THE PHYLOGENETIC POSITION OF *SINEOAMPHISBAENA HEXATABULARIS* REEXAMINED

MAUREEN KEARNEY

Field Museum of Natural History, Department of Zoology, Division of Amphibians and Reptiles, Chicago, Illinois 60605,
mkearney@fmnh.org

ABSTRACT—*Sineoamphisbaena hexatabularis*, a fossil squamate recovered from Upper Cretaceous deposits in Inner Mongolia, China, was reported to be the oldest known amphisbaenian and the sister group to all other amphisbaenians. However, the conclusion of amphisbaenian affinities was based on a partitioned analysis that excluded relevant data and included reconstructed characters. When characters for analysis are limited to those that are observable on the fossils and all evidence is included and analyzed simultaneously, results do not support *S. hexatabularis* as an amphisbaenian, but instead suggest that *S. hexatabularis* may be related to macrocephalosaurids. Several potential synapomorphies of *S. hexatabularis* and macrocephalosaurids are provided, including: presence of lateral process of palatal ramus of pterygoid; postorbital large, extending posteriorly beyond supratemporal fenestra, and approaching posterior edge of cranial roof; and tall, narrow, dorsal process of maxilla. *S. hexatabularis* is tentatively reassigned to the Macrocephalosauridae. The origin of amphisbaenians remains obscure.

INTRODUCTION

Amphisbaenians are burrowing squamate reptiles of enigmatic affinities. Most are completely limbless, but three species within the genus *Bipes* possess front limbs only. Previous hypotheses of sister groups to amphisbaenians are numerous, including almost every non- or reduced-limbed lizard group (e.g., Cope, 1892; Böhme, 1981; Rieppel, 1981; Greer, 1985; Estes et al., 1988; Schwenk, 1988; Reeder, 1995; Hallermann, 1998; Lee, 1998), as well as snakes (Rage, 1982). Some have also suggested that amphisbaenians are a freestanding taxon separate from snakes or other lizards (Vanzolini, 1951; Gans, 1974, 1978; Bellairs and Gans, 1983). The anatomy of amphisbaenians is very specialized, making phylogenetic comparisons difficult since many potential features for comparison are absent or highly transformed. The difficulty encountered with morphological convergence due to fossoriality in phylogenetic studies of squamates has become a classic problem in vertebrate systematics, and part of this problem centers specifically around amphisbaenians. Thus, it was of some importance when a newly discovered fossil from the Gobi Desert of Inner Mongolia, China, was reported to be the oldest and most primitive known amphisbaenian (Wu et al., 1993).

Wu et al. (1996) subsequently described *Sineoamphisbaena hexatabularis*, from the Cretaceous of Inner Mongolia, China (Fig. 1), and interpreted it as the oldest known amphisbaenian and the sister taxon to all other amphisbaenians based on a cladistic analysis of osteological characters scored for all squamate families. A detailed scenario regarding the origin and early evolution of amphisbaenians was suggested based on this analysis:

"amphisbaenians evolved in Central Asia during the Cretaceous in response to the transition from a perennially lacustrine environment to a dry, semiarid, eolian environment. The relatively primitive morphology indicates that *Sineoamphisbaena hexatabularis* was not permanently subterranean. The further derived modifications of later forms are associated with tunneling in an environment of more compact soils" (Wu et al., 1996:541).

The interpretation of *S. hexatabularis* as the sister group to amphisbaenians is highly significant not only because amphisbaenian affinities within squamates have been enigmatic for decades (Bogert, 1964; Gans, 1978; Estes et al., 1988; Rieppel,

1988), but also because it implies an Asian origin, which is significantly different than previously proposed hypotheses that have emphasized the predominantly North American, Tertiary amphisbaenian fossil record (e.g., Berman, 1973; Gans, 1978). Furthermore, as indicated in the above quote, the morphological gap between *S. hexatabularis* and any fossil or extant amphisbaenian is very large (see also Gao and Hou, 1996). *S. hexatabularis* exhibits a mixture of primitive features (e.g., well-developed limbs, large and complete orbits, complete temporal arcade, paired parietals) and derived features (e.g., braincase completely enclosed by bone) relative to amphisbaenians.

The published interpretation of *S. hexatabularis* as the sister group to amphisbaenians is called into question here via a reanalysis that addresses analytical problems in the original study, such as the exclusion of characters that could not be scored for the new fossil in order to avoid missing data, and the partitioning of the analysis into a three-step procedure that did not adequately test phylogenetic relationships. Also, several character states that were based on reconstructions of the fossil in the published analysis are deleted, others are reinterpreted based on this author's anatomical studies of amphisbaenians, and several potential synapomorphies shared by *S. hexatabularis* and macrocephalosaurid lizards are provided.

METHODS AND RESULTS OF PUBLISHED STUDY

Wu et al. (1996) described two specimens for *S. hexatabularis*. The holotype (IVPP V10593) consists of an almost-complete skull with a partial skeleton. The paratype (IVPP V10612) consists of a partial skull with a partial left mandible. Both specimens were recovered from the Upper Cretaceous Djadokhta Formation, Bayan Mandahu, Inner Mongolia, China.

Specific features of the fossil were suggested to indicate amphisbaenian affinities and the authors then grouped features of *S. hexatabularis* into four classes (autapomorphic, apomorphic, plesiomorphic, and variable) in relation to a taxon "Other Amphisbaenians" prior to analysis. Most features not falling within the apomorphic category were excluded from the data matrix. A previously published data matrix for squamates (that of Estes et al., 1988), consisting of 148 osteological and soft tissue characters, was utilized by Wu et al. (1996) as the basis for scoring features of *S. hexatabularis*. Sixty-three characters from that data matrix that could not be scored for *S. hexatabularis* due
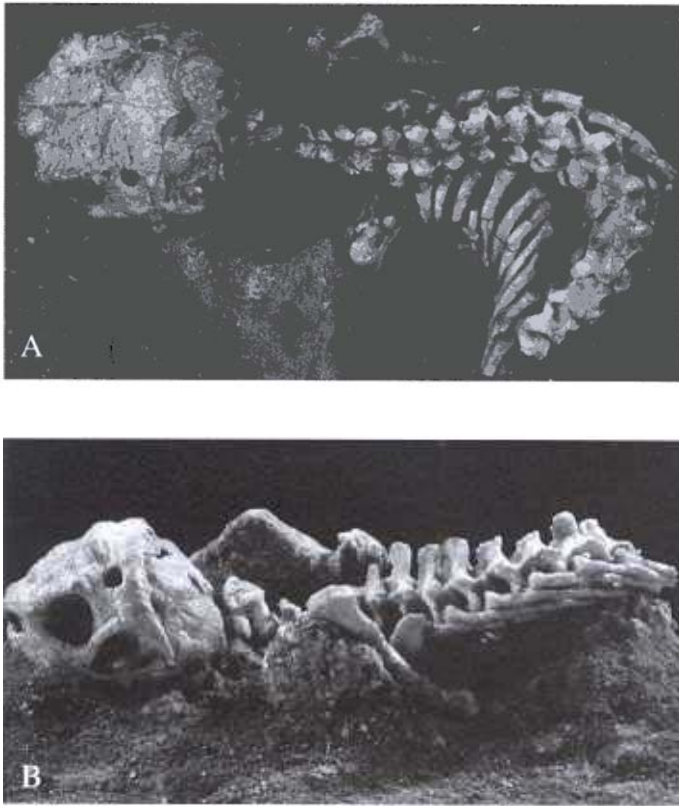
FIGURE 1. A, dorsal view of holotype of *Sineoamphisbaena hexa-tabularis* (IVPP V10593). B, left lateral view of holotype of *Sineoam-phisbaena hexatabularis* (IVPP V10593).

