



The first amphisbaenians from Texas, with notes on other squamates from the middle Eocene Purple Bench Locality

Michelle R. Stocker & E. Christopher Kirk

To cite this article: Michelle R. Stocker & E. Christopher Kirk (2016): The first amphisbaenians from Texas, with notes on other squamates from the middle Eocene Purple Bench Locality, Journal of Vertebrate Paleontology

To link to this article: <http://dx.doi.org/10.1080/02724634.2016.1094081>

 View supplementary material 

 Published online: 18 Feb 2016.

 Submit your article to this journal 

 View related articles 

 View Crossmark data 

THE FIRST AMPHISBAENIANS FROM TEXAS, WITH NOTES ON OTHER SQUAMATES FROM THE MIDDLE EOCENE PURPLE BENCH LOCALITY

MICHELLE R. STOCKER^{*,1,2,†} and E. CHRISTOPHER KIRK^{2,3}

¹Department of Geological Sciences, Jackson School of Geosciences, 1 University Station, C1100, The University of Texas at Austin, Austin, Texas 78712, U.S.A. ;

²Vertebrate Paleontology Laboratory, Jackson School of Geosciences, J. J. Pickle Research Campus, 10100 Burnet Road, PRC 6-VPL R7600, The University of Texas at Austin, Austin, Texas 78712, U.S.A.;

³Department of Anthropology, 1 University Station, C3200, The University of Texas at Austin, Austin, Texas 78712, U.S.A., eckirk@austin.utexas.edu

ABSTRACT—The shift to a cooler and drier climate through the Paleogene has been interpreted as the driver for changes in diversity and biogeographic distributions among mammalian taxa during the Eocene, leading to hypotheses of continued tropical climatic refugia in West Texas through the middle and late Eocene. However, the presence of ectothermic reptiles during that time has not been documented in detail and would potentially provide additional climatic indicators. We provide the first description of the herpetofauna from the Devil's Graveyard Formation (DGF), West Texas, the southernmost, well-sampled middle Eocene basin in North America. Specimens are derived from beds correlated with the Ui3 biochron of the late Uintan North American Land Mammal 'Age' (~45–40 Ma). We report the first amphisbaenians known from Texas, expanding our spatial and climatic understanding of rhineurid distribution, as well as the first glyptosaurine anguimorphs and alethinophidian snakes from the Purple Bench assemblage. These new amphisbaenians preserve a jugal posteriorly enclosing the orbit and an extremely short retroarticular process and are recovered in a clade comprising †*Spathorhynchus*, †*Dyticonastis*, †*Ototriton*, and †*Hyporhina*. The documentation of the amphisbaenians and other squamates provides biogeographic range extensions of these taxa to West Texas. Despite suggestions that West Texas was a middle and late Eocene climatic refugium for mammals adapted to subtropical forested environments, rhineurid amphisbaenians show a wide range of temperature tolerances up to the beginning of the Neogene.

<http://zoobank.org/urn:lsid:zoobank.org:pub:3E55D6BF-0691-4220-9212-0407F454BE53>

SUPPLEMENTAL DATA—Supplemental materials are available for this article for free at www.tandfonline.com/UJVP

Citation for this article: Stocker, M. R., and E. C. Kirk. 2016. The first amphisbaenians from Texas, with notes on other squamates from the middle Eocene Purple Bench locality. *Journal of Vertebrate Paleontology*. DOI: 10.1080/02724634.2016.1094081.

INTRODUCTION

Amphisbaenians constitute a clade of fossorial squamates whose morphology is characterized by an elongate body form, limblessness (in all but the Bipedidae), and modifications to the skull that reflect its use in head-first burrowing (Gans, 1974; Kearney, 2003). Recent total evidence analyses of their relationships with respect to other squamates (e.g., Townsend et al., 2004; Vidal and Hedges, 2005; Müller et al., 2011; Hipsley and Müller, 2014) recover amphisbaenians as the sister group to Lacertidae. Within Amphisbaenia, five major clades generally are recognized, but controversy exists as to which North American clade is the most basally diverging: the limbed Bipedidae according to morphological data (Kearney, 2003; Gauthier et al., 2012) or Rhineuridae as indicated by molecular evidence (Kearney and Stuart, 2004; Macey et al., 2004; Vidal et al., 2008; Wiens et al., 2012).

Extinct North American amphisbaenians are perhaps the best understood of the known amphisbaenian fossils, and they are

represented by multiple skulls and postcrania from the Paleocene to the Recent (e.g., Estes, 1983; Sullivan, 1985; Kearney, 2003). The Paleogene fossil record of amphisbaenians in North America primarily includes specimens from the northern Great Plains and Rocky Mountain regions (Berman, 1973, 1976, 1977; Hutchison, 1992; Williamson and Lucas, 1993; Kearney, 2003; Smith, 2006, 2009, 2011; Hembree, 2007), California (Brattstrom, 1958; Walsh and Estes, 1985), and Baja California (Novacek et al., 1987). Nearly all of those specimens were identified as rhineurids closely related to the extant *Rhineura floridana*, the Florida worm lizard (e.g., Kearney, 2003). *Rhineura floridana* currently is known from the Pliocene to Recent of the Florida peninsula and part of Georgia (e.g., Gans, 1967a, 1967b; Zug, 1968; Estes, 1983; Mulvaney et al., 2005; Hipsley and Müller, 2014). This geographic restriction could be the result of phylogenetic niche conservatism, in which evolutionary constraints limited the geographic distribution of *R. floridana* to environments that resemble those inhabited by extinct members of Rhineuridae (Wiens and Graham, 2005; Losos, 2008; Wiens, 2008; Wiens et al., 2010). However, an analysis of environmental tolerances within Rhineuridae demonstrated that extinct rhineurids were able to tolerate environmental conditions that were drier and cooler than the habitats currently occupied by *R. floridana* (Hipsley and Müller, 2014).

Here we describe the first amphisbaenian fossils known from Texas. These specimens represent a new rhineurid taxon that

*Corresponding author.

†Current address: Department of Geosciences, 4044 Derring Hall, Virginia Polytechnic Institute and State University, Blacksburg, Virginia 24061, U.S.A.; stockerm@vt.edu

Color versions of one or more of the figures in this article can be found online at www.tandfonline.com/ujvp.

currently is known only from the late Uintan (Ui3) Purple Bench locality of the Devil's Graveyard Formation (middle Eocene). We also provide preliminary descriptions and identifications for other squamate fossils recovered from the Purple Bench locality, including glyptosaurine anguimorphs and alethinophidian snakes. These new descriptions complement the already well-known mammalian fauna and provide a more comprehensive documentation of the Purple Bench faunal assemblage.

Institutional Abbreviations—TMM, Jackson School of Geosciences Vertebrate Paleontology Laboratory, The University of Texas at Austin, Austin, Texas; USNM, Smithsonian Institution National Museum of Natural History, Washington, D.C.

GEOGRAPHIC AND GEOLOGIC SETTING

The fossils described herein were collected between 2005 and 2014 at Midwestern State University's Dalquest Desert Research Site (Fig. 1). Located in the Big Bend region of southwest Texas, the Dalquest Desert Research Site presents extensive exposures of the middle Eocene Devil's Graveyard Formation (DGF), including the highly fossiliferous Purple Bench locality (TMM 41672). This locality occurs within the unnamed middle member of the DGF and was mapped by Stevens and colleagues in their initial description of the formation (Stevens et al., 1984; Wilson, 1984, 1986; Williams and Kirk, 2008; Campisano et al., 2014). The DGF primarily includes fluviially deposited volcanoclastic sediments derived from volcanic sources in Chihuahua and the Trans-Pecos volcanic field of West Texas (Stevens et al., 1984; Runkel, 1988, 1990). These sediments accumulated within the Tornillo Basin, the southernmost Laramide-aged intermontane basin in the North American cordillera (Lehman, 1991). In the vicinity of the Dalquest Desert Research Site and adjacent Agua Fria Ranch, the DGF is bounded unconformably below by Late Cretaceous marine sediments and above by the ~33.28 Ma Mitchell Mesa Rhyolite (Stevens et al., 1984; Henry et al., 1998).

A variety of relative and numerical dating techniques indicate that the DGF spans the middle Eocene to early Oligocene (Wilson, 1986; Robinson et al., 2004; Campisano et al., 2014). The Purple Bench locality occurs stratigraphically above a series of localities in the lower member of the DGF that have yielded mammalian fossils characteristic of the early Uintan North American Land Mammal 'Age' or NALMA (i.e., biochron Ui1b; Campisano et al., 2014). Dating of volcanic tuffs bracketing those Ui1b localities by the $^{40}\text{Ar}/^{39}\text{Ar}$ method has yielded statistically indis-

tinguishable ages of 44.88 ± 0.04 and 45.04 ± 0.10 Ma (Campisano et al., 2014). Mammalian fossils characteristic of the Duchesnean NALMA also occur stratigraphically above the Purple Bench locality (Wilson, 1986; Robinson et al., 2004). Based on $^{40}\text{Ar}/^{39}\text{Ar}$ dates from the Lapoint Tuff in the Duchesne River Formation in eastern Utah, the beginning of the Duchesnean NALMA can be no later than 39.75 ± 0.04 Ma (Prothero and Swisher, 1992). Accordingly, the absolute age of fossils recovered from Purple Bench must be between approximately 45 and 40 Ma. These dates are consistent with the characteristically late Uintan (biochron Ui3) mammalian fauna that has been recovered from Purple Bench and other DGF middle member localities constituting the Serendipity Local Fauna (Wilson, 1986; Robinson et al., 2004; Williams and Kirk, 2008). The Ui3 faunas in the Uinta Basin were dated by paleomagnetic correlation to span the transitions between Chrons C20r and C18r, with radiometric dates of 43.432–41.154 Ma (Robinson et al., 2004; Gradstein et al., 2012). Previous paleomagnetic data indicated deposition of the lower and middle members of the DGF during Chrons C20r and C20n, but magnetostratigraphic data were unresolved for the Serendipity Local Fauna (Walton, 1992; Prothero, 1996; Williams and Kirk, 2008). Revisions to that timescale and modified correlations for the DGF by Prothero (1996) placed the Purple Bench locality in Chron C18r (i.e., 41.154 Ma–40.145 Ma; Gradstein et al., 2012).

SYSTEMATIC PALEONTOLOGY

SQUAMATA Oppel, 1811, sensu Merrem, 1820

AMPHISBAENIA Gray, 1844

RHINEUROIDEA Vanzolini, 1951

RHINEURIDAE Vanzolini, 1951

SOLASTELLA COOKEI, gen. et sp. nov.

(Figs. 2–4)

Etymology—Generic epithet combines Latin 'sola' ('alone') and 'stella' ('star'), in reference to Texas, the 'Lone Star State.' Specific epithet honors Dr. William B. Cook, botanist and professor of biology at Midwestern State University.

Holotype—TMM 41672-246, partial skull and articulated left mandibular ramus missing anterior portion of the premaxilla, right maxilla, right circumorbital elements, and right side of the occipital condyle.

Paratype—TMM 41672-243, skull with complete mandible.

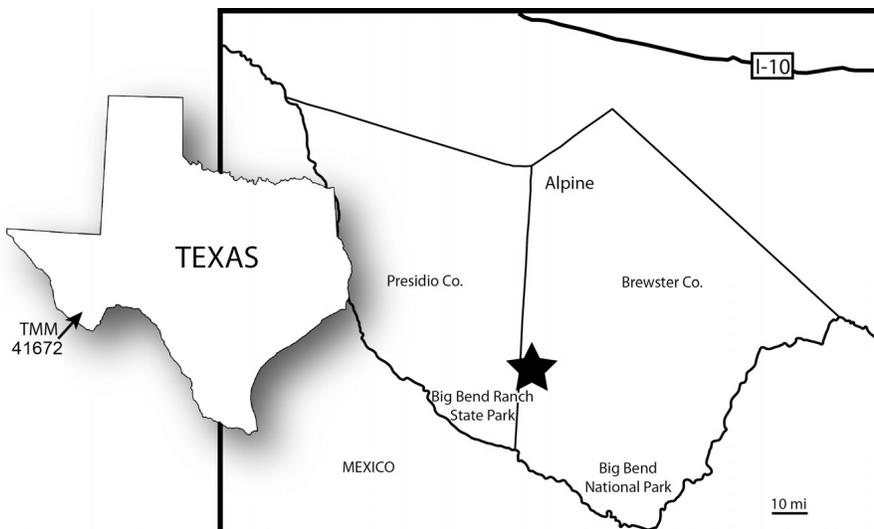


FIGURE 1. Map of West Texas, U.S.A., showing relative position of exposures of the Purple Bench locality (TMM 41672). Detailed map of area surrounding the Dalquest Desert Research Site, including Big Bend National Park and Big Bend Ranch State Park. Star indicates the approximate geographic provenance of specimens discussed in the text.

