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

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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. amblycephs, R. minutus, and R. attenuatus are synonymized with Rhineura hatchetii. In addition, Hyporrhina 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 hatcheti gen. nov., Hadrorhineura hibbardi gen. nov., Spalthyrinus fossorium, S. natronicus, Dyticonastis rensbergeri, Macrorhineura skinneri, Ototriton solidus, Hyporrhina 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; Gauthier, 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, Tropidonophidae, 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 rineurids 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 hatcheri* 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 *Platybarchis coloradensis* (Cope, 1873), collected from the White River Formation of Colorado, as *Rhineura coloradensis* (Gilmore, 1928).

An amphisbaenian skull collected from the White River Group in southern Wyoming identified as *Rhineura hatcheri* 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 preconoroidial portion of the dentary. Another amphisbaenian fossil diagnosed by its smaller size, *Rhineura minuta* (Gilmore, 1938), was collected from the same locality but was later revised by Vanzolini (1951) as *Pseudohyrina minuta*. This new genus was supported by the presence of elongate nasals and a posterior position of the fenestra 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 amphibiaenians and stratigraphic and geographic locality information; *, taxa included in this analysis.

<table>
<thead>
<tr>
<th>Fossil Taxa</th>
<th>Age</th>
<th>Stratigraphic Location</th>
<th>Geographic Location</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Plesiornionea tsentasi</td>
<td>Late Paleocene</td>
<td>Upper Nacimiento Formation</td>
<td>New Mexico</td>
<td>Sullivan, 1985</td>
</tr>
<tr>
<td>Spathorhynchus fassorium</td>
<td>Middle Eocene (Wasatchian)</td>
<td>Bridger Formation, Wind River Formation, Lost Cabin Member</td>
<td>Sweetwater County, Wyoming, Natrona County, Wyoming</td>
<td>Berman, 1973</td>
</tr>
<tr>
<td>Ototrition solidus</td>
<td>Middle Eocene (Wasatchian)</td>
<td>Wind River Formation, Lysite Member</td>
<td>Big Horn County, Wyoming</td>
<td>Loomis, 1919; Gilmore, 1928</td>
</tr>
<tr>
<td>Jepsiabena minor</td>
<td>Middle Eocene (Wasatchian)</td>
<td>Wind River Formation, Lost Cabin Member</td>
<td>Natrona County, Wyoming</td>
<td>Gilmore and Jepson, 1945</td>
</tr>
<tr>
<td>Spathorhynchus natunicus</td>
<td>Early Oligocene</td>
<td>White River Formation</td>
<td>Natrona County, Wyoming</td>
<td>Berman, 1977</td>
</tr>
<tr>
<td>Hyporhina tertia</td>
<td>Early Oligocene</td>
<td>White River Formation</td>
<td>Freemont County, Wyoming</td>
<td>Berman, 1972</td>
</tr>
<tr>
<td>Rhineura coloradoensis</td>
<td>Early Oligocene</td>
<td>White River Formation</td>
<td>Logan County, Colorado</td>
<td>Gilmore, 1928; Taylor, 1951</td>
</tr>
<tr>
<td>Rhineura (Gilmorea) attenuatus</td>
<td>Middle Oligocene</td>
<td>Lower Brule Formation</td>
<td>Converse County, Wyoming</td>
<td>Taylor, 1951</td>
</tr>
<tr>
<td>Hyporhina galbreath</td>
<td>Middle Oligocene</td>
<td>White River Formation</td>
<td>Logan County, Colorado</td>
<td>Taylor, 1951</td>
</tr>
<tr>
<td>Rhineura hatcheri</td>
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<td>White River Group</td>
<td>Shannon County, South Dakota</td>
<td>Gilmore, 1928; Taylor, 1951</td>
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</tr>
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<td>White River Formation</td>
<td>Logan County, Colorado</td>
<td>Taylor, 1951</td>
</tr>
<tr>
<td>Rhineura hibbardi</td>
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<td>Logan County, Colorado</td>
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<td>Lower Brule Formation</td>
<td>Converse County, Wyoming</td>
<td>Taylor, 1951</td>
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<td>Hyporhina antiqua</td>
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<td>Dytiiconasis rensbergeri</td>
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<td>Turtle Cove Member, John Day Formation</td>
<td>Oregon</td>
<td>Berman, 1976</td>
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<tr>
<td>Macrorhineura Skinneri</td>
<td>Early Miocene (Arikareen)</td>
<td>Sharps Formation</td>
<td>Shannon County, South Dakota</td>
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<td>Rhineura marslandensis</td>
<td>Early Miocene (Hemmingfordian)</td>
<td>Marsland Formation</td>
<td>Box Butte County, Nebraska</td>
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<td>Rhineura sepulcra</td>
<td>Early Miocene (Hemmingfordian)</td>
<td>Rosebud Formation</td>
<td>Bennet County, South Dakota</td>
<td>Holman, 1979</td>
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<td>Rhineura floridana</td>
<td>Pleistocene (Illinoian)</td>
<td>Crystal River Formation</td>
<td>Levy County, Florida</td>
<td>Holman, 1959</td>
</tr>
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size (17.6 vs. 32 mm). Gilmore and Jepson (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 galbrathi, Rhineura amhiphys, R. bibrardi, and R. wilsoni. Taylor (1951) also described a new genus and species, Gilmorea 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 (Bridgegan) to late Eocene (Chadronian) of Wyoming. The two species, Spathorhynchus fossorium and S. natroniensis, 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 central Oregon, Dyticonastis rensbergei. 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 marlandensis, 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 marlandensis differs from R. batcheri 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 Bennett County, South Dakota. This material was described as another new species of amphisbaenian, Rhineura septaluna, 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 America was made by Sullivan and Holman (1996), who synonymized several Oligocene species of Rhineura, Gilmorea, and Pseudorhineura. The most important result of this study was that Rhineura hibbardi, R. sternbergii, Pseudorhineura minutus (i.e., R. minutus), R. attenuatus (i.e., Gilmorea attenuatus), R. bibrardi, R. amphipectus, and R. wilsoni were all synonymized into the single species Rhineura batcheri. 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 amblycephys*, *R. attenuatus*, *R. minutus*, and *R. wilsoni* were synonymized with *Rhineura batherti*. For similar reasons, *Hyporhina tertia* was synonymized with *Hoprhina galeaethri*. 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 bipes* (*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 excluded because of their presence in the outgroups. The g 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 amblycephys*, *R. attenuatus*, *R. minutus*, and *R. wilsoni*) are considered diagnostic of *Rhineura batherti* (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 batherti*.

