THE UNIVERSITY OF KANSAS

PALEONTOLOGICAL CONTRIBUTIONS

April 30, 2007 Number 15

# PHYLOGENETIC REVISION OF RHINEURIDAE (REPTILIA: SQUAMATA: AMPHISBAENIA) FROM THE EOCENE TO MIOCENE OF NORTH AMERICA

**Daniel I. Hembree**

Department of Geological Sciences, Ohio University, 316 Clippinger Laboratories, Athens, Ohio 45701, USA
hembree@ohio.edu

*Abstract.*—This paper presents a cladistic analysis of morphological characters of Eocene–Miocene North American Amphisbaenia to resolve the phylogenetic relationships among the family Rhineuridae. All North American fossil amphisbaenians are placed within the family Rhineuridae as a result of this analysis. Five taxa previously afforded species rank including *Jepsibaena minor, R. wilsoni, R. amblyceps, R. minutus,* and *R. attenuatus* are synonymized with *Rhineura hatcherii.* In addition, *Hyporhina antiqua* and *H. tertia* are synonymized. Two new genera, *Protorhineura* gen. nov. and *Hadrorhineura* gen. nov. are proposed for Oligocene taxa assigned previously to the genus *Rhineura.* Fossil Rhineuridae are therefore represented by seven genera and nine species: *Protorhineura hatcherii* gen. nov., *Hadrorhineura hibbardi* gen. nov., *Spathorhynchus fossorium, S. natronicus, Dyticonastis rensbergeri, Macrorhineura skinneri, Ototriton solidus, Hyporhina antiqua,* and *H. galbreathi.* Revision of the North American fossil Amphisbaenia has important evolutionary and paleobiogeographic implications for the family Rhineuridae. The inclusion of all North American fossil amphisbaenians in Rhineuridae extends the paleogeographic range of the family, which is known from the Paleocene to the Miocene as well as the Pleistocene and Holocene. Fossil Rhineuridae occur from Oregon to Florida, yet their distribution is concentrated in the North American midcontinent (Colorado, South Dakota, and Wyoming) in Eocene and Oligocene strata. The characters defining different rhineurid clades seem to be related to adaptations for improved burrowing efficiency. Changes in character states related to burrowing co-occur with changes in other characters; this suggests that although burrowing adaptations are related to speciation events in Rhineuridae, the recovered relationships are not simply artifacts of convergent evolution.

Key words: amphisbaenian, Cenozoic, fossorial, phylogeny, biogeography.

## INTRODUCTION

Species-level phylogenetic relationships among the fossil amphisbaenians of North America are examined herein. Amphisbaenians are burrowing lizards grouped into the squamate suborder, Amphisbaenia, which includes five families containing 24 extant genera and approximately 170 species (Zug, Vitt, and Caldwell, 2001; Pough et al., 2003). Habitats of extant amphisbaenians vary from clay-rich to sandy soils in warm-humid to relatively xeric climates (Gans, 1974). Amphisbaenians are distributed across continents on both sides of the Atlantic and into the Middle East (Fig. 1.1). Although amphisbaenians long have been considered closely related to lizards (Sauria), their precise relationship among saurians has remained a subject of debate (Estes, De Queiroz, and Gauthier, 1988; Rieppel, 1988; Lee, 1998; Kearney, 2003; Townsend et al., 2004). It is difficult to determine the phylogenetic position of amphisbaenians among tetrapodal saurians, because these reptiles have a highly derived morphology (Lee, 1998).

Relationships within Amphisbaenia are equally problematic. A recent morphological phylogenetic study of amphisbaenian genera by Kearney (2003) revealed some relationships at the generic and family levels that are inconsistent with the previously accepted taxonomy. This analysis placed the limbed Bipedidae as the most basal lineage and suggested several African and South American genera of the Amphisbaenidae were closely related to the endemic North American family Rhineuridae. A more recent molecular phylogenetic study by Kearney and Stuart (2004), however, produced results that were partially in conflict with the morphology-based tree topology; North American Rhineuridae appear as the most basal lineage and the sister group to Blanidae, Bipedidae, Trogonophidae, and Amphisbaenidae (Kearney and Stuart, 2004). A less densely sampled molecular analysis by Macey et al. (2004) that did not include Blanidae also resulted in the basal position of Rhineuridae.

The unique morphology of amphisbaenians is the result of a series of adaptations to fossorial habitats. Among these features are the total or partial loss of limbs, an elongate body form, a compact and highly ossified skull, a modified snout, a transparent

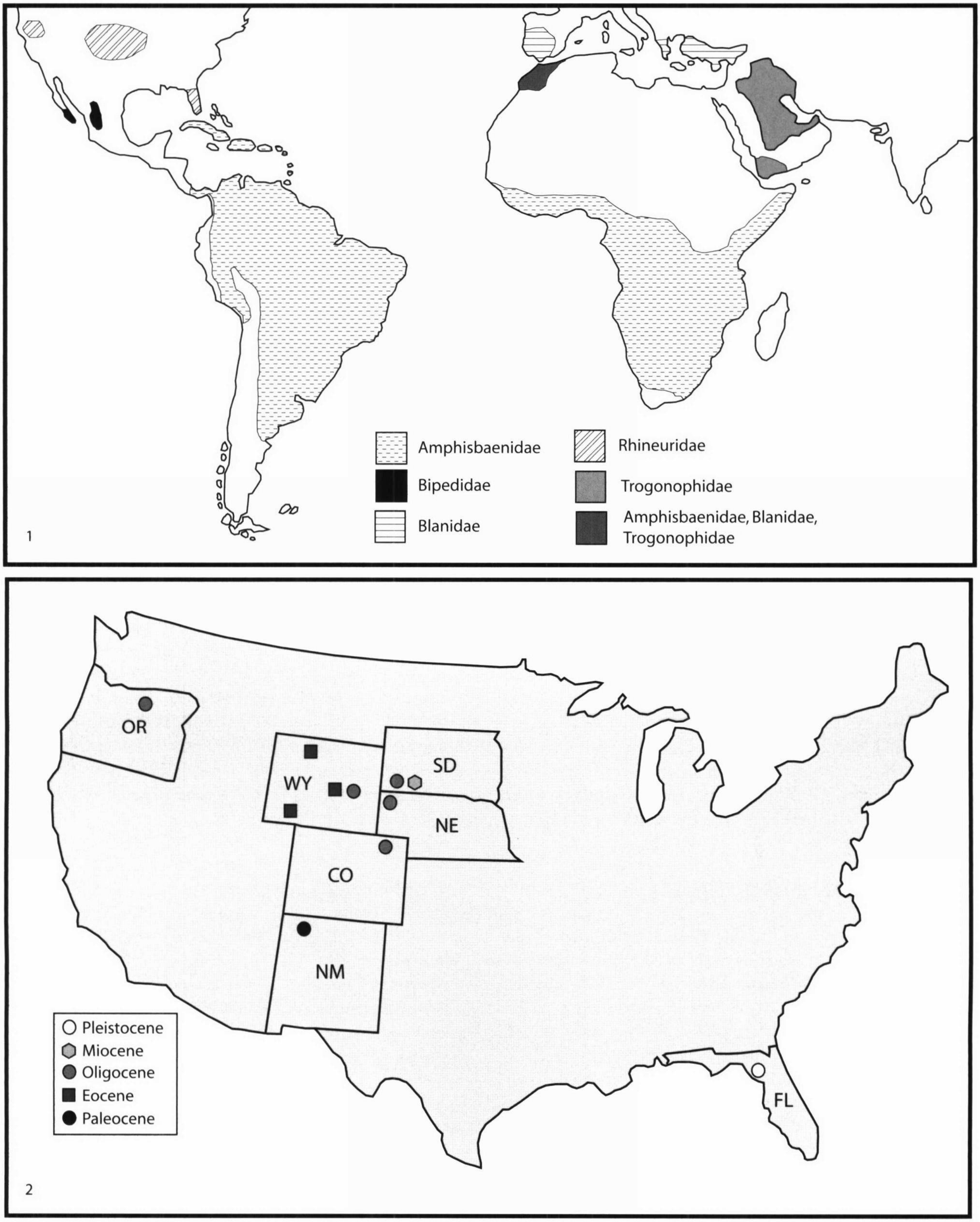


Figure 1. Distribution of extant and fossil amphisbaenian species. *1,* Map showing worldwide distribution of five families of Amphisbaenia. *2,* Map showing localities within United States from which fossil amphisbaenians are known (new).

lower eyelid fused to the upper lid, and an annulated scale pattern and pinnate muscle fiber arrangement that allows for forward and backward movement within tunnels (Gans, 1968, 1969; Berman, 1973; Wake, 1993). Amphisbaenian taxa differ from one another in the morphology of their skulls. Although most amphisbaenian species have cone-shaped skulls with blunt snouts, some have sloping skulls with horizontally flattened snouts or vertically oriented, bony keels (Gans, 1969). These variations in skull morphology indicate adaptations for different burrowing behaviors (Gans, 1969, 1974).

A full understanding of the evolutionary history of a group requires consideration of its fossil record (e.g., Donoghue et al., 1989). Despite their small size and fossorial habitat, amphisbaenians have a relatively good fossil record. Numerous, well-preserved amphisbaenian fossils have been collected from Tertiary floodplain paleosols of the Rocky Mountain region of North America (Fig. 1.2; Baur, 1893; Loomis, 1919; Walker, 1932; Gilmore and Jepsen, 1945; Taylor, 1951; Galbreath, 1953; Estes, 1965; Berman, 1972, 1973, 1976, 1977; Holman, 1979). The widespread distribution of North American amphisbaenians in the Tertiary is in striking contrast to their modern restriction to northern Florida. Since their first description in the late nineteenth century, North American fossil amphisbaenians have reached a relatively high diversity of 9 genera and 22 species (Table 1). A number of these taxa, however, are known from single specimens and consist only of fragmentary cranial or vertebral material. Therefore a taxonomic revision of these extinct taxa will increase the utility of fossil amphisbaenian taxa in phylogenetic studies with extant amphisbaenians.

## NORTH AMERICAN FOSSIL AMPHISBAENIANS

With their first appearance in the Paleocene (Estes, 1965) amphisbaenians are well represented in the fossil record of the North American Cenozoic. The recognized fossil species are represented by a combination of well-preserved cranial material and disarticulated vertebrae. These fossil amphisbaenians resemble extant rhineurids morphologically, most likely because both are or were fossorial and both have highly derived, shovel-shaped skulls. In previous studies, most fossil amphisbaenians of North America have been placed into two closely related families, the Rhineuridae and the Hyporhinidae (Estes, 1983). One fossil genus has been assigned to the family Amphisbaenidae (MacDonald, 1970).

Members of the family Rhineuridae are distinguished by a strong craniofacial angle, a flattened facial surface, a shovel-like snout with a sharp horizontal edge, ventrally oriented nostrils, and a broad, triangular nasal process of the premaxilla (Vanzolini, 1951; Berman, 1973). The extant Rhineuridae is represented by a single species, *Rhineura floridana*, which is restricted to Florida and Georgia in the United States. *Rhineura* represents one of only two genera of extant amphisbaenians present in North America (Zug, Vitt, and Caldwell, 2001; Pough et al., 2003).

Members of the family Hyporhinidae are distinguished by the presence of long, posteriorly directed, paired palatal processes of the premaxilla that form part of the palatine shelf; junction of the premaxilla, nasals, and frontals at a common point on the dorsal surface of the skull; and a short, blunt snout (Berman, 1972). The Hyporhinidae is composed entirely of fossil species occurring in the Eocene and Oligocene strata of the central United States.

*Taxonomic history.*—The first recognized fossil amphisbaenians consist of two skulls collected from the Oligocene White River Group of South Dakota (Baur, 1893). *Rhineura hatcherii* was described as similar to *Rhineura floridana,* differentiated primarily by a more slender skull and more maxillary teeth (Baur, 1893). *Hyporhina antiqua* was assigned to a new family, Hyporhinidae (Baur, 1893), due to the presence of a postorbital bar, a character unique to modern amphisbaenians. Soon after, Loomis (1919) described a new amphisbaenian, *Ototriton solidus,* from a badly weathered skull without a lower jaw collected from the lower Eocene Lysite Member (Wind River Formation) of Wyoming. Loomis, however, originally described the specimen as an amphibian apparently because it has an elongate, seemingly double-headed occipital condyle (Loomis, 1919). Gilmore (1928) revised the diagnosis of *Ototriton solidus,* classifying it as a new genus and species of the Rhineuridae. Gilmore (1928) also recognized amphisbaenian remains among fossils collected by Marsh (1871, 1885). One specimen is a single, dorsal vertebra collected from the middle Eocene Bridger Formation, Uinta County, Wyoming, and originally described as *Glyptosaurus anceps* by Marsh (1871). Gilmore (1928) redescribed the specimen as the amphisbaenian *Ototriton anceps,* based on its possession of amphisbaenian vertebral characters. The specimen was placed in the genus *Ototriton* because of its large size and occurrence in the Eocene of Wyoming. Gilmore (1938) later compared *O. anceps* to *Lestophis crassus* (Marsh, 1885), also represented by a single vertebra, and determined that both belonged to the same genus. Comparison of Oligocene fossil lizards to *Rhineura floridana* led Gilmore to reclassify a series of vertebrae originally named *Platyrhachis coloradoensis* (Cope, 1873), collected from the White River Formation of Colorado, as *Rhineura coloradoensis* (Gilmore, 1928).

