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# New specimens of *Eilenodon* (Reptilia, Sphenodontia) from the Morrison Formation (Upper Jurassic) of Colorado and Utah

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## ABSTRACT

New sphenodontian specimens, representing four individuals of the genus *Eilenodon*, provide the first evidence of the structure of the upper jaw of the genus and offer clues to the life orientation of the maxilla and dentary and their associated tooth wear facets. The maxilla of *Eilenodon* is, like the dentary, a robust bone with a lightly sculpted external surface and transversely expanded teeth possessing single wear facets on a plane perpendicular to the root-crown axis. *Eilenodon* is a rare taxon previously identified from the type locality at the Fruita Paleontological Area in Colorado and subsequently reported from one other site. The new specimens increase the known distribution of large sphenodontians in the Morrison Formation of the western United States and are from four localities, in Grand County, Utah, and Mesa, Montrose, and Fremont counties, Colorado.

## INTRODUCTION

Sphenodontians are an ancient order of lepidosauromorph reptiles represented by the extant genus *Sphenodon*, which is known only from islands around New Zealand (Evans, 1984; Benton, 1985; Robb, 1986). Three named genera are known from the Upper Jurassic deposits of North America: *Opisthias* (Gilmore, 1909), *Theretairus* (Simpson, 1926), and *Eilenodon* (Rasmussen and Callison, 1981). All are from the Morrison Formation of the Rocky Mountain region. Of these, *Opisthias* is the most common, with *Theretairus* known only from two specimens. *Theretairus* has been considered a juvenile form of *Opisthias* by Hoffstetter (1953), but this assessment is not fully established. Evans (1992) noted that *Theretairus* has two caniniform teeth near the front of the dentary, whereas *Opisthias* appears to lack the caniniform. *Eilenodon* was named by Rasmussen and Callison (1981) on the basis of two lower jaw fragments from the Fruita Paleontological Area in western Colorado. This genus is different from all other sphenodontid taxa, except *Toxolophosaurus*, in having robust, labiolingually expanded teeth (Rasmussen and Callison, 1981; Olson, 1960; Throckmorton et al., 1981). Several new specimens of *Eilenodon* have been identified in the Morrison Formation in recent years, and these are described here.

One new specimen was collected in 1977 by Lance Eriksen and was identified on the accession form for the

Museum of Western Colorado only as having been collected from the Upper Jurassic of "Westwater, Utah." This refers to outcrops of the Morrison Formation along the Colorado River about 4 miles west of the Utah-Colorado border, at the northeastern end of Westwater Canyon. The most probable site is in the Bitter Creek drainage north of Westwater, which Eriksen apparently worked in the 1970s. The Westwater name can, however, refer to the canyon, a point along the nearby railroad, and a boat ramp along the river; unfortunately, there is a lot of Morrison Formation exposure in this area, and the specimen could well have been found anywhere within a few miles of this point along the Colorado River.

Another specimen was collected from the Dry Mesa Quarry, southwest of Delta, Colorado, in 1993, and is in the collections at the Brigham Young University Earth Science Museum. This specimen was found in the lower Brushy Basin Member in the same deposit as the pterosaur *Mesadactylus*, the theropod *Torvosaurus*, and the large sauropod *Supersaurus* (Jensen and Padian, 1989; Britt, 1991; Miller et al., 1991).

A third specimen was collected by Bryan Small in 1992 at the Green Acres locality at Garden Park in Fremont County, Colorado. This specimen is at the Denver Museum of Nature and Science and consists of both dentaries, fragments of both maxillae, and other fragments.

The last specimen was collected from a site near Uravan in Montrose County, Colorado, and was among sphenodon-

tian material reported but not described by Scheetz (1991). This locality is in the lower Brushy Basin Member of the Morrison Formation.

*Institutional Abbreviations*—BYU, Earth Science Museum, Brigham Young University, Provo; DMNH, Denver Museum of Nature and Science, Denver; LACM, Natural History Museum of Los Angeles County; MWC, Museum of Western Colorado, Grand Junction.

