

DISCUSSION

Phylogenetic relationships of *Sineoamphisbaena hexatabularis*: further considerations¹

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The authors (K. Gao and L. Hou) criticized the proposal by Wu et al. (1993a) that *Sineoamphisbaena hexatabularis* is the oldest and most primitive amphisbaenian yet known and the attendant hypothesis that the Amphisbaenia and Macrocephalosauridae (sensu Sulimski 1975) are sister-groups. We contest that their criticisms are neither justified nor supported by available evidence and thus offer the following consideration of their concerns.

Especially, the authors expressed reservations about several of the characters listed by Wu et al. (1993a) in support of an Amphisbaenia–Macrocephalosauridae clade. Although the authors followed the classification by Wu et al. (1993a) while awaiting more detailed information on the taxa, they are clearly dissatisfied with the conclusion.

Before considering the character-based questions that were raised by the authors, differences in basic assumptions concerning the operational taxonomic units (OTU) appropriate for this analysis must be addressed. The authors followed Estes et al. (1988) in including the Macrocephalosauridae (represented by *Macrocephalosaurus* and *Darchansaurus*; Sulimski 1975), Polyglyphanodontidae (represented by *Polyglyphanodon*, *Paraglyphanodon*, *Erdenetesaurus*, and *Chermisaurus*; Sulimski 1975), and Adamisauridae (represented by *Adamisaurus*; Sulimski 1978) in the Polyglyphanodontinae of the family Teiidae, whereas Wu et al. (1993a) followed Sulimski and treated these three as separate taxonomic units in their analysis (also see Wu et al. 1993b, 1996). This was done because significant differences are present in the palate, maxilla, and temporal region of these taxa and extant teiids and because the monophyly of the Teiidae sensu Estes

(1983) and Estes et al. (1988) has not yet been established by way of cladistic analysis of the relevant taxa mentioned above. Thus, the authors' criticisms of the taxonomic relationships proposed by Wu et al. (1993a) were founded upon assumptions of relationships that were not accepted by Wu et al.

Wu et al. (1993a) listed two character complexes in support of the amphisbaenian–macrocephalosaurid relationship, one describing the peculiar modification of the palate and the other summarizing the specialization of the temporal region. These are uniquely shared by the two taxa. The two character complexes are as follows: (1) "the palatal ramus of the pterygoid is forked into a medial process, which extends along the medial side of the palatine and contacts or nearly reaches the vomer, and a lateral process which meets the ectopterygoid (sometimes the maxilla too) along the lateral side of the palatine and closes the suborbital fenestra" (Wu et al. 1993a, p. 59); and (2) "a large postorbital is posteriorly broad, extends posteriorly over the temporal fenestrae, meets or closely approaches the parietal, and is excluded from the infratemporal fenestra by the contact of the jugal and squamosal" (Wu et al. 1993a, p. 59). The authors (p. 593) rightly questioned the strength of some of the individual characters in these complexes. However, this problem was largely dealt with in Wu et al. (1993a, 1993b), where the individual characters of the two complexes are included in a matrix of characters, and the resulting cladogram is the result of a PAUP analysis of this data matrix (see also Wu et al. (1996) for details).

With reference to the characters discussed by the authors, we offer the following comments:

(1) Length of the vomer: "Vomer elongate, approaching pterygoid" has been recognized as a teiid synapomorphy of the Teiidae (Romer 1956; Estes et al. 1988)" (p. 594). Romer (1956, p. 546) considered "vomeres elongate" as a teiid feature, while Estes et al. (1988) redefined this character by adding the qualifier "approaching pterygoid" and listed it as a synapomorphy of Teiidae. However, in their cladistic analysis, Estes et al. (1988) used the definition of "vomer elongate posteriorly, extends one half or more the length of the maxillary tooth row and usually restricting internal naris" (p. 129) and recognized it as a synapomorphy of the Scleroglossa (p. 151), as in our analysis (Wu et al. 1996, p. 565). Therefore, this character state does not help resolve relationships between the Amphisbaenia and any of the taxa of the Teiidae sensu Estes (1983) and Estes et al. (1988).