to non-preservation (18 soft-tissue characters and 45 skeletal characters) were excluded because of concerns regarding potential ambiguity caused by missing data.

The cladistic analysis of Wu et al. (1996) was divided into three steps based on a concern regarding computational constraints. In the first step, data for *S. hexatabularis*, 25 other squamate taxa (including amphisbaenians), and an outgroup taxon were analyzed simultaneously; this resulted in a grouping of *S. hexatabularis* with amphisbaenians, and that clade in an unresolved position (Fig. 2A). In the second step, the taxon "Other Amphisbaenians" was deleted from the matrix and the matrix reanalyzed: "Once *Sineoamphisbaena* had been consistently referred to the Amphisbaenia, we used this species as the representative of the Amphisbaenia, because of its primitiveness, and reanalyzed the data matrix, with the six amphisbaenian autapomorphies (characters 86–91) eliminated" (Wu et al., 1996:563). This second analysis resulted in a more resolved topology, and yielded a grouping of *S. hexatabularis* with "Macrocephalosauridae" and that clade as the sister group to "Polyglyphanodontidae" (Fig. 2B). The final hypothesis preferred by Wu et al. (1996) (Fig. 2C)—that of an ((Other Amphisbaenians, *S. hexatabularis*) Macrocephalosauridae)) group—was based on a synthesis of the first two cladograms, with an "Other Amphisbaenians"-*S. hexatabularis* clade accepted from the first analysis (Fig. 2A), and a *S. hexatabularis*-macrocephalosaurid clade accepted from the second analysis (Fig. 2B). However, this result does not stand when all taxa are included and analyzed together. As described below under "Reanalyses and Results," simultaneous analysis of all the data, in combination with correction of characters that were based on reconstructions, supports only a grouping of *S. hexatabularis* with macro-

cephalosaurids and a grouping of "Other Amphisbaenians" with dibamid lizards.

SYSTEMATIC PALEONTOLOGY

LEPIDOSAUROMORPHA Gauthier et al., 1988a
LEPIDOSAURIFORMES Gauthier et al., 1988a
LEPIDOSAURIA Haeckel, 1866
SQUAMATA Oppel, 1811
MACROCEPHALOSAURIDAE Sulimski, 1975
SINEOAMPHISBAENA Wu et al., 1993

Emended Diagnosis—Although the status of Macrocephalosauridae is beyond the scope of this paper, the following derived features may be used provisionally to diagnose this taxon as a macrocephalosaurid: (1) nasal-prefrontal contact; (2) presence of a lateral process of the palatal ramus of the pterygoid; (3) postorbital large and extending posteriorly beyond supratemporal fenestra, approaching posterior edge of cranial roof; (4) tall, narrow, dorsal process of maxilla; (5) deep prefrontal-lacrimal complex excluding maxilla from orbit; and (6) slender, long and pointed supratemporal process of parietal contacting squamosal.

Holotype—IVPP 10593, a nearly complete skull and partial skeleton.

Distribution—Late Cretaceous of Inner Mongolia, China.

REANALYSES AND RESULTS

The holotype and paratype of *S. hexatabularis* were examined and compared to specimens of all the taxa included in the published study. The data of Wu et al. (1996) were reanalyzed as described below. All search options were identical to those used by Wu et al. (1996).

Addition of Excluded Characters

The 63 excluded characters from the Estes et al. (1988) data set were added to the matrix of Wu et al. (1996) and the data set was reanalyzed using the same search conditions and algorithm in PAUP version 3.1.1 (Swofford, 1993) that were used in the published study. Inclusion of these characters resulted in a data matrix that contained 18.9% missing data, compared to 5.6% missing data in the reduced data set of the published study. Thus, Wu et al. (1996) were correct in their concern that including these characters would increase the percentage of question marks in the data matrix. However, inclusion of these characters resulted in only two most parsimonious trees and a significantly more resolved strict consensus tree (Fig. 3) than that obtained from the reduced data set (compare to Fig. 2A). Simultaneous analysis of all of the data results in a cladogram grouping *S. hexatabularis* with amphisbaenians and this clade as the sister group to dibamids, then snakes. Several of the excluded characters were apparently important in uniting amphisbaenians with dibamids and snakes.