#### SYSTEMATIC PALEONTOLOGY

Class REPTILIA Linnaeus, 1758

Order SPHENODONTIA Williston, 1925

Family SPHENODONTIDAE Cope, 1870

Genus *EILENODON* Rasmussen and Callison, 1981

*EILENODON ROBUSTUS* Rasmussen and Callison, 1981

Figure 1

*Age and distribution*.—Morrison Formation, Late Jurassic, North America; Fruita Paleontological Area and Dry Mesa Quarry, Mesa County, Colorado; Uravan Locality, Montrose County, Colorado; Green Acres, Fremont County, Colorado; Westwater Canyon area, Grand County, Utah. Also reported from Ninemile Hill, Carbon County, Wyoming.

*Referred Specimens*.—MWC 2907, fragment of right dentary with six teeth, from near Westwater Canyon; BYU 11460, dentary fragment with seven teeth, from Dry Mesa Quarry; MWC 1200, left maxilla fragment with five teeth, from Uravan Locality; DMNH 10685, right dentary fragment with seven teeth, left dentary fragment with six teeth, left maxilla fragment with four teeth, right maxilla fragment with three teeth, two unidentified elements with teeth, unworn isolated tooth, plus many fragments, all from one individual, from Green Acres.

*Revised Diagnosis*.—Lower jaw elements as described by Rasmussen and Callison (1981). Maxilla has relatively thick (~2–4mm) bone with anteroposteriorly oriented sculpting on lateral and dorsal surfaces. Maxilla curves strongly medially above level of tooth row (~50–80 degrees to vertical in anterior or posterior view) so that much of outer surface of the element apparently faces dorsally. Maxillary teeth similar in dimensions to dentary teeth but with wear facet only on top of tooth (lacking secondary wear facet on labial or lingual surface).

#### Maxilla

Maxilla MWC 1200 has a length of 10 mm as preserved, with five teeth (Fig. 1e–f). Teeth are 1–2 mm long and 3.5–5.0 mm wide. The anterior-most two teeth are well-worn on top of the crown but not on the sides; more posterior teeth are nearly unworn and shorter anteroposteriorly than the anterior teeth. The maxilla is thick and

sculpted (though abraded slightly) with a strong medial curve 2–3 mm above the tooth row. The curve makes an angle of nearly 90 degrees in anterior or posterior view. The width of the dorsal-facing surface of the maxilla is at least 5 mm as preserved.

The left maxilla fragment of DMNH 10685 is 14 mm long with at least four teeth (Fig. 1k–n); wear of the anterior teeth is so heavy that it can not be determined how many teeth are present. Teeth are 1.5–2.0 mm long and 3.0–4.0 mm wide. Unlike the dentary teeth, there is only one wear facet on each tooth, and it is nearly horizontal; there are no clear vertical wear facets on either side of the teeth. The dorsolateral surface of the maxilla is sculpted with many thin postero-medially directed gooves; these begin about 3 mm dorsal to the level of the tooth row. Between the tooth row and the lower end of sculpting on the external surface is a thin and shallow, antero-posteriorly directed groove. The maxilla curves strongly medially within about 3 mm above the level of the tooth row so that the snout of animal appears to have been low. The thickness of the maxilla both at the tooth row and its most medial preserved extent is about 4 mm.

DMNH 10685 also includes a right maxilla fragment 9 mm long with four fragmentary teeth, the anterior two of which are highly worn. The dorsal part of the preserved bone above the tooth row also possesses a shallow groove above the tooth row and postero-medially directed sculpting on the outer surface.

#### Dentary

MWC 2907 is 27 mm long and consists of the upper section of a dentary along the tooth row (Fig. 1a–b). The six teeth in the posterior part of the dentary are unworn to heavily worn and 1–2 mm long and 5 mm wide. The posterior teeth are shorter in anteroposterior length than are the anterior teeth. The posterior two teeth are unworn, and the anterior four teeth are progressively more heavily worn toward the front tooth positions. Lateral wear facets of the teeth are nearly vertical in the anterior four teeth. The dentary is broken anteriorly, posteriorly, and above the Meckelian groove. Anterior teeth are covered by bone of an unknown element, apparently diagenetically attached to the dentary; the unknown bone does not appear similar to maxilla fragments in other specimens described below but may be part of the palatine.