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(2) Vomer–pterygoid contact: “‘Vomer–pterygoid contact’ occurs in *Macrocephalosaurus* and *Adamisaurus*, but not in the closely related *Polyglyphanodon*” (p. 594). Because of the absence of the vomer–pterygoid contact in the latter, the authors do not believe that the shared presence of this character in the Macrocephalosauridae and Amphisbaenia is a homology. This argument has to assume, a priori, that *Polyglyphanodon*, *Adamisaurus*, and the macrocephalosaurids form a monophyletic group. That the authors make this assumption is implied in their statement that *Polyglyphanodon*, *Adamisaurus*, and the macrocephalosaurids are closely related. Our evidence argued against a monophyletic clustering of these taxa (see also Wu et al. 1996, Figs. 13B, 14B), and thus called into question the utility and significance of the term “closely related” as employed by the authors. A vomer–pterygoid contact in *Adamisaurus* is a noncongruent character state in our phylogenetic analysis. Actually, the detailed structure of this region is significantly different between *Adamisaurus* and the clade Macrocephalosauridae plus Amphisbaenia, and this character state is reasonably interpreted as having been acquired independently in each (see Wu et al. 1996). In the former the contact between the vomer and pterygoid is a result of the extreme anterior elongation of the palatal ramus of the pterygoid and a short vomer (Sulimski 1978, Fig. 1c; Estes 1983, Fig. 18c), whereas in the latter the vomer is elongate.

(3) Closure of the suborbital fenestra: The authors (p. 594) did not accept that the suborbital fenestra is closed in *Macrocephalosaurus*, yet they provided no reasons for this claim. The original descriptions reported that the suborbital fenestra is closed in *Macrocephalosaurus gilmorei* (Sulimski 1975, p. 37; Estes 1983, p. 85) and *Macrocephalosaurus chulsanensis* (sometimes punctured by a small foramen, Sulimski 1975, p. 49). Sulimski (1975, p. 74) and Estes (1983, p. 80) argued that the suborbital fenestra is closed in *Darchansaurus* as well. Furthermore, the authors (p. 594) argued that the Macrocephalosauridae and polyglyphanodontids resemble other teiids in the suppression of the suborbital fenestra. We do not think so, because the fenestra is completely closed by the development of a lateral process of the palatal ramus of the pterygoid in the Macrocephalosauridae (Sulimski 1975) and in the Amphisbaenia. Within the Teiidae sensu Estes (1983) and Estes et al. (1988), this lateral process of the pterygoid is present only in *Cherminisaurus* (Polyglyphanodontidae; Sulimski 1975), but the suborbital fenestra, although small, remains open in this taxon (Sulimski 1975; Estes 1983).

(4) Size of the postorbital: “A large postorbital can be seen in many groups of squamates with suppression of the upper temporal fenestra (e.g., Xantusiidae, Cordylidae, and Xenosauridae; see Estes et al. 1988)” (p. 594). Wu et al. (1993a) did not use the state “a large postorbital” in the analysis. It is not useful due to the fusion of the postorbital with the postfrontal within many squamate groups, such as the Xantusiidae (see Rieppel 1984; Estes et al. 1988, p. 144) and Xenosauridae (see Estes et al. 1988, p. 146). The character used by Wu et al. is “a large postorbital extends posteriorly, beyond the supratemporal fenestra.” This character is not applicable to taxa (such as the Cordylidae) in which the supratemporal fenestrae are closed. Among the taxa with a postorbital that can be placed in relationship to

the supratemporal fenestra, the similarity in size of the postorbital in macrocephalosaurids of Sulimski (1975) and *Sineoamphisbaena* is striking.

(5) Posterior contact between the postorbital and parietal: “‘Macrocephalosaurids’ (including *Adamisaurus*) do not have a posterior contact between postorbital and parietal (K. Gao, personal observation)” (p. 594). Wu et al. (1993a) did not use the relationships between the postorbital and parietal as an individual character in their analysis (also see Wu et al. 1996) because it is a reflection of the posterior extent of the postorbital (see the previous comment). A related, but independent, character is the degree to which the squamosal enters the supratemporal fenestra (also see character 101 in Wu et al. 1996). In both the Macrocephalosauridae and *Sineoamphisbaena*, the squamosal is excluded by the postorbital–parietal contact or postorbital–supratemporal contact from the supratemporal fenestra.