Character Reinterpretations

Fourteen of the characters used in the original analysis were reinterpreted or rescored based on examination of specimens. Character numbers are taken from Wu et al. (1996). However, the criterion used by Wu et al. (1996) for scoring polymorphic characters is not adopted here. Those authors scored the plesiomorphic state for any taxon in which both plesiomorphic and apomorphic states occurred, assuming that the apomorphic state evolved within the group. Here, those characters are scored as polymorphic. Furthermore, the criterion of Wu et al. (1996) was inconsistently applied to amphisbaenians—for some characters (e.g., characters 57, 79, 80), the plesiomorphic condition for amphisbaenians was assumed to be that occurring in the extant
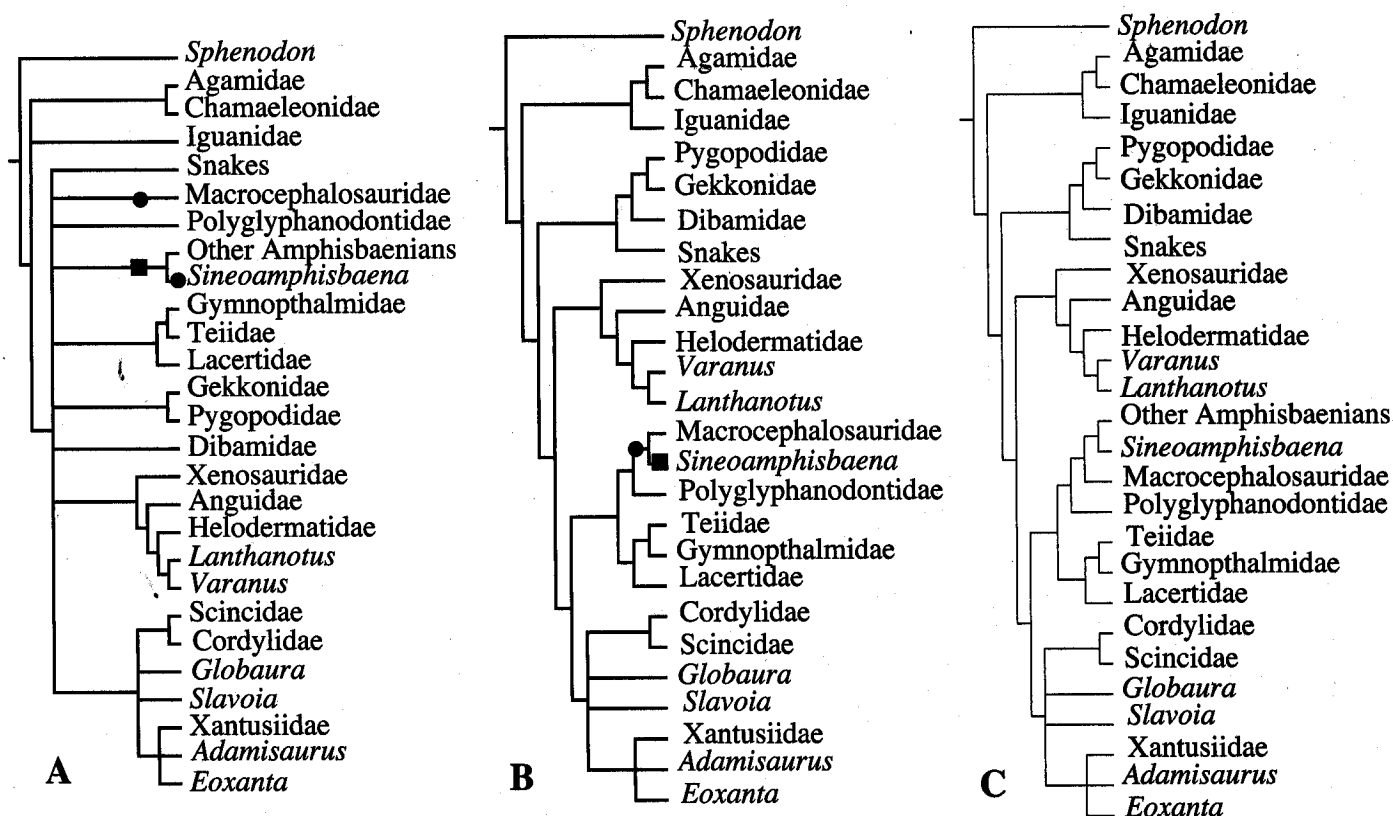
FIGURE 2. A, step one of Wu et al.'s (1996) analysis: Strict consensus cladogram of 28 most parsimonious trees (length = 317, CI = 0.39, RI = 0.56) based on a data set including all taxa and excluding 63 characters unscorable for *S. hexatabularis*. This data set contains 5.6% missing data. According to this topology, numerous characters (represented by circular dots) shared by Macrocephalosauridae and *Sineoamphisbaena* must be interpreted as homoplasies. The square represents character states interpreted as synapomorphies of the group consisting of *Sineoamphisbaena* and "Other Amphisbaenians." B, step two of Wu et al.'s (1996) analysis: strict consensus cladogram of 9 most parsimonious trees (length = 306, CI = 0.39, RI = 0.54) based on data set excluding the taxon "Other Amphisbaenians," and excluding 63 characters unscorable for *Sineoamphisbaena*. The circle represents the character states that are now interpreted as synapomorphies of *Sineoamphisbaena* and Macrocephalosauridae, previously interpreted as homoplasies in A. The square represents the character states that are now interpreted as autapomorphies of *Sineoamphisbaena*, previously interpreted as synapomorphies of *Sineoamphisbaena* and "Other Amphisbaenians" in A. C, final phylogenetic hypothesis concluded by Wu et al. (1996) based on a regrafting of "Other Amphisbaenians" onto the *Sineoamphisbaena* branch of Figure 3B.

Bipes and, for other characters (e.g., characters 5, 12, 31, 54, 84, 92, 104), the plesiomorphic condition for amphisbaenians was assumed to be that occurring in fossil rhineurids. Because ingroup relationships among amphisbaenians are enigmatic and therefore plesiomorphic vs. apomorphic conditions are poorly understood within the group, it is difficult to apply Wu et al.'s (1996) criterion, even if one desired to do so.

Character 5—Prefrontal contact with posterior orbital bones: no contact with postorbital, postfrontal, or fused postorbital-postfrontal above orbit (0); contact with postorbital, postfrontal, or fused postorbital-postfrontal above orbit (1). This character was scored by Wu et al. (1996) as 1 (contact present) in amphisbaenians and *S. hexatabularis*. However, among amphisbaenians, only two species (the fossil taxa *Spathorhynchus fossorium* and *Spathorhynchus natronicus*) exhibit a postfrontal bone at all and these taxa exhibit a prefrontal-postfrontal contact (Berman, 1973). In all other amphisbaenians, the postfrontal is absent, indicating that this character must be scored as inapplicable (−) for most amphisbaenians.

Character 13—Postfrontal forking: subtriangular, not forked medially (0); semilunate, forked medially, clasping frontoparietal suture (1). This character was scored 0 (not forked) in amphisbaenians and *S. hexatabularis*. The comments made above for character 5 apply for this character as well and the character is rescored here as inapplicable (−) for most amphisbaenians.