BYU 11460 is 18 mm long and consists of a dentary fragment with seven teeth (Fig. 1c–d). The jaw fragment is in a piece of pebbly sandstone matrix, and the teeth are highly worn due to postmortem transport; the enamel is broken off and dentine exposed on six of the teeth, and on the seventh, enamel appears to have been removed due to normal wear during life. Teeth are 1.5–2 mm long and 3–4

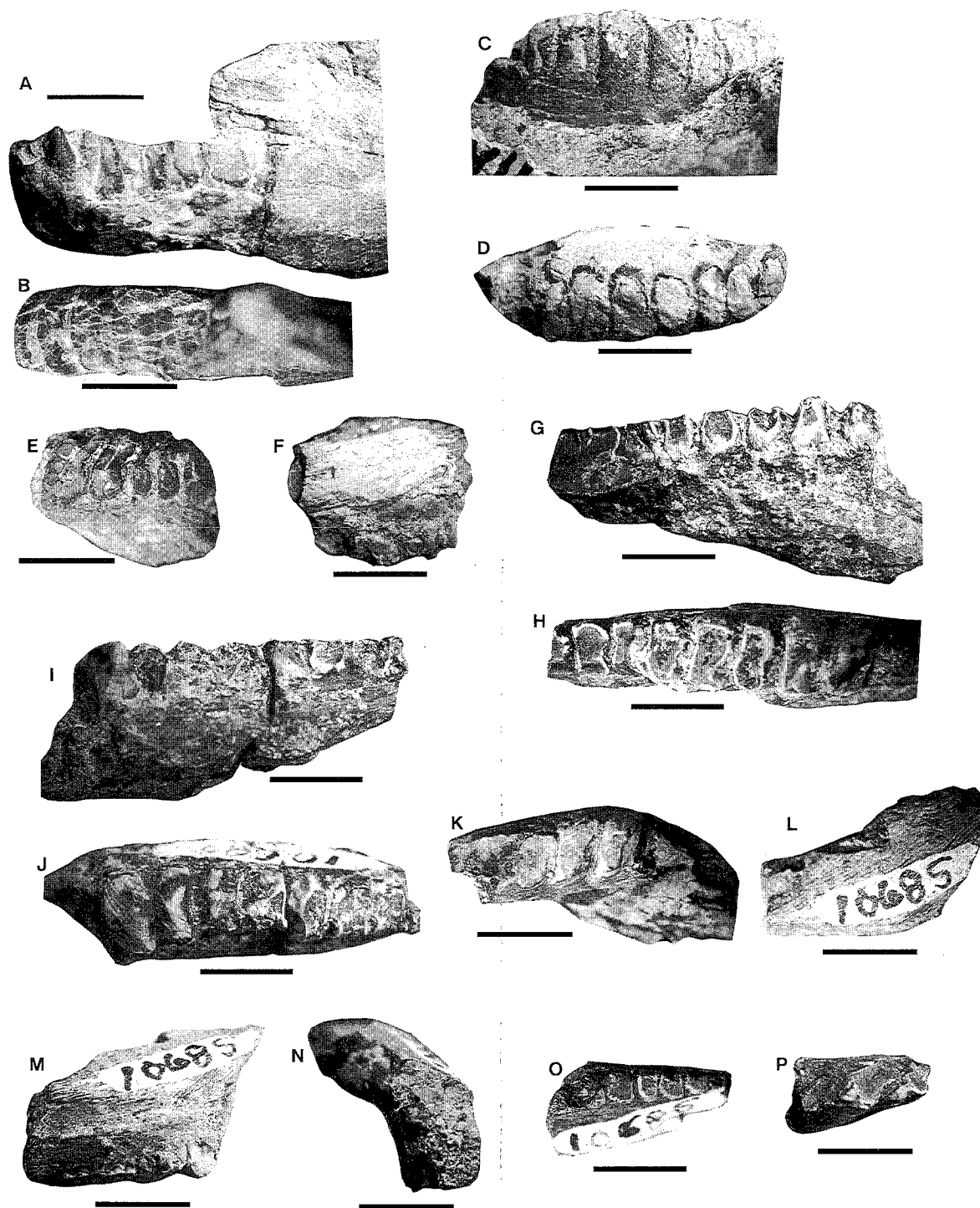


Figure 1. *Eilenodon robustus* material from the Morrison Formation of Utah and Colorado. (A–B) MWC 2907, fragment of right dentary in lateral (A) and occlusal (B) views, from Westwater area, Grand County, Utah. (C–D) BYU 11460, fragment of dentary in lateral (C) and occlusal (D) views, from Dry Mesa Quarry, Mesa County, Colorado. (E–F) MWC 1200, fragment of left maxilla in occlusal (E) and lateral (F) views, from Uraivan Locality, Montrose County, Colorado. (G–P) DMNH 10685, (G–H), left dentary in lateral (G) and occlusal (H) views, (I–J) right dentary in lateral (I) and occlusal (J) views, (K–N) fragment of left maxilla in occlusal (K), dorsal (L), lateral (M), and anterior (N) views, (O) unidentified element of jaw in occlusal view, (P) unidentified element (possibly palatine) with two diagonally oriented teeth in occlusal view, from Green Acres, Garden Park area, Fremont County, Colorado. All scale bars = 5mm.

mm wide. Because of transport damage to most of the teeth, it is difficult to determine if the dentary fragment is a right or left, but based on an apparent lateral wear facet on the undamaged tooth, and apparent size increase of the teeth in one direction along dentary, the jaw may be a right.

DMNH 10685 includes a left dentary fragment, broken above the level of the Meckelian groove, that is 21 mm long and preserves seven teeth (Fig. 1g-h). The teeth are 1.5–2.0 mm long and 3–4 mm wide, with the posterior-most tooth unworn and the next six teeth progressively more worn. The anterior-most tooth is worn down almost to the dentary bone. Wear facets are flat on the tooth crowns and nearly vertical on the lateral sides. As with the type specimen (LACM 120462), the unworn tooth is inclined steeply laterally and less steeply medially.