An amphisbaenian skull collected from the White River Group in southern Wyoming identified as *Rhineura hatcherii* later was used to define a new species, *Rhineura sternbergii* (Walker, 1932), based on a shorter length of the skull, elongate nasals, a rounded maxilla, and a shorter precoronoidal portion of the dentary. Another amphisbaenian fossil diagnosed by its smaller size, *Rhineura minutus* (Gilmore, 1938), was collected from the same locality but was later revised by Vanzolini (1951) as *Pseudorhineura minutus.* This new genus was supported by the presence of elongate nasals and a posterior position of the fenetra ovalis.

Gilmore later reported a new saurian, *Oligodontosaurus wyomingensis* (Gilmore, 1942), represented by a left mandibular ramus with a complete dental series of nine homodont teeth. *Oligodontosaurus wyomingensis* was assigned to the Amphisbaenia by Estes (1965) because of 1) the low tooth count; 2) pleurodont implantation of the teeth; 3) the interdental bone ridges and nutritive foramina as seen in *Amphisbaena alba;* and 4) the short postcoronoid portion of the jaw. Gilmore and Jepsen (1945) also described a second species of *Ototriton* from the Lost Cabin Member of the early Eocene Wind River Formation collected from Converse County, Wyoming. *Ototriton minor* consists of a single skull with articulated lower jaws; it is distinguished from *Ototriton solidus* by its smaller

Table 1. The 22 described species of North American fossil amphisbaenians and stratigraphic and geographic locality information; *, taxa included in this analysis.

| Fossil Taxa | Age | Stratigraphic Location | Geographic Location | Reference |
|---|---|---|---|---|
| *Oligodontosaurus wyomingensis* | Paleocene | Polecat Bench Formation<br>Fort Union Formation | Park County, Wyoming | Estes, 1965, 1976 |
| *Plesiorhineura tsentasi* | Late Paleocene (Torrejonian) | Upper Nacimiento Formation | New Mexico | Sullivan, 1985 |
| *Spathorhynchus fossorium* | Middle Eocene (Wasatchian) | Bridger Formation<br>Wind River Formation, Lost Cabin Member | Sweetwater County, Wyoming<br>Natrona County, Wyoming | Berman, 1973 |
| *Ototriton solidus* | Middle Eocene (Wasatchian) | Wind River Formation, Lysite Member | Big Horn County, Wyoming | Loomis, 1919; Gilmore, 1928 |
| *Jepsibaenia minor* | Middle Eocene (Wasatchian) | Wind River Formation, Lost Cabin Member | Natrona County, Wyoming | Gilmore and Jepson, 1945 |
| *Spathorhynchus natronicus* | Early Oligocene (Chadronian) | White River Formation | Natrona County, Wyoming | Berman, 1977 |
| *Hyporhina tertia* | Early Oligocene (Chadronian) | White River Formation | Freemont County, Wyoming | Berman, 1972 |
| *Rhineura coloradoensis* | Early Oligocene (Chadronian) | White River Formation | Logan County, Colorado | Gilmore, 1928; Taylor, 1951 |
| *Rhineura (Gilmoreia) attenuatus* | Middle Oligocene (Orellan) | Lower Brule Formation | Converse County, Wyoming | Taylor, 1951 |
| *Hyporhina galbreathi* | Middle Oligocene (Orellan) | White River Formation | Logan County, Colorado | Taylor, 1951 |
| *Rhineura hatcherii* | Middle Oligocene (Orellan)–<br>Late Oligocene (Whitneyan) | White River Group<br>White River Formation<br>White River Group | Shannon County, South Dakota<br>Logan County Colorado<br>Sioux County, Nebraska | Gilmore, 1928; Taylor, 1951 |
| *Rhineura amblyceps* | Middle Oligocene (Orellan) | White River Formation | Logan County, Colorado | Taylor, 1951 |
| *Rhineura wilsoni* | Middle Oligocene (Orellan) | White River Formation | Logan County, Colorado | Taylor, 1951 |
| *Rhineura hibbardi* | Middle Oligocene (Orellan) | White River Formation | Logan County, Colorado | Taylor, 1951 |
| *Pseudorhineura minuta* | Middle Oligocene (Orellan) | Lower Brule Formation | Converse County, Wyoming | Taylor, 1951 |
| *Rhineura sternbergii* | Middle Oligocene (Orellan) | Lower Brule Formation | Converse County, Wyoming | Walker, 1932; Taylor, 1951 |
| *Hyporhina antiqua* | Late Oligocene (Whitneyan) | White River Formation | Shannon County, South Dakota | Baur, 1893; Taylor, 1951 |
| *Dyticonastis rensbergeri* | Late Oligocene (Whitneyan)–<br>Early Miocene (Arikareen) | Turtle Cove Member, John Day Formation | Oregon | Berman, 1976 |
| *Macrorhineura skinneri* | Early Miocene (Arikareen) | Sharps Formation | Shannon County, South Dakota | MacDonald, 1970 |
| *Rhineura marslandensis* | Early Miocene (Hemingfordian) | Marsland Formation | Box Butte County, Nebraska | Yatkola, 1976 |
| *Rhineura sepultura* | Early Miocene (Hemingfordian) | Rosebud Formation | Bennet County, South Dakota | Holman, 1979 |
| *Rhineura floridana* | Pleistocene (Illinoian) | Crystal River Formation | Levy County, Florida | Holman, 1959 |

size (17.6 vs. 32 mm). Gilmore and Jepsen (1945) thought the two specimens were of equivalent developmental stages, and relative size was a specific indicator for other amphisbaenian taxa.

Taylor (1951) described 13 specimens, mostly skulls, collected from the White River Formation of Logan County, Colorado, by the University of Kansas Museum of Natural History Expedition of 1946 under the direction of C. W. Hibbard. From this collection, Taylor (1951) named four new species including *Hyporhina galbreathi, Rhineura amblyceps, R. hibbardi,* and *R. wilsoni.* Taylor (1951) also described a new genus and species, *Gilmoreia attenuatus,* collected by G. F. Sternberg from the White River Group near Douglas, Wyoming, the type locality of both *Rhineura (Pseudorhineura) minutus* and *Rhineura sternbergii.*

MacDonald (1970) described a new amphisbaenian genus and species, *Macrorhineura skinneri*, from the Miocene Sharps Formation of South Dakota. The species is represented by a single specimen consisting of a partial skull with an articulated lower jaw. This genus and species was assigned to Amphisbaenidae, which occurs currently in South America and Africa.

Berman (1972) described a third species of the genus *Hyporhina* from the late Eocene (Chadronian) White River Formation in Fremont County, Wyoming. The new species, *Hyporhina tertia,* was described from a single specimen consisting of the anterior portion of a skull, from the premaxilla to the middle of the frontals. Berman redefined the genus *Hyporhina,* arguing that the presence of a postorbital bone was not a character unique to *Hyporhina.* Berman (1972) diagnosed the genus on the following characters: 1) presence of long, posteriorly directed, paired palatal processes of the premaxilla that form part of the palatine shelf; 2) the junction of the premaxilla, nasals, and frontals at a common point on the dorsal surface of the skull; and 3) possession of a short, blunt snout. Berman (1973) also described a new amphisbaenian genus from North America, *Spathorhynchus,* based on material from the middle Eocene (Bridgerian) to late Eocene (Chadronian) of Wyoming. The two species, *Spathorhynchus fossorium* and *S. natronicus,* were described from relatively complete skulls and articulated vertebrae. The genus is characterized by the presence of both postorbital and postfrontal bones, which form an enclosed orbit (Berman, 1973, 1977). *Spathorhynchus* also possesses a laterally widened snout that has an exaggerated spade shape (Berman, 1973). Although most fossil rhineurids have been collected from the Great Plains of the United States, Berman (1976) described a new genus and species from the Oligocene-Miocene John Day Formation of north-central Oregon, *Dyticonastis rensbergeri.* This species, represented by eight specimens including well-preserved skulls and articulated vertebrae, represents the westernmost record of rhineurids in North America. Notably, *Dyticonastis,* which occurs primarily in strata dated as Oligocene in age (Berman, 1976), possesses many of the same characters as the late Eocene species *Spathorhynchus fossorium.*

Additional amphisbaenian taxa have been described from relatively incomplete material including elements of the mandible and vertebral column. Yatkola (1976) described a new species, *Rhineura marslandensis,* from the middle Miocene Marsland Formation of Nebraska. The specimen is represented only by a partial left dentary, a partial maxilla, and five vertebrae. Yatkola (1976) provided four morphological characters from the lower jaw that are diagnostic of amphisbaenians—few pleurodont teeth, a closed Meckelian groove, a tube-shaped dentary, and a prominent mandibular symphysis. *Rhineura marslandensis* differs from *R. hatcherii* only in having six dentary teeth (Yatkola, 1976). Specimens consisting primarily of partial lower jaws and isolated vertebrae were collected by Holman (1979) from the Miocene Rosebud Formation in Bennet County, South Dakota. This material was described as another new species of amphisbaenian, *Rhineura sepultura,* diagnosed by six, recurved dentary teeth; a short, stout dentary; splenial extending to the fifth dentary tooth; and coronoid extending to the most posterior maxillary tooth. The last new North American fossil amphisbaenian was described by Sullivan (1985). This material was collected from the upper part of the middle Paleocene Nacimiento Formation of New Mexico. The new species, *Plesiorhineura tsentasi,* consists of the medial part of the right lower jaw and was diagnosed by the position of the coronoid, surangular, and anterior inferior alveolar foramen (Sullivan, 1985). *Plesiorhineura tsentasi* was assigned to Rhineuridae because of the morphology, number, and position of the dentary teeth.

A revision of the fossil amphisbaenians of North American was made by Sullivan and Holman (1996), who synonymized several Oligocene species of *Rhineura*, *Gilmoreia*, and *Pseudorhineura.* The most important result of this study was that *Rhineura hatcherii, R. sternbergii, Pseudorhineura minutus* (i.e., *R. minutus*), *R. attenuatus* (i.e., *Gilmoreia attenuatus*), *R. hibbardi, R. amblyceps,* and *R. wilsoni* were all synonymized into the single species *Rhineura hatcherii.* Sullivan and Holman (1996) did not, however, place these taxa in a phylogenetic framework or provide an emended diagnosis for the synonymized taxa.

Kearney (2003) performed a morphological phylogenetic analysis of the entire Amphisbaenia using extant and fossil taxa. In the analysis, Kearney found Rhineuridae to be paraphyletic because it included the fossil specimens of the family Hyporhinidae. Kearney therefore placed hyporhinids within Rhineuridae and removed the family Hyporhinidae. The cladistic analysis also resulted in paraphyletic relationships between most of the fossil taxa (Kearney, 2003). The only well-resolved clade was that of *Spathorhynchus* and *Dyticonastis.* No revision of the systematics of the fossil taxa was made, but several fossil taxa were removed from the analysis. Despite the removal of these taxa, the paraphyletic relationships of the fossil rhineurids were not resolved. The results of Kearney's (2003) analysis demonstrate the need to revise the taxonomy of Rhineuridae.

## PHYLOGENETIC ANALYSIS

*Characters and taxa analyzed.*—A phylogenetic analysis was conducted using 79 cranial characters derived from previous studies of extant amphisbaenians (Gans, 1978; Estes, De Queiroz, and Gauthier, 1988; Rieppel, 1988; Kearney, 2003). Characters and character states are given in Appendix 1. Cranial characters were used exclusively, because the skull is the most commonly preserved part of the amphisbaenian skeleton, and they offer the greatest amount of morphological information (Zangerl, 1944, 1945; Gans, 1960, 1978). Character codings are given in Appendix 2.

Specimens representing 15 fossil species belonging to the family Rhineuridae and Hyporhinidae were originally analyzed. These species are considered to be from Eocene to Miocene in age. All Paleogene and Neogene taxa for which sufficient cranial morphological information exists were incorporated into this phylogenetic analysis (Table 1). Species known only from isolated vertebrae or poorly preserved cranial elements were not included (i.e., *Rhineura coloradoensis* Cope, 1873; *Oligodontosaurus wyomingensis* Gilmore, 1942) because they lack sufficient character information. This exclusion removed all Paleocene amphisbaenians from the phylogenetic analysis. After the cranial characters of the original 15 species were coded, 2 groups of species were found to have the same character states (Appendix 2). As a result of this similarity, in the original phylogenetic analyses these species formed monophyletic groups. Because of similarities in diagnostic character states and the absence of any known difference in other characters, *Jepsibaena minor*, *Rhineura amblyceps*, *R. attenuatus*, *R. minutus*, and *R. wilsoni* were synonymized with *Rhineura hatcherii*. For similar reasons, *Hyporhina tertia* was synonymized with *Hyporhina galbreathi*. The analysis presented here was performed following the removal of these six species.

*Sphenodon punctatus*, *Gekko gekko*, and *Boa constrictor* were used as outgroups to polarize the character states because of their presumed sister-group relationship to the Amphisbaenia (Estes, De Queiroz, and Gauthier, 1988; Lee, 1998; Kearney, 2003; Townsend et al., 2004). A single extant species of each of the other five families of Amphisbaenia, *Blanus cinereus* (Blanidae), *Bipes biporus* (Bipedidae), *Amphisbaena alba* (Amphisbaenidae), and *Trogonophis wiegmanni* (Trogonophidae), were included with the ingroup to test the monophyly of the fossil and extant Rhineuridae.

