anterior tip. However, the evidence from other characters indicates that these must be interpreted as reversals (see diagnoses of Varanoidea and Serpentes).

Finally, it should be noted that the robust position of snakes deep within varanoids supports the initial, tentative decision to include snakes in the ingroup (Platynota). As noted in the introduction, while is some evidence that snakes are platynotans, this arrangement is not beyond doubt. If snakes were indeed platynotans, then their inclusion in an analysis

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of platynotan relationships should not cause problems regarding homoplasy and instability in the resultant tree. Snakes would have been expected to have slotted neatly into the final cladogram, with little homoplasy, and their position would have been robust and stable. This is indeed what has happened in this analysis. Snakes possess not just the (admittedly few) diagnostic characters of platynotans as a whole, but also a particular set of derived features that allow them to be placed in various nested subgroups of platynotans (e.g. varanoids, thecoglossans, pythonomorphs). The initial tentative decision to include snakes in the ingroup (Platynota) was strongly supported by the results of the subsequent cladistic analysis, which showed that snakes also possess the synapomorphies of various nested subgroups of platynotans and are thus embedded deeply within Platynota. This reasoning might sound dangerously circular, but it is not. If snakes were not platynotans, inclusion of them (mistakenly) into a cladistic analysis of platynotans would not have yielded such clear results. In this scenario, snakes would not be expected to have many of the synapomorphies uniting various subgroups of platynotans. Furthermore, any apparent synapomorphies that snakes did share with some platynotans would have arisen by chance (convergently), since snakes really lie outside platynotans. Thus, the combination of derived characters found in snakes would not conform to the nested pattern of synapomorphies identified within platynotans. It is unlikely, for instance, that snakes would convergently evolve all the synapomorphies of pythonomorphs, but none of the synapomorphies of the *Varanus–Lanthanotus* clade (the sister group of pythonomorphs). Rather, snakes would be expected to have randomly evolved a few but not all of the characters of both these groups. This would mean that they cannot be placed with confidence in either group. Thus, if snakes were not platynotans, forcing them into a cladistic analysis of platynotans would have resulted in their position within the group being poorly resolved and highly unstable.

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REFERENCES

Ali, S. M. 1949 Studies on the anatomy of the tail in Sauria and Rhychocephalia. III. *Varanus monitor* (Linné). *Proc. Indiana Acad. Sci.* **30B**, 155–167.

Archibald, J. D. 1994 Metataxon concepts and assessing possible ancestry using phylogenetic systematics. *Syst. Biol.* **43**, 27–40.

Arnold, E. N. 1973 Relationships of the Palaearctic lizards assigned to the genera *Lacerta*, *Algyroides* and *Psammodromus* (Reptilia, Lacertidae). *Bull. Br. Mus. nat. Hist., Zool.* **25**, 289–366.

Arnold, E. N. 1983 Osteology, genitalia, and the relationships of *Acanthodactylus* (Reptilia: Lacertidae). *Bull. Br. Mus. nat. Hist., Zool.* **44**, 219–339.

Arnold, E. N. 1984. Variation in the cloacal and hemipenial muscles of lizards and its bearing on their relationships. *Symp. zool. Soc. Lond.* **52**, 47–85.

Arnold, E. N. 1989 Towards a phylogeny and biogeography of the Lacertidae: relationships within an old-world family of lizards derived from morphology. *Bull. Br. Mus. nat. Hist., Zool.* **55**, 209–257.

Arnold, E. N. 1990 Why do morphological phylogenies vary in quality? A study based on the comparative history of lizard clades. *Proc. R. Soc. Lond.* B **240**, 135–172.

Bahl, K. N. 1937 The skull of *Varanus monitor* (Linn.). *Rec. Ind. Mus.* **39**, 133–174.

Barrows, S. & Smith, H. M. 1947 The skeleton of the lizard *Xenosaurus grandis* (Gray). *Univ. Kansas Science Bull.* **31**, 227–281.

Baur, G. 1890 On the characters and systematic position of the large sea-lizards, Mosasauridae. *Science* **16**, 262.

Bell, G. L. 1994 A phylogenetic revision of Mosasauridae and closely related taxa. *J. vert. Paleont.* **14**, 17A.

Bell, C. J., Mead, J. I. & Fay, L. P. 1995 Neogene history of *Anniella* Gray, 1852 (Squamata, Anniellidae) with comments on postcranial osteology. *Copeia* **1995**, 719–726.

Bellairs, A. d'A. 1949 Observations on the snout of *Varanus*, and a comparison with that of other lizards and snakes. *J. Anat.* **83**, 116–146.

Bellairs, A. d'A. 1950 Observations on the cranial anatomy of *Anniella*, and a comparison with other burrowing lizards. *Proc. zool. Soc. Lond.* **119**, 887–904.

Bellairs, A. d'A. 1972 Comments on the evolution and affinities of snakes. In *Studies on vertebrate evolution* (eds K. A. Joysey & T. S. Kemp), pp. 157–172. Edinburgh: Oliver and Boyd.

Bellairs, A. d'A. & Underwood, G. 1951 The origin of snakes. *Biol. Rev.* **26**, 193–237

Bogert, C. M. & del Campo, R. M. 1956 The gila monster and its allies. *Bull. Am. Mus. nat. Hist.* **109**, 1–238.

Borsuk-Bialynicka, M. 1984 Anguimorphans and related lizards from the Late Cretaceous of the Gobi Desert, Mongolia. *Palaeont. Polonica* **46**, 5–105.

Borsuk-Bialynicka, M. 1986 On the diagnosis of the *Xenosauridae* (Anguimorpha). In *Studies in herpetology* (ed. Z. Rocek), pp. 213–218. Prague.

Boulenger, G. A. 1891 Notes on the osteology of *Heloderma horridum* and *H. suspectum*, with remarks on the systematic position of the Helodermatidae and on the vertebrae of the lacertilia. *Proc. zool. Soc. Lond.* **1891**, 109–118.

Bremer, K. 1988 The limits of amino-acid sequence data in angiosperm phylogenetic reconstruction. *Evolution* **42**, 795–803.

Brock, G. T. 1932 The skull of *Leptotyphlops* (*Glauconia nigricans*). *Anat. Anz.* **73**, 199–204.

Brongersma, L. D. 1958 Upon some features of the respiratory and circulatory systems in Typhlopidae and some other snakes. *Arch. néerl. Zool.* **13**, 120–127.

Bryant, H. N., & Russell, A. P. 1992 The role of phylogenetic analysis in the inference of unpreserved attributes of extinct taxa. *Phil. Trans. R. Soc. Lond.* B **337**, 405–418.

Bryant, H. N. & Russell, A. P. 1993 The occurrence of clavicles within Dinosauria: implications for the homology

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of the avian furcula and the utility of negative evidence. *J. vert. Paleont.* **13**, 171–184.

Bullett, P. 1942 Beiträge zur Kenntnis des Gebisses von *Varanus salvator* Laur. *Vierteljahresschr. Naturforsch. Ges. Zür.* **87**, 139–192.

Cadle, J. E., Dessauer, H. C., Gans, C. & Gartside, D. F. 1990 Phylogenetic relationships and molecular evolution in uropeltid snakes (Serpentes: Uropeltidae): allozymes and albumin immunology. *Biol. J. Linn. Soc.* **40**, 293–320.