Character 27—Lacrimal: present, either separate or fused to

prefrontal (0); absent (1). This character was scored 0 (present, either separate or fused to prefrontal) in amphisbaenians and *S. hexatabularis*. Wu et al.'s (1996) discussion of this feature admits the difficulty of distinguishing fusion of the lacrimal and the prefrontal from the loss of the lacrimal in squamates, and the authors rely on the position of the lacrimal foramen as an indicator of whether a lacrimal is present/fused or absent, indicating that the same state does not occur in amphisbaenians and *S. hexatabularis*. The authors state: "The lacrimal foramen is typically situated between the prefrontal and maxilla, or between the prefrontal and jugal, and is largely exposed laterally in lepidosaurians that do not have the lacrimal [including amphisbaenians]. ... Where a lacrimal is present, the lacrimal foramen is located within the lacrimal or between the lacrimal and prefrontal and is not visible laterally. The lacrimal foramen in *S. hexatabularis* is deep and located on the medial surface of the prefrontal, a position similar to that of the lepidosaurians that have a lacrimal. This suggests that the prefrontal here includes the lacrimal in fusion. The sutural pattern of the bone with the neighbouring elements ... also indicates that the prefrontal and lacrimal are fused" (Wu et al., 1996:548). Thus, by their own criteria, the laterally exposed condition in amphisbaenians is indicative of having no lacrimal whereas the deep condition in *S. hexatabularis* is indicative of having a fused lacrimal-prefrontal and it is not clear why both taxa were scored with "lacrimal present."
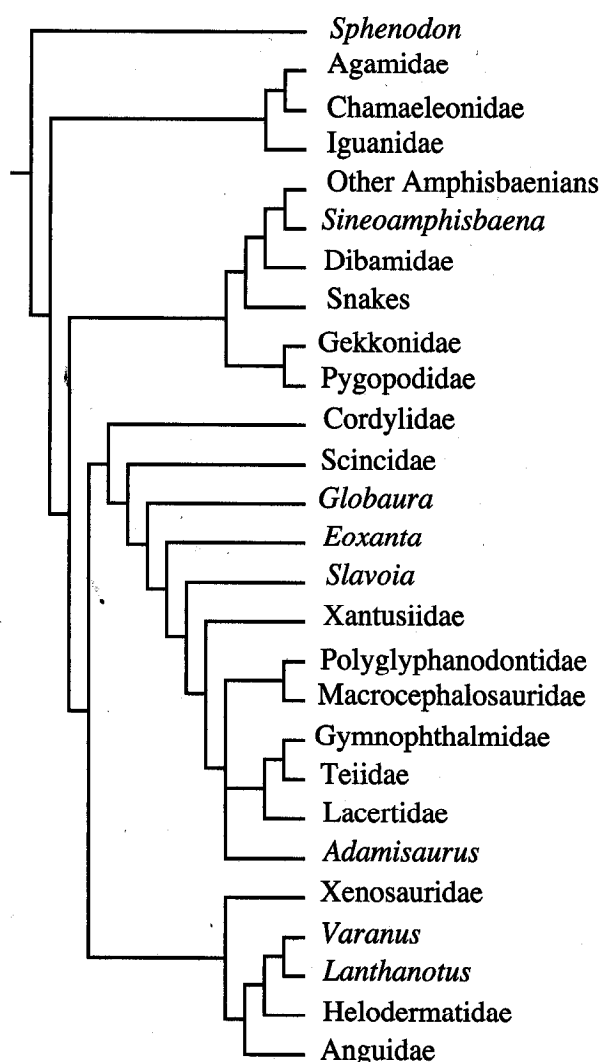
FIGURE 3. Strict consensus of two most-parsimonious trees (length = 509, CI = 0.40, RI = 0.58) resulting from analysis of all taxa and all characters in a data set containing 18.9% missing data.

Estes et al. (1988) and Gans (1978) considered the lacrimal to be absent in amphisbaenians, although Romer (1956) considered some amphisbaenians to have a fused lacrimal-prefrontal. Additionally, the size of the purported prefrontal-lacrimal complex in *S. hexatabularis* is much larger compared to the size of the prefrontal in amphisbaenians; it forms the entire anteroventral margin of the orbit in *S. hexatabularis*, whereas in amphisbaenians, the prefrontal is restricted to a small area immediately anterior to the orbit. This is consistent with the hypothesis that the lacrimal is fused to the prefrontal in *S. hexatabularis* but absent in amphisbaenians. Finally, a recent study of an amphisbaenian embryonic series indicates that there is never an independent ossification of a lacrimal element (Montero et al., 1999) and these authors therefore considered the bone to be lost in amphisbaenians. Amphisbaenians are scored here for the absence of a lacrimal and *Sineoamphisbaena* is scored for the presence of a lacrimal.

Character 28—Lacrimal fusion: separate (0); fused to prefrontal (1). *S. hexatabularis* and amphisbaenians were scored 1 for this character (lacrimal fused to prefrontal). Because of the comments made above for Character 27, amphisbaenians are rescored here as inapplicable (−) for this character, the same

state given by the authors to other taxa such as dibamids, gekkonids, and snakes, that lack a lacrimal.

Character 45—Epipterygoid: present (0); absent (1). This character was scored as 1 (absent) in *S. hexatabularis* and amphisbaenians by Wu et al. (1996). The epipterygoid is absent in all amphisbaenians with the exception of *Trogonophis* (Gans, 1960; Bellairs and Kamal, 1981). However, the presence or absence of an epipterygoid is not observable in *S. hexatabularis*; the assignment of an absent state was based on the absence of a pit on the pterygoid for the epipterygoid. Thus, this character is here rescored as unknown (?) for *S. hexatabularis* and polymorphic (0/1) for "Other Amphisbaenians."

Character 53—Subdental shelf size: small or absent (0); large (1). This character was scored as 0 (small or absent) in amphisbaenians and in *S. hexatabularis*. However, the presence or absence of a subdental shelf cannot be directly observed in *S. hexatabularis* due to poor preservation. Although the authors indicate this with their statement that the medial surface of the mandibular elements is not visible, they conclude that a small subdental shelf is "indicated." *S. hexatabularis* is rescored here as unknown (?) for this character.

Character 86—Orbitosphenoid: absent (0); present (1). This character was scored as 1 (present) for *S. hexatabularis* and amphisbaenians. This character, and several related ones which follow, relate to the bony, anteriorly closed braincase in *S. hexatabularis*, and figure prominently in Wu et al.'s (1996) hypothesis that *S. hexatabularis* shares a close relationship with "Other Amphisbaenians."

An enlarged orbitosphenoid closing the anterior braincase has long been recognized as a unique feature of the Amphisbaenia (Gans, 1978). Bellairs and Gans (1983) reported that the orbitosphenoid in amphisbaenians is an unpaired element of membrane origin and questioned the homology of this structure with the small, paired orbitosphenoids that are cartilage-replacement bones in other lizards. Montero and Gans (1999) recently renamed this element the "tabulosphenoid" in order to reflect its unique nature and morphology. Most recently, Montero et al. (1999) reported the observation that, embryologically, the orbitosphenoid (=tabulosphenoid) in amphisbaenians is formed both by the orbitosphenoid cartilage replacement bones of lizards, as well as a contribution of membrane bone.

Wu et al. (1996) interpreted the ossification closing the anterior braincase in *S. hexatabularis* as an orbitosphenoid, but there are some major differences between these structures in the two taxa. In most amphisbaenians, the anterior braincase is closed ventrolaterally by the azygous orbitosphenoid and anteriorly by the descending process of the frontals, and the suture between each frontal and the orbitosphenoid is visible in lateral view (Fig. 4A). The frontals in amphisbaenians form a complete ring around the olfactory lobes of the brain and are underlain partially by the anterior edge of the orbitosphenoid. Wu et al. (1996) interpreted the bony element(s) closing the anterior braincase in *S. hexatabularis* as an orbitosphenoid but there is no suture delineating that element from the descending processes of the frontals (Fig. 4B). This lack of a suture was explained by a hypothesis of fusion of the descending processes of the frontals with the purported orbitosphenoid. However, there is no evidence to support this hypothesis of fusion, and such a fusion does not exist in any amphisbaenian.