*Parsimony analysis.*—Phylogenetic analysis was performed using PAUP* 4.0b10 (Swofford, 2000). The data set was subjected to a heuristic search using a random addition sequence with 1,000 random replications, with tree-bisecting reconnection as the branch-swapping algorithm. Forty-eight of the characters were treated as ordered (Appendix 1). Twenty-one of the characters that had no consistent criterion on which to order them were treated as unordered (Appendix 1). Characters were optimized with the accelerated transformation (ACCTRAN) option.

A single most parsimonious tree with 123 steps was recovered (Fig. 2). The consistency index (CI) for the tree is 0.650 and the retention index (RI) is 0.781. The consistency index exceeds those derived from sets of similarly sized matrices constructed from random data (CI = 0.16) at the 0.05 level of significance (Klassen, Mooi, and Locke, 1991).

Support for specific nodes within the recovered cladogram were characterized by bootstrap and jackknife analyses. These analyses provide information about the stability of the position of branches when a portion of the taxa or character data are eliminated (Felsenstein, 1985; Sanderson, 1989). Both the bootstrap and jackknife analyses were performed using a full heuristic search with 1,000 replicates and a 10% deletion of taxa and characters, respectively. Groups compatible with the 50% majority rule consensus were retained. The confidence values for the nodes duplicated in these analyses are presented in Figure 2.

Support for the cladogram was further constrained by the $g_1$ statistic, a measure of the skewness of tree length distributions used as a measure of phylogenetic signal (Hillis, 1991). The $g_1$ statistic was calculated using PAUP*4.0b10, which averages the values of 10 replicate calculations of the $g_1$ statistic for 1,000 random trees. The $g_1$ statistic for a random data set of 8 taxa is –0.05 (Hillis, 1991). The value obtained for this data set was –0.635, which is a phylogenetic signal much stronger than that of a random data set and significant at the P = 0.05 level (Hillis, 1991).

## RESULTS AND TAXONOMIC IMPLICATIONS

*Fossil amphisbaenian taxonomy.*—Six genera and 9 species of North American fossil amphisbaenians are retained from the 7 genera and 15 species analyzed. After preliminary analyses, 5 species (*Jepsibaena minor, Rhineura amblyceps, R. attenuatus, R. minutus,* and *R. wilsoni)* are synonymized with *Rhineura hatcherii* (Fig. 3). The character analysis presented in Appendix 2 shows that there is little if any morphological difference among these 5 fossil species and *Rhineura hatcherii.*

Each of these five species is represented by only a few, and in some cases a single, specimen(s) that is incomplete and poorly preserved. In two instances the unique morphology of these species could be attributed to missing cranial elements, such as the nasals, frontals, maxillaries, and premaxillae (e.g., *Rhineura attenuatus;* Taylor, 1951). *Rhineura amblyceps* was considered a new species simply because it is larger than specimens of *Rhineura hatcherii* (Taylor, 1951). In contrast, other specimens were described as new species because they were smaller than *Rhineura hatcherii* (e.g., Gilmore, 1938). The holotype of *Rhineura minutus* (Fig. 3.5), for example, does appear different superficially from *R. hatcherii. Rhineura minutus* was diagnosed originally by a skull length of 7.8 mm, low craniofacial angle, absence of sculpturing on the anterodorsal surface of the skull, and absence of a sagittal crest (Gilmore, 1938). Some of these features, including the absent sculpturing and sagittal crest, are artifacts of preservation (Estes, 1983). The holotype is heavily worn, and some cranial elements are broken or missing. Other features such as the small size and low craniofacial angle are likely ontogenetic artifacts (Estes, 1983). While the skull is completely ossified, ossification occurs early in extant amphisbaenians including *Rhineura floridana* (Estes, 1983). *Jepsibaena minor* was diagnosed by the presence of three premaxillary teeth, seven maxillary teeth, and eight dentary teeth (Gilmore and Jepsen, 1945). Specific numbers of teeth have been found to vary within living species of amphisbaenians, depending on the size of the individual (Estes, 1983). Therefore, tooth counts are unreliable as diagnostic characters. All other cranial characters considered diagnostic of *J. minor* are also present in *R. hatcherii. Rhineura wilsoni* was described from a single specimen missing the squamosal, quadrate, and entire lower jaw. It was diagnosed by the presence of seven maxillary teeth, elongate prefrontals, ventrally oriented nostrils, and a slender skull. Tooth counts are unreliable, and the other diagnostic characters occur in specimens of *R. hatcherii.*

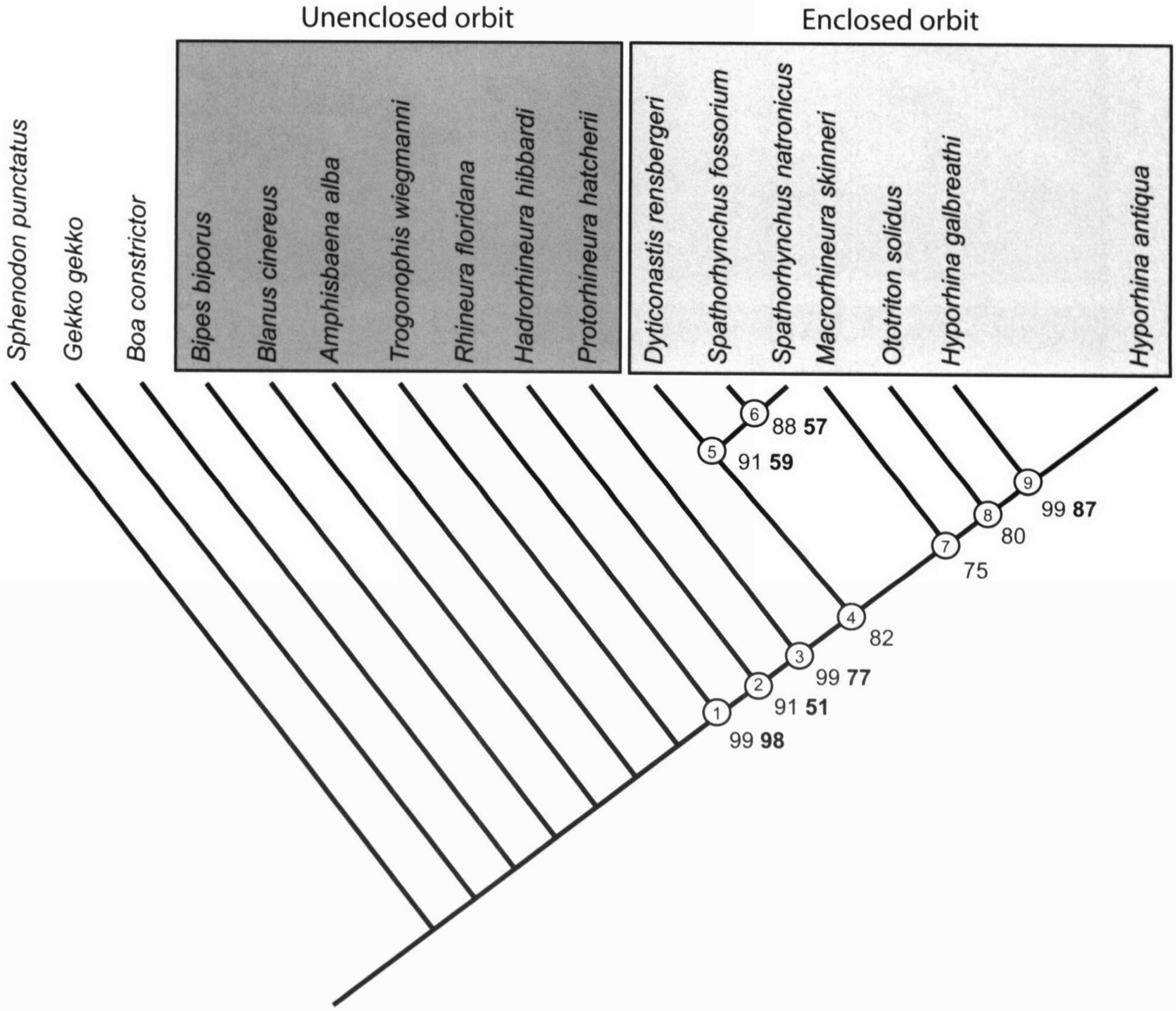


Figure 2. The single most parsimonious tree produced from the analysis of character data in Appendix 1 with PAUP* 4.0b10 (Swofford, 2002). Nodes within the Rhineuridae are indicated by circled numbers 1–9. Tree length is 123 steps; retention index is 0.78; consistency index is 0.650; g1 statistic is –0.635. Bootstrap (bold) and jackknife (normal) values, calculated with a 10 percent deletion, are indicated next to the node they support. Apomorphic characters that change below each node and species are listed in parentheses. Node 1: 13 (0), 19 (3), 49 (0); node 2: 66 (0); *Hadrorhineura hibbardi:* 10 (1); node 3: 18 (0), 25 (1), 33 (1), 34 (1), 67 (1), 72 (0), 78 (0); *Protorhineura hatcherii:* 31 (2), 73 (1); node 4: 31 (0), 51 (0); node 5: 6 (1); *Dyticonastis rensbergeri:* 53(0); node 6: 30 (0); *Spathorhynchus natronicus:* 73 (1), 78 (1); node 7: 79 (0); *Macrorhineura skinneri:* 8 (0), 10 (1), 49 (0); node 8: 33 (0); node 9: 1 (1); 11 (1), 22 (0), 56 (1); *Hyporhina galbreathi:* 21 (1); *Hyporhina antiqua:* 15 (1), 65 (1), 67 (0) (new).

*Hyporhina tertia,* represented only by the preorbital portion of the skull, was synonymized with *Hyporhina galbreathi,* leaving two species in the genus *Hyporhina. Hyporhina tertia* was originally diagnosed from a single specimen consisting of approximately one half of the anterior portion of the skull (Berman, 1972). The specimen was considered unique because an ascending process of the maxilla displaces the sutural contact between the maxilla, frontal, and prefrontal. Examination of the material available in the single specimen of *H. tertia,* however, indicates that all other cranial character states are identical to *H. galbreathi* (Appendix 2). The incomplete nature of the specimen, therefore, makes its diagnosis as a separate species questionable.

The phylogenetic analysis also indicated that the genus *Rhineura,* consisting of two fossil species, *Rhineura hatcherii* and *R. hibbardi,* and the modern species *R. floridana,* is paraphyletic (Fig. 2). Both fossil species originally were assigned to the genus *Rhineura* based on similarities in cranial morphology (Baur, 1893; Taylor, 1951). *Rhineura hatcherii* and *R. hibbardi,* however, possess 11 cranial characters that differ from *R. floridana.* These differences suggest that *R. hatcherii* and *R. hibbardi* belong to separate genera. *Rhineura*

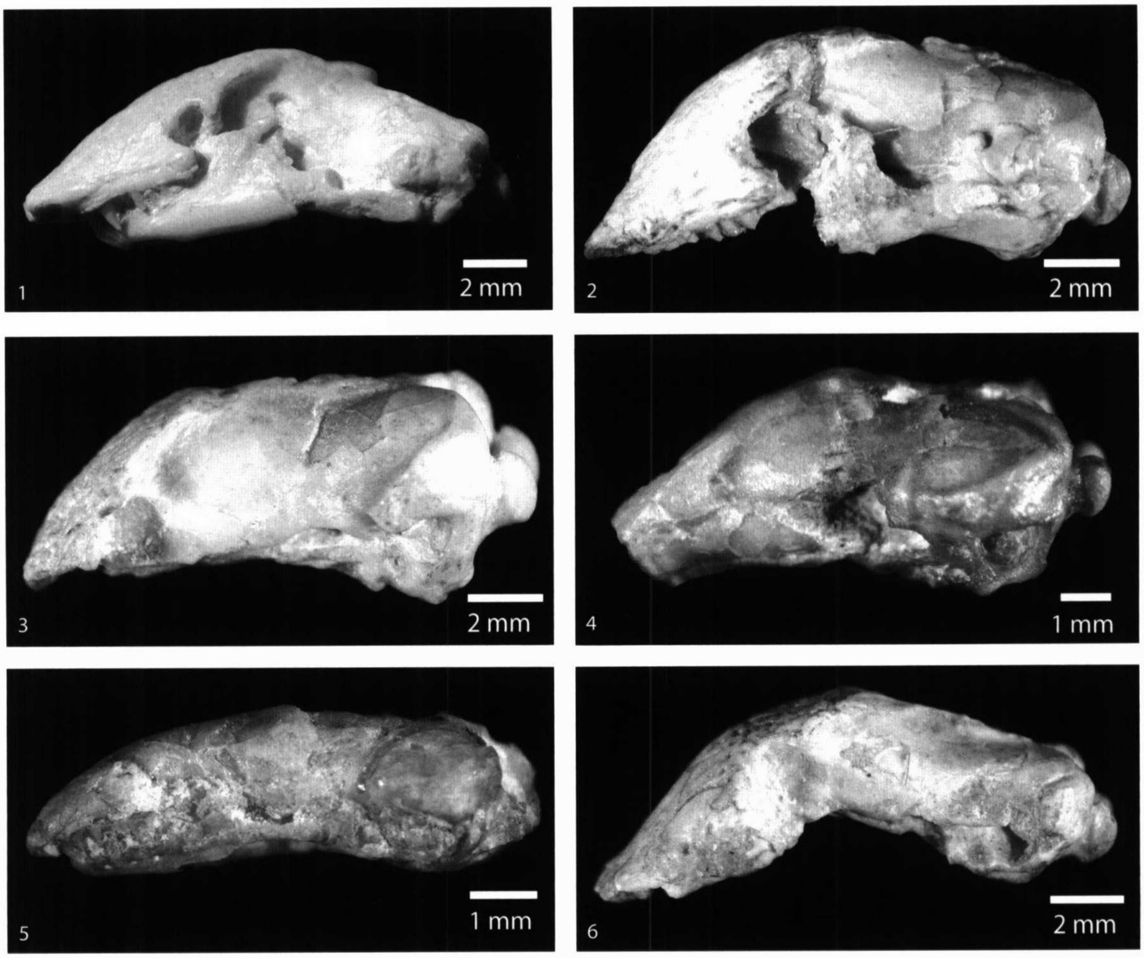


Figure 3. Specimens of the fossil taxa synonymized under *Protorhineura hatcherii: 1, Rhineura hatcherii* (KUVP 133197). *2, Rhineura amblyceps* (UMMP 25430). *3, Rhineura amblyceps* (KUVP 7649). *4, Rhineura attenuatus* (USNM 133197). *5, Pseudorhineura minuta* (USNM 12158). *6, Rhineura wilsoni* (UMMP 25429) (new).