Caldwell, M. W. 1996 Ontogeny and phylogeny of the mesopodial skeleton in mosasauroid reptiles. *Zool. J. Linn. Soc.* **116**, 407–436.

Caldwell, M. W., Carroll, R. L. & Kaiser, H. 1995 The pectoral girdle and forelimb of *Carsosaurus marchesetti* (Aigialosauridae), with a preliminary phylogenetic analysis of mosasauroids and varanoids. *J. vert. Paleont.* **15**, 516–531.

Callison, G. 1967 Intracranial mobility in mosasaurs. *Univ. Kansas Paleont. Contr.* **26**, 1–15.

Camp, C. L. 1923 Classification of the lizards. *Bull. Am. Mus. nat. Hist.* **48**, 289–481.

Camp, C. L. 1942 California mosasaurs. *Univ. Calif., Memoirs* **13**, 1–68.

Carroll, R. L. & M. DeBraga. 1992 Aigialosaurs: mid–Cretaceous varanoid lizards. *J. vert. Paleont.* **12**, 66–86.

Clos, L. M. 1995 A new species of *Varanus* (Reptilia: Sauria) from the Miocene of Kenya. *J. vert. Paleont.* **15**, 254–267.

Coe, W. & Kunkel, B. 1906 Studies on the California limbless lizard, *Anniella*. *Trans. Connecticut Acad. Arts Sci.* **12**, 349–403.

Cooper, J. S. 1966 Tooth replacement in the slow worm (*Anguis fragilis*). *J. Zool.* **150**, 235–248.

Cope, E. D. 1869 On the reptilian orders Pythonomorpha and Streptosauria. *Proc. Boston Soc. nat. Hist.* **12**, 250–266.

Cope, E. D. 1878 Professor Owen on the Pythonomorpha. *Bull. U.S. geol. Surv.* **4**, 299–311.

Cope, E. D. 1900 The crocodilians, lizards and snakes of North America. *Ann. Rept. Smithsonian Inst.* **1898**, 155–1294.

Costelli, J. & Hecht, M. K. 1971 The postcranial osteology of the lizard *Shinisaurus*: the appendicular skeleton. *Herpetologica* **27**, 87–98.

Criley, B. B. 1968 The cranial osteology of gerrhonotiform lizards. *Am. Midl. Nat.* **80**, 199–219.

Cundall, D. & Rossman, D. A. 1993 Cephalic anatomy of the rare Indonesian snake *Anomochilus weberi*. *Zool. J. Linn. Soc.* **109**, 235–273.

Cundall, D., Wallach, V. & Rossman, D. A. 1993 The systematic relationships of the snake genus *Anomochilus*. *Zool. J. Linn. Soc.* **109**, 275–299.

Daudin, F. M. 1803 *Histoire naturelle, générelle et particuliere, des reptiles*, Vol. 2. Paris: Dufart.

DeQueiroz, K. & Gauthier, J. 1992 Phylogenetic taxonomy. *A. Rev. Ecol. Syst.* **23**, 449–480.

DeBraga, M. & Carroll, R. L. 1993 The origin of mosasaurs as a model of macroevolutionary patterns and processes. *Evol. Biol.* **27**, 245–322.

Denton, R. K. & O'Neill, R. C. 1995 *Prototeius stageri*, gen. et. sp. nov., a new teiid lizard from the Upper Cretaceous Marshalltown Formation of New Jersey, with a preliminary phylogenetic revision of the Teiidae. *J. vert. Paleont.* **15**, 235–253.

Dobie, J. L., Womochel, D. R. & Bell, G. L., Jr 1986 A unique sacroiliac contact in mosasaurs (Sauria, Varanoidea, Mosasauridae). *J. vert. Paleont.* **6**, 197–199.

Dollo, L. 1889 Premiere note sur les mosasauriens de Mesvin. *Bull. Soc. Belg. Géol. Paléontol. Hydrol.* **3**, 271–304.

Dollo, L. 1894 Nouvelle note sur l'ostéologie des mosasauriens. *Bull. Soc. Belg. Géol. Paléont. Hydrol.* **6**, 219–259.

Dollo, L. 1904 Les mosasauriens de la Belgique. *Anna. Soc. Scient. Bruxelles* **18**, 18–207.

Dollo, L. 1905 Un nouvel opercule tympanique de *Plioplatecarpus*. *Mem. Soc. Belg. Géol. Paléont. d'Hydrol.* **19**, 125–131.

Dollo, L. 1924 *Globidens alabamaensis*, mosasaurien américain retrouvé dans le Craie d'Obourg du Hainaut, et les mosasauriens de la Belgique en général. *Arch. Biol.* **34**, 167–213.

Deurden, J. E. & Essex, R. 1928 The pelvic girdle of the snake *Typlops*. *S. Afr. J. Nat. Hist.* **4**, 173–186.

Dunn, E. R. 1941 Notes on the snake genus *Anomalepis*. *Bull. Mus. comp. Zool.* **87**, 511–526.

Dunn, E. R. & Tihen, J. A. 1944 The skeletal anatomy of *Liotyphlops albirostris*. *J. Morph.* **74**, 287–295.

Edmund, A. G. 1969 Dentition. In *Biology of the reptilia*, Vol. 1. (eds C. Gans, A. d. Bellairs & T. S. Parsons), pp. 117–200. London: Academic Press.

Eernisse, D. J. & Kluge, A. G. 1993 Taxonomic congruence versus total evidence, and amniote phylogeny inferred from fossils, molecules and morphology. *Mol. Biol. Evol.* **10**, 1170–1195.

El–Toubi, M. R. 1938 The osteology of the lizard *Scincus scincus* (Linn.). *Bull. Facult. Sci., Egyptian Univ.* **14**, 1–38.

Essex, R. 1927 Studies in reptilian degeneration. *Proc. zool. Soc. Lond.* **4**, 879–945.

Estes, R. 1964 Fossil vertebrates from the late Cretaceous Lance Formation, eastern Wyoming. *Univ. Calif. Publ. geol. Sci.* **49**, 1–186.

Estes, R. 1983 *Handbuch der Paläoherpetologie. Teil 10A. Sauria Terrestria*. Stuttgart: Gustav Fischer Verlag.

Estes, R., de Queiroz, K. & Gauthier, J. A. 1988 Phylogenetic relationships within Squamata. In *Phylogenetic relationships of the lizard families* (eds R. Estes & G. K. Pregill), pp. 119–281. Stanford: Stanford University Press.

Estes, R., Frazetta, T. H. & Williams, E. E. 1970 Studies on the fossil snake *Dinilysia patagonica* Woodward: Part 1. Cranial morphology. *Bull. Mus. comp. Zool.* **140**, 25–74.

Evans, H. E. 1955 Osteology of the worm snake, *Typhlops jamaicensis* (Shaw). *Anat. Rec.* **112**, 381–396.

Evans, S. E. 1995 A new anguimorph lizard from the Jurassic and Lower Cretaceous of England. *Palaeontology* **37**, 33–49.

Farris, J. S. 1989 The retention index and the rescaled consistency index. *Cladistics* **5**, 417–419.

