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Non-anguimorph Lizards of the Late Oligocene and Early Miocene of Florida and Implications for the Reorganization of the North American Herpetofauna

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by
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ABSTRACT

Non-anguimorph Lizards of the Late Oligocene and Early Miocene of Florida and Implications for the Reorganization of the North American Herpetofauna

by

Kevin R. Chovanec

Paleokarst deposits from the Oligo-Miocene of northern Florida preserve undescribed herpetofaunal remains that fill important temporal and geographic gaps in our understanding of Cenozoic lizard evolution. Here I describe and discuss the non-anguimorph lizard diversity of the Brooksville 2 (Ar2) and Miller (He1) local faunas to test for patterns of regional and latitudinal provincialism in the contemporary North American record. Collectively, the sites are significant for documenting 1) extralimital occurrences of the tropical clades *Anolis* and Corytophaninae, 2) a substantial temporal range extension of the modern southeastern endemic Rhineuridae, 3) the earliest record of eublepharid gekkotans from North America, and 4) the early Miocene arrival of "cnemidophorine" teiids from South America. This work complements recent studies of older, Eocene lizards by others and lends paleontological support to aspects of the tropical conservatism hypothesis: lineages now confined to the tropics were present at higher latitudes when megathermal climates were more extensive.

ACKNOWLEDGEMENTS

Thank you to Drs. Blaine Schubert, Jim Mead, and Wally “Steven” Wallace for their guidance, patience, and support. Fellow graduate students helped shape this endeavor into the experience that it has been. Jeff Martin, in particular, has been a dependable source of useful and not-so-useful discussion. He also fixed my car and helped make significant improvements to my oral presentation; I feel compelled to thank him on behalf of my audience for the latter. Mark Hutchinson provided some encouraging words at the start of my program that were (and still are) much appreciated. Richard Hulbert and Kenneth Krysko of the Florida Museum of Natural History facilitated access to fossil and modern specimens under their care, and Andreas Kerner kindly donated material from the Miller locality.

Not a single aspect of this project would have been possible without the help of Sandy Swift. Sandy showed me the art of picking and sorting, taught me much of what I know of small vertebrate anatomy, and tried her best to get me to produce the same kinds of high-quality figures that she does. My questions were always met with enthusiasm, and her curiosity has been infectious. She filled equally important roles of mentor and total distraction, so thanks to her for being a source of chocolate and of motivation.

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CHAPTER 1

INTRODUCTION

It has long been hypothesized that the late Oligocene and early Miocene represent an important time for the modernization of the North American lizard fauna (Tihen 1964; Estes 1970), but geographic, temporal, collection, and taxonomic biases have so far precluded a thorough characterization of this transition. The snake fauna changed demonstrably at this time, and the gradual (and near-total) supersession of henophidians by an invading caenophidian radiation beginning in the Arikareean Land Mammal Age (LMA) and ending in the Hemphillian LMA is well documented (Parmley and Holman 1995; Williams 2009). Tihen (1964) suggested the replacement of “archaic” lizards known from the early Tertiary (e.g., anguids, xenosaurids, and varanids) by modern groups (e.g., teiids, scincids, and iguanids) was relatively abrupt and argued such a change would be better explained by the geographic redistribution of existing lineages in response to climatic changes than by the sudden proliferation of novel clades. Estes (1970; 1976; 1983b) advocated a similar idea; taxa that vanished from the record in the latter half of the Cenozoic either went extinct or else sought asylum at lower latitudes after climate cooled in the Oligocene. Importantly, both authors conceded the inadequacy of the record from tropical Central America and the southern and southeastern United States for elaborating their models any further.

In his study of early Eocene lizards from Wyoming, Gauthier (1982) contrasted the dominance of (presumably) mesic anguimorphs in the Paleogene with the increased abundance and diversity of xeric iguanids in the Neogene. His observation, however, pertained to the western portion of the continent where the fossil record is more complete and where living lineages are necessarily adapted to drier environments. While lizard communities in arid and semiarid regions of the western United States today are certainly dominated by iguanid species (Pianka 1967), they belong to a few subclades (phrynosomatines, iguanines, and crotaphytines) that represent only a fraction of the taxonomic and ecological diversity of the family as a whole (Smith 2006). Gauthier (1982) did not systematically describe the iguanid remains from his sample but estimated that they accounted for roughly one-fifth of the total number of lizard species recovered. Although ultimately their relationships to modern, extant taxa remained obscure, Gauthier's study was significant for highlighting the presence of iguanians at all at a time when published Paleogene accounts of them remained scarce.