*hibbardi* differs from *R. floridana* by possessing a straight tooth orientation (characters 19 and 66) as well as lacking a nasal-maxillary contact (character 10). *Rhineura hatcherii* also possesses a straight tooth orientation (characters 19 and 66). *Rhineura hatcherii* differs from both *R. floridana* and *R. hibbardi* by possessing a straight suture between the frontals, paired subcircular depressions near the anteromedial edge of the parietal, anterolateral, and posterolateral processes on the maxillae, six to eight maxillary teeth, a separated dentary symphysis, and a postcoronoid region of the mandible equal in length to the precoronoid region (characters 18, 25, 33, 34, 67, 72, and 78), as well as by lacking a jugal and by possessing a retroarticular process that extends posteriorly (characters 31 and 73).

Both groups appear robust and have bootstrap and jackknife values of 0.51 and 0.91 (node 2) and 0.77 and 0.99 (node 3), respectively. *Rhineura hibbardi* is reassigned therefore to *Hadrorhineura* n. gen., and *Rhineura hatcherii* is reassigned to *Protorhineura* n. gen. (Fig. 4).

*Phylogenetic relationships.*—Several patterns emerge in the cladogram in Figure 2. First, *Rhineura floridana* consistently occupies a basal position, and the remaining fossil taxa form a well-supported monophyletic assemblage. The extant species, *Rhineura floridana*, and all the fossil species of North American amphisbaenians form a well-supported monophyletic clade with *R. floridana* at its base. Bootstrap and jackknife values of 0.98 and 0.99 at node 1 and 0.51 and 0.91 at node 2 support the clade. The results of this phylogenetic analysis agree therefore with those of Kearney (2003) and suggest that all North American fossil amphisbaenians should be grouped into Rhineuridae. Hyporhinidae does not seem to be valid, because characters once attributed only to members of this family, including the presence of a postorbital arch, are present within members of both families. This revision is due primarily to fossil species of Rhineuridae described by Berman (1973, 1976, 1977). *Macrorhineura* also groups within Rhineuridae and not within Amphisbaenidae as originally described (MacDonald, 1970).

Each clade recovered in this analysis is supported by specific character evidence. The monophyly of the North American fossil amphisbaenian clade is supported by a narial margin enclosed by the maxilla and nasal only; a W-shaped frontoparietal suture; absence of elongate, paired palatal processes of the maxillae; and straight tooth orientation (characters 13, 19, 49, and 66). *Hadrorhineura hibbardi* occupies the base of this clade as the sister species to the rest of the fossil taxa. Within this larger monophyletic group there are several smaller clades.


Figure 4. Fossil Rhineuridae: *1, Protorhineura hatcherii* (KUVP 133197), dorsal view; *2,* right lateral view; *3,* left lateral view; *4,* ventral view. *5, Hadrorhineura hibbardi* (UMMP 25431), dorsal view; *6,* right lateral view; *7,* left lateral view; *8,* ventral view (new).

*Protorhineura hatcherii, Dyticonastis rensbergeri, Spathorhynchus fossorium, S. natronicus, Macrorhineura skinneri, Ototriton solidus, Hyporhina galbreathi,* and *H. antiqua* form a monophyletic group united by the presence of a straight suture between the frontals; paired, subcircular depressions near the anteromedial edge of the parietal; anterolateral and posterolateral processes on the maxillae; six to eight maxillary teeth; an unfused dentary symphysis; and postcoronoid and precoronoid regions of the mandible equal in length (characters 18, 25, 33, 34, 67, 72, 78). This clade is supported by bootstrap and jackknife values of 0.77 and 0.99. *Protorhineura hatcherii* is the sister species to the remaining group of fossil taxa. *Dyticonastis rensbergeri, Spathorhynchus fossorium, S. natronicus, Macrorhineura skinneri, Ototriton solidus, Hyporhina galbreathi,* and *H. antiqua* form a monophyletic clade supported by the presence of a well-developed jugal and a pterygoid-vomer contact (characters 31 and 51). This clade is supported by a jackknife value of 0.82.

A clade consisting of the two species of *Spathorhynchus* as sister taxa and *Dyticonastis rensbergeri* as the sister species of that group is supported by bootstrap and jackknife values of 0.59 and 0.91. This clade is consistent with that of Kearney's (2003) final phylogeny. The *Spathorhynchus-Dyticonastis* clade is united by the presence of a spatulate rostral process formed by an extension of the premaxillary (character 6). The sister-group relationship of *Spathorhynchus fossorium* and *S. natronicus* is defined by the presence of a postfrontal (character 30) and is supported by bootstrap and jackknife values of 0.57 and 0.88. The material representing *Spathorhynchus fossorium, S. natronicus,* and *Dyticonastis rensbergeri* are some of the best-preserved amphisbaenian fossils known. Few cranial characters in these species are unknown. The relationships among these taxa are well constrained, therefore, as are their relationships with extant amphisbaenians.

The monophyletic clade of fossil amphisbaenians that includes members of three genera, *Macrorhineura*, *Ototriton*, and *Hyporhina*, is characterized by the possession of dentary teeth with a uniform size (character 79). This clade is supported by a jackknife value of 0.75. The final monophyletic clade consists of the two species of the genus *Hyporhina* as sister taxa and *Ototriton solidus* as the sister species of that group. Members of this clade are united by the absence of an anterolateral process on the premaxilla (character 33), and the lineage is supported by a jackknife value of 0.80. The relatively incomplete nature of the single specimen of *Ototriton minor* makes this assignment questionable. Given the fossil material present, however, *Ototriton* does seem to be related more closely to *Hyporhina* than to *Rhineura*, contrary to the results of previous studies. Bootstrap and jackknife values of 0.87 and 0.99 support the sister-group relationship of *Hyporhina galbreathi* and *H. antiqua.* The sister-group relationship of *Hyporhina galbreathi* and *H. antiqua* is united by a strong (>60°) craniofacial angle; contact between the premaxilla, nasals, and frontals at a single point; absence of a sagittal crest on the parietal; and an elevated, enlarged occipital condyle with the foramen magnum opening dorsally (characters 1, 11, 22, 56).

## DISCUSSION

*Evolutionary and ecological implications.*—The results of this study allow new interpretations for both the diversity and temporal range of North American fossil Rhineuridae. The phylogeny presented here reveals a lower diversity of fossil amphisbaenians in North America at both the family and species level than previously thought. The fossil taxa included in this analysis have been reduced to a single family with nine species. This reduction in diversity alters the interpretation of the evolutionary history of North American Amphisbaenia. At the family level, the inclusion of all North American fossil amphisbaenians into the Rhineuridae extends the stratigraphic occurrence of this family into the Miocene. This revision leaves the Pliocene as the only epoch in the Cenozoic for which rhineurid fossils are not known. Such gaps in the fossil record of Amphisbaenia may be due less to low preservational potential and more to the proper recognition and classification of collected fossil material.

Many of the characters indicating evolutionary changes and speciation within Rhineuridae involve aspects of reorganization of cranial elements. Changes in size or relative proportions of the skull do not seem to be as important. The unique morphology of the amphisbaenian skull is considered the result of a series of adaptations to fossorial life and the use of the head as a digging tool (Gans, 1974). At the base of Rhineuridae, one of the defining characters is a complex W-shaped suture pattern between the frontals and parietals. Complex, sinuous sutures between these cranial bones increase their strength and ability to resist torsional forces (Gans, 1974).

*Hyporhina* is characterized by the development of a stronger craniofacial angle and an elevated and enlarged occipital condyle with a dorsally opening foramen magnum. Gans (1974) demonstrated through experiments with living shovel-headed amphisbaenians that tunnels are constructed by first forcing the snout edge into the soil. The head is then swung upward about the occipital condyle, rotating the dorsal surface of the spade into a horizontal position and compressing the displaced soil into the tunnel roof (Gans, 1974). The increased craniofacial angle allows for more soil to be displaced in this process.

A similar adaptation diagnoses the base of the *Dyticonastis-Spathorhynchus* clade. These genera are characterized by an anterior extension of the premaxilla that forms a spatulate rostral process. This extension of the premaxilla creates an elongate cutting edge that extends past the lower jaw (Fig. 5.2–5.3), providing a larger surface that can be forced deeper into the soil of the tunnel wall (Gans, 1974). The spatulate rostral process therefore represents another adaptation to displace more soil during soil construction, thereby increasing burrowing efficiency.

Of particular note in the amphisbaenian phylogeny is the position of taxa with and without enclosed orbits (Fig. 2). All extant members of Amphisbaenia lack an enclosed orbit (Gans, 1978). Most species also lack fully functional eyes, with the exception of members of *Bipes,* which do possess well-developed eyes (Gans, 1978; Kearney, 2003). The level of eye reduction varies considerably among the different amphisbaenian clades. Remnants of a nonvascular lens and a poorly developed retina are always present; although in *Rhineura floridana,* visual cells do not develop (Gans, 1978). The trogonophids *Agamodon*, *Trogonophis*, and *Diplometopon* also possess remnants of eye muscles (Gans, 1978). The development of the orbital bones, however, has no relationship to the reduction of the eye in extant species (Kearney, 2003). *Bipes* has the best-developed eye but does not have an enclosed orbit. Other species with poorly developed eyes have orbits that are partially enclosed by modified projections of the parietal or frontal (Kearney, 2003). Absence of an enclosed orbit occurs in members of many other reptile groups, especially those that occupy fossorial habitats. Burrowing reptiles such as the skinks *Typhlosaurus lineatus, T. vermis,* and *T. aurantiacus* and the dibamid, *Dibamus novaeguineae* have reduced eyes and unenclosed orbits (Rieppel, 1993). The reduction of eyes and loss of cranial elements enclosing the orbits therefore probably are adaptations to fossoriality.

Differences in the level of eye reduction and in patterns of cranial development around the orbits among the amphisbaenian families, as well as the results of this study, argue for multiple, independent losses of the fully enclosed orbit, including the reduction or loss of the postfrontal, postorbital, and jugal. This would require the independent loss of the enclosed orbit in Bipedidae, Blanidae, Amphisbaenidae, Trogonophidae, and a few species of

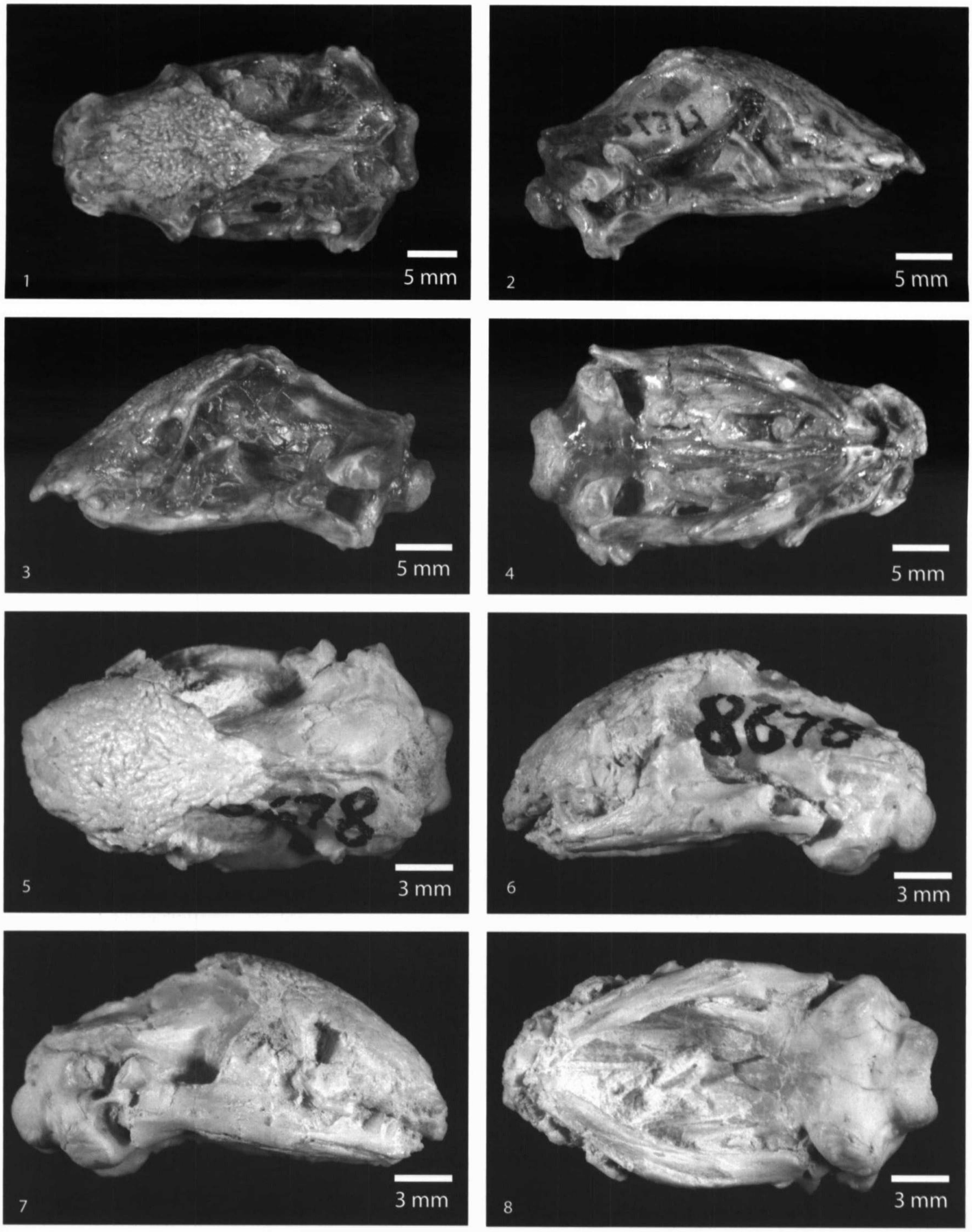


Figure 5. Fossil Rhineuridae: *1, Spathorhynchus fossorium* (USNM 25431), dorsal view; *2,* right lateral view; *3,* left lateral view; *4,* ventral view. *5, Spathorhynchus natronicus* (AMNH 8678), dorsal view; *6,* right lateral view; *7,* left lateral view; *8,* ventral view (new).