Fejérváry, G. J. 1918 Contributions to a monograph on fossil Varanidae and Megalanidae. *Ann. Mus. Nat. Hungarici* **16**, 341–467.

Fejérváry, G. J. 1935 Further contributions to a monograph of the Megalanidae and fossil Varanidae, with notes on recent varanians. *Ann. Hist. nat. Mus. Hungarici, Pars Zool.* **29**, 1–130.

Felsenstein, J. 1985 Confidence limits on phylogenies: an approach using the bootstrap. *Evolution* **39**, 783–791.

Fisher, D. L. & Tanner, W. W. 1970 Osteological and myological comparisons of the head and thorax regions of *Cnemidophorus tigris septentrionalis* Burger and *Ameiva undulata parva* Barbour and Noble (Family Teiidae). *Brigham Young Univ. Sci. Bull. Biol. Ser.* **11**, 1–41.

Forstner, M. R. J., Davis, S. K. & Arevalo, E. 1995 Support for the hypothesis of anguimorph ancestry for the suborder Serpentes from phylogenetic analysis of mitochondrial DNA sequences. *Mol. Phyl. Evol.* **4**, 93–102.

Frazetta, T. H. 1970 Studies on the fossil snake *Dinilysia patagonica* Woodward. Part II. Jaw machinery in the earliest snakes. *Forma Functio* **2**, 205–221.

Frazetta, T. H. 1983 Adaptation and function of cranial kinesis in reptiles: a time–motion analysis of feeding in alligator lizards. In *Advances in herpetology and evolutionary*

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biology (eds A. Rhodin & Miyata), pp. 222–244. Cambridge MA: Museum of Comparative Zoology.

Gans, C. 1975 Vertebrate limblessness: evolution and functional corollaries. *Am. Zool.* **15**, 455–467.

Gao, K.-Q. & Fox, R. C.. 1991 New teiid lizards from the Upper Cretaceous Oldman Formation (Judithian) of southeastern Alberta, Canada, with a review of the Cretaceous record of teiids. *Ann. Carnegie Museum* **60**, 145–162.

Gauthier, J. A. 1980 *Anniella* (Sauria, Anguidae) from the Miocene of California. *PaleoBios* **31**, 1–7.

Gauthier, J. A. 1982 Fossil xenosaurid and anguid lizards from the early Eocene Wasatch Formation, southeast Wyoming, and a revision of the Anguioidea. *Contr. Geol., Univ. Wyoming* **21**, 7–54.

Gauthier, J., Kluge, A. G. & Rowe, T. 1988 Amniote phylogeny and the importance of fossils. *Cladistics* **4**, 105–209.

Gilmore, C. 1922 A new description of *Saniwa ensidens* Leidy, an extinct varanid from Wyoming. *Proc. U.S. nat. Mus.* **60**, 1–28.

Gilmore, C. W. 1928 Fossil lizards of North America. *Natl. Acad. Sci. Mem.* **22**, 1–169.

Gilmore, C. W. 1943 Fossil lizards of Mongolia. *Bull. Am. Mus. nat. Hist.* **81**, 361–384.

Good, D. A. 1987*a* An allozyme analysis of anguid subfamilial relationships (Lacertilia: Anguidae). *Copeia* **1987**, 696–701.

Good, D. A. 1987*b* A phylogenetic analysis of the cranial osteology in the gerrhonotine lizards (Lacertilia: Anguidae). *J. Herpet.* **21**, 283–295.

Gray, J. 1827 A synopsis of the genera of saurian reptiles, in which some new genera are indicated and the others reviewed by actual examination. *Ann. Philos.* **2**, 54–58.

Greer, A. E. 1970 A subfamilial classification of scincid lizards. *Bull. Mus. comp. Zool.* **139**, 151–183.

Greer, A. E. 1985 The relationships of the lizard genera *Anelytropsis* and *Dibamus*. *J. Herpet.* **19**, 116–156.

Greer, A. E. 1990 *The biology and evolution of Australian lizards.* Sydney: Surrey Beatty and Sons.

Groombridge, B. C. 1979 A previously unreported throat muscle in Scolecophidia (Reptilia: Serpentes), with comments on other Scolecophidian throat muscles. *J. nat. Hist.* **13**, 661–680.

Haas, G. 1930*a* Über das kopfskelett und die Kaumuskulatur der Typhlopiden und Glauconiiden. *Zool. Jahrb.* **52**, 1–94.

Haas, G. 1930*b* Über die Kaumuskulatur und die Schädelmechanik einiger Wuhlschlangen. *Zool. Jahrb.* **52**, 95–218.

Haas, G. 1931 Über die Morphologie der Kiefermuskulatur und die Schädelmechanik einiger Schlangen. *Zool. Jahrb.* **54**, 333–416.

Haas, G. 1964 Anatomical observations on the head of *Liotyphlops albirostris* (Typhlopidae, Ophidia). *Acta Zool.* **45**, 1–62.

Haas, G. 1968 Anatomical observations on the head of *Anomalepis aspinosus* (Typhlopidae, Ophidia). *Acta Zool.* **49**, 62–139.

Haines, R. W. 1969 Epiphyses and sesamoids. In *Biology of the reptilia* (eds C. Gans, A. d. Bellairs & T. S. Parsons), pp. 81–115. London: Academic Press.

Hecht, M. K. 1975 The morphology and relationships of the largest known terrestrial lizard, *Megalania prisca* Owen, from the Pleistocene of Australia. *Proc. R. Soc. Victoria* **87**, 239–249.

Hecht, M. K. 1982 The vertebral morphology of the Cretaceous snake, *Dinilysia patagonica* Woodward. *Neues Jahrb. geol. Palaeontol. Monatsh.* **1982**, 523–532.

Hecht, M. K. & Costelli, J. 1969 The postcranial osteology of the lizard *Shinisaurus*. 1. The vertebral column. *Am. Mus. Novit.* **2378**, 1–21.

Heise, P. J., Maxson, L. R., Dowling, H. G. & Hedges, S. B. 1995 Higher-level snake phylogeny inferred from mitochondrial DNA sequences of 12S rRNA and 16S rRNA genes. *Mol. Biol. Evol.* **12**, 259–265.

Hikida, T. 1978 Postembryonic development of the skull of the Japanese skink, *Eumeces latiscutatus* (Scincidae). *Jap. J. Herpet.* **7**, 56–72.

Hillis, D. M. 1991 Discriminating between phylogenetic signal and random noise in DNA sequences. In *Phylogenetic analysis of DNA sequences* (eds M. M. Miyamoto & J. Cracraft), pp. 278–294. Oxford: Oxford University Press.

Hoffstetter, R. 1949 Les reptiles subfossiles de l'ile Maurice. I. Les Scincidae. *Ann. Paleont.* **35**, 45–72.

Hoffstetter, R. 1957 Un saurien helodermatide (*Eurheloderma gallicum* nov. gen. et sp.) dans la faune fossile des Phosphorites du Quercy. *Bull. geol. Soc. France* **7**, 775–786.

Hoffstetter, R. 1967 Coup d'oeil sur les sauriens (= lacertiliens) des couches de Purbeck (Jurassique Supérieur d'Angleterre). *Coll. Int. CNRS* **163**, 349–371.