Referred Specimens—TMM 41672-244, partial skull with partial left mandibular ramus; TMM 41672-245, partial skull with left mandibular ramus; TMM 41672-247, partial skull; TMM 41672-249, partial skull. Nearly all of the fossils are preserved in nodules. Mechanical preparation by pin vise and pneumatic tool (HW-1 aircscribe or Microjack no. 4) removed the encrusting matrix on the outer surfaces of the elements in all places where stability of the fossil was not compromised.

Type Locality—Purple Bench locality (TMM 41672), unnamed middle member, Devil's Graveyard Formation, Brewster County, Texas, U.S.A. All specimens included in this study were derived from surface exposures of the Purple Bench locality and were surface collected during multiple field expeditions. The Purple Bench locality crops out in multiple local, though dis-junct, geographic areas, and the vertebrate skeletal materials were collected and sorted according to those sublocalities. Detailed provenance data for these specimens are on file at the TMM.

Age—Late Uintan (U13), middle Eocene.

Diagnosis—Autapomorphies of this new taxon include presence of jugal articulation with parietal at posterodorsal corner of orbit and retroarticular process extremely short. This new taxon also preserves the following combination of characters: shares with Rhineuroidea presence of a strong craniofacial angle and enlarged 'U'-shaped occipital condyle (Kearney, 2003); shares with Rhineuridae presence of ventrally open nares, low premaxillary tooth count, and presence of pterygoid-vomer contact; shares with †*Dyticonastis*, †*Spathorhynchus*, and †*Hyporhina* presence of jugal that encloses orbit posteriorly; and shares with †*Spathorhynchus* unforked posteromedial process of premaxilla.

COMPARATIVE MORPHOLOGICAL DESCRIPTION

TMM 41672-246 is a mostly complete cranium (Fig. 2), but the anterior and right lateral portions of the skull are damaged (Fig. 2C–E). An accurate anteroposterior length of the skull cannot be determined for TMM 41672-246 because the anterior portion of the premaxilla is missing. What is preserved measures approximately 12.3 mm anteroposteriorly along the midline of the skull from the partial premaxilla to the occipital condyle. The anteroposterior length of the skull of TMM 41672-243 (Fig. 3) is 13.8 mm in comparison; the skull measures 9.2 mm at its widest across the lateral edges of the jugals. Furthermore, in TMM 41672-243, postorbital skull length (8.7 mm) is 63% of total skull length. Such elongation of the postorbital region of the skull is characteristic of Amphisbaenia and several other fossorial squamate clades (e.g., anniellids, snakes, dibamids; Berman, 1973; Kearney, 2003:character 26). There is a strong craniofacial angle between the preorbital rostral, or facial, segment and the postorbital occipital, or cranial, segment of the skull (Figs. 2, 3), which is diagnostic for Rhineuroidea (Kearney, 2003). This results in the snout being depressed relative to the neurocranium. The snout is prognathous.

Premaxilla

A single tooth is visible in TMM 41672-243 at the midline (Fig. 3D), although single small teeth may have been present on either side. The zygous premaxilla has an unforked posteromedial process in anterior view (Fig. 2E). That process is narrow and separates the nasals at least in the medial portions of their contacts, and the process does not contact the frontals externally. The extent of the premaxilla, with respect to the formation of a spatulate anterior process (Kearney, 2003:character 30), cannot be determined for TMM 41672-246. More of the anterior portion of the premaxilla is preserved in TMM 41672-243 and TMM 41672-247, and in these specimens the premaxilla appears prognathous but not spatulate. Among extinct rhineurids, Kearney

(2003) coded †*Spathorhynchus* and †*Dyticonastis* as possessing a spatulate rostral process of the premaxilla. However, Berman's (1973, 1976, 1977) images for each of those taxa do not show a premaxillary morphology similar to that shown by Kearney (2003), as illustrated in her figure 13 for the amphisbaenian †*Listromycter*. Because of the incomplete preservation of this area in all currently known specimens from the Purple Bench locality and the need to clarify the meaning of a 'spatulate process' of the premaxilla, we coded this character as '?' for †*Solastella*.

Maxilla

The maxilla is a roughly triangular element in lateral view (Figs. 2A, 3B), articulating anteromedially with the nasal, dorsally with the frontal, and posteriorly with the jugal. The external surface of the facial process is perforated by three or four labial foramina that are roughly parallel to the ventral margin of the maxilla. Along its dorsal margin, the blunt edge of the frontal process of the maxilla contacts the frontal in a straight suture and excludes the nasal from contacting the element interpreted here as a potential prefrontal (see below). The type of contact with the prefrontal is unclear because of damage in this area of the skull in TMM 41672-246. The external surfaces of the cranial elements are too abraded in TMM 41672-243 to aid in this determination. The posteroventral process of the maxilla forms the anteroventral margin of the orbit, and the posterior corner of this process laterally overlaps an anterior process of the jugal.

A deep overhang of the lateral edge of the maxilla lateral to the tooth row (Fig. 2A, B, G) results in an 'L'-shaped coronal cross-section. An additional five foramina open ventrally along the length of this overhang and roughly correspond to the alveoli. Five pleurodont maxillary teeth are visible in TMM 41672-243, whereas there are four visible maxillary teeth in TMM 41672-246. Kearney (2003) reported six or seven maxillary teeth for extinct rhineurids. There is a small diastema posterior to the second mesial-most maxillary tooth that may have accommodated a small additional tooth. All teeth taper to a point and are slightly recurved at their tips (Figs. 2, 3).

Nasal

The nasals are paired elements that articulate with the frontals, maxillae, and premaxilla on the external surface of the skull. The anterodorsal portions of most of both nasals are missing in TMM 41672-246 and TMM 41672-243 so that natural endocasts of the nasal passages are visible in anterior and dorsal views. The nasal passages are directed anterolaterally and would have opened through ventrally oriented nares (Fig. 2C–F). Small foramina preserved in the posterolateral corners of the nasals may have been present over more of the dorsal surface of these elements. The contact with the maxilla extends posterodorsally along the anterolateral corner of the rostral blade of the snout. The nasals contact each other posteriorly at the midline, and together they articulate with the frontals in a roughly coronally oriented suture.

Frontal

The paired frontals contact each other on the dorsal surface of the skull by a nearly straight interfrontal suture that trends along the midline (Fig. 2C–F). The dorsal surfaces (= dorsal plates of Kearney et al., 2005) of the frontals are pierced by multiple foramina. These foramina are arranged in anteroposteriorly oriented columns, with one column situated closer to the midline suture and the remaining foramina concentrated in the posterolateral regions of the frontals in TMM 41672-246. Such foramina more evenly cover the frontal surfaces in TMM 41672-245.

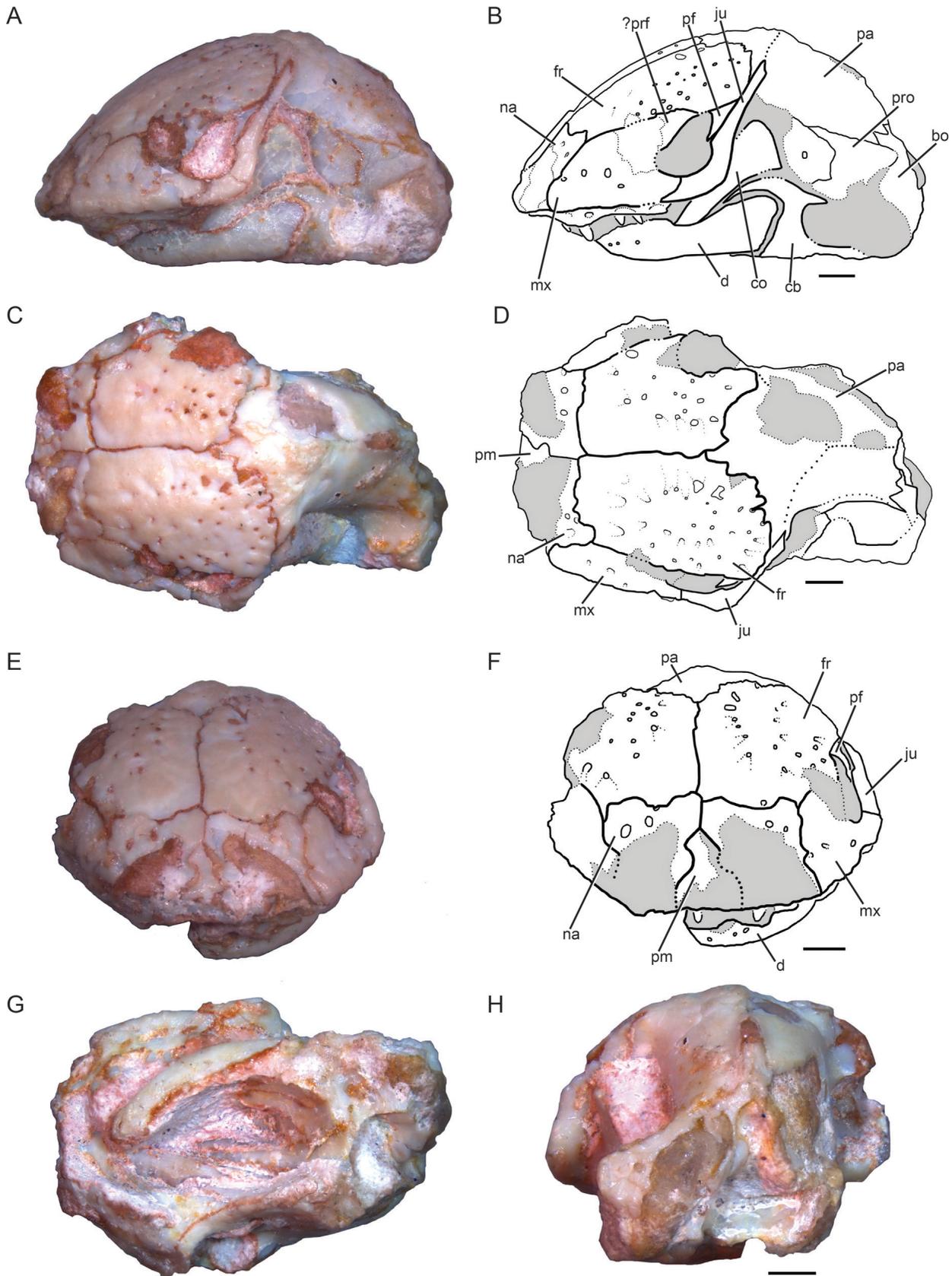


FIGURE 2. †*Solastella cookei*, new genus and species, TMM 41672- 246 (holotype). **A, B**, skull in left lateral view with interpretive line drawing; **C, D**, skull in dorsal view with interpretive line drawing; **E, F**, skull in anterior view with interpretive line drawing; **G**, skull in ventral view (anterior to the left); **H**, skull in posterior view. **Abbreviations:** **bo**, basioccipital; **cb**, compound bone; **co**, coronoid; **d**, dentary; **fr**, frontal; **ju**, jugal; **mx**, maxilla; **na**, nasal; **pa**, parietal; **pf**, postfrontal; **pm**, premaxilla; **?prf**, possible prefrontal; **pro**, prootic. Scale bars equal 1 mm.