Rhineuridae (Fig. 2). The enclosed orbit is retained in *Dyticonastis-Spathorhynchus* and *Hyporhina* clades of Rhineuridae (Fig. 2). The single specimens of *M. skinneri* and *O. solidus* are too incomplete to interpret the presence or absence of an enclosed orbit. Considering their close relationship to the *Dyticonastis-Spathorhynchus* and *Hyporhina* clades on the phylogeny, it is likely they also possessed enclosed orbits.

The use of characters related to the function of the amphisbaenian skull as a digging tool potentially may lead to problems of convergence in a phylogenetic analysis. These functionally adaptive characters, however, are paired with other characters that are unrelated to burrowing, including the closure of the orbit in the species of *Spathorhynchus* (Fig. 5.2, 5.7) and *Hyporhina* (Fig. 6.6), the number and orientation of maxillary teeth, and the type

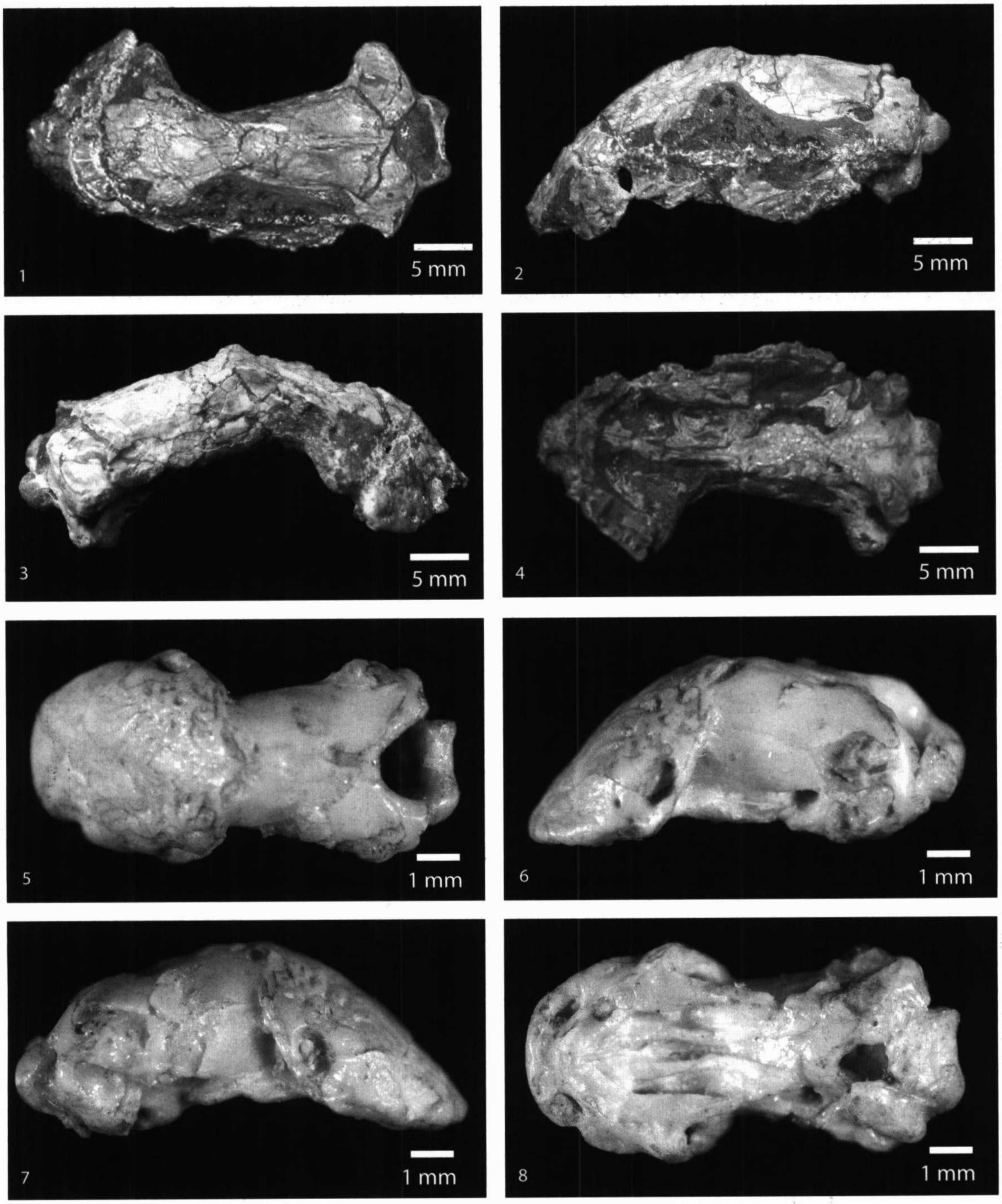


Figure 6. Fossil Rhineuridae: *1, Ototriton solidus* (ACM 3639), dorsal view; *2,* left lateral view; *3,* right lateral view; *4,* ventral view. *5, Hyporhina galbreathi* (KUVP 8221), dorsal view; *6,* left lateral view; *7,* right lateral view; *8,* ventral view (new).

of tooth implantation. The presence of these characters reduces the likelihood of artificial clades forming simply as a result of similarities in behavior and habitat.

*Paleobiogeographic implications.*—The phylogenetic revision of Rhineuridae results in an overall extension of the paleogeographic range of the family and its species. The removal of all fossil taxa from the genus *Rhineura* restricts this genus to the southeastern United States. The oldest fossils attributed definitively to *Rhineura* are found in Pleistocene strata of Florida (Holman, 1959). This evidence implies that while the origin of the family Rhineuridae is at least within the late Paleocene, the genus *Rhineura* is relatively recent in origin.

Through the occurrence of well-represented fossils of Eocene and Oligocene rhineurids in the central United States and Pleistocene to recent rhineurids in the southeastern United States, it has been inferred that rhineurids continued to inhabit these regions throughout the Neogene. Fossil evidence for this interpretation, however, has been lacking. Miocene rhineurid fossil specimens have consisted only of dentary and vertebral material that comprise the fossil species *Rhineura marslandensis* and *R. sepultura* (Yatkola, 1976; Holman, 1979). The precise taxonomic placement of these species is not well constrained, because they are based on such limited fossil material (Estes, 1983). The inclusion of the relatively well-preserved Miocene amphisbaenian, *Macrorhineura*, into Rhineuridae extends both the stratigraphic and geographic range of the family. The occurrence of fossil rhineurids within the central United States in the Miocene provides additional evidence that extant rhineurids in Florida may be the remnants of a more broadly distributed North American population. The absence of Miocene fossil rhineurids in regions where they were once abundant in the Oligocene may indicate the gradual contraction of their range in conjunction with continued cooling and drying of the North American climate during the Neogene (Prothero and Berggren, 1992; Prothero, Ivany, and Nesbitt, 2003).

The creation of the new monotypic genus *Protorhineura* from six fossil species results not only in a long-lived species but also one that was widely distributed. *Protorhineura* has a paleogeographic range that includes middle Eocene to middle Oligocene basins of Colorado, Nebraska, South Dakota, and Wyoming. The presence of a single, long-lived species of a limbless, fossorial reptile across such a broad area implies that these basins may not always have been isolated. This result suggests instead that the basins were periodically connected to permit free movement and gene flow within the population, thereby limiting chances of vicariant speciation.

*Dyticonastis*, present in Oligocene strata of Oregon, represents the farthest westward expansion of the Rhineuridae in North America. Members of this genus, however, retain morphological features common among Eocene rhineurids of the midcontinent, including a closed orbit, well into the Oligocene. The retention of these primitive characters in the *Dyticonastis* clade has been attributed to the geographic isolation of this group (Berman, 1976). This analysis corroborates the close phylogenetic relationship between the Eocene-Oligocene genus *Spathorhynchus* and the Oligocene genus *Dyticonastis*. This relationship implies the potential speciation by vicariance of these clades from a common ancestor after the Laramide orogeny resulted in the uplift of the Rocky Mountains in the Paleocene.

## CONCLUSIONS

Taxonomic names have been applied to most amphisbaenian fossils that have been collected. Many fossil amphisbaenian species are based on poorly preserved and incomplete specimens. This has resulted in a confused taxonomy and an artificial diversity of ancient North American amphisbaenians. Cranial characters provide an ideal data set for determining the relationships of fossil amphisbaenians. A phylogenetic analysis of the North American fossil rhineurids provides support for the synonymy of at least seven species. This study suggests that *Jepsibaena minor, Rhineura hatcherii, R. wilsoni, R. amblyceps, R. minutus,* and *R. attenuatus* are synonymous. In addition, *Hyporhina galbreathi* and *H. tertia* are considered synonymous. All North American fossil amphisbaenians are placed in Rhineuridae. Fossil rhineurids are represented by seven genera and nine species, *Protorhineura hatcherii* gen. nov., *Hadrorhineura hibbardi* gen. nov., *Spathorhynchus fossorium*, *S. natronicus*, *Dyticonastis rensbergeri*, *Macrorhineura skinneri*, *Ototriton solidus, Hyporhina antiqua*, and *H. galbreathi*.

Revision of the North American fossil Amphisbaenia has important evolutionary and paleobiogeographic implications for the family Rhineuridae. The inclusion of all North American fossil amphisbaenians into Rhineuridae extends the stratigraphic and paleogeographic range of the family. Rhineurid fossils are known from the Paleocene to the Miocene as well as the Pleistocene and Holocene. They occur as far west as Oregon and as far east as Florida. Their distribution is concentrated, however, in the North American midcontinent during the Eocene and Oligocene. Although it may seem that the characters that define the rhineurid clades are based on convergent adaptations to the soil ecosystem and improved burrowing efficiency, the changes in the burrowing-related character states occur along with other unrelated characters. This suggests that burrowing adaptations are in fact directly related to speciation events within the Rhineuridae, and the recovered relationships are not simply artifacts of convergent evolution.

## SYSTEMATIC PALEONTOLOGY

*Institutional abbreviations.*—ACM, Pratt Museum of Natural History, Amherst; AMNH, American Museum of Natural History, New York; CM, Carnegie Museum of Natural History, Pittsburg; KUVP, University of Kansas Natural History Museum, Lawrence; LACM, Natural History Museum of Los Angeles, Los Angeles; UCMP, University of California Museum of Paleontology, Berkeley; UF, Florida Museum of Natural History, Gainesville; UMMP, University of Michigan Museum of Paleontology, Ann Arbor; USNM, Smithsonian Institution, Washington, D.C.; YPM, Yale Peabody Museum, New Haven.

### Class REPTILIA Laurenti, 1768
### Suborder AMPHISBAENIA Gray, 1844
### Family RHINEURIDAE Vanzolini, 1951
### Genus PROTORHINEURA new genus

*Rhineura* Cope, 1861, p. 75

*Ototriton* Loomis, 1919, p. 217, fig. 1.

*Gilmoreia* Taylor, 1951, p. 527, fig. 1, pl. 58,*3–5*.

*Jepsibaena* Vanzolini, 1951, p. 116.

*Pseudorhineura* Vanzolini, 1951, p. 116.

*Type species.*—*Rhineura hatcherii* by monotypy.

*Diagnosis.*—Slight craniofacial angle (30°); narial margin enclosed by maxilla and nasal; straight suture between frontals; W-shaped frontoparietal suture; paired, subcircular depressions near anteromedial edge of parietal present; jugal absent; anterolateral and posterolateral processes on maxilla present; elongate, paired, palatal processes of maxilla absent; straight tooth orientation; 6–8 maxillary teeth; dentary symphysis unfused; retroarticular process extending posteriorly; postcoronoid and precoronoid regions of mandible equal in length.