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 amblycephys* was considered a new species simply because it is larger than specimens of *Rhineura batherti* (Taylor, 1951). In contrast, other specimens were described as new species because they were smaller than *Rhineura batherti* (e.g., Gilmore, 1938). The holotype of *Rhineura minutus* (Fig. 3.5), for example, does appear different superficially from *R. batherti*. *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. batherti*. *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. batherti*. 
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); Hadromineura hibbardi: 10 (1); node 3: 18 (0), 25 (1), 33 (1), 34 (1), 67 (1), 72 (0), 78 (0); Protobineura batcheri: 31 (2), 73 (1); node 4: 31 (0), 51 (0); node 5: 6 (1); Dyticonastis rensergenri: 53 (0); node 6: 30 (0); Spathorhyncbus natronicus: 73 (1), 78 (1); node 7: 79 (0); Macrorbineura 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 batcheri 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 batcheri and R. hibbardi, however, possess 11 cranial characters that differ from R. floridana. These differences suggest that R. batcheri and R. hibbardi belong to separate genera. Rhineura
Figure 3. Specimens of the fossil taxa synonymized under Protorhineura batcheri: 1, Rhineura batcheri (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).

*bibbardi* 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 batcheri* also possesses a straight tooth orientation (characters 19 and 66). *Rhinocera hatcheni* differs from both *R. floridana* and *R. bibhardi* by possessing a straight suture between the frontals, paired subcircular depressions near the anteromedial edge of the parietal, anterolateral, and postero-lateral 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 bibbardi* is reassigned therefore to *Hadrorhineura* n. gen., and *Rhineura batcheri* 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). *Macro rhineura* 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 bibbardi* 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 bibbardi (UMMP 25431), dorsal view; 6, right lateral view; 7, left lateral view; 8, ventral view (new).