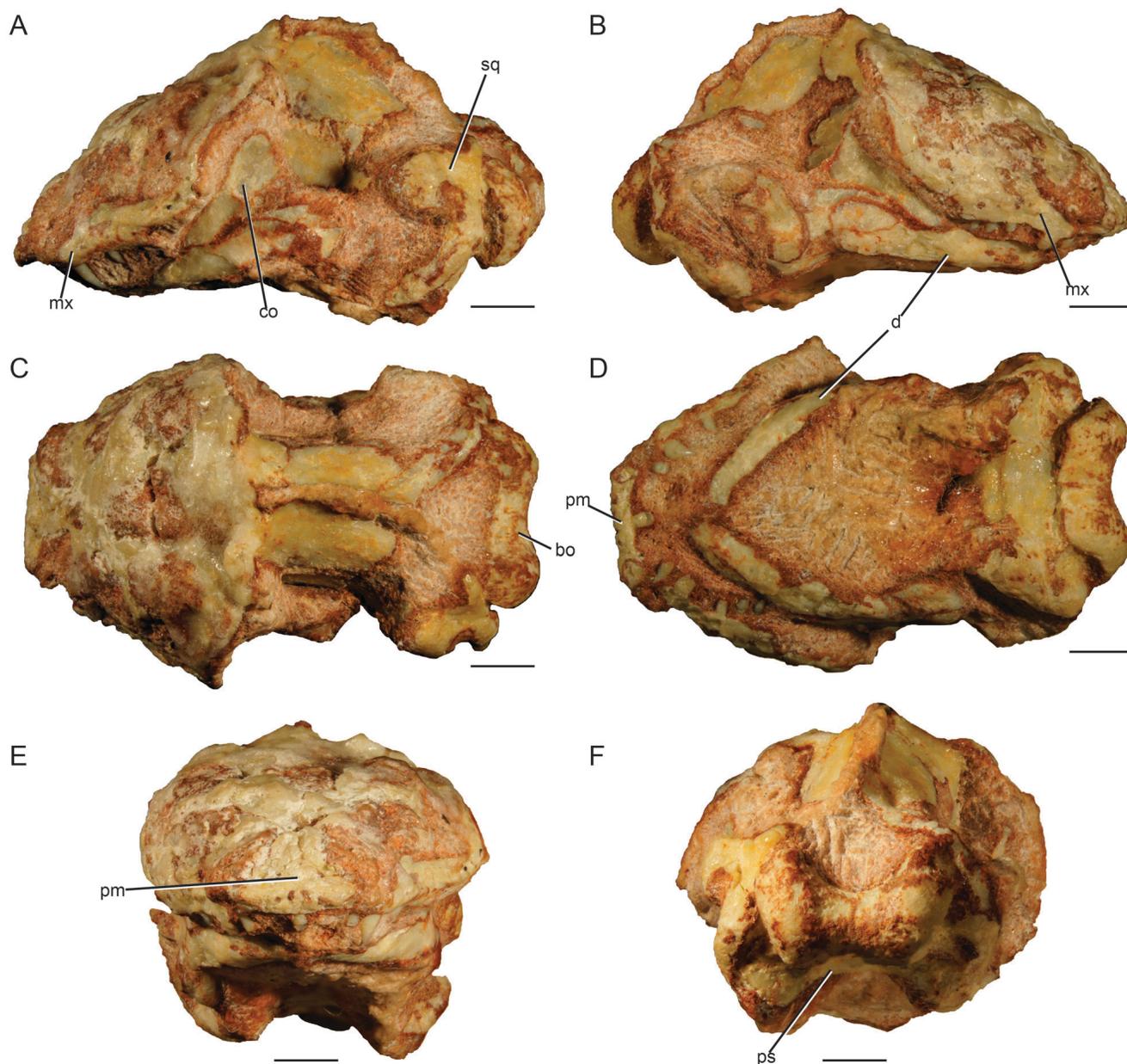


FIGURE 3. †*Solastella cookei*, new genus and species, TMM 41672-243 (paratype). **A**, skull in left lateral view; **B**, skull in right lateral view; **C**, skull in dorsal view (anterior to the left); **D**, skull in ventral view (anterior to the left); **E**, skull in anterior view; **F**, skull in posterior view. **Abbreviations:** **bo**, basioccipital; **co**, coronoid; **d**, dentary; **mx**, maxilla; **ps**, parabasisphenoid; **pm**, premaxilla; **sq**, squamosal. Scale bars equal 1 mm.

Similar foramina were reported for †*Rhineura hatcheri* (Kearney et al., 2005), and they were hypothesized to communicate with the cutaneous sensory branches of the trigeminal nerve (cranial nerve [CN] V) based on the description of *Ctenosaura* by Oelrich (1956).

On the dorsal surface of the skull, the posterior portions of the frontals are separated from each other by a small anterior process of the parietal (= the apical process). The frontal-parietal suture is a rounded ‘W’ shape in dorsal view (Fig. 2), and the dorsal process of the jugal (see below) articulates with the frontal along the posterolateral corner of that suture.

Jugal and Circumorbital Region

The most distinctive feature of †*Solastella* is the presence of an enclosed orbit (Figs. 2, 3). This feature also is reported in †*Dyticonastis*, †*Spathorhynchus*, and †*Hyporhina* (Berman, 1973, 1976, 1977; Kearney, 2003). The posterior margin of the orbit is enclosed by a complete jugal, which is slender and rounded in TMM 41672-246 and bears two externally visible processes: an anteroventral and a dorsal. These processes form an ~110° angle, and the apex of that angle forms the mediolaterally widest portion of the skull. The anteroventral process of the jugal is rounded ventrally and slightly expanded in width relative to the dorsal process of the jugal. This process extends further

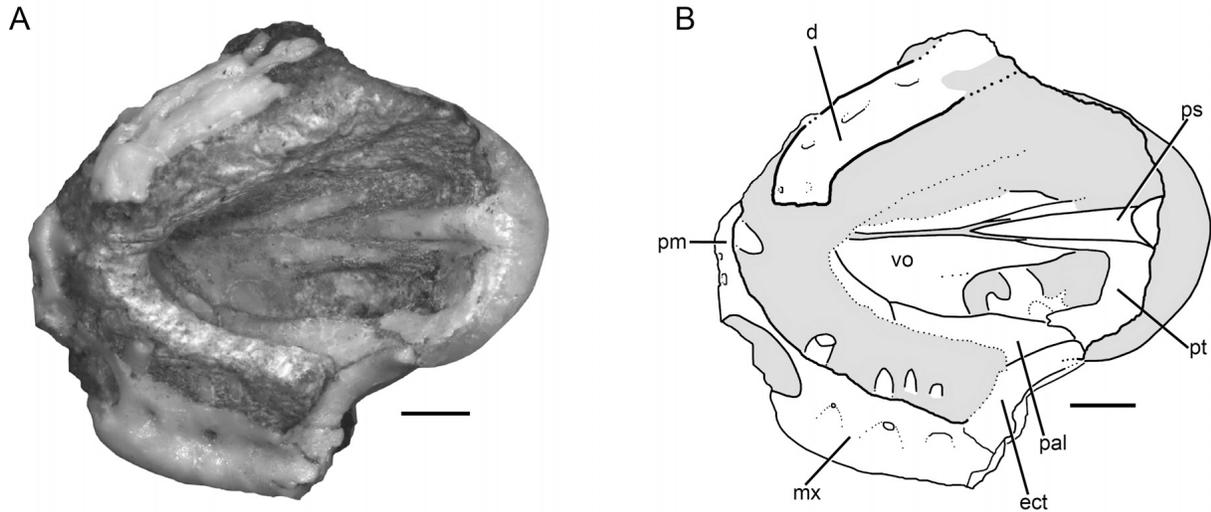


FIGURE 4. †*Solastella cookei*, new genus and species, TMM 41672-244. **A, B**, skull in ventral view with interpretive line drawing (anterior to the left). **Abbreviations:** **d**, dentary; **ect**, ectopterygoid; **mx**, maxilla; **pal**, palatine; **pm**, premaxilla; **ps**, parabasisphenoid; **pt**, pterygoid; **vo**, vomer. Scale bars equal 1 mm.

anteriorly than the anteroventral process of the jugal in †*Spathorhynchus fossorium* (USNM 26317). The rod-like dorsal process of the jugal articulates with the anterolateral corner of the parietal, just posterior to the frontal.

A prefrontal may be present in †*Solastella* based on interpretations of a small portion of bone exposed anterodorsal to the orbit in TMM 41672-246. What remains of this small element articulates between the frontal and the frontal process of the maxilla. There appears to be a postfrontal in TMM 41672-246 as well (Fig. 2). A postfrontal previously was reported for †*Spathorhynchus*, †*Dyticonastis*, †*Hyporhina*, and †*Ototriton* (Kearney, 2003) but not †*Rhineura hatcherii* (Kearney et al., 2005). However, poor preservation in this area in TMM 41672-246 prohibits definitive knowledge of whether both a prefrontal and a postfrontal were present in this specimen or whether the potential prefrontal is actually a portion of the maxilla separated by damage. None of the other †*Solastella* specimens from Purple Bench preserve this region of the skull without damage.

Parietal

The parietal is a single, fused element with no parietal foramen, and it contributes to most of the postorbital length of the skull (Figs. 2, 3). A sagittal crest is present along the anteroposterior midline of this element, terminating anteriorly in the apical process and posteriorly just dorsal to the foramen magnum. In TMM 41672-246, this apical process is small and triangular, but in TMM 41672-245, the process is larger and divides the frontals nearly to their midpoints. Anterodorsally, the parietal contributes to the deflected facial portion of the skull, so that the anterior-most portion of the parietal is on the facial plane of the skull (Fig. 2). There appears to be a small anterolateral process of the parietal along the canthus rostralis just anterior to the dorsal process of the jugal, but this feature differs from that observed by Berman (1973) for †*Spathorhynchus fossorium*, in which the process is wedged between the prefrontal and postfrontal. Posterior to the canthus rostralis, the parietal is constricted mediolaterally along the lateral wall of the braincase. These lateral walls are enclosed dorsally by the temporal laminae of the parietal that extend ventrally to contact the alar processes of the prootics (Fig. 2). The parietal is contacted along its

posterior margin by the supraoccipital medially and the remainder of the occipital complex laterally (see below).

Palate

The palate is strongly vaulted and is formed by the vomers, palatines, pterygoids, and ectopterygoids (Fig. 4). Anteriorly, each vomer has a single foramen penetrating the ventral surface (Figs. 2G, 4b). The lateral edges of the vomers are concave approximately halfway along their anteroposterior length, and they form the medial margins of the fenestrae vomeronasalis. The lateral margin of the fenestra vomeronasalis appears to be formed by a medial process of the maxilla. The ectopterygoid is slender and articulates medially with the posterior corner of the maxilla, medial to the body of the jugal. Posterolaterally, the pterygoids have plate-like surfaces that articulate to the lateral edges of the cultriform process of the parabasisphenoid. The anterodorsally oriented cultriform process is elongated and separates the tapered posterior processes of the vomers at its anterior extent (Fig. 4b; Kearney, 2003:character 95[2]). None of the palatal elements have teeth, as is typical for amphisbaenians (Kearney, 2003:characters 90, 91).

Postorbital Region and Occipital Complex

As in many amphisbaenians, the posterior elements of the cranium fuse to form a single, complex element (= the occipital complex; Kearney et al., 2005) that encloses the braincase and posterior portions of the skull (Figs. 2, 3). This complex articulates with the posterior edge of the parietal dorsal to the foramen magnum and laterally with or including the alar processes of the prootics. The widest portion of this region of the skull is across the otic region. A small hooked squamosal appears to be attached to the lateral surface of the otic region posterodorsal to the anterodorsally rounded quadrate in TMM 41672-243.

Ventrally, the parabasisphenoid bears laterally expanded basiptyergoid processes. None of the currently known specimens of †*Solastella* clearly preserve 'Element X' (epiphyseal caps of questionable homology) on the ventrolateral processes, although they may be fused (Kearney et al., 2005). The posterior portion of the body of the parabasisphenoid/occipital complex slopes

posterodorsally to meet the discrete ventral edge of the occipital condyle without forming a distinct condylar neck (Fig. 3D, F).

In posterior view, the occipital condyle is a large ‘U’-shaped bar (Kearney, 2003:character 106[2]; Fig. 3) similar to that of †*Spathorhynchus fossorium* (USNM 26317). The occipital condyle is elevated above the ventrolateral processes of the basicranium and enlarged so that the foramen magnum opens posterodorsally. The foramen magnum is narrow at its dorsal extent and rounded and wide ventrally. The ventrolateral processes are more laterally positioned than the lateral edges of the occipital condyle, and they are slightly pointed and angled medially, unlike the gently rounded ventrolateral processes in †*Rhineura hatcherii* (Kearney et al., 2005). Between the ventrolateral processes, the occipital condyle, and the posterior portions of the otic capsules are narrow and deep occipital recesses.