Hoffstetter, R. 1968 Présence des Varanidae (Reptilia: Sauria) dans le Miocène de Catalogne. Considérations sur l'histoire de la famille. *Bull. Mus. natn. Hist. Nat.* **40**, 1051–1064.

Hoffstetter, H. & Gasc, J.–P. 1968 Observations sur le squelette cervical et spécialement sur les hypapophyses des sauriens varanoides actuels et fossiles. *Bull. Mus. natn. Hist. Nat.* **39**, 1028–1043.

Holman, J. A. 1973 A huge new xenosaurid lizard from the Upper Miocene of Nebraska. *Proc. biol. Soc. Wash.* **86**, 105–112.

Jenkins, F. J., Jr 1983 The functional anatomy of the shoulder of the savannah monitor lizard (*Varanus exanthematicus*). *J. Morph.* **175**, 195–216.

Jenkins & Goslow 1983

Jollie, M. J. 1960 The head skeleton of the lizard. *Acta Zool.* **41**, 1–64.

Jörg, E. 1965 *Ophisaurus acuminatus* nov. spec. (Anguidae, Rept.) von der pontischen Wirbeltier-Fundstätte Hewenegg/Hegau. *Beitr. Narturk. Forsch. SW-Deutchl.* **24**, 21–30.

Kallersjö, M., Farris, J. S., Kluge, A. G. & Bult, C. 1992 Skewness and permutation. *Cladistics* **8**, 275–287.

King, D., King, M. & Baverstock., P. 1991 A new phylogeny of the Varanidae. *Mertensiella* **2**, 211–219.

Kingman, R. H. 1932 A comparative study of the skull in the genus *Eumeces* of the Scincidae (a preliminary paper). *Univ. Kansas Sci. Bull.* **20**, 273–295.

Kluge, A. G. 1989 Progress in squamate classification. *Herpetologica* **45**, 368–379.

Kluge, A. G. 1991 Boine snake phylogeny and research cycles. *Misc. Publ. Mus. Zool. Univ. Mich.* **178**, 1–58.

Kornhuber, A. 1901 Eine neue fossile Eidechse aus der anteren Kreideschichten von Lesina in Dalmatien. *Abh. Kaiserlich–Koniglichen geol. Reichanstalt* **17**, 1–24.

Kuhn, O. 1940 Die placosauriden und Anguiden aus dem mittleren Eozän des Geiseltales. *Nova Acta Leopoldina* **8**, 461–486.

Landsmeer, J. M. 1984 Morphology of the anterior limb in relation to sprawling gait in *Varanus*. *Symp. zool. Soc. Lond.* **52**, 27–45.

Lang, M. 1991 Generic relationships within Cordyliforms (Reptila: Squamata). *Bull. Inst. R. Sci. Nat. Belg.* **61**, 121–188.

Lécuru, S. 1968*a* Étude des variations morphologiques du sternum, des clavicules et de l'interclavicule des lacertiliens. *Ann. Sci. Nat., Zool.* **10**, 511–544.

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Lécuru, S. 1968*b* Remarques sur le scapulo-coracoide des lacertiliens. *Ann. Sci. Nat., Zool.* **10**, 511–544.

Lee, M. S. Y. 1995 Historical burden in systematics and interrelationships of 'parareptiles'. *Biol. Rev.* **70**, 459–547.

Lee, M. S. Y. 1996*a* Snake-like tooth replacement in mosasaurian lizards. *J. nat. Hist.* (In the press.)

Lee, M. S. Y. 1996*b* Stability in meaning and content of taxon names: an evaluation of crown-clade definitions. *Proc. R. Soc. Lond.* B **263**, 1103–1109.

Lingham-Soliar, T. 1988 The mosasaur *Goronyosaurus* from the Upper Cretaceous of Sokoto State, Nigeria. *Palaeontology* **31**, 747–762.

Lingham-Soliar, T. 1991*a* Locomotion in mosasaurs. *Mod. Geol.* **16**, 229–248.

Lingham-Soliar, T. 1991*b* Mosasaurs from the Upper Cretaceous of Niger. *Paleontology* **34**, 653–670.

Lingham-Soliar, T. 1992 The tylosaurine mosasaurs of Europe and Africa. *Bull. Inst. R. Sci. Nat. Belg.* **62**, 171–194.

Lingham-Soliar, T. 1994 The mosasaur *Plioplatecarpus* (Reptilia, Mosasauridae) from the Upper Cretaceous of Europe. *Bull. Inst. R. Sci. Nat. Belg.* **64**, 177–211.

Lingham-Soliar, T. 1995 Anatomy and functional morphology of the largest marine reptile known, *Mosasaurus hoffmani* (Mosasauridae, Reptilia) from the Upper Cretaceous, Upper Maastrichtian of The Netherlands. *Phil. Trans. R. Soc. Lond.* B **347**, 155–180.

Lingham-Soliar, T. & Nolf, D. 1989 The mosasaur *Prognathodon* (Reptilia, Mosasauridae) from the upper Cretaceous of Belgium. *Bull. Inst. R. Sci. Nat. Belg.* **59**, 137–190.

Linneaus, C. 1766 *Systema Naturae. Classis III Amphibia. Laurentii Salvii, Holmiae.* 1963 Reprint, Ohio Herpeological Society (not seen).

List, J. C. 1966 Comparative osteology of the snake families Typhlopidae and Leptotyphlopidae. *Ill. Biol. Mono.* **36**, 1–112.

Lönnberg, E. 1903 On the adaptations to a molluscivorous diet in *Varanus niloticus*. *Arch. Zool.* **1**, 65–83.

Mahendra, B. C. 1936 Contributions to the osteology of the Ophidia. I. The endoskeleton of the so-called 'blind snake' *Typhlops braminus Daud. Proc. Indiana Acad. Sci.* **3**, 128–142.

Malan, M. E. 1941 Cranial anatomy of the genus *Gerrhosaurus*. *S. Afr. J. Sci.* **37**, 192–217.

McDowell, S. B. 1967*a* Osteology of the Typhlopidae and Leptotyphlopidae: a critical review. *Copeia* **1967**, 686–692.

McDowell, S. B. 1967*b* The extracolumella and tympanic cavity of the 'earless' monitor lizard, *Lanthanotus borneensis*. *Copeia* **1967**, 154–159.

McDowell, S. B. 1972 The evolution of the tongue of snakes and its bearing on snake origins. *Evol. Biol.* **6**, 191–273.

McDowell, S. B. 1987 Systematics. In *Snakes: ecology and evolutionary biology* (eds R. A. Siegel, J. T. Collins & S. S. Novak), pp. 3–50. New York: Macmillan.

McDowell, S. B. & Bogert, C. M. 1954 The systematic position of *Lanthanotus* and the affinities of anguinomorphan lizards. *Bull. Am. Mus. nat. Hist.* **105**, 1–142.

Merriam, J. C. 1894 Ueber die pythonomorphen der Kansas–Kreide. *Palaeontographica* **41,** 1–39.

Mertens, R. 1942*a* Die Familie der Warane (Varanidae). Dritter Teil: Taxonomie. *Abh. Senck. Naturf. Ges.* **466**, 235–391.