Protorhineura hatcherii, Dyticonastis renbergeri, 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 renbergeri, 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 renbergeri 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 Spalthorbuschus-Dytonastis clade is united by the presence of a spatalate rostral process formed by an extension of the premaxillary (character 6). The sister-group relationship of Spalthorbuschus 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 Spalthorbuschus fossilim, S. natronicus, and Dytonastis renbergeri 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 gallorea and H. antiqua. The sister-group relationship of Hyporhina gallorea and H. antiqua is united by a strong (>60°) cranial 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 Dytonastis-Spathorbyschus clade. These genera are characterized by an anterior extension of the premaxilla that forms a spatalate 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 spatalate 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 floridanana, visual cells do not develop (Gans, 1978). The trogonophids Agamodons, 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 Typhlopsaurus lineatus, T. vermis, and T. aurantiacus and the dibamid, Dibamus norvegicae 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, Blindidae, Amphisbaenidae, Trogonophidae, and a few species of
Rhineuridae (Fig. 2). The enclosed orbit is retained in *Dytonastis-Spathorhynchus* and *Hyporrhina* 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 *Dytonastis-Spathorhynchus* and *Hyporrhina* 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 *Hyporrhina* (Fig. 6.6), the number and orientation of maxillary teeth, and the type
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 Pleisto-
cene to recent rhineurids in the southeastern United States, it has
been inferred that rhineurids continued to inhabit these regions

Figure 6. Fossil Rhineuridae: 1, Ototriton solidus (ACM 3639), dorsal view; 2, left lateral view; 3, right lateral view; 4, ventral view. 5, Hyporbina galbreathi (KUVP 8221), dorsal view; 6, left lateral view; 7, right lateral view; 8, ventral view (new).
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. sepulcrala (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 batcherti, R. wilsoni, R. amblyceps, R. minutus, and R. attenuatus are synonymous. In addition, Hyporhina galbraathii 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 batcherti gen. nov., Hadrorhineura bibbardii gen. nov., Spathorhynchus fossorium, S. matronicus, Dyticonastis rensbergeri, Macrorhineura skinneri, Ototriton solidus, Hyporhina antiqua, and H. galbraathi.

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


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.
Gilmoria Taylor, 1951, p. 527, fig. 1, pl. 58,3–5.
Type species.—Rhineura batcherti by monotypy.

Diagnosis.—Slight craniocfacial 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 precoronid regions of mandible equal in length.

Etymology.—From Greek, proto, 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 minutus* Gilmore, 1938, by monotypy.
*Ototriton minor* Gilmore and Jepsen, 1945, p. 31, fig. 1.
*Gilmoreia attenuata* Taylor, 1951, p. 527, fig. 1; pl. 58, 1–3;
*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.
Revised diagnosis.—Slight craniofacial angle (30°); narial margin enclosed by maxilla and nasal; straight suture between frontals; W-shaped frontoarticular 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 and dentary teeth; retroarticular process deflected ventrally; postcoronoid region of mandible short relative to precoronal region.

Material examined.—*Rhineura hatcherii*: YPM 11389 (holotype), KUVP 8220, 8960, CM423A; *Rhineura wilsoni*: KUVP 7651 (holotype), UMMP 25429; *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 hatcheri* 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 ontogenetic 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; sinusoid suture between frontals; W-shaped frontoarticular 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 precoronal 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 frontoarticular suture and a straight tooth orientation and in the absence of a 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; sinusoid suture between frontals; W-shaped frontoarticular 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 precoronal 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. hatcheri* 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 postrolateral 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 symphys; 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 postrolateral 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 symphys; 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 postrolateral 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 symphys; retroarticular process of dentary extending posteriorly; postcoronoid region of mandible short relative to precoronoid region.

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

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 postrolateral 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 symphys; 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; postrolateral 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 Amphisbaenida (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 premxillary 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

*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.**—KUPV 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 premxillary 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 premaxilla. From the preserved cranial elements, this fossil species was found to lie within Rhineuridae.

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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 sinuose; (2) strongly interdigitating.
19. Frontotemporal 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. Parietals contribute 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. Triadrate 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. Postorbital: (0) present; (1) absent.

32. Supratemporal process of parietal: (0) present; (1) absent.

33. Squamosal: (0) present; (1) absent.

34. Posterolateral process on maxillae: (0) absent; (1) present.

35. Anterolateral process on maxillae: (0) absent; (1) present.

36. Supratemporal: (0) present; (1) absent.

37. Supraoccipital: (0) positioned ventrally or posteroventrally in relation to parietal, forming a posttemporal fenestra; (1) tightly contacts parietal along its entire anterior margin, posttemporal fenestra absent.

38. Position of nuchal crest: (0) not extending beyond maxillary teeth; (1) extending beyond first maxillary tooth; (2) extending posteriorly to contact ectopterygoid.