One criterion used to support the orbitosphenoid identification was: "The bone is underlain by the parasphenoid cultriform process" (Wu et al., 1996:551). This, too, is inferred and not observed. In both specimens of *S. hexatabularis*, the cultriform process is a very short, pointed tip on the anterior parasphenoid (Fig. 4C, D), but Wu et al. (1996:550) surmise that it has been broken in *S. hexatabularis* and reconstruct it as extending anteriorly, similar to the condition occurring in amphisbaenians. In contrast, the orbitosphenoid in most amphis-
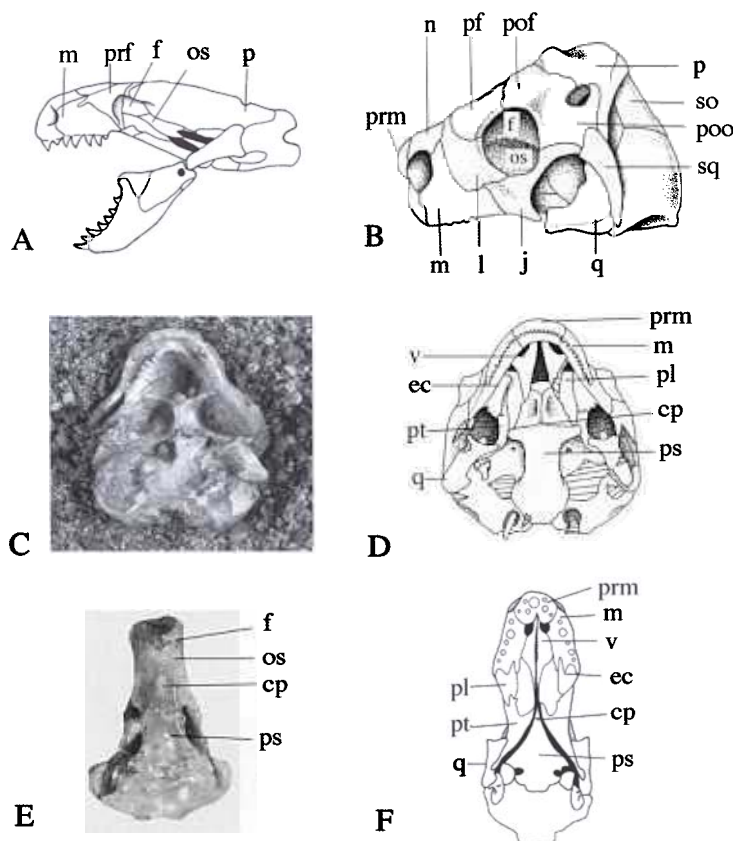
FIGURE 4.   A, left lateral view of *Amphisbaena alba* showing relationship between frontals and orbitosphenoid (=tabulosphenoid) (redrawn from Zangerl, 1944). **B**, reconstruction of elements in *S. hexatabularis* by Wu et al. (1996) (redrawn from Wu et al., 1996:fig. 6C.). The frontals are assumed to be fused with the orbitosphenoid in *S. hexatabularis* but this condition never occurs in amphisbaenians. **C**, condition of the cultriform process in paratypic skull of *S. hexatabularis*. This condition is essentially the same in the holotypic skull. **D**, illustration of ventral surface of holotypic skull of *S. hexatabularis*. **E**, ventral view of the braincase (underlying elements absent) of the amphisbaenian fossil *Lophocranion rusingense* (BMNH R-8293) showing large cultriform process of the parasphenoid which substantially underlies the orbitosphenoid in amphisbaenians. **F**, ventral view of the skull of the extant *Amphisbaena alba* (redrawn from Zangerl, 1944) showing anteriorly elongated cultriform process of the parasphenoid. This relationship of an enlarged cultriform process underlying an orbitosphenoid element was reconstructed by Wu et al. (1996) for *S. hexatabularis*. **Abbreviations**: **cp**, cultriform process of parasphenoid; **ec**, ectopterygoid; **f**, frontal; **j**, jugal; **l**, lacrimal; **m**, maxilla; **n**, nasal; **os**, orbitosphenoid; **p**, parietal; **ps**, parasphenoid; **pl**, palatine; **prf**, prefrontal; **prm**, premaxilla; **poo**, postorbital; **pof**, postfrontal; **ps**, parasphenoid; **pt**, pterygoid; **q**, quadrate; **so**, supraoccipital; **sq**, squamosal; **v**, vomer.

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baenians is significantly underlain by a very large cultriform process (Fig. 4E, F). Therefore, if the cultriform process of the parasphenoid is to be interpreted as underlying the purported orbitosphenoid in *S. hexatabularis*, this must be based on a reconstruction in both specimens, and the process must be assumed to be broken in both specimens.

In addition, examination of the holotype and paratype skulls of *S. hexatabularis* indicates that the ossification in question is a paired element (Fig. 4C, D), not a single one as is usually the case in amphisbaenians (Bellairs and Gans, 1983; Montero and Gans, 1999). The purported orbitosphenoid in *S. hexatabularis* is concave on either side of the midline and exhibits a ridged suture medially. This is not the case in most amphisbaenians, in which the ventral surface of the single element is usually flat and smooth anteriorly, hence the new name, "tabulosphenoid," assigned by Montero and Gans (1999) (e.g., Fig. 4E). While these elements might be large, paired orbitosphenoids, this would be homologous to the conditions occurring in some basal squamates, and not to the unique conditions occurring in amphisbaenians. The most significant problem with this identification, however, is that it rests upon the assumption that there is no suture delineating the descending processes of the frontals from the purported orbitosphenoid due to

fusion of these elements. Such a fusion between frontals and orbitosphenoids is unknown among any amphisbaenian or other squamate. The enclosures of the optic foramina are indeed orbitosphenoid-like but, if these are orbitosphenoids, they are quite dissimilar to the orbitosphenoid of amphisbaenians. A few amphisbaenians have paired orbitosphenoids but, in those cases, the orbitosphenoids are greatly reduced in size, do not contain optic foramina, and are topologically dissimilar to this condition. For all the above reasons, I take an agnostic position on the identification of this element and the character is rescored here as unknown (?) for *S. hexatabularis*. "Other Amphisbaenians" are scored with state 1; all other taxa are scored with state 0.