Mertens, R. 1942*b* Die Familie der Warane (Varanidae). Erster Teil: Allgemeines. *Abh. Senck. Naturf. Ges.* **462**, 1–116.

Mertens, R. 1942*c* Die Familie der Warane (Varanidae). Zweiter Teil: der Schädel. *Abh. Senck. Naturf. Ges.* **465**, 117–234.

Mertens, R. 1959 Über die schadel einiger bermerkenswerter Warane Australiens. *Sond. Viertelj. Naturforsch. Gesell. Zürich* **104**, 115–128.

Meszoely, C. M. A. 1970 North American fossil anguid lizards. *Bull. Mus. comp. Zool.* **139**, 87–150.

Meszoely, C. A. M., Estes, R. & Haubold, H.. 1978 Eocene anguid lizards from Europe and a revision of the genus *Xestops*. *Herpetologica* **34**, 156–166.

Molnar, R. E. 1990 New cranial elements of a giant varanoid from Queensland. *Mem. Queensland Mus.* **29**, 437–444.

Nash, D. F. & Tanner, W. W. 1970 A comparative study of the head and thoracic osteology and myology of the skinks *Eumeces gilberti* van Denburgh and *Eumeces skiltonianus* (Baird and Girard). *Brigham Young Univ. Sci. Bull. Biol. Ser.* **12**, 1–32.

Nopsca, F. 1908 Zur kenntnis der fossilen Eidechsen. *Beitr. Paläont. geol. Österreih-Ungarns* **21**, 33–62.

Nopsca, F. 1923 *Eidelosaurus* und *Pachyophis*: Zwei neue Neucom-reptilien. *Palaeontographica* **65**, 99–154.

Norell, M. A., McKenna, M. C. & Novacek, M. J. 1992 *Estesia mongoliensis*, a new fossil varanoid from the Late Cretaceous Barun Goyot Formation of Mongolia. *Am. Mus. Novit.* **3045**, 1–24.

Odermatt, C. 1940 Beiträge zur Kenntnis des Gebisses von *Heloderma*. *Vierteljahresschr. Naturforsch. Ges. Zür.* **85**, 98–141.

Osborn, H. F. 1899 A complete mosasaur skeleton, osseous and cartilaginous. *Am. Mus. nat. Hist., Mem.* **1**, 167–188.

Owen, R. 1851 *A Monograph on the Fossil Reptiles of the Cretaceous Formations. Part* 1. London: Palaeontological Society.

Owen, R. 1877 On the rank and affinities in the reptilian class of the Mosasauridae, Gervais. *Q. Jl. geol. Soc.* **34**, 748–753.

Plisnier-Ladame, F. & Coupatez, P. 1969 Étude morphologique de l'Anneau sclérotique de *Mosasaurus hoffmanni* Mantell, 1829. *Bull. Soc. Belg. Géol. Paléont. Hydrol.* **78**, 253–265.

Pregill, G. K., Gauthier, J. A. & Greene, H. W. 1986 The evolution of helodermatid squamates, with description of a new taxon and an overview of Varanoidea. *Trans. San Diego Soc. nat. Hist.* **21**, 167–202.

Presch, W. 1980 Evolutionary history of the South American microteiid lizards (Teiidae, Gymnophthalminae). *Copeia* **1980**, 36–56.

Presch, W. 1988 Cladistic relationships within the Scincomorpha. In *Phylogenetic relationships of the lizard families* (ed. R. Estes and G. Pregill), pp. 471–491. Stanford: Stanford University Press.

Radovanovic, M. 1937 Osteologie des Schlangenkopfes. *Jena Z. Naturw.* **71**, 179–312.

Rage, J.-C. 1974 Les serpents des phosphorites du Quercy. *Palaeovertebrata* **6**, 274–303.

Rage, J.-C. 1982 La phylogénie des Lépidosauriens (Reptilia): une approche cladistique. *C. r. Acad. Sci., Paris* **294**, Ser. II, 563–566.

Rage, J.-C. 1984 *Handbuch der paläoherpetologie. Teil* 11. *Serpentes*. Stuttgart: Gustav Fischer Verlag.

Rage, J.-C. 1987 Fossil history. In *Snakes: ecology and evolutionary biology* (eds R. A. Seigel, J. T. Collins & S. S. Novak), pp. 51–76. New York: Macmillan.

Renous, S., Raynaud, A., Gasc, J.-P. & Pieau, C. 1976 Caractères rudimentaires, anatomiques et embryologiques, de la ceinture pelvienne et des appendices postérieurs du Python réticulé (*Python reticulatus* Schneider, 1801). *Bull. Mus. natn. Hist. Nat.* **267**, 547–583.

Renous-Lécuru, S. 1973 Morphologie comparée du carpe chez les lépidosauriens actuels (rhynchocéphales, lacer-

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tiliens, amphisbéniens). *Gegenbaur's Morphol. Jahrb.* **119**, 727–766.

Rieppel, O. 1977*a* The naso-frontal joint in *Anilius scytale* (Linneaus) and *Cylindrophis rufus* (Schlegel): Serpentes, Aniliidae. *J. nat. Hist.* **11**, 545–553.

Rieppel, O. 1977*b* Studies on the skull of the Henophidia (Reptilia, Serpentes). *J. Zool.* **181**, 145–173.

Rieppel, O. 1978*a* The braincase of *Anniella pulchra* Gray (Lacertilia, Anniellidae). *Rev. Suisse Zool.* **85**, 617–624.

Rieppel, O. 1978*b* The evolution of the naso-frontal joint in snakes and its bearing on snake origins. *Z. zool. Syst. Evolutionsforsch* **16**, 14–27.

Rieppel, O. 1979*a* The braincase of *Typhlops* and *Leptotyphlops* (Reptilia, Serpentes). *Zool. J. Linn. Soc.* **65**, 161–176.

Rieppel, O. 1979*c* The evolution of the basicranium in the Henophidia (Reptilia, Serpentes). *Zool. J. Linn. Soc.* **66**, 411–431.

Rieppel, O. 1979*d* A cladistic classification of snakes based on skull structure. *Z. zool. Syst. Evolutionsforsch* **17**, 140–150.

Rieppel, O. 1980*a* The phylogeny of anguimorph lizards. *Denkschr. Schweiz. Naturforsch. Ges.* **94**, 1–86.

Rieppel, O. 1980*b* The postcranial skeleton of *Lanthanotus borneensis* (Reptilia, Lacertilia). *Amphibia–Reptilia* **1**, 95–112.

Rieppel, O. 1980*c* The sound-transmitting apparatus in primitive snakes and its phylogenetic significance. *Zoomorphology* **96**, 45–62.

Rieppel, O. 1981 The skull and jaw adductor musculature in some burrowing scincomorph lizards of the genera *Acontias*, *Typhlosaurus* and *Feylinia*. *J. Zool.* **195**, 493–528.

Rieppel, O. 1983 A comparison of the skull of *Lanthanotus borneensis* (Reptilia: Varanoidea) with the skull of primitive snakes. *Z. zool. Syst. Evolutionsforsch* **21**, 142–153.

Rieppel, O. 1984 The cranial morphology of the fossorial lizard genus *Dibamus* with a consideration of its phylogenetic relationships. *J. Zool.* **204**, 289–327.