Mandible

The mandible is composed of the dentary anteriorly, a large coronoid, and the postdentary elements (= compound bone). The left and right mandibular rami may have been loosely joined at the symphysis posteroventral to the prognathous premaxilla. The rami gently curve posterolaterally to their posterior edges just posterior to the quadrate articulation (Fig. 3b). The dentary tooth count is between five and seven teeth, based on unpublished high-resolution X-ray computed tomographic (CT) data for TMM 41672-243 and depending on the presence of replacement teeth in that specimen (Kearney, 2003:character 119[0]). These teeth appear to be pointed and are restricted to the anterior half of the dentary.

The coronoid is a dorsoventrally tall element in †*Solastella*, with an anterior process that contacts the dorsolateral surface of the dentary. The dorsal margin is not sharply angled as in †*Spathorhynchus* (Berman, 1973, 1977) and is more similar to the more rounded dorsal margin in †*Dyticonastis* (Berman, 1976). As preserved in TMM 41672-246 and TMM 41672-243, the anterior portion of the coronoid is medial to the jugal.

The postdentary compound bone appears to be anteroposteriorly short (Figs. 2A, B; 3B), with little to no retroarticular process. The quadrate-articular contact is nearly at the ventral margin of the mandible and is oriented posterodorsally, indicating that the distal end of the quadrate was oriented anteromedially.

Postcrania

We attribute several isolated vertebrae to Amphisbaenia (e.g., TMM 41672-254, TMM 41672-261; Fig. 5), and these may also be remains of †*Solastella*. The dorsal surfaces of the nearly flat neural arches are striated as in †*Hyporhina*, †*Spathorhynchus*, and †*Dyticonastis*, and this may be a shared feature of rhineurids (Berman, 1972, 1973, 1976). The transverse processes are medio-laterally wide, and there is an anteroposterior connection between the prezygapophyses and the postzygapophyses.

PHYLOGENETIC ANALYSES

We explored the systematic relationships of our new amphisbaenian material using two main analyses in order to account for the differences in topologies that arise as a result of morphological versus molecular analyses of amphisbaenian relationships (e.g., Kearney, 2003; Kearney and Stuart, 2004; Macey et al., 2004; Vidal et al., 2008; Gauthier et al., 2012; Wiens et al., 2012, also see Supplemental Data). First, we added †*Solastella* to the total evidence matrix used most recently by Hipsley and Müller (2014), which incorporated 162 morphological characters from Kearney (2003) and molecular sequence data consisting of 2842 base pairs from CMOS and RAG1. Character states for †*Solastella* are listed in Appendix 1. We performed a Bayesian

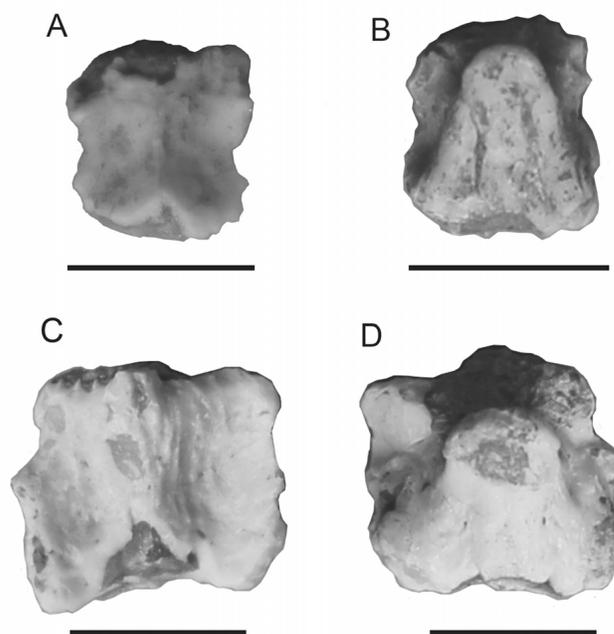


FIGURE 5. Amphisbaenia. Isolated vertebrae from the Purple Bench locality. **A**, TMM 41672-261 in dorsal view; **B**, TMM 41672-261 in ventral view; **C**, TMM 41672-254 in dorsal view; **D**, TMM 41672-254 in ventral view. Scale bars equal 5 mm.

phylogenetic analysis of the combined data sets in MrBayes 3.2.1 (Huelsenbeck and Ronquist, 2005) using the same parameters as Hipsley and Müller (2014). Results of our Bayesian analysis (average standard deviation of split frequencies = 0.010972) were congruent with those reported by Hipsley and Müller (2014), with some clades collapsed into polytomies and posterior probabilities slightly lower for most nodes. We recovered †*Solastella* as the sister taxon to a †*Spathorhynchus* + †*Dyticonastis* clade (Fig. 6).

We performed a secondary parsimony analysis in PAUP* 4.0b10 (Swofford, 2002) in order to minimize the effect of missing sequence data while still reflecting the molecular signal for the relationships among major amphisbaenian clades. For this analysis, we used the morphological partition of our Bayesian analysis (162 characters), using the same taxa ($n = 26$) as in that analysis and constrained all relationships other than those within Rhineuridae to those of the total evidence topology. Parsimony settings were set to collapse zero-length branches if minimum branch length was zero ('amb-'). Search parameters included heuristic search, 1000 random addition (RA) replicates, and tree-bisection-reconnection (TBR) branch swapping. All multistate characters were unordered, all characters were equally weighted, and multistate taxa were treated as polymorphisms, as in Kearney's (2003) analysis. Trees were rooted with Lacertidae.

Our parsimony analysis resulted in 411 most parsimonious trees (MPTs) of length (TL) 182, consistency index [CI] 0.754, retention index [RI] 0.812, and rescaled consistency index [RC] 0.612. Relationships among the rhineurids are poorly resolved in both the strict (Fig. 7A) and Adams (Fig. 7b) consensus trees, although we recover †*Hyporhina* as monophyletic in each, and †*Solastella* is recovered as part of the polytomy including all rhineurid taxa. Two additional parsimony analyses were conducted to reflect the taxonomic deletions by Kearney (2003) as a result of her determination of which taxa were equivalents. In these analyses, we deleted †*Rhineura amblyceps*, †*Rhineura hibbardi*, †*Rhineura hatcherii*, and †*Rhineura wilsoni* and performed

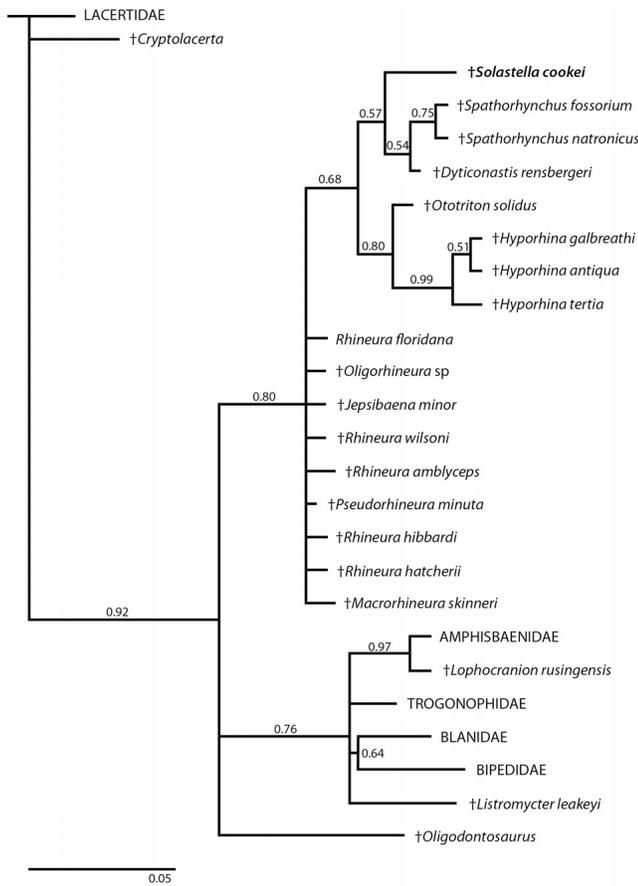


FIGURE 6. Results of Bayesian phylogenetic analysis using the matrix and parameters of Hipsley and Müller (2014) and including †*Solastella cookei*. †*Solastella* is recovered as the sister taxon to a †*Spathorhynchus* + †*Dyticonastis* clade.

the heuristic search with the constraint tree in place. The consensus topologies for these analyses were more resolved than those of the initial parsimony analysis. This additional analysis resulted in three MPTs (Fig. 7C, D; TL = 182, CI = 0.758, RI = 0.814, and RC = 0.617). Here, †*Solastella* was recovered in a polytomy with †*Dyticonastis*, †*Spathorhynchus*, †*Ototriton*, and †*Hyporhina* in the strict consensus, and in a polytomy with the †*Dyticonastis* + †*Spathorhynchus* clade and the †*Ototriton* + †*Hyporhina* clade in the Adams consensus.

DISCUSSION

Relationships of †*Solastella*

We assessed the systematic relationships of the new amphisbaenian taxon from Purple Bench, †*Solastella cookei*, by utilizing one of the most recent and most comprehensive analyses of amphisbaenian phylogenetic relationships available (Hipsley and Müller, 2014; hereafter, ‘HM2014,’ see also Longrich et al., 2015). That publication included both morphological and molecular data in order to account for the perceived conflict those two data sets present independently with respect to the systematic relationships within Amphisbaenia and the larger relationships of amphisbaenians within Squamata. We recovered †*Solastella* as a rhineurid amphisbaenian most closely related to †*Dyticonastis*, †*Spathorhynchus*, †*Ototriton*, and †*Hyporhina* (Figs. 6, 7).

The clade comprising *Rhineura*, †*Spathorhynchus*, †*Dyticonastis*, †*Ototriton*, †*Hyporhina*, and †*Solastella* is

supported by multiple apomorphic character states, but few of those characters are unambiguous synapomorphies. However, the clade comprising only the extinct taxa †*Spathorhynchus*, †*Dyticonastis*, †*Ototriton*, †*Hyporhina*, and †*Solastella* is supported by five unambiguous synapomorphies in our analysis. The rugose surface of the facial bones (HM2014:character 33[1]), presence of anterolateral parietal processes along the canthus rostralis (HM2014:character 56[1]), presence of elongated, paired, palatal processes of the maxillae (HM2014:character 94 [1]), presence of a pterygoid-vomer contact that separates the palatines (HM2014:character 96[1]), and presence of replacement teeth (HM2014:character 111[1]) all diagnose that clade.

The Fossil Record of Amphisbaenians in North America

These amphisbaenian fossils from Purple Bench represent the first members of the clade known from Texas. Amphisbaenians are known from approximately 180 extant species that are distributed worldwide (Gans, 1974, 2005; Uetz, 2013). However, only two clades are represented in North America—the three species of Bipedidae, known from Baja California and parts of western Mexico with no recognized fossil record (Estes, 1983), and the Rhineuridae. Extant rhineurids are known only from limited parts of the southeastern U.S.A. (Gans, 1967a, 1967b; Zug, 1968), but fossils from western North America have been assigned to Rhineuridae because of the shared presence of a strong craniofacial angle and a shovel-headed cranial morphology, along with multiple additional apomorphies supporting rhineurid monophyly (Kearney, 2003). However, discussions questioning monophyly of the more inclusive Rhineurioidea (Gans, 1974; Kearney, 2003) were centered on the possibility that those characters were convergently acquired through the fossorial adaptations of the group or a potential influence from geographic similarity (i.e., all shovel-headed amphisbaenians from North America may be rhineurids, but not all shovel-headed amphisbaenians worldwide constitute a monophyletic Rhineurioidea). Our data, including the new Texas specimens, do not conflict with an exclusively rhineurid North American fossil record. However, whether the similar morphologies observed in *Monopeltis* and other shovel-headed South American and African amphisbaenians are convergent or homologous remains to be tested, because detailed phylogenetic and morphological data for these taxa are still lacking.