Character 87—Anterior braincase floor: no floor formed (0); floored by orbitosphenoid, parasphenoid cultriform process underlying orbitosphenoid (1); or floored by parasphenoid cultriform process (2). *S. hexatabularis* and amphisbaenians were scored with state 1 for this character (floored by orbitosphenoid, parasphenoid cultriform process underlying orbitosphenoid) in the analysis of Wu et al. (1996). Although this is the case in amphisbaenians, in *S. hexatabularis* this scoring can only be based on a reconstruction of an enlarged cultriform process and
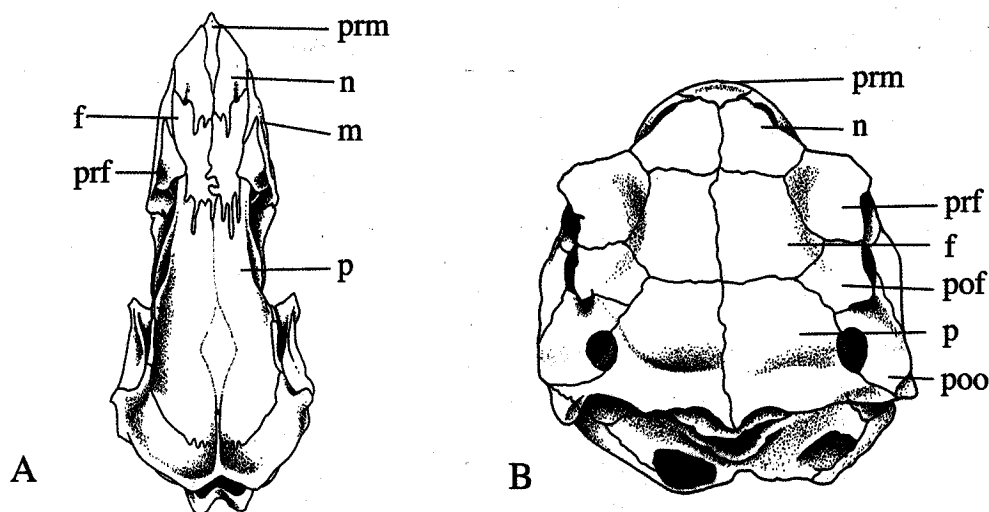
FIGURE 5. Comparison of suture patterns among cranial roofing bones. A, dorsal view of skull of *Amphisbaena caeca* (redrawn from Gans and Alexander, 1962:pl. 2). B, dorsal view of skull of *S. hexatabularis*. Abbreviations as in Figure 4.

of an orbitosphenoid fused to the descending frontal processes. This character is here rescored as ? for *S. hexatabularis*.

Character 88—Skull solidarity: cranial elements loosely connected and palate not firmly attached to braincase floor (0); cranial elements tightly connected and palate firmly attached to braincase floor (1). *S. hexatabularis* and amphisbaenians were scored by Wu et al. (1996) with state 1 (cranial elements tightly connected and palate firmly attached to braincase floor) for this character. However, cranial elements are strongly interdigitated in most amphisbaenians with highly sinuous sutures (Fig. 5A), whereas in *S. hexatabularis*, the sutures are only slightly sinuous (Fig. 5B). Second, the palatal-braincase contact in *S. hexatabularis* is not any tighter than in typical squamates and certainly does not approach the condition in amphisbaenians and dibamids, in which the braincase/cranial elements are in tight contact with the palatal bones. In *S. hexatabularis*, the cranial/braincase elements are exposed in ventral view. Additionally, in *S. hexatabularis* (but not in amphisbaenians or dibamids), the metakinetic joint is preserved (seen clearly in Figs. 1B and 4B). A tight basicranial articulation occurs in amphisbaenians and dibamids, but not in *S. hexatabularis*. *S. hexatabularis* is rescored here with state 0 for this character.

Character 89—Enlarged median tooth on fused premaxillae: absent (0); present (1). *S. hexatabularis* and amphisbaenians were both scored with state 1 (enlarged median tooth present) for this character. However, the median premaxillary tooth in *S. hexatabularis* is just barely larger than its surrounding premaxillary teeth (see Fig. 4D). This is similar to the condition that occurs in some scincids, *Dibamus*, and in the fossil *Slavoia*, but not at all like the condition in amphisbaenians in which the median premaxillary tooth is greatly enlarged, representing the replacement for the hatchling egg tooth (see Fig. 4F). This was acknowledged in the original study, but nevertheless coded as a homologous state: "A median tooth is present, and although it is only slightly larger than the others, this can be interpreted as an early stage in the evolution of the condition seen in the later amphisbaenians" (Wu et al., 1996:558). *S. hexatabularis* is rescored here as state 0 (the same state given to other squamate taxa such as *Dibamus* that exhibit a slightly enlarged median premaxillary tooth).

Character 91—Size of quadrate ramus of pterygoid: long and large, loosely connecting to quadrate (0); short and small, tightly wrapping around posteromedial (ventromedial if quadrate horizontally oriented) surface of quadrate (1). *S. hexata-*

bularis and amphisbaenians were scored with state 1 (short and small, tightly wrapping around posteromedial [ventromedial if quadrate horizontally oriented] surface of quadrate). In most amphisbaenians, the pterygoid is long and gently curves posterolaterally to clasp the quadrate due to the extreme lengthening of the postorbital region of the skull (see Fig. 4F). In *S. hexatabularis*, however, the pterygoid is short and sharply curves laterally to contact the quadrate just posterior to the orbit due to the extreme shortness of the postorbital region of the skull (see Fig. 4D). Amphisbaenians are rescored here with state 0.

Character 92—Contact of pterygoid with vomer: present, palatal ramus of pterygoid meeting vomer anteriorly (0); absent (1). Wu et al. (1996) coded this character as present in amphisbaenians and *S. hexatabularis*. This character is polymorphic in amphisbaenians. In most amphisbaenians, including *Bipes*, the pterygoid does not contact (nor even approach) the vomer (see Fig. 4F), while in some fossil rhineurids with a strong craniofacial angle, pterygoid-vomer contact occurs via an extremely long palatal ramus of the pterygoid. This character is here recoded as polymorphic (0/1) for amphisbaenians.

Character 93—Lateral process of palatal ramus of pterygoid: absent (0); present, a lateral process of palatal ramus developed along lateral border of palatine (1). This character was scored with state 1 for *S. hexatabularis* and "Other Amphisbaenians." However, this condition only occurs in two fossil amphisbaenian taxa, *Dyticonastis rensbergeri* and *Spathorhynchus fossorium*. Thus, amphisbaenians are recoded here as polymorphic (0/1) for this character. The character is also polymorphic for Macrocephalosauridae (Gao, 1997).