Rieppel, O. 1988 A review of the origin of snakes. *Evol. Biol.* **22**, 37–130.

Robinson, P. L. 1975 The functions of the hooked fifth metatarsal in lepidosaurian reptiles. *Coll. Int. CNRS* **218**, 461–483.

Russell, D. A. 1964 Intracranial mobility in mosasaurs. *Postilla* **86**, 1–19.

Russell, D. A. 1967 Systematics and morphology of American mosasaurs. *Bull. Peabody Mus. nat. Hist.* **23**, 1–237.

Russell, D. A. 1975 A new species of *Globidens* from South Dakota, and a review of globidentine mosasaurs. *Fieldiana, Geol.* **33**, 235–256.

Sanderson, M. J. & Donoghue, M. J. 1989 Patterns of variation in levels of homoplasy. *Evolution* **43**, 1781–1795.

Savage, J. M. 1963 Studies on the lizard family Xantusiidae. IV. The genera. *Contr. Sci. Los Angeles County Mus.* **71**, 1–38.

Schwenk, K. 1988 Comparative morphology of the lepidosaur tongue and its relevance to squamate phylogeny. In *Phylogenetic relationships of the lizard families* (eds R. Estes & G. Pregill), pp. 568–598. Stanford: Stanford University Press.

Shine, R. 1986 Evolutionary advantages of limblessness: evidence from the pygopodid lizards. *Copeia* **1986**, 525–529.

Shufeldt, R. W. 1890 Contribution to the study of *Heloderma suspectum*. *Proc. zool. Soc. Lond.* **1890**, 148–244.

Siebenrock, F. 1892 Zur kenntniss des Kopfskelettes der Scincoiden, Anguiden, und gerrhosauriden. *Ann. K. K. Naturhist. Hofmus. Wien* **7**, 163–196.

Siebenrock, F. 1894 Das skelett der *Lacerta simonyi* Steind. und der Lacertidenfamilie überhaupt. *Sitz.–Ber. Math.-Nat. Kl. Acad. Wiss. Wien* **103**, 205–292.

Skinner, M. M. 1973 Ontogeny and adult morphology of the skull of the South African skink, *Mabuya Capensis* (Gray). *Ann. Univ. Stellenbosch* **48**, 1–116.

Slowinski, J. B. 1993 'Unordered' versus 'ordered' characters. *Syst. Biol.* **42**, 155–165.

Slowinski, J. B. & Guyer, C. 1989 Testing the stochasticity of patterns of organismal diversity: an improved null model. *Am. Nat.* **134**, 907–921.

Slowinski, J. B. & Savage, J. M. 1995 Urotomy in *Scaphiodontophis*. Evidence for the multiple tail break hypothesis in snakes. *Herpetologica* **51**, 338–341.

Smit, A. L. 1949 Skedelmorfologie en -kinese van *Typhlops delalandii* (Schlegel). *S. Afr. J. Sci.* **45**, 117–140.

Sprackland, R. G. 1991 The origin and zoogeography of monitor lizards of the subgenus *Odatria* gray (Sauria: Varanidae): A re-evaluation. *Mertensiella* **2**, 240–252.

Steindachner, F. 1878 Über zwei neue Eidechsen-Arten aus Sud-America und Borneo. *Denkschr. Akad. Wiss. Wien* **38**, 93–96.

Stevens, M. 1977 Further study of Castolon local fauna (Early Miocene), Big Bend National Park, Texas. *Pearce-Sellards Ser., Texas Memorial Mus.* **28**, 1–69.

Sullivan, R. M. 1979 Revision of the Paleogene genus *Glyptosaurus* (Reptilia, Anguidae). *Bull. Am. Mus. nat. Hist.* **163**, 1–72.

Sullivan, R. M. 1989 *Proglyptosaurus huerfanensis*, new genus, new species: Glyptosaurine lizard (Squamata: Anguidae) from the Early Eocene of Colarado. *Am. Mus. Novit.* **2949**, 1–8.

Swofford, D. 1993 PAUL: Phylogenetic Analysis Using Parsimony. Version 3.1.1. Illinois Natural History Survey, Champagne.

Tihen, J. A. 1945 Notes on the osteology of typhlopid snakes. *Copeia* **1945**, 204–210.

Tihen, J. A. 1949 The genera of gerrhonotine lizards. *Am. Midl. Nat.* **41**, 580–601.

Toerien, M. J. 1950 The cranial morphology of the californian lizard *Anniella pulchra* Gray. *S. Afr. J. Sci* **46**, 321–342.

Underwood, G. 1957*a* *Lanthanotus* and the anguimorphan lizards. *Copeia* **1957**, 20–30.

Underwood, G. 1957*b* On lizards of the family Pygopodidae. A contribution to the morphology and phylogeny of the Squamata. *J. Morph.* **100**, 207–268.

Underwood, G. 1967 A contribution to the classification of snakes. *British Museum (Natural History) Publications* **653**, 1–179.

Underwood, G. 1970 The eye. In *The biology of the reptilia*, Vol. 2 (eds C. Gans & T. Parsons), pp. 1–98. New York: Academic Press.

Underwood, G. 1976 Simplification and degeneration in the course of evolution of squamate reptiles. *Coll. Int. CNRS* **266**, 341–352.

Underwood, G. 1984 Scleral ossicles in lizards: an exercise in character analysis. *Symp. Zool. Soc. Lond.* **52**, 483–502.

Vaeth, R. H., Rossman, D. A. & Shoop, W. 1985 Observations of tooth surface morphology in snakes. *J. Herpet.* **19**, 20–26.

Vaughn, P. P. & Dawson, M. R. 1956 On the occurrence of calcified tympanic membranes in the mosasaur *Platecarpus*. *Transactions of the Kansas Academy of Science* **59**, 382–384.

Walls, G. 1942 *The vertebrate eye and its adaptive radiation*. New York: Hafner.

Warner, R. 1946 Pectoral girdles vs. hyobranchia in the snake genera *Liotyphlops* and *Anomalepis*. *Science* **103**, 720–722.

Watkinson, G. B. 1906 The cranial nerves of *Varanus bivittatus*. *Morph. Jahrb.* **35**, 450–472.

Wiley, E. O., Siegel-Causey, D., Brooks, D. R. & Funk, V.

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A. 1991 The compleat cladist. *Univ. Kansas Mus. nat. Hist. Spec. Publ.* **19**, 1–158.

Wilkinson, M. 1992 Ordered versus unordered characters. *Cladistics* **8**, 375–385.

Wilkinson, M. 1994 Common cladistic information and its consensus representation: reduced Adams and reduced cladistic consensus trees and profiles. *Syst. Biol.* **43**, 343–368.

Wilkinson, M. 1995 Coping with abundant missing entries in phylogenetic inference using parsimony. *Syst. Biol.* **44**, 501–514.

Wilkinson, M. & Benton, M. J. 1995 Missing data and rhynchosaur phylogeny. *Hist. Biol.* **10**, 137–150.

Williams, E. E. 1959 The occipito–vertebral joint in the burrowing snakes of the family Uropeltidae. *Breviora* **106**, 1–10.

Williston, S. W. 1898 Mosasaurs. *Kansas Univ. geol. Surv.* **4**, 83–221.