*Etymology.*—From Greek, protos, meaning first, and from the genus *Rhineura,* to which this genus is most closely related.

*Occurrence.*—Middle Eocene, Wind River Formation, Wyoming, to middle Oligocene, Brule and White River formations, South Dakota, Wyoming, and Colorado.

*Discussion.*—This new genus includes fossil taxa from the Eocene to Oligocene of Colorado, South Dakota, and Wyoming. Although these fossil taxa previously were considered to belong to different genera, in this analysis they were found to possess identical cranial characters (Appendix 1). Other fossil taxa included in this new genus were considered to belong within the extant genus *Rhineura.* These fossil species differ from the extant species *Rhineura floridana* by 11 morphological characters (Appendix 1), requiring their placement in a separate genus.

## PROTORHINEURA HATCHERII (Baur, 1893) new combination

Figure 4.1–4.4

*Rhineura hatcherii* Baur, 1893, p. 998.

*Rhineura sternbergii* Walker, 1932, p. 225.

*Rhineura minutus* Gilmore, 1938, p. 12, fig. 1.

*Ototriton minor* Gilmore and Jepsen, 1945, p. 31, fig. 1.

*Jepsibaena minor* Vanzolini, 1951, p. 116.

*Gilmoreia attenuatus* Taylor, 1951, p. 527, fig. 1; pl. 58,*3–5.*

*Rhineura amblyceps* Taylor, 1951, p. 543, fig. 5; pl. 59,*1;* pl. 61,*1–5;* pl. 62,*1–3;* pl. 67,*1–3.*

*Rhineura wilsoni* Taylor, 1951, p. 548, fig. 7; pl. 58,*1–2;* pl. 59,*2–3;* pl. 63,*1–3.*

*Pseudorhineura minutus* Vanzolini, 1951, p. 116.

*Rhineura attenuatus* Estes, 1983, p. 198.

*Rhineura hatcherii* emendation Estes, 1983, p. 199.

*Revised diagnosis.*—Slight craniofacial angle (30°); narial margin enclosed by maxilla and nasal; straight suture between frontals; W-shaped frontoparietal suture; paired, subcircular depressions near anteromedial edge of parietal present; jugal absent; anterolateral and posterolateral processes on maxilla present; elongate, paired, palatal processes of maxilla absent; straight tooth orientation; 6–8 maxillary teeth; dentary symphysis unfused; retroarticular process extending posteriorly; postcoronoid and precoronoid regions of mandible equal in length.

*Material examined.*—*Rhineura hatcherii:* YPM 11389 (holotype), KUVP 8220, 8960, CM423A; *Rhineura wilsoni:* KUVP 7651 (holotype), UMMP 25429; *Rhineura attenuatus:* USNM 16308 (holotype); *Rhineura amblyceps:* KUVP 7649 (holotype), 7650, UMMP 25430; *Jepsibaena minor* YPM 13460 (holotype).

*Occurrence.*—Middle Eocene, Wind River Formation, Wyoming, to middle Oligocene, Brule and White River formations, South Dakota, Wyoming, and Colorado.

*Discussion.*—The original descriptions of the fossils included in this species often are based on a single specimen or a few specimens collected from a single locality. Characters used to differentiate these various species included differences in collecting locality, overall size, and the absence of characters owing to poorly preserved fossil specimens. The morphologies of these species, however, are indistinguishable. All of the species synonymized with *Protorhineura hatcherii* share the synapomorphies of loss of the jugal and possession of retroarticular process that extends posteriorly (characters 31 and 73). Differences among the smaller fossils are considered onotogenetic in nature (Estes, 1983; Sullivan and Holman, 1996).

## Genus HADRORHINEURA new genus

*Rhineura* Cope, 1861

*Type species.*—*Rhineura hibbardi* Taylor, 1951, p. 539, by monotypy.

*Diagnosis.*—Strong craniofacial angle (60°); nasals and maxillary not in contact; narial margin enclosed by maxilla and nasal only; nasals rise above frontals on facial surface; sinuous suture between frontals; W-shaped frontoparietal suture; jugal present but reduced; anterolateral and posterolateral processes on maxilla absent; elongate, paired palatal processes of maxilla absent; straight tooth orientation; 7 maxillary and dentary teeth; retroarticular process deflected ventrally; postcoronoid region of mandible short relative to precoronoid region.

*Etymology.*—From Greek, hadros, meaning well developed, stout, or bulky, and from the genus *Rhineura,* which this genus resembles.

*Occurrence.*—Lower Oligocene, White River Formation, Logan County, northeastern Colorado.

*Discussion.*—The single species of this genus, *Hadrorhineura hibbardi,* was placed in the genus *Rhineura.* The new genus *Hadrorhineura* differs from *Rhineura* by possessing a W-shaped frontoparietal suture and a straight tooth orientation and in the absence of a nasal-maxillary contact (characters 10, 19, and 66).

## HADRORHINEURA HIBBARDI (Taylor, 1951) new combination

Figure 4.5–4.8

*Rhineura hibbardi* Taylor, 1951, p. 539, fig. 4; pl. 60,*1–3.*

*Revised diagnosis.*—Strong craniofacial angle (60°); nasals and maxillary not in contact; narial margin enclosed by maxilla and nasal only; nasals rise above frontals on facial surface; sinuous suture between frontals; W-shaped frontoparietal suture; jugal present but reduced; anterolateral and posterolateral processes on maxilla absent; elongate, paired palatal processes of maxilla absent; straight tooth orientation; 7 maxillary and dentary teeth; retroarticular process deflected ventrally; postcoronoid region of mandible short relative to precoronoid region.

*Material examined.*—UMMP 25431 (holotype); KUVP 133202.

*Occurrence.*—Lower Oligocene, White River Formation, Logan County, northeastern Colorado.

*Discussion.*—This taxon was originally known from a single specimen collected in northeastern Colorado. Additional, previously undescribed specimens were located in the collections of the University of Kansas Natural History Museum and studied for this analysis. Although Sullivan and Holman (1996) determined that *Rhineura hibbardi* and *R. hatcherii* were synonymous, significant differences between these two species were found using the new specimens.

## Genus SPATHORHYNCHUS Berman, 1973

*Spathorhynchus* Berman, 1973, p. 705, fig. 1–3.

*Type species.*—*Spathorhynchus fossorium* Berman, 1973, p. 705.

*Diagnosis.*—Slight craniofacial angle (30°); anterior extension of premaxilla forming spatulate rostral process; narial margin enclosed by maxilla and nasal only; straight suture between frontals; W-shaped frontoparietal suture; paired subcircular depressions near anteromedial edge of parietal; postfrontal enclosing orbit from behind; jugal present; anterolateral and posterolateral processes on maxilla; elongate, paired palatal processes of maxilla absent; palatines in medial contact separating pterygoid and vomer; straight tooth orientation; 6–8 maxillary teeth; separated dentary symphysis; postcoronoid and precoronoid regions of mandible of equal length.

*Occurrence.*—Middle Eocene to lower Oligocene, Bridger, Wind River and White River formations, Wyoming.

*Discussion.*—The middle Eocene genus *Spathorhynchus* (Berman, 1973) consists of two species, *S. fossorium* (Berman, 1973) and *S. natronicus* (Berman, 1977). Berman (1977) cited a number of characters that separate the two species, and the genus has been considered valid by others (Estes, 1983; Sullivan and Holman, 1996).

## SPATHORHYNCHUS FOSSORIUM Berman, 1973

Figure 5.1–5.4

*Spathorhynchus fossorium* Berman, 1973, p. 705, fig. 1–3.

*Diagnosis.*—Slight craniofacial angle (30°); anterior extension of premaxilla forming spatulate rostral process; narial margin enclosed by maxilla and nasal only; straight suture between frontals; W-shaped frontoparietal suture; paired subcircular depressions near anteromedial edge of parietal; postfrontal enclosing orbit from behind; jugal present; anterolateral and posterolateral processes on maxilla; elongate, paired palatal processes of maxilla ansent; palatines in medial contact separating pterygoid and vomer; straight tooth orientation; 6–8 maxillary teeth; separated dentary symphysis; postcoronoid and precoronoid regions of mandible of equal length.

*Material examined.*—USNM 26317 (holotype), USNM 26318, CM 25475.

*Occurrence.*—Middle Eocene Bridger (Bridgerian) and Wind River (Wasatchian) formations, western and central Wyoming respectively.

## SPATHORHYNCHUS NATRONICUS Berman, 1977

Figure 5.5–5.8

*Spathorhynchus natronicus* Berman, 1977, fig. 1.

*Diagnosis.*—Slight craniofacial angle (30°); anterior extension of premaxilla forming spatulate rostral process; narial margin enclosed by maxilla and nasal only; straight suture between frontals; W-shaped frontoparietal suture; paired subcircular depressions near anteromedial edge of parietal; postfrontal enclosing orbit from behind; jugal present; anterolateral and posterolateral processes on maxilla; elongate, paired palatal processes of maxilla absent; palatines in medial contact separating pterygoid and vomer; straight tooth orientation; 6–8 maxillary teeth; separated dentary symphysis; retroarticular process of dentary extending posteriorly; postcoronoid region of mandible short relative to precoronoid region.

*Material examined.*—AMNH 8677 (holotype), AMNH 8678.

*Occurrence.*—Lower Oligocene White River Formation, Natrona County, Wyoming.

## Genus DYTICONASTIS Berman, 1976
## DYTICONASTIS RENSBERGERI Berman, 1976

*Dyticonastis rensbergeri* Berman, 1976, p. 165, fig. 1–2.

*Diagnosis.*—Slight craniofacial angle (30°); anterior extension of premaxilla forming spatulate rostral process; narial margin enclosed by maxilla and nasal only; straight suture between frontals; W-shaped frontoparietal suture; paired subcircular depressions near anteromedial edge of parietal; jugal present; anterolateral and posterolateral processes on maxilla; elongate, paired palatal processes of maxilla absent; palatines in medial contact separating pterygoid and vomer; no contact between palatine and ectopterygoid; 3 premaxillary teeth; straight tooth orientation; 7 maxillary teeth; 8 dentary teeth; separated dentary symphysis; postcoronoid and precoronoid regions of mandible of equal length.

*Material examined.*—UCMP 76878–76883.

*Occurrence.*—Upper Oligocene (Whitneyan) to lower Miocene (Arikareean), John Day Formation, north-central Oregon.

## Genus OTOTRITON Loomis, 1919
## OTOTRITON SOLIDUS Loomis, 1919

Figure 6.1–6.4

*Ototriton solidus* Loomis, 1919, p. 217, fig. 1.

*Diagnosis.*—Slight craniofacial angle (30°); premaxilla, nasals, and frontals meeting at a single point; narial margin enclosed by maxilla and nasal only; straight suture between frontals; W-shaped frontoparietal suture; paired subcircular depressions near anteromedial edge of parietal; jugal present; posterolateral processes on maxilla; elongate, paired palatal processes of maxilla absent; pterygoid and vomer in contact; 3 premaxillary teeth; acrodont dentition; straight tooth orientation; 6–8 maxillary teeth.

*Material examined.*—ACM 3539 (holotype)

*Occurrence.*—Lower to middle Eocene, Wind River Formation, Lysite Member, Big Horn County, Wyoming.

Discussion.—This species is one of the earliest described fossil amphisbaenians and is known from only a single, poorly preserved specimen. Despite the limited material available, this genus and species possesses sufficient synapomorphies to remain a valid taxon.

## Genus HYPORHINA Baur, 1893

*Hyporhina* Baur, 1893, p. 998.

*Type species.*—*Hyporhina antiqua* Baur, 1893, p. 998.

*Diagnosis.*—Strong (60°) craniofacial angle; premaxilla, nasals, and frontals meeting at a single point; narial margin enclosed by maxilla and nasal only; straight suture between frontals; W-shaped frontoparietal suture; sagittal crest absent; paired subcircular depressions near anteromedial edge of parietal; jugal present; posterolateral processes on maxilla; elongate, paired palatal processes of maxilla absent; pterygoid-vomer contact; elevated and enlarged occipital condyle with dorsal foramen magnum; straight tooth orientation; 6–8 maxillary teeth; separated dentary symphysis; postcoronoid and precoronoid regions of mandible of equal length; dentary teeth maintaining constant size.

*Occurrence.*—Late Eocene to middle Oligocene, White River Formation, Colorado and Wyoming.

*Discussion.*—The genus *Hyporhina* was one of the earliest described fossil genera of the Amphisbaenia (Baur, 1893). The fossil specimens were considered unique enough to be placed into their own family (Baur, 1893). Since the original description, three species of *Hyporhina* (Baur, 1893) have been named based on five specimens, *H. antiqua* (Baur, 1893), *H. galbreathi* (Taylor, 1951), and *H. tertia* (Berman, 1972). In this analysis, all members of *Hyporhina* grouped within the clade Rhineuridae; therefore, the family Hyporhinidae has been found to be invalid.

## HYPORHINA ANTIQUA Baur, 1893

*Hyporhina antiqua* Baur, 1893, p. 998.