Other Characters Added

The characters assumed a priori to be autapomorphic or plesiomorphic for *S. hexatabularis* and excluded from the data matrix in that analysis were added to the data matrix here. This is important because, of the 13 excluded characters assumed to be autapomorphic, the following are also present in many macrocephalosaurids: a tall, narrow, dorsal process of the maxilla (Sulimski, 1975); a deep prefrontal-lacrimal complex which excludes the maxilla from the orbit (Gao and Norell, 1999); and a slender, long, and pointed supratemporal process of the parietal contacting the squamosal (Sulimski, 1975). Similarly, of the 22 characters judged to be plesiomorphic for *S. hexatabu-*

laris and excluded from the analysis, at least one is considered to be an apomorphic reversal for other squamate taxa in recent studies: an enlarged posteroventral process of the jugal is considered a synapomorphic reversal for polyglyphanodontines by Gao and Norell (1999) and Sulimski (1975).

The resulting combined and revised data matrix in NEXUS format can be found in TreeBASE (http://www.treebase.org/ treebase/index.html).

Reinterpretation of Phylogenetic Placement of *S. hexatabularis*

When these recodings and additional characters are incorporated into the data matrix and all data are analyzed simultaneously, an *S. hexatabularis*-macrocephalosaurid clade is found, as well as a clade uniting amphisbaenians with dibamids, then snakes (Fig. 6). This cladogram is similar to that obtained from the simultaneous analysis of all taxa and all characters in Figure 3 except that *S. hexatabularis* is the sister group to macrocephalosaurids rather than "Other Amphisbaenians." Seven unequivocal synapomorphies support the grouping of *S. hexatabularis* with macrocephalosaurids: nasal-prefrontal contact; presence of lateral process of the palatal ramus of pterygoid; postorbital large and extending posteriorly beyond supratemporal fenestra approaching posterior edge of cranial roof; tall, narrow, dorsal process of maxilla; deep prefrontal-lacrimal complex contacting jugal and excluding maxilla from orbit; and slender, long and pointed supratemporal process of parietal contacting squamosal. Of the 22 characters judged to be plesiomorphic for *S. hexatabularis* and excluded from the analysis, at least one is considered to be an apomorphic reversal for other squamate taxa in recent studies and is found here to provide support for a *S. hexatabularis*-macrocephalosaurid clade: enlarged, blunt, posteroventral process of jugal. The jugal is lost completely in most amphisbaenians; however, in *S. hexatabularis* and macrocephalosaurids, this bone has expanded, particularly in the development of a strong posterior extension. Figure 7 illustrates some of these features in the fossil *Macrocephalosaurus chulsanensis*. Several other potential synapomorphies of *S. hexatabularis* and these taxa exist, but these occur sporadically among polyglyphanodontids and macrocephalosaurids, and require further exploration: parietal rugose anteriorly but smooth posteriorly; posterodorsal process of jugal enlarged and contacting both postorbital and squamosal; humerus with slender shaft and expanded proximal and distal ends capped by ossified epiphyses; supratemporal fossa small and oval-shaped; cultriform process short; sculpturing of dermal cranial bones; and maxillary toothrow entirely antorbital.

DISCUSSION

Affinities of *Sineoamphisbaena hexatabularis*

Wu et al.'s (1996) conclusions were based on the hypothesis that *S. hexatabularis* shares numerous similarities with both amphisbaenians and macrocephalosaurids. Gao and Hou (1996) criticized the conclusions of Wu et al. (1996), and suggested that there were no compelling similarities between the *S. hexatabularis*-Other Amphisbaenians grouping and macrocephalosaurids. Wu et al. (1997) took issue with the criticisms of Gao and Hou (1996). Gao (1997) replied again, and reiterated his objection to the validity of an Amphisbaenia-Macrocephalosauridae sister-group relationship. In contrast to both these previous studies, I conclude that *S. hexatabularis* does share homologous characters with macrocephalosaurids, but not with amphisbaenians. Based on the reanalysis here, the available evidence suggests that the affinities of *S. hexatabularis* may lie with macrocephalosaurids, although the relationships of that group are currently poorly known.
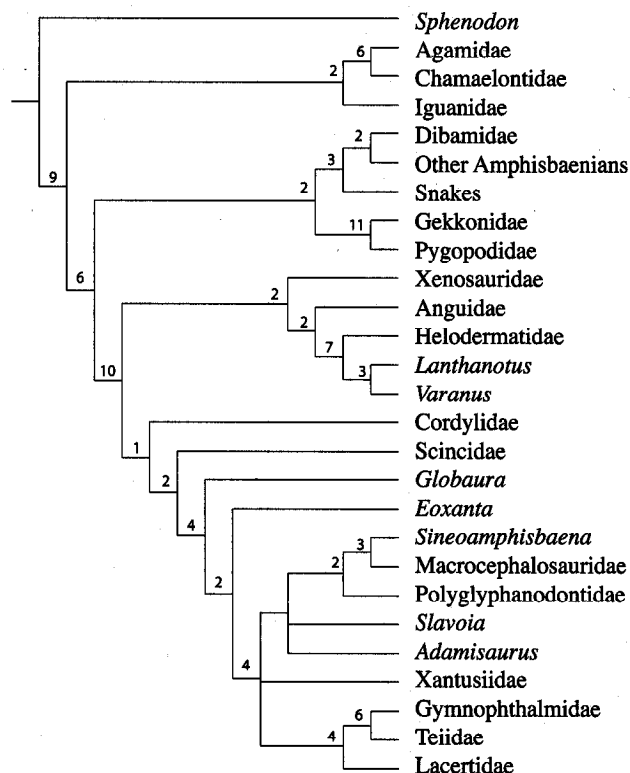

FIGURE 6. Strict consensus of three most-parsimonious cladograms (length = 533, CI = 0.40, RI = 0.57) resulting from simultaneous analysis of all characters and taxa after recoding and addition of new characters. Numbers at nodes are Bremer decay values (Bremer, 1988).

Macrocephalosauridae are a highly problematic and poorly understood group. Gilmore (1942) defined the Polyglyphanodontinae (including macrocephalosaurs) as a subfamily of the Iguanidae. Sulimski (1975, 1984) recognized the Macrocephalosauridae, Adamisauridae and Polyglyphanodontidae as separate families, suggesting that they could not be placed in the Teiidae and that they were scincomorphs of unknown affinities. However, Estes (1983) placed these three groups into the subfamily Polyglyphanodontinae within the family Teiidae. Alifanov (1993) followed Sulimski (1975) and resurrected the familial rank for Macrocephalosauridae. Most recently, Gao and Norell (1999) questioned this status again. *S. hexatabularis* appears to share synapomorphic features with macrocephalosaurids; however, Gao and Norell (1999) have raised doubts regarding the monophyly of this group and relationships among all these taxa require additional study.

Finally, it should be noted that a recent study by Lee (1998) also suggested a close relationship between *S. hexatabularis* and amphisbaenians (although in this case dibamids were the sister group to amphisbaenians and *S. hexatabularis* was the sister group to that clade). However, the Lee (1998) analysis, like the Wu et al. (1996) analysis, excluded soft tissue characters and the Lee (1998) study did not include macrocephalosaurids.