Wu, X., Brinkman, D. B., Russell, A. P., Dong, Z., Currie, P. J., Hou, L. & Cul, G. 1993 Oldest known amphisbaenian from the Upper Cretaceous of Chinese Inner Mongolia. *Nature* **366**, 57–59.

Yatkola, D. A. 1976 Fossil *Heloderma* (Reptilia, Helodermatidae). *Occ. Pap. Mus. nat. Hist., Univ. Kansas* **51**, 1–14.

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APPENDIX 1. SOURCES OF ANATOMICAL INFORMATION

Anatomical information used in this study was derived primarily from examination of specimens, supplemented by published descriptions. Only the more important specimens examined are listed below. Fossil forms are denoted by asterisks; all other specimens are skeletal preparations. The chief literature sources on skeletal anatomy consulted for each group are also listed.

(*a*) *Lacertoidea*

Lacertidae: *Acanthodactylus vulgaris* (BMNH 1907.6.22.10), *Ichnotropis capensis* (AMS R76368), *Lacerta viridis* (BMNH 63.2.21.25; MMS R1234), *Nuras taeniolata* (AMS R76373), *Podarcis sicula* (BMNH 1920.1.20.800), *Psammodromis algirus* (BMNH 56.9.2.16). Polyglyphodontidae: *Euspondylus brevifrontalis* (BMNH 1905.5.31.37). Teiidae: *Ameiva festiva* (AMS R73364), *Callopistes maculatus* (BMNH 1904.1.25.12), *Neusticurus ecpleopus* (AMS R73364), *Pholidobolus montium* (AMS R73403), *Proctoporus ventrimaculatus* (AMS R81741), *Tupinambis nigropunctatum* (BMNH 1964.1825). Xantusiidae: *Xantusia henshawi* (BMNH 1969.2961), *Xantusia vigilis* (AMS R4581). Literature: Arnold (1973, 1983, 1989), Camp (1923), Edmund (1969), Estes (1983), Estes *et al.* (1988), Fisher & Tanner (1970), Hoffstetter & Gasc (1969), Jollie (1960), Lécuru (1968*a*, *b*), Presch (1988), Savage (1963), Siebenrock (1894).

(*b*) *Scincoidea*

Cordylidae: *Chamaesaura anguina* (AMS unreg.), *Platysaurus intermedius* (AMS R76360). *Pseudocordylus microlepidotus* (BMNH 64.2.21.27), Gerrhosauridae: *Gerrhosaurus flavigularis* (BMNH 63.2.21.30), *Tetradactylus seps* (AMS R93618), *Zonosaurus madagascarensis* (BMNH 63.5.14.4). Scincidae: *Chalcides ocellatus* (BMNH 63.2.21.29), *Ctenotus taeniolatus* (AMS R64219), *Eumeces algeriensis* (BMNH 93.2.24.1), *Eumeces obsoletus* (BMNH 89.7.3.32), *Leiopisma platynotum* (AMS R123335), *Tiliqua scincoides* (AMS R66047), Literature: Camp (1923), Edmund (1969), El Toubi (1938), Estes *et al.* (1988), Greer (1970), Hikida (1978), Hoffstetter (1949), Hoffstetter & Gasc (1969), Kingman (1932), Lang (1991), Lécuru (1968*a*, *b*), Malan (1941), Nash & Tanner (1970), Presch (1988), Rieppel (1981), Siebenrock (1892), Skinner (1973).

(*c*) *Anguidae*

Anguinae: *Anguis fragilis* (AMS R95419), *Ophisaurus apodus* (AMNH 75481, 73228), *Ophisaurus compressus* (USNM 284142), *Ophisaurus ventralis* (USNM 14142, 161277). Diploglossinae: *Diploglossus stenurus* (AMS R97328). Gerrhonotidae: *Abronia mixteca* (AMNH 91001), *Abronia oaxacae* (AMNH 93208), *Barisia imbricata* (USNM 32166), *Elgaria coerula* (USNM 313411), *Elgaria kingii* (USNM 292554, 292555), *Elgaria multicarinata* (AMNH 141091; USNM 11298, 292548, 313412), *Gerrhonotus liocephalus* (AMNH 72638, 104476; USNM 25085), *Gerrhonotus gadovis* (AMNH 90944, as *Mesaspis*). Literature: Bell *et al.* (1995), Bellairs (1950), Camp (1923), Coe & Kunkel (1906), Cooper (1966), Criley (1968), Estes (1964, 1983), Frazetta (1983), Gauthier (1980, 1982), Good (1987*b*), Hoffstetter & Gasc (1969), Jörg (1965), Kuhn (1940), Lécuru (1968*a*, *b*), Meszoely (1970), Rieppel (1978, 1980*a*), Siebenrock (1892), Sullivan (1972, 1989), Tihen (1949), Toerien (1950).

(*d*) *Xenosauridae*

Shinisaurus crocodilurus (AMNH 44928), *Xenosaurus grandis* (AMNH 19380, 103212; USNM 111531). Literature: Barrows & Smith (1947), Camp (1923), Costelli & Hecht (1971), Hecht & Costelli (1969), Hoffstetter & Gasc (1969), Holman (1973), Lécuru (1968*a*, *b*), Rieppel (1980*a*).

(*e*) *Helodermatidae*

Heloderma horridus (AMNH 56439, 57863, 57868, 64128, 71664, 118700, 118701), *Heloderma suspectum* (AMNH 56432, 66998, 71082, 71864, 72646, 72908, 72999, 73771, 74777, 74778, 109521, 110174, 118698, 139670; UMZC R9319, 9320, 9321). Literature: Bogert & del Campo (1956), Boulenger (1891), Estes (1983), Lécuru (1968*a*, *b*), Odermatt (1942), Pregill *et al.* (1986), Shufeldt (1890), Stevens (1977).

(*f*) **Estesia mongoliensis*

(AMNH MAE14; cast of MAS M3/14 in AMNH). Literature: Norell *et al.* (1992).

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(*g*) ****Telmasaurus grangeri***

(AMNH 6645, 6646). Literature: Borsuk-Bialynicka (1984), Estes (1983), Gilmore (1943).

(*h*) ****Saniwa***

Saniwa ensidens (USNM 2185), *Saniwa* sp. (AMNH 1020A, 7292; USNM 4119, 16534–8). Literature: Estes (1983), Gilmore (1922, 1928).

(*i*) ***Varanus***

Varanus albigularis (BMNH 1974.2480), *Varanus bengalensis* (BMNH 1930.1.10.2, 1974.2479), *Varanus exanthematicus* (BMNH 1920.1.20.3660, 1974.2480),*Varanus giganteus* (UMZC R9586, R9587), *Varanus gilleni* (BMNH 1910.5.28.13), *Varanus gouldii* (BMNH R1983.1132), WAM R28281, R70345), *Varanus griseus* (BMNH 71.6.6.2, 1974.2481–3), *Varanus indicus* (BMNH 1932.7.19.2), *Varanus komodoensis* (BMNH 1934.8.2.2, 1985.1226; USNM 228163, 101444), *Varanus mertensi* (BMNH 1983.1132 – ασ *V. gouldii*), *Varanus niloticus* (BMNH 1970.183; UMZC R9551), *Varanus panoptes* (AMS R100500), *Varanus salvator* (BMNH 1972.2160–2), *Varanus tristis* (WAM R106054), *Varanus varius* (BMNH 1987.2154; CSIRO REPS13). Literature: Ali (1949), Bahl (1937), Bellairs (1949), Brongerma (1958), Bullet (1942), Clos (1995), Fejérváry (1918, 1935), Hoffstetter & Gasc (1968), Jenkins & Goslow (1983), Landsmeer (1984), Lécuru (1968*a*, *b*), Lönnberg (1903), Mertens (1940*a*, *b*, c, 1959), Watkinson (1906).