*Diagnosis.*—Strong (60°) craniofacial angle; premaxilla, nasals, and frontals meeting at a single point; narial margin enclosed by maxilla and nasal only; prefrontals reduced and restricted to facial region by descending process of frontal; straight suture between frontals; W-shaped frontoparietal suture; sagittal crest absent; paired subcircular depressions near anteromedial edge of parietal; jugal present; jugal forming postorbital bar in connection with maxilla, frontal, and parietal; posterolateral processes on maxilla; elongate, paired palatal processes of maxilla absent; pterygoid-vomer contact; elevated and enlarged occipital condyle with dorsal foramen magnum; 1 premaxillary tooth; acrodont dentition; straight tooth orientation; 4 maxillary teeth; separated dentary symphysis; postcoronoid region of mandible equal in length to precoronoid region; dentary teeth maintaining constant size.

*Material examined.*—YPM 11390 (holotype).

*Occurrence.*—Early to middle Oligocene (Orellan to Whitneyan), White River Formation, eastern Wyoming and northeastern Colorado.

## HYPORHINA GALBREATHI Taylor, 1893

Figure 6.5–6.8

*Hyporhina galbreathi* Taylor, 1951, p. 532, fig. 2–3; pl. 58,*6–8;* pl. 59,*4–5.*

*Hyporhina tertia* Berman, 1972, p. 3, fig. 1.

*Revised diagnosis.*—Strong (60°) craniofacial angle; premaxilla, nasals, and frontals meeting at a single point; narial margin enclosed by maxilla and nasal only; prefrontal forming part of orbital border; straight suture between frontals; W-shaped frontoparietal suture; lateral processes of anterior parietal contributing to deflected facial portion of skull; sagittal crest absent; paired subcircular depressions near anteromedial edge of parietal; jugal present; posterolateral processes on maxilla; elongate, paired palatal processes of maxilla absent; pterygoid-vomer contact; elevated and enlarged occipital condyle with dorsal foramen magnum; straight tooth orientation; 6 maxillary teeth; separated dentary symphysis; postcoronoid and precoronoid regions of mandible of equal length; dentary teeth maintaining constant size.

*Material examined.*—KUVP 8219, 8221 (holotype), 8222; CM 17179

*Occurrence.*—Early to middle Oligocene, White River Formation, Logan County, northeastern Colorado; late Eocene (Chadronian), White River Formation, Fremont County, Wyoming.

Discussion.—*Hyporhina galbreathi* was described from fairly complete material collected from northeastern Colorado. In addition to the holotype and paratype, other specimens of *H. galbreathi* were identified within the collections of the University of Kansas Natural History Museum and used in this analysis. *Hyporhina tertia* is known from a single specimen consisting only of the preorbital portion of the skull.

## Genus MACRORHINEURA MacDonald, 1970
## MACRORHINEURA SKINNERI MacDonald, 1970

*Macrorhineura skinneri* MacDonald, 1970, p. 18, fig. 3.

*Revised diagnosis.*—Slight (30°) craniofacial angle; smooth facial bones; nasal-maxillary contact absent; anterior extension of frontals meeting premaxilla and nasals at single point; narial margin enclosed by maxilla and nasal only; prefrontal forming part of orbital border; straight suture between frontals; W-shaped frontoparietal suture; paired subcircular depressions near anteromedial edge of parietal; jugal present; anterolateral and posterolateral processes of maxilla; elongate, paired palatal processes of maxilla absent; pterygoid-vomer contact; single, enlarged, median premaxillary tooth; pleurodont dentition; straight tooth orientation; 6 maxillary teeth; 6 dentary teeth; separated dentary symphysis; dentary teeth maintaining constant size.

*Material examined.*—LACM 9249 (holotype).

*Occurrence.*—Early Miocene, Sharps Formation, Wounded Knee, Shannon County, South Dakota.

*Discussion.*—This species was originally reported by MacDonald (1970) as belonging to the family Amphisbaenidae. The specimen consists only of the anterior portion of skull, from parietal-frontal suture to premaxillary. From the preserved cranial elements, this fossil species was found to lie within Rhineuridae.

## ACKNOWLEDGMENTS

I thank Michael Caldwell (University of Alberta) and Linda Trueb (University of Kansas) for their careful reviews and suggestions that greatly improved this manuscript. I thank Stephen Hasiotis, Bruce Lieberman, and Alycia Stigall for discussions and comments on earlier versions of this manuscript. The following people graciously arranged the loan of specimens in their care: Carl Mehling (AMNH), Desui Miao (KUVP), Kenneth Krysko (UF), Greg Gunnell (UMMP), and Mark Florence (USNM). This research was supported by the Department of Geology, University of Kansas, the Paleontological Society (Stephen J. Gould Grant-in-aid), the Geological Society of America, Colorado Scientific Society, and the Society of Vertebrate Paleontology (Bryan Patterson Award).

## REFERENCES


Baur, G. 1893. The discovery of Miocene amphisbaenians. American Naturalist 27:998–999.

Berman, D. S. 1972. *Hyporhina tertia*, new species (Reptilia: Amphisbaenia), from the early Oligocene (Chadronian) White River Formation of Wyoming. Annals of the Carnegie Museum 44:1–10.

Berman, D. S. 1973. *Spathorhynchus fossorium*, a middle Eocene amphisbaenian (Reptilia) from Wyoming. Copeia 4:704–721.

Berman, D. S. 1976. A new amphisbaenian (Reptilia: Amphisbaenia) from the early Oligocene of Wyoming. Journal of Paleontology 50:165–174.

Berman, D. S. 1977. *Spathorhynchus natronicus*, a new species of rhineurid amphisbaenian (Reptilia) from the early Oligocene of Wyoming. Journal of Paleontology 51:986–991.

Cope, E. D. 1861. Specimens of *Lepidosternum floridanum* Baird were exhibited. Proceedings, Academy of Natural Sciences. Philadelphia. p. 75.

Cope, E. D. 1873. Synopsis of new Vertebrata from Tertiary of Colorado, obtained during the summer of 1873. United States Government Printing Office. Washington, D.C. 19 p.

Donoghue, M. J., J. A. Doyle, J. Gauthier, A. G. Kluge, and T. Rowe. 1989. The importance of fossils in phylogeny reconstruction. Annual Review of Ecology and Systematics 20:431–460.

Estes, R. 1965. Notes on some Paleocene lizards. Copeia 1965:104–106.

Estes, R. 1983. *Sauria terrestria,* Amphisbaenia: Handbuch der Palaoherpetologie, Part 10a. Gustav Fisher Verlag. Stuttgart. 249 p.

Estes, R., K. De Queiroz, and J. Gauthier. 1988. Phylogenetic relationships within Squamata. *In* R. K. Estes, and G. Pregill, eds., Phylogenetic Relationships of the Lizard Families. Stanford University Press. Stanford. p. 119–281.

Felenstein, J. 1985. Confidence limits on phylogenies: An approach using the bootstrap. Evolution 39:783–791.

Galbreath, E. C. 1953. A contribution to the Tertiary geology and paleontology of northeastern Colorado, Vertebrata 4. University of Kansas Paleontological Contributions, Article 13:1–120.

Gans, C. 1960. Studies on Amphisbaenids (Amphisbaenia, Reptilia): A taxonomic revision of the Trogonophidae, and a functional interpretation of the amphisbaenid adaptive pattern. Bulletin of the American Museum of Natural History 119:129–204.

Gans, C. 1968. Relative success of divergent pathways in amphisbaenian specialization. The American Naturalist 102:345–362.

Gans, C. 1969. Amphisbaenians: Reptiles specialized for a burrowing existence. Endeavour 28:146–151.

Gans, C. 1974. Biomechanics: An approach to vertebrate biology. J. B. Lippincott Company. Philadelphia. 261 p.

Gans, C. 1978. The characteristics and affinities of the Amphisbaenia. Transactions of the Zoological Society of London 34:347–416.

Gilmore, C. W. 1928. Fossil Lizards of North America. National Academy of Sciences, Memoir 22:201 p.

Gilmore, C. W. 1938. Descriptions of new and little known lizards of North America. Proceedings of the United States National Museum 86:11–26.

Gilmore, C. W. 1942. Paleocene faunas of the Polecat Bench Formation, Park County, Wyoming: Part II Lizards. Proceedings of the American Philosophical Society 85:159–167.

Gilmore, C. W., and G. L. Jepsen. 1945. A new Eocene lizard from Wyoming. Journal of Paleontology 19:30–34.

Gray, J. E. 1844. Catalogue of the tortoises, crocodiles, and amphisbaenians in the collection of the British Museum. British Museum. London. 80 p.

Hillis, D. M. 1991. Discriminating between phylogenetic signal and random noise in DNA sequences. *In* M. Miyamoto and J. Cracraft, eds., Analysis of DNA Sequences. Oxford University Press. New York. p. 278–294.

Holman, J. A. 1959. Amphibians and reptiles from the Pleistocene (Illinoian) of Williston, Florida. Copeia 1959:96–102.

Holman, J. A. 1979. A new amphisbaenian of the genus *Rhineura* from the middle Miocene of South Dakota. Herpetologica 35:383–386.

Kearney, M. 2003. Systematics of the Amphisbaenia (Lepidosauria: Squamata) based on morphological evidence from recent and fossil forms. Herpetological Monographs 17:1–74.

Kearney, M., and B. L. Stuart. 2004. Repeated evolution of limblessness and digging heads in worm lizards revealed by DNA from old bones. Proceedings of the Royal Society of London (series B) 271:1,677–1,683.

Klassen, G. J., R. D. Mooi, and A. Locke. 1991. Consistency indices and random data. Systematic Zoology 40:446–457.

Laurenti, J. N. 1768. Specimen medicum, exhibens synopsin Reptilium emendatum cum experimentis circa venena et antidota Reptilium Austriacorum. Trattnern. Vienna. 214 p.

Lee, M. S. Y. 1998. Convergent evolution and character correlation in burrowing reptiles: Towards a resolution of squamate relationships. Biological Journal of the Linnean Society 65:369–453.

Loomis, F. B. 1919. An amphibian from the Eocene. American Journal of Science 47:217–219.

MacDonald, J. R. 1970. Review of the Miocene Wounded Knee faunas of southwestern South Dakota. Bulletin of the Los Angeles County Museum of Natural History Science 8:1–82.

Macey, J. R., T. J. Papenfuss, J. V. Kuehl, H. M. Fourcade, and J. L. Boore. 2004. Phylogenetic relationships among amphisbaenian reptiles based on complete mitochondrial genomic sequences. Molecular Phylogenetics and Evolution 33:22–31.

Marsh, O. C. 1871. Description of some new fossil serpents, from the Tertiary deposits of Wyoming. American Journal of Science 101:322–329.

Marsh, O. C. 1885. Names of extinct reptiles. American Journal of Science 29:169.

Pough, F. H., R. M. Andrews, J. E. Cadle, M. L. Crump, A. H. Savitsky, and K. D. Wells. 2003. Herpetology, 3rd ed. Benjamin Cummings. New York. 736 p.

Prothero, D. R., and W. A. Berggren, eds. 1992. Eocene-Oligocene Climatic and Biotic Evolution. Princeton University Press. New Jersey. 567 p.

Prothero, D. R., L. C. Ivany, and E. A. Nesbitt, eds. 2003. From Greenhouse to Icehouse: The Marine Eocene-Oligocene Transition. Columbia University Press. New York. 541 p.

Rieppel, O. 1988. The classification of the Squamata. *In* M. J. Benton, ed., The Phylogeny and Classification of the Tetrapods, Volume 1: Amphibians, Reptiles, Birds. Systematics Association Special Volume 35A. Clarendon Press. Oxford. p. 261–293.

Rieppel, O. 1993. Patterns of diversity in the reptilian skull. *In* J. Hanken and B. K. Hall, eds., The Skull: Volume 2, Patterns of Structural and Systematic Diversity. The University of Chicago Press. Chicago. p. 344–390.

Sanderson, M. J. 1989. Confidence limits of phylogenies: The bootstrap revisited. Cladistics 5:113–129.

Sullivan, R. M. 1985. A new Middle Paleocene (Torrejonian) rhineurid amphisbaenian, *Plesiorhineura tsentasi* new genus, new species, from the San Juan Basin, New Mexico. Journal of Paleontology 59:1,481–1,485.

Sullivan, R. M., and J. A. Holman. 1996. Squamata. *In* D. R. Prothero and R. J. Emry, eds., The Terrestrial Eocene-Oligocene Transition in North America. Cambridge University Press. Cambridge. p. 354–372.

Swofford, D. L. 2002. PAUP*. Phylogenetic Analysis Using Parsimony (*and other methods) [computer program]. Version 4.0b10. Sinauer. Sunderland.

Taylor, E. H. 1951. Concerning Oligocene amphisbaenid reptiles. University of Kansas Science Bulletin 34:521–558.

Townsend, T. M., A. Larson, E. Louis, and J. R. Macey. 2004. Molecular phylogenetics of Squamata: The position of snakes, amphisbaenians, and dibamids, and the root of the Squamate tree. Systematic Biology 53:735–757.

Vanzolini, P. E. 1951. A systematic arrangement of the family Amphisbaenidae (Sauria). Herpetologica 7:113–123.

Walker, M. V. 1932. A new burrowing lizard from the Oligocene of central Wyoming. Transactions of the Kansas Academy of Science 35:224–231.

Wake, M. H. 1993. The skull as a locomotor organ. *In* J. Hanken and B. K. Hall, eds., The Skull, Vol. 3: Functional and Evolutionary Mechanisms. The University of Chicago Press. Chicago. p. 215–220.

Yatkola, D. A. 1976. Mid-Miocene lizards from western Nebraska. Copeia 1976:645–654.

Zangerl, R. 1944. Contributions to the osteology of the skull of the Amphisbaenidae. The American Naturalist 31:417–454.