It should be noted that the (amphisbaenian, dibamid) snake)) grouping obtained here after reanalysis is supported by some characters that are often considered to be correlated with a fossorial lifestyle (e.g., Lee, 1998). In this respect, the group may be regarded with some skepticism. However, the data of Wu et al. (1996) do not support an alternative hypothesis for a sister-group relationship between amphisbaenians and *Sineoamphisbaena* when all the data are analyzed simultaneously. This
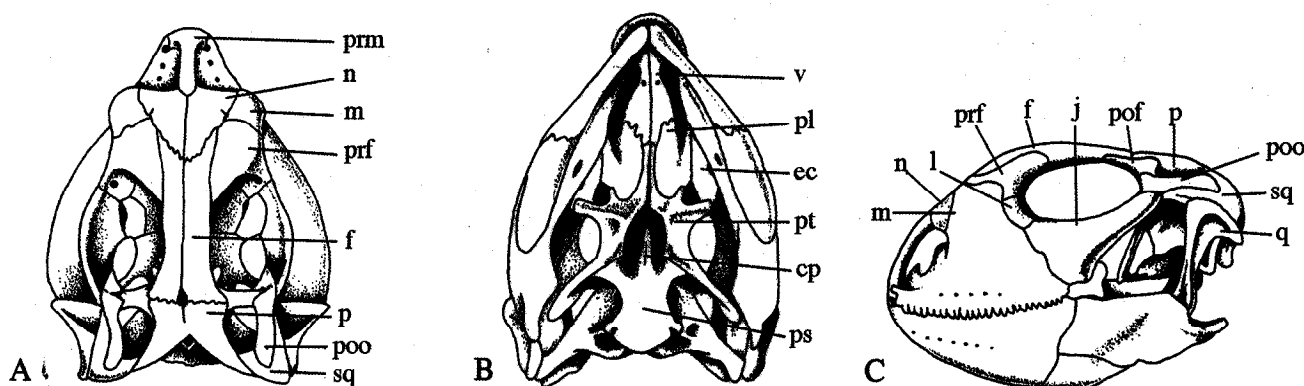
FIGURE 7. A, dorsal; B, ventral, and C, lateral views of *Macrocephalosaurus chulsanensis* (ZPAL MgR-I/14) (redrawn from Sulimski, 1975). Abbreviations as in Fig. 4.

placement of amphisbaenians with dibamids and snakes is obtained repeatedly in many morphology-based squamate phylogenetic studies (Estes et al., 1988; Hallermann, 1998; Rieppel and Zaher, 2000) and, although it is typically viewed with suspicion due to the preponderance of "fossorial characters" supporting the group, no other well-supported placement for amphisbaenians has been found. This grouping is unlikely to be broken on the basis of traditional morphological data alone or without the discovery of fossil amphisbaenians related to basal forms such as *Bipes* and/or fossil dibamids.

Simultaneous Analysis vs. Missing Data

Wu et al. (1996) expressed concern about the consequences of missing data entries in their data matrix and, on this basis, excluded all characters that were unscorable for the fossil taxon of interest. However, as shown above, the "added missing data" that resulted from the inclusion of these characters did not obscure relationships; instead the added character states further resolved relationships.

The effect of missing data on systematic analyses containing both living and extinct taxa has become an issue of concern in the recent paleontological literature (e.g., Wilkinson, 1995; Norell and Gao, 1997; Grande and Bemis, 1998) and many misconceptions have been perpetuated (Kearney and Clark, 2003). Missing data are often blamed for increased ambiguity in such analyses, manifested in large numbers of primary trees and relatively unresolved consensus trees. However, as shown here, extent of missing data in a data matrix is not necessarily a predictor of degree of resolution. Instead, resolution of relationships depends on the exact combination of question marks and character covariation in the data matrix (Novacek, 1992). Thus, it should not be assumed a priori that adding characters which must be scored as missing in fossils will result in increased ambiguity or that omitting such characters is "safe" (Kearney, 2002). Indeed, exclusion of characters or taxa from a phylogenetic analysis is in conflict with the philosophy of "total evidence" advocated by many systematists (Kluge, 1989; Eernisse and Kluge, 1993; Nixon and Carpenter, 1996).

It should be noted that the approach of excluding taxa or characters in order to reduce the percentage of missing data in matrices is becoming commonplace to the point where certain classes of data (typically non-osteological) are often excluded in paleontological studies with little justification. Missing data exclusion strategies preclude the possibility that fragmentary taxa or fragmentary characters that can only be partially scored in a data matrix might still contribute important information, a point that has been demonstrated empirically (e.g., Norell and de Queiroz, 1991; this study). The criterion for inclusion of

characters or taxa in phylogenetic studies should not be how much missing data they contribute to the matrix, because any amount of character data constitutes additional homology statements that may contribute to the hypothesis of relationships.

Taxonomic Sampling/Data Partitioning

Examination of the three-step analysis of Wu et al. (1996) reveals that several characters that were initially interpreted as homoplasies of *S. hexatabularis* and "macrocephalosaurids" in the first step of their analysis were subsequently interpreted as synapomorphies of those two taxa in the second step of their analysis when the taxon "Other Amphisbaenians" was removed (Fig. 3A, B). This is because the removal of the taxon "Other Amphisbaenians" altered the balance of character distributions in such a way as to favor the secondary signal in the matrix for a *S. hexatabularis*-macrocephalosaurid grouping, and the characters that had supported an *S. hexatabularis*-"Other Amphisbaenians" clade became autapomorphies of *S. hexatabularis*. To generalize this issue to one of taxonomic sampling, missing taxa cause a shift in the balance between homologous and homoplastic characters and this causes changes in topology—what were seen as homoplasies now appear as homologies and what were seen as homologies now appear as autapomorphies when taxa are removed from an analysis. If the test of character congruence is considered important in cladistic analysis, then complete taxon sampling is crucial because missing taxa ultimately translate into "missing character congruence." The test of congruence relies on the interaction of character states among taxa, and excluding taxa (along with their characters) diminishes the severity of that test.

The issue of taxon sampling in cladistic analysis has been the subject of considerable debate in the recent systematics literature (Doyle and Donoghue, 1987; Gauthier et al., 1988b; Kluge, 1989; Huelsenbeck, 1991; Wiens and Reeder, 1995; Hillis, 1996; Siddall, 1996; Graybeal, 1998; Poe, 1998). Some have argued for limiting the number of taxa based on criteria of consistency or accuracy. Others argue for increasing the number of taxa based on a desire to break up long branches, or to increase severity of test. If relying on the test of character congruence as the basis for inferring relationships, then inclusion of all relevant taxa (and the character evidence that they bear) is important because missing taxa will detract from that test.

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