†*Solastella cookei* from Purple Bench also represents the first record of a late middle Eocene (i.e., Uintan or Duchesnean) amphisbaenian from North America. The rhineurid fossil record spans the Paleocene to the Recent in North America (Estes, 1965; Kearney, 2003; Hembree, 2007; Hipsley and Müller, 2014), and includes all known fossils of North American amphisbaenians. However, there is a temporal gap in that record between the Miocene (Hemingfordian records of †*Rhineura marslandensis* and †*Rhineura sepultura* of Nebraska and South Dakota, respectively; Kearney, 2003), and Pleistocene localities in Florida that were reported to have rhineurid specimens (Holman, 1958, 1959). Furthermore, the Miocene record is problematic because Kearney (2003) considered both †*Rhineura marslandensis* and †*Rhineura sepultura* only to share diagnostic character states with Rhineuridae. Within the Eocene, the rhineurid taxa †*Spathorhynchus* (Wasatchian and Chadronian), †*Lestophis* (Bridgerian, but not included in any of our phylogenetic analyses because it was considered to be a taxonomic equivalent of Rhineuridae; Kearney, 2003), †*Jepsibaena* (Wasatchian), and †*Ototriton* (Wasatchian) are all known from Wyoming (Estes, 1983; Kearney, 2003). †*Dyticonastis* is known from the late Whitneyan (Oligocene) of the John Day Formation in Oregon (Berman, 1976). †*Hyporhina* is known by three species from the White River Formation (?Whitneyan) of

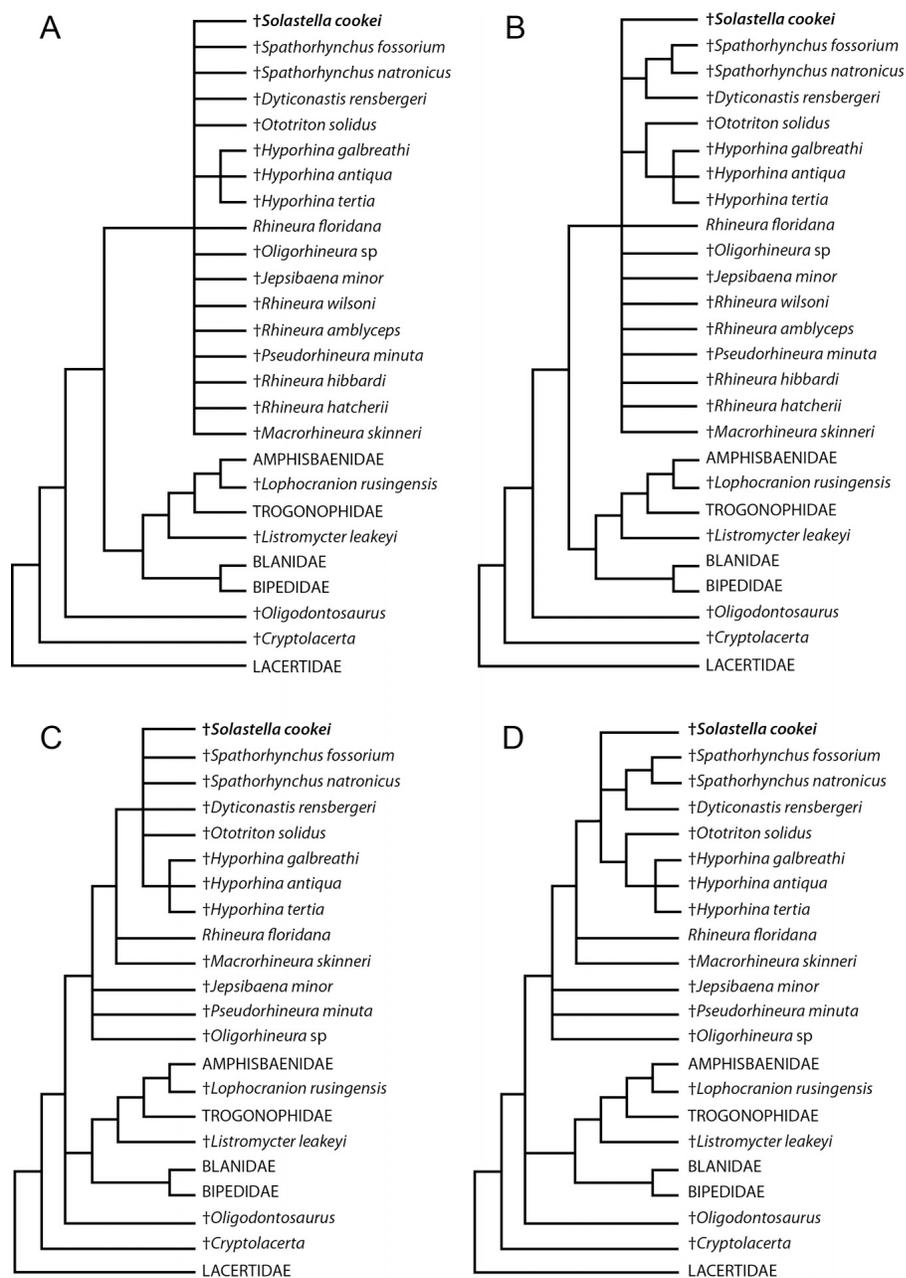


FIGURE 7. Results of parsimony-based phylogenetic analyses using the morphological portion of the matrix and parameters of Hipsley and Müller (2014) and including †*Solastella cookei*. **A**, strict consensus tree for analysis including †*Solastella cookei* based on full taxon sampling following Hipsley and Müller (2014); **B**, Adams consensus tree for analysis including †*Solastella cookei* based on full taxon sampling following Hipsley and Müller (2014). In both **A** and **B**, †*Solastella cookei* is recovered as part of a polytomy of all Rhineuridae. **C**, strict consensus tree for analysis including †*Solastella cookei* based on reduced taxon sampling following Kearney (2003). †*Solastella cookei* is recovered as part of a polytomy including †*Dyticonastis*, †*Spathorhynchus*, †*Ototriton*, and †*Hyporhina*; **D**, Adams consensus tree for analysis including †*Solastella cookei* based on reduced taxon sampling following Kearney (2003). In both **C** and **D**, †*Solastella cookei* is more closely related to †*Dyticonastis*, †*Spathorhynchus*, †*Ototriton*, and †*Hyporhina* than to *Rhineura floridana*.

Colorado, South Dakota, and Wyoming (Gilmore, 1928; Estes, 1983). These extinct taxa all share the presence of enclosed orbits and a shovel-headed cranial shape, in contrast to extant *Rhineura*, which does not have a posteriorly enclosed orbit (Kearney, 2003).

Other Squamate Material from Purple Bench

Multiple specimens were collected from Purple Bench that we identified as various taxa within Squamata (Fig. 8) strictly based on preserved morphological characteristics outlined by Estes (1983), Kearney (2003), Conrad (2008), Evans (2008), and Gauthier et al. (2012).

Some squamate vertebrae are procoelous, and we attribute these (e.g., TMM 41672-265, TMM 41672-266, TMM 41672-267, TMM 41672-268) to alethinophidian snakes because of the presence of the following characters determined to be diagnostic for the group by Head (2002). The anterior cotyles are expanded and have sharply delineated margins. The ventral surfaces of the vertebrae bear subcentral paralympathic fossae, paired and symmetrical subcentral foramina, and a sharp midline hemal keel, which terminates in a point just anterior to the sharply rimmed condyles. There are also distinct zygosphenes-zygantrum complexes present in these vertebrae.

SERPENTES Linnaeus, 1766
ALETHINOPHIDIA Nopcsa, 1923
(Fig. 8A–C)

ANGUIMORPHA Fürbringer, 1900
ANGUIDAE Gray, 1825
GLYPTOSAURINAE McDowell and Bogert, 1954
(Fig. 8D–H)

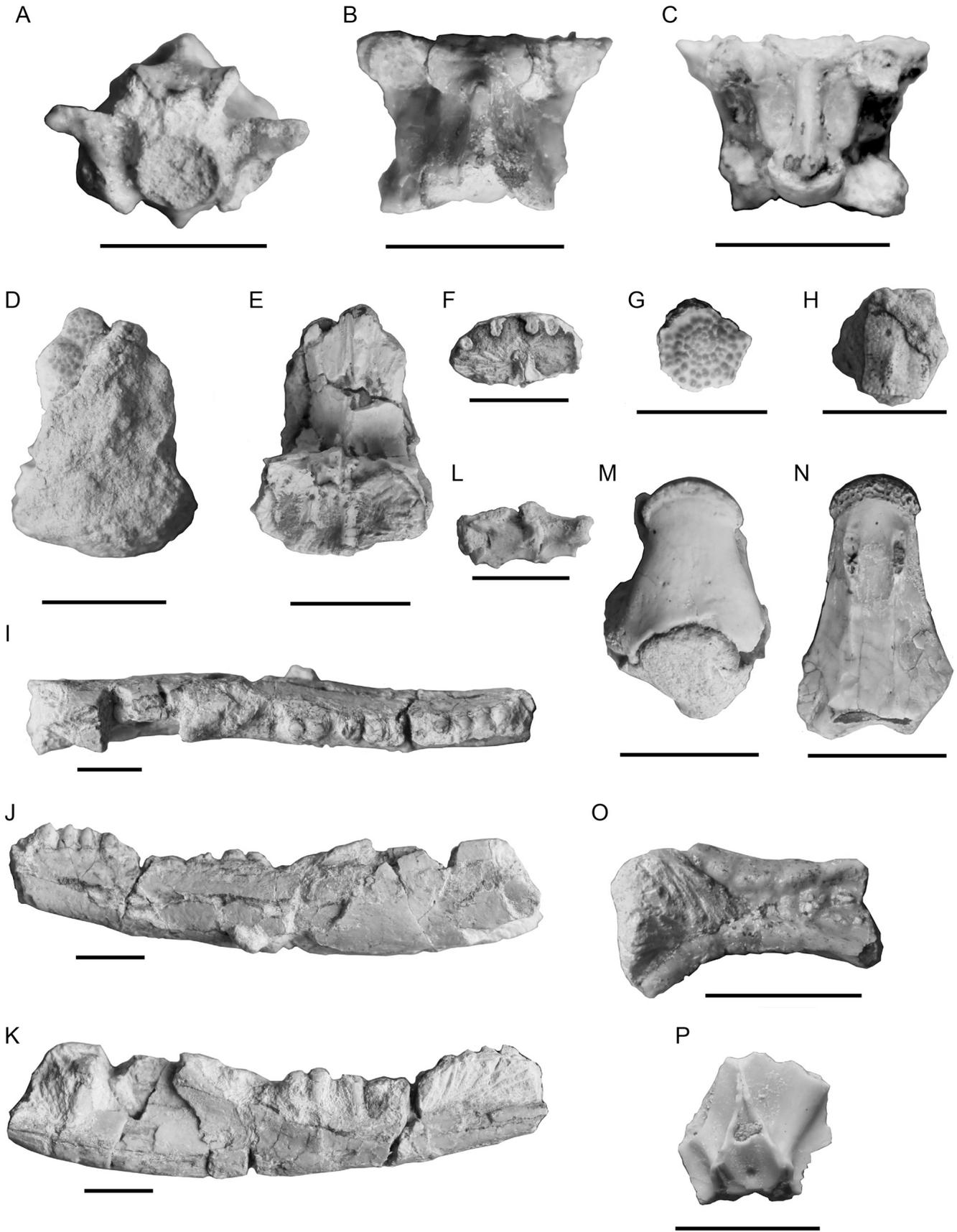


FIGURE 8. Other squamate material from Purple Bench. **A–C**, TMM 41672-266, Alethinophidia snake vertebra. **A**, anterior view; **B**, dorsal view; **C**, ventral view. **D–H**, Glyptosaurinae specimens. **D**, TMM 41672-257, premaxilla in dorsal view; **E**, TMM 41672-257, premaxilla in ventral view; **F**, TMM 41672-256, premaxilla in ventral view; **G**, TMM 41672-269, cranial osteoderm in dorsal view; **H**, TMM 41672-271, postcranial osteoderm in dorsal view. **I–P**, Squamata specimens. **I–K**, TMM 41672-253, left mandible in **I**, occlusal view; **J**, lateral view; and **K**, medial view. **L**, TMM 41672-276, fused vertebrae in lateral view; **M**, TMM 41672-272, trunk vertebra in ventral view; **N**, TMM 41672-274, caudal vertebra in ventral view; **O**, TMM 41672-259, azygous frontal in dorsal view; **P**, TMM 41672-258, azygous parietal in ventral view. For all images, scale bars equal 1 cm.