(6) Jugal–squamosal contact: “Once again, a jugal–squamosal contact is a well-recognized teiid synapomorphy . . . (see Estes et al. 1988)” (p. 594). Estes et al. (1988) did not employ “jugal–squamosal contact” as a character state and do not consider it exclusively as a synapomorphy of their Teiidae. They defined the derived state of this character as “contact present or bones approach each other very closely” (see Estes et al. 1988, p. 129), and further detailed its distribution within the Squamata (see Estes 1988, p. 147): “in iguanians, scincids, teiids, xenosaurs, . . . the jugal and squamosal are in contact or nearly in contact.” Finally, they considered the condition “jugal–squamosal contact on supratemporal arch present or close” as a synapomorphy of their Teiidae, with convergence in other squamates (see Estes et al. 1988, p. 215). Actually, in the Teiidae sensu Estes (1983) and Estes et al. (1988) the separation of the jugal from the squamosal commonly occurs in extant forms (such as *Tupinambis nigropunctatus*; Estes 1988, Fig. 23) as well as in the fossil *Adamisaurus* (Estes 1983, Fig. 18A). Wu et al. (1993a) restricted the jugal–squamosal relationship to the contact of the two bones, which completely excludes the postorbital from the infratemporal fenestra, and thus interpret teiids of their usage and *Adamisaurus* as having the plesiomorphic condition of jugal–squamosal separation.

We also disagree with the authors’ comments on the character state “parietals separate” in *S. hexatabularis*. They (p. 594) claimed that “If ‘parietals separate’ is indeed a primitive condition in amphisbaenians, and the latter group is the sister group of ‘Macrocephalosauridae’ as Wu et al. (1993) advocated, there would have been at least two reversals in this particular aspect in the evolution of the Amphisbaenia Once again, this character state casts doubt on the relationships of the Amphisbaenia with other squamate groups” (p. 594). We feel that this argument is flawed. The authors demonstrated that they are aware that all amphisbaenians (except *S. hexatabularis*) and macrocephalosaurids (Sulimski 1975) have fused parietals, and that an ontogenetic fusion of the parietals is probably a synapomorphy of the Squamata, with reversals occurring in a couple of families (Estes et al. 1988). In this case, “parietal fusion” is plesiomorphic for any taxon within the Squamata and “parietals separate” in any taxon of the group represents an apomorphic reversal. Therefore, the presence of “parietals separate” in *S. hexatabularis* represents only one reversal,

rather than the two reversals advocated by the authors in this particular feature in the history of the Amphisbaenia. The state "parietals separate" in *S. hexatabularis* is revealed, by its congruence with other character states, as an apomorphic reversal within the Amphisbaenia (see Wu et al. 1996, Fig. 13, *Sineoamphisbaena* . . . 21(0) . . .), and thus is neutral with respect to the relationships of the Amphisbaenia. Without having considered its congruence with other characters, any conclusion about relationships of a taxon made based on the plesiomorphic state of a single character is unjustifiable.

The authors (p. 594) also pointed out that "*Sineoamphisbaena* is no longer the oldest known amphisbaenian: Nessov (1985) described *Hodzhakulia*, based on maxillaries and dentaries that clearly show amphisbaenian affinities (Nessov and Gao 1993)." This indicates that the authors consider *Hodzhakulia* to be the oldest representative of the Amphisbaenia. As far as we know, the data presented to date do not provide adequate support for this. The cited relevant publication by the authors, a short abstract, simply stated that "*Hodzhakulia magma* Nessov, 1985 is of special importance, as it shows affinities with the Amphisbaenia and may be the earliest fossil record of the group" (see Nessov and Gao 1993). *Hodzhakulia magma* is represented by incomplete(?) maxillae and dentaries (Nessov 1985, Pl. I, figs. 4–6, Pl. II, fig. 15) and was originally referred to the (?)Teiidae. If it does prove to be an amphisbaenian, its occurrence is consistent with our prediction that amphisbaenians originated earlier than the Campanian in central Asia.

It is almost inevitable that we have made mistakes in our interpretation of the morphology and relationships of *S. hexatabularis*, and we welcome criticisms based on these. We feel, however, that the authors' criticisms of our statements are unsubstantiated.

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