39. Tooth implantation (unordered): (0) pleurodont; (1) acrodont.

40. Tooth orientation: (0) straight; (1) recurved.

41. Epipterygoid: (0) present; (1) absent.

42. Palate: (0) not in contact with braincase; (1) tightly contacting ventral surface of braincase.

43. Palatines: (0) flat; (1) scroll-like, with a medial extension forming a secondary palate.

44. Palatal processes of maxilla: (0) absent; (1) present.

45. Maxillary tooth row (unordered): (0) in continuous line with premaxillary region; (1) extremely shortened relative to prefrontal region.

46. Extended maxillary palatal processes (unordered): (0) not extending as far as maxillary teeth; (1) extending beyond first maxillary tooth; (2) extending posteriorly to contact ectopterygoid.

47. Pterygoid teeth: (0) present; (1) absent.

48. Palatine teeth: (0) present; (1) absent.

49. Pterygoid-vomer contact: (0) present, separating palatines; (1) absent, palatines in medial contact.

Dentition and Mandible

50. Epipterygoid: (0) present; (1) absent.

51. Palatine-ectopterygoid contact (unordered): (0) absent; (1) present anteromedially only; (2) present along entire medial border of ectopterygoid and lateral border of palatine.

52. Suborbital fenestra: (0) present, large; (1) present, small; (2) absent, closed.

53. Palatine-ectopterygoid 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 unextended, foramen magnum opens posteriorly; (1) condyle elevated strongly and enlarged, foramen magnum opens dorsally.

57. Frontal and sphenoid: (0) do not meet along midline dorsally, supraoccipital forms dorsal border of foramen magnum; (1) meet along midline, excluding supraoccipital from foramen magnum.

58. Posterocondral edge of supraoccipital flared, large occipital crest: (0) absent; (1) present.

59. Epipterygoid: (0) present; (1) absent.

60. Length/width ratio (unordered).

61. Length/height ratio (unordered).

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 symphysis (unordered): (0) separate; (1) fused.

73. Meckel's canal: (0) open anteriorly; (1) closed anteromedially.

74. Mandible: (0) small or absent; (1) well developed.

75. Subdental shelf (unordered): (0) small or absent; (1) well developed.

76. Premaxillary tooth count (unordered): (0) between 0 and 3; (1) 12 or more.

77. Subdental shelf (unordered): (0) small or absent; (1) well developed.

78. Compound postdental bone: (0) absent; (1) present.

79. Postcoronoid region of mandible: (0) about equal in length to precornoroid region; (1) extremely shortened relative to precornoroid region.

80. Dentary tooth 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 hatcheri* in final analysis using character states of *Rhineura hatcheri*; ^, taxa synonymized with *Hyporhina galbreathi* in the final analysis using characters states of *Hyporhina galbreathi*; ?, missing data.

| Taxon                     | Character 1 | Character 2 | Character 3 | Character 4 | Character 5 | Character 6 | Character 7 | Character 8 | Character 9 | Character 10 | Character 11 | Character 12 | Character 13 | Character 14 | Character 15 | Character 16 | Character 17 | Character 18 | Character 19 | Character 20 | Character 21 | Character 22 | Character 23 | Character 24 | Character 25 | Character 26 | Character 27 | Character 28 | Character 29 | Character 30 | Character 31 | Character 32 | Character 33 | Character 34 | Character 35 | Character 36 | Character 37 | Character 38 | Character 39 | Character 40 | Character 41 | Character 42 | Character 43 | Character 44 | Character 45 | Character 46 | Character 47 | Character 48 | Character 49 | Character 50 | Character 51 | Character 52 | Character 53 | Character 54 | Character 55 | Character 56 | Character 57 | Character 58 | Character 59 | Character 60 | Character 61 | Character 62 | Character 63 | Character 64 | Character 65 | Character 66 | Character 67 | Character 68 | Character 69 | Character 70 | Character 71 | Character 72 | Character 73 | Character 74 | Character 75 | Character 76 | Character 77 | Character 78 | Character 79 | Character 80 | Character 81 | Character 82 | Character 83 | Character 84 | Character 85 | Character 86 | Character 87 | Character 88 | Character 89 | Character 90 | Character 91 | Character 92 | Character 93 | Character 94 | Character 95 | Character 96 | Character 97 | Character 98 | Character 99 | Character 100 |