Two large premaxillae (TMM 41672-256 and TMM 41672-257) represent glyptosaurine anguimorphs. Both of these premaxillae are large and unpaired. In dorsal view, TMM 41672-256 preserves several large foramina in the anterolateral portions of the element, whereas TMM 41672-257 preserves osteoderms articulated to its dorsal surface (Fig. 8D). Those osteoderms are small, either four- or five-sided, and bear small tubercles arranged in a generally concentric pattern. In lateral view, a small facet for the articulation with the maxilla is present at the anteroventral corner of the naris. This articular facet is larger in the larger specimen (TMM 41672-257). In ventral view, both premaxillae preserve a widely spaced, pleurodont dentition. In TMM 41672-257, the nasal facets are preserved on the posteroventral surfaces of the posterodorsal process. Large foramina for the ophthalmic branch of CN V perforate the palatal surface of the premaxilla.

Both cranial and postcranial osteoderms can be identified as Glyptosaurinae (e.g., TMM 41672-269, TMM 41672-270, TMM 41672-271; Fig. 8G, H). The rounded cranial osteoderms (TMM 41672-269 and TMM 41672-270) are approximately six-sided and ornamented with roughly concentric whorls of small tubercles on their dorsal surfaces, similar to the osteoderms that remain attached to the premaxilla, TMM 41672-257. The rectangular postcranial osteoderms (e.g., TMM 41672-271) are generally thinner than the rounded cranial osteoderms. The tuberculate postcranial osteoderms are rectangular with an anterior lamina, which is interpreted as a smooth gliding surface when imbricated (McDowell and Bogert, 1954; Gauthier, 1982). Some of these rectangular osteoderms additionally have an anteroposteriorly oriented keel on their ornamented surfaces.

SQUAMATA Oppel, 1811 sensu Merrem, 1820 (Fig. 8I–P)

Specimen TMM 41672-253 is a large (anteroposterior length greater than 6 cm) partial left mandible missing the anterior-most portion with the symphysis as well as the retroarticular process (Fig. 8I–K). On the lateral surface, a crack follows the positions of the mental foramina along the long axis of the mandible. The Meckelian canal appears to be closed, but the ventral portion of the mandible may be vertically distorted so closure cannot be confirmed anterior to the splenial. The dentary is distinctly bowed ventrally along its long axis (Gauthier et al., 2012:character 357[1]). The anterior process of the coronoid is preserved in articulation, but the dorsal angle of the coronoid is missing so that the dorsal extent of this process cannot be ascertained. The base of the articular is preserved posterior to the mandibular fenestra as a slight medial expansion. There are at least 10 pleurodont teeth preserved in place. Most of these teeth are either broken transversely or have cusps with worn to rounded distal surfaces, although one of the posterior teeth appears globidont as in teiids (e.g., *Tupinambus*, *Dracaena*). The anterior four of the preserved teeth are more pointed and triangular as in the anterior dentary teeth of both *Tupinambus* and *Dracaena*, and unlike the teeth of *Peltosaurus granulatus* (USNM 84302), which has teeth with squared dorsal margins (Conrad, 2008:character 212[6]). However, the lateral margin of the dentary of TMM 41672-253 extends further dorsally than seen in *Tupinambus*, creating a more pleurodont dentition in TMM 41672-253. In this respect, the Purple Bench specimen is more similar to specimens referred to *Paraplicosauriops*, a glyptosaurine taxon from the Phosporites du Quercy in France (Augé and Sullivan, 2006). *Paraplicosauriops* also appears to have dentary teeth that are more globidont posteriorly and more pointed anteriorly. If this specimen does support the presence of a large teiid in the Purple Bench assemblage, this would be evidence that the group survived the Cretaceous-Paleogene extinction event in North America. However, until additional skeletal material of this taxon is collected, its identification as either a

teiid or melanosaurin are tantalizing but unconfirmed possibilities.

Some squamate vertebrae (e.g., TMM 41672-272, TMM 41672-273, TMM 41672-274, TMM 41672-275, and TMM 41672-276) are anteroposteriorly longer than they are dorsoventrally tall and lack diagnostic features of alethinophidian snakes (Fig. 8L–N). The neural spines are present along the anteroposterior length of the vertebrae and are low anteriorly. The neural arches are dorsoventrally taller posteriorly. The ventral surfaces of the vertebrae are smooth and flat; caudal vertebrae preserve articulation facets for hemal arches (Fig. 8N). In lateral view, these vertebrae bear strong posterodorsally inclined keels along the lateral surfaces of the centra. None of the caudal vertebrae of this morphology bear autotomic septa, and one specimen (TMM 41672-276; Fig. 8L) preserves fusion between two caudal vertebrae.

Specimen TMM 41672-259 is an unpaired frontal (Fig. 8O). The frontal is narrow near its midpoint. The dorsal surface bears an ornamentation of rough, small tubercles between raised orbital margins. Sharp, triangular facets for articulation with the frontals are present on the anterolateral surfaces of the frontal. Fused frontals are present in iguanids, gekkonids, teiids, lacertids, some xantusiids, cordylids, and xenosaurids (Estes, 1983).

Specimen TMM 41672-258 is the body of a large parietal with the posterior margin of a parietal foramen preserved along its anterior margin (Fig. 8P). The dorsal surface is lightly sculptured, with small tubercles arranged randomly. The posterior processes are broken off at their bases. In ventral view, the parietal processes are extremely pronounced.

Implications for the Evolution of the Paleogene Fauna in West Texas

The middle Eocene was a crucial time of climate fluctuation and associated diversity changes from the warm early part of the Cenozoic to the much cooler late Eocene and early Oligocene (Gradstein et al., 2012). First occurrences and extinctions of mammalian taxa in North America are relatively well known during this time period (Robinson et al., 2004; Gunnell et al., 2009; Woodburne et al., 2009). Indeed, the terrestrial Eocene deposits of western North America underwent intensive sampling of and research on the mammalian fossils over the past century, resulting in a robust mammalian biochronology (Wood, 1941; Woodburne, 2004). However, that preferential documentation of mammalian fossils has led most inferences of Eocene faunal dynamics in North America to be based primarily on changes in biodiversity and biogeographic ranges of the mammalian taxa rather than on a comprehensive understanding of the total extinct biodiversity from a time or locality. Our examination and description of the herpetofauna from the Purple Bench locality addresses a missing aspect of that faunal assemblage and provides additional data with respect to climatic changes and their effects on the evolution of terrestrial vertebrates in the southern Rocky Mountain region.

The squamate specimens from Purple Bench mostly consist of disarticulated material, which can create difficulties for specimen identification. However, apomorphies present in those materials allow our identification of alethinophidian snakes, glyptosaurine anguimorphs, and rhineurid amphisbaenians. Additionally, turtle fossils, preliminarily identified as Carettochelyidae and Testudinoidea (Burroughs et al., 2011), and crocodylians (Stocker et al., 2012; Stocker, 2013) are recognized from Purple Bench. Squamate fossils previously were not described from any other portion of the DGF. However, multiple reptile fossils, including the crocodylians '*Allognathosuchus*' and †*Boverisuchus*, the tortoise †*Hadrianus*, several aquatic turtles, glyptosaurine anguimorphs, and the aquatic snake †*Pterosphenus*, were reported from the possibly coeval late middle Eocene (Uintan) Casa Blanca Local

Fauna near Laredo, Texas (Westgate, 1988, 1989, 2012). Well-documented mid-latitude terrestrial Eocene squamate assemblages do exist outside of West Texas, but they are constrained to either the early Eocene (earliest Wasatchian: Smith, 2009; late Wasatchian-Bridgerian: Walker, 1999) or late Eocene (Chadronian: Sullivan and Holman, 1996; Smith, 2006, 2011). There currently are no late middle Eocene (~48–38 Ma) terrestrial squamate assemblages documented from the mid-latitudes of North America (Smith, 2011). Major components of the Purple Bench assemblage such as glyptosaurine anguimorph lizards and rhineurid amphisbaenians are known from both older and younger mid-latitude assemblages (Walker, 1999; Smith, 2011); thus, the Purple Bench assemblage fills an important temporal gap in the ranges of these groups.

Paleoecological interpretations for West Texas previously were centered on mammalian taxa and subsequently focused on early primates. As ectotherms, squamates should be a better indicator of climate change because of their potentially restricted window of climatic and environmental tolerances. Despite that potential physiological restriction, it is the mammalian taxa that appear to be more affected by the cooling and drying pattern through the end of the Paleogene, taking advantage of the middle Eocene tropical paleoenvironment of West Texas along with the squamate taxa documented here, whereas rhineurid amphisbaenians continue to inhabit their more northern distribution up to the beginning of the Neogene.

Paleoclimatic reconstructions of western North America have been based on a variety of methods (e.g., leaf margin analysis: Wing et al., 2005; carbonate clumped isotope thermometry of paleosols: Snell et al., 2013), and these resulted in mean annual temperature (MAT) estimates of approximately 20–38°C for the Bighorn Basin during the Paleocene-Eocene Thermal Maximum (PETM). A substantially cooler MAT of ~15°C was estimated at the Eocene-Oligocene boundary in the northern Great Plains (Zanazzi et al., 2007). Estimations for the early middle Eocene of East Texas based on stable isotope profiles of shallow water gastropods hypothesized a MAT of ~23°C, with a seasonality of 8–9°C (Andreasson and Schmitz, 2000). The Lake Casa Blanca assemblage in southern Texas has been interpreted as a tropical estuarine environment in which water temperatures likely could be greater than 24°C (Westgate, 1989), and this warm temperature estimate agrees with inferences for West Texas based on fossils of the gastropod *Lysinoe* (Roth, 1984).

A subtropical climate also was inferred for the latest Eocene of West Texas based on the presence of primates (Westgate and Gee, 1990; Williams and Kirk, 2008; Kirk and Williams, 2011). Primates are well known from the DGF of West Texas; these include the omomyiforms †*Diablomomys dalquesti* and †*Omomys carteri* and the adapiforms †*Mahgarita stevensi* and †*Mescalerolemur horneri* (Wilson, 1986; Williams and Kirk, 2008; Kirk and Williams, 2011). The presence of those taxa in the DGF of West Texas supported the hypothesis that climatic changes in the central Rocky Mountains, from humid subtropical forests to cooler and seasonally drier forests through the Eocene, caused taxa to take refuge in the humid, subtropical environment that persisted later in the Eocene in southern North America (Westgate, 1989; Williams and Kirk, 2008).

However, Walker (1999) reported diversification of squamates through the Wasatchian and Bridgerian of Wyoming and attributed that diversification to the climatic warming during the early Eocene Climatic Optimum (EECO). More recently, two hypotheses were proposed by Smith (2006, 2011) to explain the northern and mid-latitude biogeographic trends of currently tropical groups of squamates through the early Cenozoic. These were an extirpation model, under which taxa that could not adapt to the changing climatic conditions went extinct, and a concentration model, where taxa that were adapted to warm and frost-free conditions tracked those climatic conditions south through the

Paleogene. With respect to the concentration model, southern shifts in geographic ranges are recognized for multiple taxa (Matthew, 1939; Estes, 1970; Estes and Hutchison, 1980; Markwick, 1998; Nesbitt et al., 2011).

An additional hypothesis regarding the apparent southern shift of taxa concerns phylogenetic niche conservatism (PNC), and this was specifically investigated for rhineurid amphisbaenians (Hipsley and Müller, 2014). Extinct rhineurids were found to occupy various climatic conditions, not limited to their extant preference for a warm and humid subtropical climate. For instance, the high MAT estimated for the middle Eocene of Texas (Andreasson and Schmitz, 2000) exceeds the MAT range for extant *Rhineura floridana*, as well as paleoclimatic estimates for other extinct rhineurid amphisbaenians (Hipsley and Müller, 2014). The presence of †*Solastella* in West Texas during the late middle Eocene adds to that extended range of paleoclimatic tolerances of rhineurid amphisbaenians.