(*j*) ***Lanthanotus***

Literature: Borsuk-Bialynicka (1984), Hoffstetter & Gasc (1968), Lécuru (1968*a*, *b*), McDowell (1967*b*), McDowell & Bogert (1954), Rieppel (1980, 1980*b*, 1983), Underwood (1957).

(*k*) ****Aigialosauridae***

Aigialosaurus dalmaticus, (BSP 1902II501), *Opetiosaurus buccichi* (NMW unnumberred specimen, additional unnumbered fragments in GBW), *Carsosaurus marchesetti* (MCSNT 11430–11432) Literature: Caldwell *et al.* (1995), Trieste Aigialosaur (MCNST). Literature: Carroll & DeBraga (1993), Kornhuber (1901).

(*l*) ****Mosasauridae***

Clidastes sp. (AMNH 192, 1548; BMNH R2946; USNM 3765, 3778, 11627, 11719), *Globidens* sp. (USNM 4993), *Halisaurus* sp. (USNM 418442), *Liodon* sp. (AMNH 1401), *Mosasaurus* sp. (AMNH 1391), *Platecarpus* sp. (AMNH 126, 127, 1488, 1491, 1820, 14788, 14800; BMNH R4002; USNM 3774, 3791, 18274), *Tylosaurus* sp. (AMNH 1543, 4909; BMNH R3616, 35622, 35625; USNM 3764). Literature: Callison (1967), Camp (1942), DeBraga & Carroll (1993), Dobie *et al.* (1986), Dollo (1924), Edmund (1969), Lingham-Soliar (1991*a*, *b*, 1992, 1994, 1995), Lingham-Soliar & Nolf (1989), Osborn (1899), Plisnier-Ladame & Coupatez (1969), Russell (1964, 1967, 1975), Williston (1898).

(*m*) ***Scolecophidia***

Anomalepidae: *Helminthophis* (AMNH 38123). Leptotyphlopidae: *Leptotyphlops humilis* (USNM 222795), *Leptotyphlops macrolepis* (BMNH 1904.6.30.5). Typhlopidae Ramphotyphlops australis (AMS unreg.), *Ramphotyphlops ligatus* (AMS 119116), *Ramphotyphlops nigriscens* (AMS R11893 and unreg.), *Typhlops angolensis* (AMNH 11633), *Typhlops diardi* (BMNH 1930.5.8.1–5), *Typhlops humilis* (USNM 222795), *Typhlops punctatus* (BMNH 1975.567; USNM 320704), *Typhlops reticulatus* (AMNH 3001), *Typhlops* sp. (USNM 16433). Literature: Brock (1932), Duerden & Essex (1928), Dunn (1941), Dunn & Tihen (1944), Essex (1927), Evans (1955), Haas (1930, 1964, 1968), List (1966), Mahendra (1936), McDowell (1967*a*), Rage (1984), Rieppel (1979, 1979*a*, 1988), Smit (1949), Tihen (1945), Underwood (1967), Warner (1946).

(*n*) ***Alethinophidia***

Aniliidae: *Anilius scytale* (BMNH 56.10.16; 58.8.23.48). Cylindrophidae: *Cylindrophis rufus* (BMNH 1930.5.8.47, 1947.1.1.8), *Cylindrophis maculatus* (AMS R131356; BMNH 1930.5.8.48, 1930.5.8.51). **Dinilysia*: cast of holotype (BMNH R3154). Uropeltidae: *Melanophidium punctatum* (BMNH 1930.5.8.118), *Platyplecturus madurensis* (BMNH 1930.5.8.110), *Uropeltis ceylanicus* (BMNH 1930.5.8.81–82, 1930.5.8.85–88, 1930.5.8.91, 1930.5.8.94–96), *Uropeltis woodmasoni* (BMNH 1930.5.8.75, as *Silybura nigra*). Xenopeltidae: *Xenopeltis unicolor* (BMNH 1947.1.1.9–12, 1930.5.8.130, 1930.5.8.132, 66.7.10.6; USNM 258746, 287277). Literature: Cundall & Rossman (1993), Cundall *et al.* (1993), Estes *et al.* (1970), Frazetta (1970), Haas (1930, 1931), Hecht (1982), Radovnovic (1938), Rage (1974, 1984), Rieppel (1977*a*, *b*, 1979, 1979*a*, *b*, *c*, 1980*c*, 1988), Underwood (1967), Williams (1959).

APPENDIX 2. ABBREVIATIONS

(*a*) *Institutional*

AMNH	American Museum of Natural History, New York
AMS	Australian Museum, Sydney
BSP	Bayerische Staatssammlung für Paläontologie und historische Geologie, München (Munich)
CSIRO	Australian National Wildlife Collection, CSIRO, Canberra
GBW	Geologische Bundesanstalt, Wien (Vienna)
MCSNT	Museo Civico di Storia Naturale, Trieste
MMS	Macleay Museum, University of Sydney

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NMW	Naturhistorisches Museum, Wien (Vienna)
QM	Queensland Museum, Brisbane
RMM	Redpath Museum, Montreal
UMZC	University Museum of Zoology, Cambridge
USNM	United States National Museum, Washington
WAM	Western Australian Museum, Perth

(*b*) ***Anatomical***

ac	fanterior coracoid foramen
af	adductor fossa
an	angular
at	atlas vertebra
ax	axis vertebra
bo	basioccipital
bpt	basipterygoid process
bs	basisphenoid
cc	crista circumfenestralis
co	coronoid
col	columella auris (stapes)
cor	coracoid
cp	compound postdentary element
de	dentary
ds	dorsum sellae
ec	ectopterygoid
ep	epipterygoid
eph	epiphysis
ex	exoccipital
fe	femur
fi	fibula
fo	fenestra ovalis
fp	fenestra perilymphatica
fr	frontal
gle	glenoid
hy	hypapophysis
il	ilium
isc	ischium
ju	jugal
la	lacrimal
mg	Meckelian groove
mx	maxilla
na	nasal
op	opisthotic
pa	parietal
pal	palatine
pcf	posterior coracoid foramen
pm	premaxilla
pof	postorbitofrontal
pra	prearticular
prf	prefrontal
pro	prootic
pt	pterygoid
pu	pubis
qa	quadrate
sa	surangular
sca	scapula
sm	septomaxilla
so	supraoccipital
sor	supraorbital
sp	splenial
sq	squamosal
st	supratemporal
sym	symphyseal area
ti	tibia
tp	transverse process
vc	vidian canal (exit)
vo	vomer
zyg	zygosphene
VII	facial foramen