Zangerl, R. 1945. Contributions to the osteology of the post-cranial skeleton of the Amphisbaenidae. The American Naturalist 33:764–780.

Zug, G. R., L. J. Vitt, and J. P. Caldwell. 2001. Herpetology: An Introductory Biology of Amphibians and Reptiles. Academic Press. San Diego, California. 630 p.

# APPENDIX 1

A list of the cranial characters and character states that were used in this phylogenetic analysis. Characters were derived from previous studies of extant amphisbaenians (Gans, 1978; Estes, De Queiroz, and Gauthier, 1988; Rieppel, 1988; Kearney, 2003). The characters are arranged from the anterior to posterior along the skull. Characters that were unordered in the analysis are indicated by (unordered) prior to the list of character states. Characters 14, 26, 40, 59, 60, 61, 62, 74, 75, and 77 were found to be uninformative and excluded from the final analysis.

**Cranial Osteology**

1. Craniofacial angulation: (0) absent (0°); (1) slight (30°); (2) strong (60°).
2. Snout shape (unordered): (0) rounded, convex along dorsal surface; (1) snout depressed; (2) laterally compressed; (3) laterally compressed with dorsal keel.
3. Postorbital length of skull as percentage of total skull length: (0) 50% or less; (1) 62% or greater.
4. Upper jaw: (0) meets lower jaw without overlap; (1) prognathous.
5. Closure of lateral braincase wall: (0) lateral braincase not enclosed by bone; (1) lateral braincase wall closed by parietal downgrowths; (2) lateral braincase closed completely by parietal downgrowths and an anterior extension of the prootic.
6. Anterior premaxillary extension forming spatulate rostral process: (0) absent; (1) present.
7. Premaxillary dorsal foramina (unordered): (0) absent; (1) present, single pair; (2) present, two pairs.
8. Surface of facial bones: (0) smooth; (1) rugose.
9. Nasals: (0) elongated anteriorly, with anterior margin extending as far as maxillae and premax; (1) truncate anteriorly with concave anterior margin.
10. Nasal-maxillary contact: (0) present; (1) absent.
11. Contact of premax, nasals, and frontals at a single point: (0) absent; (1) present, medial anterior extension of the frontals extends to meet the premax between nasals.
12. Position of external nares (unordered): (0) anterolateral; (1) ventrolateral; (2) ventral.
13. Narial margins (unordered): (0) enclosed by maxilla and nasal only; (1) enclosed by maxilla, nasal, and premax; (2) enclosed by nasal and septomaxilla.
14. Nasals:(0) level with frontals; (1) raised above frontals.
15. Prefrontals (unordered): (0) contributing to facial surface and inner wall of orbit; (1) reduced and restricted to facial area; (2) reduced and confined to inner walls of orbit; (3) absent.
16. Prefrontal-nasal contact: (0) present, separates maxilla from frontal; (1) absent, nasal and prefrontal separated by an anterolateral process of frontal contacting maxilla.
17. Frontal fusion: (0) frontals unfused; (1) frontals fused.
18. Suture between frontals: (0) straight; (1) slightly sinuous; (2) strongly interdigitating.

19. Frontoparietal suture in superficial view (unordered): (0) forms a straight transverse line; (1) strongly interdigitating continuously across the suture; (2) U-shaped; (3) W-shaped.
20. Parietal fusion: (0) absent; (1) present.
21. Parietal contributes to deflected facial portion of skull: (0) absent; (1) present, anterior portion of parietal occurs on facial plane.
22. Sagittal crest on parietal: (0) absent; (1) present.
23. Triradiate boss on parietal: (0) absent; (1) present.
24. Parietal foramen: (0) present; (1) absent.
25. Paired subcircular depressions near anteromedial edge of parietal: (0) absent; (1) present.
26. Anterolateral process of parietal: (0) absent; (1) parietal with anterolateral processes along canthus rostralis.
27. Parietofrontal fusion: (0) absent; (1) present.
28. Supratemporal process of parietal: (0) present; (1) absent.
29. Lateral parietal flanges: (0) absent; (1) present.
30. Postfrontal: (0) present; (1) absent.
31. Jugal: (0) present; (1) reduced; (2) absent.
32. Postorbital: (0) present; (1) absent.
33. Anterolateral process on maxillae: (0) absent; (1) present.
34. Posterolateral process on maxillae: (0) absent; (1) present.
35. Squamosal: (0) present; (1) absent.
36. Supratemoral: (0) present; (1) absent.
37. Supratemporal fenestra: (0) present; (1) absent.
38. Supraoccipital: (0) positioned ventrally or posteroventrally in relation to parietal, forming a postemporal fenestra; (1) tightly contacts parietal along its entire anterior margin, posttemporal fenestra absent.
39. Position of quadrate in lateral view (unordered): (0) nearly horizontal; (1) angled anteroventrally; (2) nearly vertical; (3) angled posteroventrally.
40. Anteriorly elongated extracolumella (unordered): (0) cartilaginous; (1) at least partially ossified; (2) absent.
41. Stapedial footplate: (0) small relative to size of skull; (1) large relative to size of skull.
42. Epipterygoid: (0) present; (1) absent.
43. Palate: (0) not in contact with braincae; (1) tightly contacting ventral surface of braincase.
44. Palatines: (0) flat; (1) scroll-like, with a medial extension forming a secondary palate.
45. Palatal processes of premaxilla: (0) absent; (1) present.
46. Extent of premaxillary palatal processes (unordered): (0) not extending as far as maxillary teeth; (1) extending beyond first maxillary tooth; (2) extending posteriorly to contact ectopterygoid.
47. Palatine teeth: (0) present; (1) absent.
48. Pterygoid teeth: (0) present; (1) absent.
49. Elongated paired palatal processes of maxillae: (0) absent; (1) present.
50. Cultriform process of parabasisphenoid (unordered): (0) small or absent; (1) well developed; (2) extremely elongated, extending anteriorly to contact vomers.
51. Pterygoid-vomer contact: (0) present, separating palatines; (1) absent, palatines in medial contact.
52. Suborbital fenestra: (0) present, large; (1) present, small; (2) absent, closed.
53. Palatine-ectopyterygoid contact (unordered): (0) absent; (1) present anteromedially only; (2) present along entire medial border of ectopterygoid and lateral border of palatine.
54. Basipterygoid processes (unordered): (0) absent; (1) present.
55. Occipital condyle: (0) unicipital; (1) bicipital; (2) large, U-shaped bar.
56. Position and size of occipital condyle: (0) condyle unelevated, foramen magnum opens posteriorly; (1) condyle elevated strongly and enlarged, foramen magnum opens dorsally.
57. Exoccipitals: (0) do not meet on midline dorsally, supraoccipital forms dorsal border of foramen magnum; (1) meet on midline dorsally, excluding supraoccipital from foramen magnum.
58. Posterodorsal edge of supraoccipital flared, large occipital crest: (0) absent; (1) present.
59. Epihyal: (0) present; (1) absent.
60. Length/width ratio (unordered).
61. Length/height ratio (unordered).

**Dentition and Mandible**

62. Replacement teeth (unordered): (0) absent, new teeth added to posterior tooth row; (1) present.
63. Premaxillary tooth count (unordered): (0) between 0 and 3; (1) between 5 and 12.
64. Enlarged median tooth on fused premaxillary element: (0) absent; (1) present.
65. Tooth implantation (unordered): (0) pleurodont; (1) acrodont.
66. Tooth orientation: (0) straight; (1) recurved.
67. Maxillary tooth count (unordered): (0) between 3 and 5; (1) between 6 and 8; (2) 9 or more.
68. Maxillary tooth row (unordered): (0) in continuous line with premaxillary teeth; (1) lies outside row of premaxillary teeth.
69. Dentary tooth count (unordered): (0) between 5 and 9; (1) 12 or more.
70. Coronoid process of dentary (unordered): (0) absent; (1) present, extends dorsally onto anterolateral surface of coronoid.
71. Dentary process of coronoid (unordered): (0) absent; (1) present.
72. Dentary symphasis (unordered): (0) separate; (1) fused.
73. Retroarticular process (unordered): (0) absent; (1) extends posteriorly; (2) deflected ventrally.
74. Splenial: (0) present; (1) absent.
75. Meckel's canal: (0) open anteriorly; (1) closed anteriorly.
76. Subdental shelf (unordered): (0) small or absent; (1) well developed.
77. Compound postdentary bone (unordered): (0) absent; (1) present.
78. Postcoronoid region of mandible: (0) about equal in length to precoronoid region; (1) extremely shortened relative to precoronoid region.
79. Dentary teeth size (unordered): (0) dentary teeth remain constant in size from anterior to posterior; (1) dentary teeth increase in size from anterior to posterior; (2) dentary teeth decrease in size from anterior to posterior.

# APPENDIX 2

Character state distribution for taxa used in the phylogenetic analysis. Character numbers are listed across top of table; *, taxa synonymized to *Protorhineura hatcherii* in final analysis using character states of *Rhineura hatcherii;* ^, taxa synonymized with *Hyporhina galbreathi* in the final analysis using characters states of *Hyporhina galbreathi;* ?, missing data.

| | <br>123456789 | 1111111111<br>0123456789 | 2222222222<br>0123456789 | 3333333333<br>0123456789 | 4444444444<br>0123456789 | 5555555555<br>0123456789 | 6666666666<br>0123456789 | 7777777777<br>0123456789 |
|---|---|---|---|---|---|---|---|---|
| *Sphenodon punctatus* | 000000000 | 00010000?0 | 0?0?000000 | 0000001101 | 000000?010 | 1000100000 | ??01010201 | 10?1100000 |
| *Gekko gekko* | 000000000 | 0001000100 | 0?0?100000 | 0210000001 | 000000??11 | 0100101000 | ??001001?0 | 10?2001100 |
| *Boa constrictor* | 001020000 | 1002000000 | 1?1?100010 | 120001001? | 001?00?000 | 2100?00100 | ??10001201 | 00?1001100 |
| *Rhineura floridana* | 111120110 | 0020001013 | 1010100010 | 1110001012 | 1111011110 | 2122020001 | ??10101010 | 0112010112 |
| *Amphisbaena alba* | 101020101 | 0001001021 | 1?11100011 | 1210011010 | 111100?110 | 2122010011 | ??11101000 | 1010110110 |
| *Trogonophis wiegmanni* | 101120101 | 00010010?1 | 1?10100011 | 1211101010 | 110100?111 | 2122010001 | ??01111000 | 1010110110 |
| *Blanus cinereus* | 001020101 | 0001001011 | 1?0?100011 | 1210001011 | 011100?110 | 2122110000 | ??11100000 | 1010110110 |
| *Bipes biporus* | 001020000 | 00010011?? | 1??0?00110 | 1210001011 | 011100?110 | 2122110000 | ??11101000 | 10?0110110 |
| *Ototriton solidus* | 101?20110 | 0?21001003 | 101011?0?0 | 1??010101? | ??11011111 | 20??02100? | ???010011? | ?????????? |
| *Jepsibaena minor** | 1111201?0 | 0????????? | 1?1??????0 | 12?11?1?1? | ??110??110 | 20?002000? | ???010011? | 0101????0? |
| *Rhineura wilsoni** | 211120110 | 0020001003 | 101011?0?0 | 1?111?101? | ?111?1011? | ????02100? | ???010?0?? | ?????????? |
| *Rhineura amblyceps** | 211?20?10 | ????001003 | 101011?010 | ??1?111011 | ?1110????? | ??2??2100? | ????1001?? | ???1??010? |
| *Rhineura minutus** | 111120?00 | 0???001003 | 10?01??010 | 12111?1?11 | ??110????? | ?12?02000? | ???0100110 | ?111???102 |
| *Rhineura attenuatus** | 1?0?2???? | ?????????? | 10101??01? | ??????1??? | ?1???????? | ?????210?? | ?????????? | ?????????? |
| *Rhineura hibbardi* | 211120?10 | 10??10?01? | 101010?010 | 11100?1012 | 1?11???11? | ??22?2000? | ???0100010 | 0112?1?112 |
| *Rhineura hatcherii** | 111120110 | 0021001003 | 101011?0?0 | 1211101012 | ?11101111? | ?12?02000? | ???0100110 | 0101??0102 |
| *Spathorhynchus fossorium* | 201121110 | 0021001003 | 1010111010 | 0011101012 | 1?11?11111 | 202202000? | ???0100110 | 01020?0102 |
| *Spathorhynchus natronicus* | 101121110 | 0021001003 | 1010111010 | 0011101012 | ?111?1?111 | 202202100? | ???0100110 | 0101???112 |
| *Dytioconastis rensbergeri* | 101121110 | 0021001003 | 1010111010 | 1?11101012 | 1111?11111 | 202002100? | ???0100110 | 01?20?0?02 |
| *Hyporhina galbreathi*^ | 211?20110 | 0121001003 | 1100111010 | 1010101012 | ?111011111 | 202202100? | ??00100110 | 0????????0 |
| *Hyporhina tertia*^ | 11?1?01?0 | 012100100? | ?????????? | ???01????? | ?????????? | ?0???????? | ???0100110 | ?????????? |
| *Hyporhina antiqua* | 211120110 | 012101100? | 100011?010 | 1010101012 | ??11011111 | 202202100? | ??0011001? | ?????????? |
| *Macrorhineura skinneri* | 11?12??00 | 102100100? | ?0?????0?? | ???11?1??? | ??11???110 | ????????0? | ???01001?0 | 01??0????0 |