ACKNOWLEDGMENTS

This project was part of dissertation research completed by M.R.S. in partial fulfillment of a Ph.D. degree at The University of Texas at Austin; M.R.S. thanks C. Bell, J. Clarke, T. Rowe, and G. Gunnell for guidance and discussion. We thank W. Cook, N. Horner, R. Willis, and Midwestern State University for field access at the Dalquest Desert Research Site. We received skillful assistance with specimen collection, preparation, and curation from M. Brown, C. Campisano, K. Criswell, S. Egberts, H. Findlayson, J. Maisano, L. Murray, C. Sagebiel, R. Wallace, S. Sroka, T. Wicks, and G. Yearwood. Discussions with K. Claeson, J. Conrad, K. Criswell, S. Drumheller-Horton, J. Head, C. Hipsley, P. Holroyd, W. Joyce, E. Lundelius, J. Mitchell, S. Moore, J. Müller, S. Nesbitt, J. Olori, K. Smith, B. Townsend, and J. Westgate improved the quality of the manuscript. M. Eklund assisted with specimen photography. S. Nesbitt provided line drawings for Figure 2. D. Ksepka assisted with MrBayes. J. Müller and C. Hipsley provided valuable reviews, which were added to by editor J. Conrad. The Jackson School of Geosciences (Lundelius Fund Scholarship), The University of Texas at Austin (William Powers, Jr. Presidential Graduate Fellowship), the Society of Vertebrate Paleontology (Jackson School of Geosciences Student Member Travel Grant), and the University of California Museum of Paleontology (Doris and Samuel P. Welles Fund) provided funding to M.R.S. for this project.

LITERATURE CITED

- Andreasson, F. P., and B. Schmitz. 2000. Temperature seasonality in the early middle Eocene North Atlantic region: evidence from stable isotope profiles of marine gastropod shells. *Geological Society of America Bulletin* 112:628–640.
- Augé, M., and R. M. Sullivan. 2006. A new genus, *Paraplacosauriops* (Squamata, Anguillidae, Glyptosaurinae) from the Eocene of France. *Journal of Vertebrate Paleontology* 26:133–137.
- Berman, D. S. 1972. *Hyporhina tertia*, new species (Reptilia: Amphisbaenia), from the early Oligocene (Chadronian) White River Formation of Wyoming. *Annals of Carnegie Museum* 44:1–10.
- Berman, D. S. 1973. *Spathorhynchus fossorium*, a middle Eocene amphisbaenian (Reptilia) from Wyoming. *Copeia* 1973:704–721.
- Berman, D. S. 1976. A new amphisbaenian (Reptilia: Amphisbaenia) from the Oligocene-Miocene John Day Formation, Oregon. *Journal of Paleontology* 50:165–174.
- Berman, D. S. 1977. *Spathorhynchus natronicus*, a new species of rhineurid amphisbaenian (Reptilia) from the early Oligocene of Wyoming. *Journal of Paleontology* 51:986–991.
- Brattstrom, B. H. 1958. New records of Cenozoic amphibians and reptiles from California. *Bulletin of the Southern California Academy of Sciences* 57:5–12.
- Burroughs, R. W., C. J. Bell, C. J., Latimer, A. E., and E. C. Kirk. 2011. Fossil turtles from the Devil's Graveyard Formation of southwest Texas: large terrestrial turtles and a geographic range extension for

- carrettochelyid turtles. Texas Academy of Science 114th Annual Meeting Program and Abstracts Volume:91–92.
- Campisano, C. J., Kirk, E. C., Townsend, K. E. B., and A. L. Deino. 2014. Geochronological and taxonomic revisions of the middle Eocene Whistler Squat Quarry (Devil's Graveyard Formation, Texas) and implications for the early Uintan in Trans-Pecos Texas. PLoS ONE 9:e101516. doi: 10.1371/journal.pone.0101516.
- Conrad, J. L. 2008. Phylogeny and systematics of Squamata (Reptilia) based on morphology. Bulletin of the American Museum of Natural History 310:1–182.
- Estes, R. 1965. Note on some Paleocene lizards. Copeia 1965:104–106.
- Estes, R. 1970. Origin of the Recent North American lower vertebrate fauna: an inquiry into the fossil record. Forma et Functio 3:139–163.
- Estes, R. 1983. Sauria terrestria, Amphisbaenia. Handbuch der Paläoherpetologie, Teil 10A. Gustav Fischer Verlag, Stuttgart, 249 pp.
- Estes, R., and J. H. Hutchison. 1980. Eocene lower vertebrates from Ellesmere Island, Canadian Arctic Archipelago. Palaeogeography, Palaeoclimatology, Palaeoecology 30:325–347.
- Evans, S. E. 2008. The skull of lizards and tuatara; pp. 1–347 in C. Gans, A. S. Gaunt, and K. Adler (eds.), Biology of the Reptilia, Volume 20. The Skull of Lepidosauria. Society for the Study of Amphibians and Reptiles, Ithaca, New York.
- Fürbringer, M. 1900. Zur vergleichenden Anatomie des Brustschulderapparates und der Schultermuskeln. Part IV. Jenaische Zeitschrift für Naturwissenschaften 34:215–718.
- Gans, C. 1967a. *Rhineura* Cope. Wide snouted worm-lizard. Catalogue of American Amphibians and Reptiles 42:42.1–42.2.
- Gans, C. 1967b. *Rhineura floridana* (Baird). Florida worm-lizard. Catalogue of American Amphibians and Reptiles 43:43.1–43.2.
- Gans, C. 1974. Biomechanics: An Approach to Vertebrate Biology. J. B. Lippincott Company, Philadelphia, 261 pp.
- Gans, C. 2005. Checklist and bibliography of the Amphisbaenia of the world. Bulletin of the American Museum of Natural History 289:1–130.
- Gauthier, J. A. 1982. Fossil xenosaurid and anguid lizards from the early Eocene Wasatch Formation, southeast Wyoming, and a revision of the Anguioidea. Contributions to Geology, University of Wyoming 21:7–54.
- Gauthier, J. A., M. Kearney, J. A. Maisano, O. Rieppel, and A. D. B. Behlke. 2012. Assembling the Squamate Tree of Life: perspectives from the phenotype and the fossil record. Bulletin of the Peabody Museum of Natural History 53:3–308.
- Gilmore, C. W. 1928 [1978]. Fossil Lizards of North America. Memoirs of the National Academy of Sciences 22, Third Memoir. Reprinted by Riverside Museum Press, 201 pp.
- Gradstein, F. M., G. Ogg, and M. Schmitz (eds.). 2012. The Geologic Time Scale 2012, 2-Volume Set. Elsevier, Amsterdam, The Netherlands.
- Gray, J. E. 1825. A synopsis of the genera of reptiles and Amphibia, with a description of some new species. Annals of Philosophy (Series 2) 10:193–217.
- Gray, J. E. 1844. Catalogue of the Tortoises, Crocodiles, and Amphisbaenians, in the Collection of the British Museum. Trustees of the British Museum, London, 80 pp.
- Gunnell, G. F., P. C. Murphey, R. K. Stucky, K. E. B. Townsend, P. Robinson, J. P. Zonneveld, and W. S. Bartels. 2009. Biostratigraphy and biochronology of the latest Wasatchian, Bridgerian, and Uintan North American Land Mammal “Ages”; pp. 279–330 in L. B. Albright III (ed.), Papers on Geology, Vertebrate Paleontology, and Biostratigraphy in Honor of Michael O. Woodburne. Museum of Northern Arizona Bulletin 65, Flagstaff, Arizona.
- Head, J. J. 2002. Snake paleontology of the Siwalik Group (Miocene of Pakistan): correlation of a rich fossil record to environmental histories. Unpublished Ph.D. dissertation, Southern Methodist University, Dallas, Texas, 290 pp.
- Hembree, D. I. 2007. Phylogenetic revision of Rhineuridae (Reptilia: Squamata: Amphisbaenia) from the Eocene to Miocene of North America. University of Kansas Paleontological Contributions 15:1–20.
- Henry, C. D., Davis, L., Kunk, M. J., and W. C. McIntosh. 1998. Tertiary volcanism of the Bofecillos Mountains and Big Bend Ranch State Park, Texas: revised stratigraphy and $^{40}\text{Ar}/^{39}\text{Ar}$ geochronology. University of Texas at Austin, Bureau of Economic Geology, Report of Investigations 253:1–74.
- Hipsley, C. A., and J. Müller. 2014. Relict endemism of extant Rhineuridae (Amphisbaenia): testing for phylogenetic niche conservatism in the fossil record. Anatomical Record 297:473–481.
- Holman, J. A. 1958. The Pleistocene herpetofauna of Saber-tooth Cave, Citrus County, Florida. Copeia 1958:276–280.
- Holman, J. A. 1959. Amphibians and reptiles from the Pleistocene (Illinoian) of Williston, Florida. Copeia 1959:96–102.
- Huelsbeck, J. P., and F. Ronquist. 2005. Bayesian analysis of molecular evolution using MrBayes; pp. 183–232 in R. Nielsen (ed.), Statistical Methods in Molecular Evolution. Springer, New York.
- Hutchison, J. H. 1992. Western North American reptile and amphibian record across the Eocene/Oligocene boundary and its climatic implications; pp. 451–463 in D. R. Prothero and W. A. Berggren (eds.), Eocene-Oligocene Climatic and Biotic Evolution. Princeton University Press, Princeton, New Jersey.
- Kearney, M. 2003. Systematics of the Amphisbaenia (Lepidosauria: Squamata) based on morphological evidence from recent and fossil forms. Herpetological Monographs 17:1–74.
- Kearney, M., and B. L. Stuart. 2004. Repeated evolution of limblessness and digging heads in worm lizards revealed by DNA from old bones. Proceedings of the Royal Society of London, Series B 271:1677–1683.
- Kearney, M., J. A. Maisano, and T. Rowe. 2005. Cranial anatomy of the extinct amphisbaenian *Rhineura hatcherii* (Squamata, Amphisbaenia) based on high-resolution X-ray Computed Tomography. Journal of Morphology 264:1–33.
- Kirk, E. C., and B. A. Williams. 2011. New adapiform primate of Old World affinities from the Devil's Graveyard Formation of Texas. Journal of Human Evolution 61:156–168.
- Lehman, T. M. 1991. Sedimentation and tectonism in the Laramide Tornillo Basin of West Texas. Sedimentary Geology 75:9–28.
- Linnaeus, C. 1766. Systema naturae. 12th edition. Classis III Amphibia. Laurentii Salvii, Stockholm, 639 pp.
- Longrich, N. R., Vinther, J., Pyron, R. A., Pisani, D., and J. A. Gauthier. 2015. Biogeography of worm lizards (Amphisbaenia) driven by end-Cretaceous mass extinction. Proceedings of the Royal Society B 282:20143034. doi: 10.1098/rspb.2014.3034.
- Losos, J. B. 2008. Phylogenetic niche conservatism, phylogenetic signal and the relationship between phylogenetic relatedness and ecological similarity among species. Ecology Letters 11: 995–1003.
- Macey, J. R., T. J. Papenfuss, J. V. Kuehl, H. M. Fourcade, and J. L. Boore. 2004. Phylogenetic relationships among amphisbaenian reptiles based on complete mitochondrial genomic sequences. Molecular Phylogenetics and Evolution 33:22–31.
- Markwick, P. J. 1998. Crocodylian diversity in space and time: the role of climate in paleoecology and its implication for understanding K/T extinctions. Paleobiology 24:470–497.
- Matthew, W. D. 1939 [1950]. Climate and Evolution. [2nd edition, revised and enlarged, arranged by E. H. Colbert.] Special Publications of the New York Academy of Sciences, Volume 1. New York Academy of Sciences, New York, 223 pp.
- McDowell, S. B., and C. M. Bogert. 1954. The systematic position of *Lanthanotus* and the affinities of the anguimorphous lizards. American Museum of Natural History Bulletin 105:1–142.
- Merrem, B. 1820. Versuch eines Systems der Amphibien. Johann Christian Krieger, Marburg, 191 pp.
- Müller, J., C. A. Hipsley, J. J. Head, N. Kardjilov, A. Hilger, M. Wuttke, and R. R. Reisz. 2011. Eocene lizard from Germany reveals amphisbaenian origins. Nature 473:364–367.
- Mulvaney, A., Castoe, T. A., Ashton, K. G., Krysko, K. L., and C. L. Parkinson. 2005. Evidence of population genetic structure within the Florida worm lizard, *Rhineura floridana* (Amphisbaenia, Rhineuridae). Journal of Herpetology 39:118–124.
- Nesbitt, S. J., D. T. Ksepka, and J. A. Clarke. 2011. Podargiform affinities of the enigmatic *Fluviovidavis platyrhamphus* and the early diversification of Strisores (“Caprimulgiformes” + Apodiformes). PLoS ONE 6:e26350. doi: 10.1371/journal.pone.0026350.
- Nopsca, F. B. 1923. Die Familien der Reptilien. Fortschritte der Geologie und Palaeontologie 2:1–210.