The right dentary fragment of DMNH 10685 is 20 mm long and contains six complete teeth and one broken anterior tooth (Fig. 1i-j). The teeth are 1.5–2.0 mm long and 2.5–4.0 mm wide. The posterior three teeth are essentially unworn, and the anterior teeth are worn. The anterior-most tooth is worn nearly down to the jaw. Wear facets are similar to those of left dentary teeth, and unworn teeth are inclined most steeply laterally. This dentary is broken above the Meckelian groove. As in the type, there is a rounded “shelf” below the tooth row along the lateral side of the dentary. This structure is not preserved in the left dentary of DMNH 10685.

#### Other Jaw Fragments

DMNH 10685 includes an unidentified fragment with four teeth (Fig. 1o) that is 10 mm long. The largest tooth is 1 mm long and 1.5 mm wide. The teeth have wear facets similar to those of the dentary teeth (i.e. on top of the crown and one side). The bone is more lightly-built than in the dentaries. There is also in DMNH 10685 an unidentified fragment (possibly of the palatine) with two teeth (Fig. 1p). It is 7 mm long, and the larger tooth is 3 mm long and 2 mm wide. The teeth are oriented diagonally relative to the apparent long axis of the bone fragment and worn diagonally relative to the long root-crown axis of the teeth, unlike other elements of DMNH 10685.

## DISCUSSION

MWC 1200 and DMNH 10685 preserve the first known elements of the upper jaws and skull of *Eilenodon*. MWC 2907 and DMNH 10685 may preserve palatine fragments, but little morphology is apparent in these pieces. The maxillae of DMNH 10685 and MWC 1200 indicate that *Eilenodon* had a thick-boned and relatively flat snout (little vertical height to the maxilla); it also had a lightly sculpted external surface of the maxilla. The maxillary teeth were

often heavily worn, with a single wear surface on the crown.

It is likely that the wear facets on the maxillary teeth of MWC 1200 and DMNH 10685 were formed by occlusion with the lateral wear facets of the dentary teeth; the dorsal wear on the dentary teeth would then have been a result of occlusion with the palatal teeth. The orientation of the maxilla in the descriptions of MWC 1200 and DMNH 10685 presented above is based on the assumption that the tooth wear surfaces faced slightly ventromedially. If the dentary was oriented with the dorsal wear facets facing dorsomedially, its teeth would have occluded with the maxillary and palatal teeth (Fig. 2). This orientation also suggests that the ventral margins of the dentaries would have been lateral to their respective tooth rows. The arrangements of the maxillary, dentary, and palatal teeth, as indicated by these new specimens, are consistent with the propalinal jaw movement suggested for *Eilenodon* by Rasmussen and Callison (1981).

*Eilenodon* is a rare animal in the Morrison Formation, having been reported previously only from the type locality at the Fruita Paleontological Area, Mesa County, Colorado (Rasmussen and Callison, 1981), and one additional site in Carbon County, Wyoming (Trujillo, 1999). Ornithopod dinosaur material at the Uravan Locality in Montrose County,

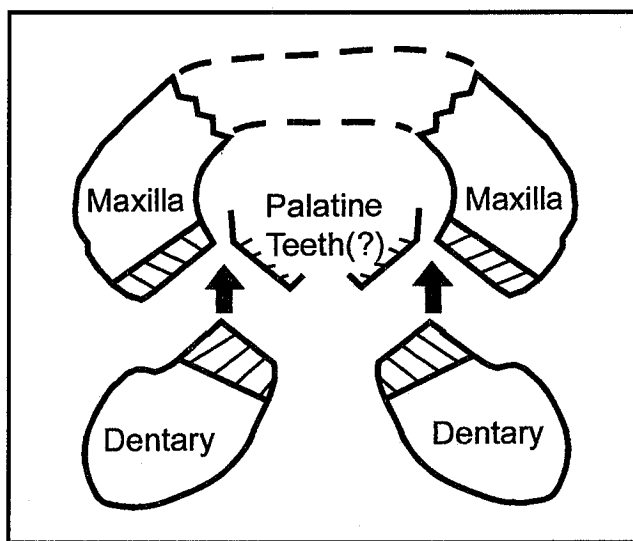


Figure 2. Schematic posterior view of a cross-section through the snout of *Eilenodon* showing proposed orientations of the dentaries and maxillae. Cross-hatching indicates teeth; arrows indicate movement of dentary teeth into contact with maxillary and palatal teeth prior to propalinal jaw stroke. The arrangement produces single, flat wear facets on maxillary teeth, single oblique wear facets on palatal teeth, and the two wear facets found on *Eilenodon* dentary teeth (with characteristic lateral facet at nearly right angles to the main facet).