- Novacek, M. J., J. J. Flynn, I. Ferrusquia-Villafranca, and R. M. Cippolletti. 1987. An early Eocene (Wasatchian) mammal fauna from Baja California. *National Geographic Research* 3:376–388.
- Oppel, M. 1811. Die Ordnungen, Familien, und Gattungen der Reptilien als Prodom einer Naturgeschichte derselben. Joseph Lindauer, Munich, 86 pp.
- Prothero, D. R. 1996. Magnetostratigraphy of the Eocene-Oligocene transition in Trans Pecos Texas; pp. 189–198 in D. R. Prothero and R. J. Emry (eds.), *The Terrestrial Eocene-Oligocene Transition in North America*. Cambridge University Press, Cambridge, U.K.
- Prothero, D. R., and C. C. I. Swisher. 1992. Magnetostratigraphy and geochronology of the terrestrial Eocene–Oligocene transition in North America; pp. 74–87 in D. R. Prothero and W. A. Berggren (eds.), *Eocene–Oligocene Climatic and Biotic Evolution*. Princeton University Press, Princeton, New Jersey.
- Robinson, P., G. F. Gunnell, S. L. Walsh, W. C. Clyde, J. E. Storer, R. K. Stucky, D. J. Foehlich, I. Ferrusquia-Villafranca, and M. C. McKenna. 2004. Wasatchian through Duchesnean biochronology; pp. 106–155 in M. O. Woodburne (ed.), *Late Cretaceous and Cenozoic Mammals of North America: Biostratigraphy and Geochronology*. Columbia University Press, New York.
- Roth, B. 1984. *Lysinoe* (Gastropoda: Pulmonata) and other land snails from Eocene-Oligocene of Trans-Pecos Texas, and their paleoclimatic significance. *The Veliger* 27:200–218.
- Runkel, A. C. 1988. Stratigraphy, sedimentology, and vertebrate paleontology of Eocene rocks, Big Bend region, Texas. Unpublished Ph.D. dissertation, The University of Texas at Austin, Austin, Texas, 310 pp.
- Runkel, A. C. 1990. Stratigraphy and depositional history of Late Cretaceous and Paleogene rocks, Trans-Pecos Texas; pp. 117–146 in P. W. Dickerson, M. S. Stevens, and J. B. Stevens (eds.), *Geology of the Big Bend and Trans-Pecos Region, South Texas Geological Society, 1989 Annual Meeting of American Association of Petroleum Geologists, Field Trip Guidebook*.
- Smith, K. T. 2006. A diverse new assemblage of late Eocene squamates (Reptilia) from the Chadron Formation of North Dakota, U.S.A. *Palaeontologia Electronica* 9(2):5A.
- Smith, K. T. 2009. A new lizard assemblage from the earliest Eocene (zone Wa0) of the Bighorn Basin, Wyoming, U.S.A.: biogeography during the warmest interval of the Cenozoic. *Journal of Systematic Paleontology* 7:299–358.
- Smith, K. T. 2011. The evolution of mid-latitude faunas during the Eocene: late Eocene lizards of the Medicine Pole Hills reconsidered. *Bulletin of the Peabody Museum of Natural History* 52:3–105.
- Snell, K. E., B. L. Thrasher, J. M. Eiler, P. L. Koch, L. C. Sloan, and N. J. Tabor. 2013. Hot summers in the Bighorn Basin during the early Paleogene. *Geology* 41:55–58.
- Stevens, J. B., Stevens, M. S., and J. A. Wilson. 1984. Devil's Graveyard Formation (new), Eocene and Oligocene age, Trans-Pecos Texas. *Texas Memorial Museum Bulletin* 32:1–21.
- Stocker, M. R. 2013. Contextualizing vertebrate faunal dynamics: new perspectives from the Triassic and Eocene of western North America. Unpublished Ph.D. dissertation. University of Texas at Austin, Austin, Texas, 297 pp.
- Stocker, M. R., C. A. Brochu, and E. C. Kirk. 2012. Spatial and temporal shifts in Paleogene crocodyliform diversity and a new globidont alligatoroid from the Middle Eocene of West Texas. *Journal of Vertebrate Paleontology, Program and Abstracts* 2012:180.
- Sullivan, R. M. 1985. A new middle Paleocene (Torrejonian) rhineurid amphisbaenian, *Plesiorhineura tsentasi* new genus, new species, from the San Juan Basin, New Mexico. *Journal of Paleontology* 59:1481–1485.
- Sullivan, R. M., and J. A. Holman. 1996. Squamata; pp. 354–372 in D. R. Prothero and R. J. Emry (eds.), *The Terrestrial Eocene-Oligocene Transition in North America*. Cambridge University Press, Cambridge, U.K.
- Swofford, D. L. 2002. PAUP*. *Phylogenetic Analysis Using Parsimony (*And Other Methods)*. Version 4. Sinauer Associates, Sunderland, Massachusetts.
- Townsend, T. M., A. Larson, E. Louis, and J. R. Macey. 2004. Molecular phylogenetics of Squamata: the position of snakes, amphisbaenians, and dibamids, and the root of the squamate tree. *Systematic Biology* 53:735–757.
- Uetz, P. (ed.) *The Reptile Database*. <http://www.reptile-database.org>. Accessed March 1, 2015.
- Vanzolini, P. E. 1951. A systematic arrangement of the family Amphisbaenidae (Sauria). *Herpetologica* 7:113–123.
- Vidal, N., and S. B. Hedges. 2005. The phylogeny of squamate reptiles (lizards, snakes, and amphisbaenians) inferred from nine protein-coding genes. *Comptes Rendus Biologies* 328:1000–1008.
- Vidal, N., A. Azvolinsky, C. Cruaud, and S. B. Hedges. 2008. Origin of tropical American burrowing reptiles by transatlantic rafting. *Biology Letters* 4:115–118.
- Walker, R. J. 1999. An analysis of the herpetofauna and paleoenvironment of the Wasatch and Bridger Formations (middle Eocene), at South Pass, Wyoming. Unpublished Ph.D. dissertation. Michigan State University, East Lansing, Michigan, 536 pp.
- Walsh, S. L., and R. Estes. 1985. Earlier ?Eocene microvertebrate fossils from San Diego County, California: a preliminary report. *San Diego Association of Geologists Field Trip Guidebook* 1985:75–83.
- Walton, A. H. 1992. Magnetostratigraphy of the lower and middle members of the Devil's Graveyard Formation (middle Eocene), Trans-Pecos, Texas; pp. 74–87 in D. R. Prothero and W. A. Berggren (eds.), *Eocene-Oligocene Climatic and Biotic Evolution*. Princeton University Press, Princeton, New Jersey.
- Westgate, J. W. 1988. Biostratigraphic implications of the first Eocene land-mammal fauna from the North American coastal plain. *Geology* 16:995–998.
- Westgate, J. W. 1989. Lower vertebrates from an estuarine facies of the middle Eocene Laredo Formation (Claiborne Group), Webb County, Texas. *Journal of Vertebrate Paleontology* 9:282–294.
- Westgate, J. W. 2012. Palaeoecology of a primate-friendly, middle Eocene community from Laredo, Texas and a review of stratigraphic occurrences of Paleogene land mammals across the Gulf Coastal Plain, USA. *Palaeobiodiversity and Palaeoenvironments* 92:497–505.
- Westgate, J. W., and C. T. Gee. 1990. Paleocology of a middle Eocene mangrove biota (vertebrates, plants, and invertebrates) from southwest Texas. *Palaeogeography, Palaeoclimatology, Palaeoecology* 78:163–177.
- Wiens, J. J. 2008. Commentary on Losos (2008): niche conservatism déjà vu. *Ecology Letters* 11:1004–1005.
- Wiens, J. J., and C. H. Graham. 2005. Niche conservatism: integrating evolution, ecology, and conservation biology. *Annual Review of Ecology, Evolution, and Systematics* 36:519–539.
- Wiens, J. J., C. R. Hutter, D. G. Mulcahy, B. P. Noonan, T. M. Townsend, J. W. Sites Jr., and T. W. Reeder. 2012. Resolving the phylogeny of lizards and snakes (Squamata) with extensive sampling of genes and species. *Biology Letters* 8:1043–1046.
- Wiens, J. J., D. D. Ackerly, A. P. Allen, B. L. Anacker, L. B. Buckley, H. V. Cornell, E. I. Damschen, T. J. Davies, J. A. Grytnes, S. P. Harrison, B. A. Hawkins, R. D. Holt, C. M. McCain, and P. R. Stephens. 2010. Niche conservatism as an emerging principle in ecology and conservation biology. *Ecology Letters* 13:1310–1324.
- Williams, B. A., and E. C. Kirk. 2008. New Uintan primates from Texas and their implications for North American patterns of species richness during the Eocene. *Journal of Human Evolution* 55:927–941.
- Williamson, T. E., and S. G. Lucas. 1993. Paleocene vertebrate paleontology of the San Juan Basin, New Mexico; pp. 105–135 in S. G. Lucas and J. Zidek (eds.), *Vertebrate Paleontology in New Mexico*. New Mexico Museum of Natural History and Science Bulletin 2. New Mexico Museum of Natural History and Science, Albuquerque, New Mexico.
- Wilson, J. A. 1984. Vertebrate faunas 49 to 36 million years ago and additions to the species *Leptoreodon* (Mammalia: Artiodactyla) found in Texas. *Journal of Vertebrate Paleontology* 4:199–207.
- Wilson, J. A. 1986. Stratigraphic occurrence and correlation of early Tertiary vertebrate faunas, Trans-Pecos Texas: Agua Fria-Green/s Valley areas. *Journal of Vertebrate Paleontology* 6:350–373.
- Wing, S. L., G. J. Harrington, F. A. Smith, J. I. Bloch, D. M. Boyer, and K. H. Freeman. 2005. Transient floral change and rapid global warming at the Paleocene-Eocene boundary. *Science* 310:993–996.
- Wood, H. E., II, R. W. Chaney, J. Clark, E. H. Colbert, G. L. Jepsen, J. B. Reeside, Jr., and C. Stock. 1941. Nomenclature and correlation of the North American continental Tertiary. *Bulletin of the Geological Society of America* 52:1–48.
- Woodburne, M. O. 2004. *Late Cretaceous and Cenozoic Mammals of North America: Biostratigraphy and Geochronology*. Columbia University Press, New York, 391 pp.

Woodburne, M. O., G. F. Gunnell, and R. K. Stucky. 2009. Climate directly influences Eocene mammal faunal dynamics in North America. *Proceedings of the National Academy of Sciences of the United States of America* 106:13399–13403.

Zanazzi, A., M. J. Kohn, B. J. MacFadden, and D. O. Terry Jr. 2007. Large temperature drop across the Eocene–Oligocene transition in central North America. *Nature* 445:639–642.

Zug, G. R. 1968. Geographic variation in *Rhinuera floridana* (Reptilia: Amphisbaenidae). *Bulletin of the Florida State Museum* 12: 185–211.

Submitted March 7, 2015; revisions received August 3, 2015; accepted August 31, 2015.
 Handling editor: Jack Conrad.

APPENDIX 1. Character codings for †*Solastella cookei* using the character-taxon matrix of Hipsley and Müller (2014); morphological character states listed only.

†*Solastella cookei*

????? ?????? ?????? ?????? ?????? 21 012? ?1?1 02?10 01?00 03211 1?0?? ?00?? 01020 0?01? ???00 ?0?0? ?????? 01???

00??2 1?2?0 ?????? 2100? ??010 00?00 1???? ?1??? ?????? ?????? ?????? ?????? ?????? ?????? ??