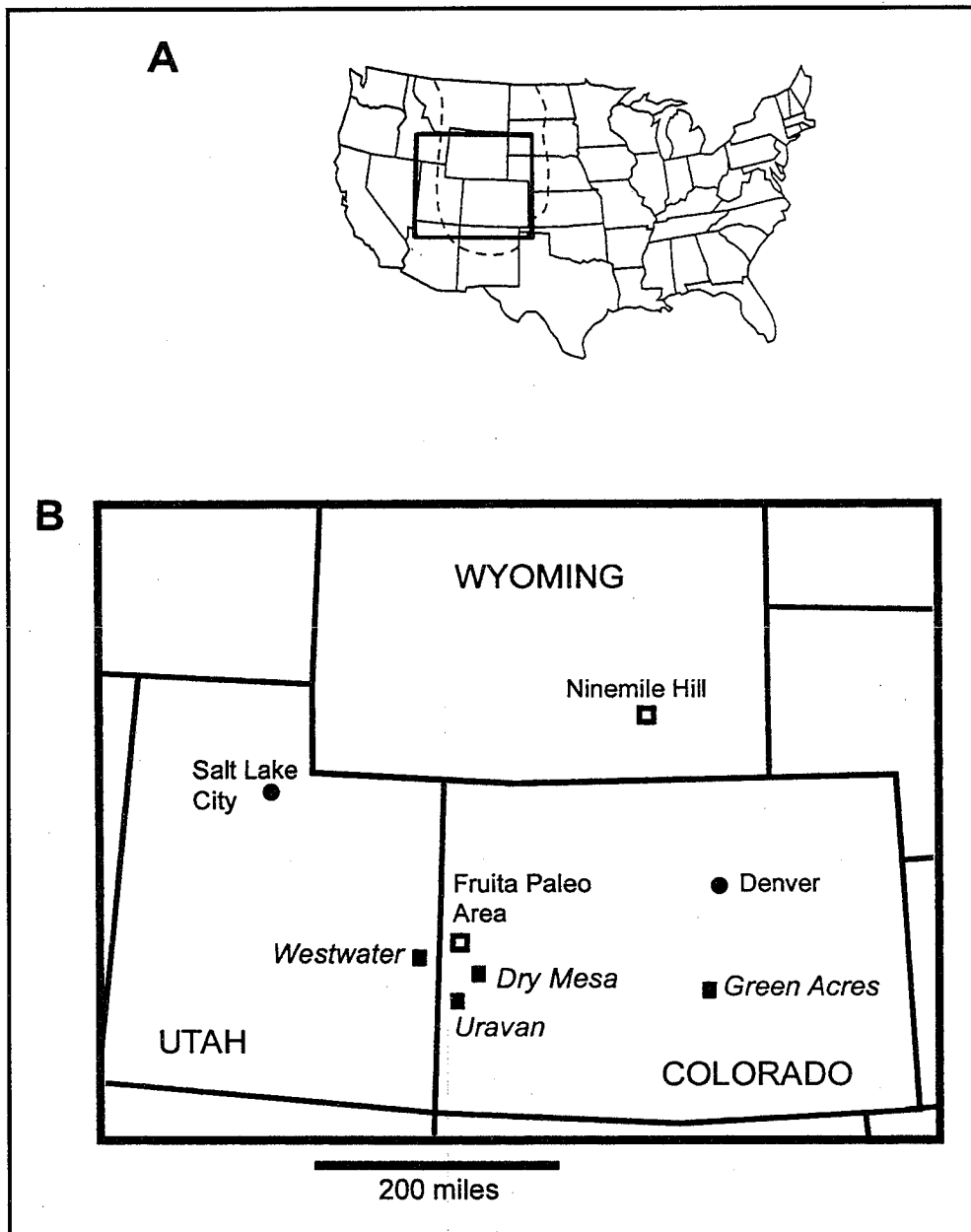


Figure 3. (A) Map of the United States with the extent of the Morrison Formation (dashed line) and area indicated in lower map (solid box). (B) Localities in the Morrison Formation at which *Eilenodon* specimens have been identified. Solid squares represent localities for specimens described in this report; open squares are previous reports. Fruita Paleontological Area in Colorado is the type locality (Rasmussen and Callison, 1981); Ninemile Hill in Wyoming reported by Trujillo (1999).

Colorado, was discussed by Scheetz (1991) and sphenodontid material was reported, but most of these specimens are similar to *Opisthias* (pers. obs.). Among the material, however, was one fragment of eilenodontine affinity (MWC 1200; Scheetz, pers. comm., 2001). With the four new specimens described here, *Eilenodon* is now known from three additional sites in Colorado and one in eastern Utah. Four

of the six known localities are thus in the Uncompahgre Plateau area (Fig. 3). The genus is unknown so far from the large microvertebrate collections from Como Bluff, Wyoming.

*Eilenodon* specimens have been found in fine-grained sediments at the Green Acres, Fruita Paleo Area, and Ninemile Hill localities, and in a coarse sandstone at the Dry

Mesa Quarry. The Westwater, Utah, specimen may have been a surface find, but in any case there is no record of the type of sediment in which it was found. Most of the vertebrate specimens from the Uraivan locality have been displaced from their original outcrop by road construction, but this material may have come from an overbank mudstone (Scheetz, 1991). MWC 1200, however, was a nearby surface find so its host matrix is unknown (Scheetz, pers. comm., 2001). The Dry Mesa specimen is somewhat worn and was likely transported some distance. Association of elements of the Fruita and Green Acres specimens suggests little postmortem transport.

Rasmussen and Callison (1981) suggested that *Eilenodon* was a herbivorous sphenodontian, and the sphenodontid *Toxolophosaurus* was probably herbivorous as well (Throckmorton et al., 1981). Reynoso (2000) described *Ankylosphenodon*, a herbivorous, aquatic sphenodontian from the Lower Cretaceous of Mexico that was until recently thought to be close to *Eilenodon* and *Toxolophosaurus* but is now placed as the sister taxon of *Sapheosaurus*. The dentary teeth of the type specimen of *Eilenodon* (LACM 120462) and those of at least two of the specimens described here, are worn down nearly level with the top of the dentary. The heavy wear on these two new specimens of *Eilenodon* suggests that indeed the type specimen is not unusual and that this sphenodontian probably fed on relatively coarse vegetation, possibly including seeds.

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