Only recently has a better understanding of North American Paleogene iguanids begun to emerge. A number of studies by Smith from the early Eocene of Wyoming (2009a; 2011a) and the late Eocene of North Dakota (2006; 2011b) showed that not only were iguanids more abundant and diverse by that time than was previously appreciated, but that they were represented by lineages that are associated almost exclusively with the New World tropics today. More recently, Smith and Gauthier (2013) revisited the undescribed portion of Gauthier's (1982) original study and confirmed a similar pattern: relatives of mid-latitude Eocene iguanids persist in the modern biota and have merely been displaced toward the equator.

Many of Smith's (2006; 2009a; 2011a; 2011b) lizards came from well-known fossil localities that had, in some cases, been explored for more than a century. He was able to demonstrate the value of a rich fraction of the record that had been overlooked, but the taxonomic resolution afforded by his sample would not have been possible without 1) screenwashing, 2) the careful study of disarticulated modern skeletons, and 3) the association of isolated elements that traditionally have rarely been considered in fossil analyses. Although screenwashing has become increasingly common since Hibbard (1949) originally outlined its utility and execution, microvertebrate fossil recovery is subject to biases introduced by pickers and sorters whose taxonomic interests (and anatomical expertise) typically lie among the mammalian branches of the vertebrate tree (Hutchison 1992; Bell and Mead 2014). Isolated cranial elements of lizards are demonstrably phylogenetically informative (Smith 2009b; Bhullar 2011), but the fossil remains of many such bones can easily go unrecognized (Bell and Mead 2014). Smith's efforts addressed these problems and helped to clarify our understanding of saurian evolution and biogeography in the Eocene.

Unfortunately, the subsequent Oligocene epoch remains somewhat of a black hole for lizard data; very little is known from North America at this time (Smith 2006). Sullivan and Holman (1996) summarized the scattered literature on Orellan-aged lizards (all from the Great Plains and Rocky Mountains regions), but otherwise published accounts of Oligocene taxa come primarily in the form of cursory descriptions of fragmentary specimens as part of broader faunal surveys (e.g., Setoguchi 1978) or are only mentioned in preliminary taxonomic lists (Patton 1969; Hayes 2000). Global climate cooled significantly at the beginning of the Oligocene before warming again towards the end (Zachos et al. 2001), and contemporary herpetofaunas from Europe show a marked decrease in diversity across the Eocene/Oligocene boundary that never fully recovered (Rage 2012). Synthetic attempts to test for analogous patterns for North American reptiles (Hutchison 1982; Hutchison 1992; Sullivan and Holman 1996; Smith 2006) suffer from a lack of data, but preliminary evidence suggests the consequences were not so catastrophic or immediate on this continent.

Still, by the late Neogene a familiar cast of characters had already appeared. What defines a "typical Neogene suite of lizard fossils" (Norell 1989: 27) in the Plio-Pleistocene varies with geography, but fossil assemblages tend to be exclusive to subfamilies and genera still living in the immediate vicinity of their respective deposits today. While most species-level designations have probably suffered from some degree of overinterpretation (Norell 1989; Bell et al. 2010), known regional fossil herpetofaunas are almost uniformly modern in composition at broader taxonomic levels (Norell 1989). Extinct groups and biogeographic anomalies from the Paleogene are gone, and some of the most ubiquitous and common elements of Pliocene-Recent lizard communities (e.g., *Plestiodon* and *Aspidoscelis*) are intercontinental immigrants (Macey et al. 2006) unknown from early Cenozoic sediments and whose arrival remains poorly constrained by the fossil record. Even if lizards in North America were not as severely impacted by the initial Eocene/Oligocene transition as they were in Europe, a drastic transformation took place sometime in the intervening Oligo-Miocene that is incompletely understood.

Early Neogene (here including also the beginning of the Arikareean) fossil lizards are not uncommon, but the record remains, as observed by Estes and Tihen (1964:465), "perhaps more tantalizing than informative." Published lacertofaunas describing multiple taxa are known primarily from Nebraska (Estes and Tihen 1964; Robinson and Van Devender 1973; Yatkola 1976; Holman 1981; Wellstead 1982), with only the Thomas Farm locality (Estes 1963) from Florida as a notable regional outlier. Much of what has been described is based on fragmentary material, so a number of species with uncertain relationships have received informal morphotypic designations in lieu of formal taxonomic assignments (Estes 1963; Estes and Tihen 1964; Yatkola 1976). In other cases identifications may have been taken too far; purported continental occurrences of the West Indian genus *Leiocephalus* in the Miocene (Estes 1963; Estes and Tihen 1964; Wellstead 1982), for example, are probably unreliable (Norell 1989; Pregill 1992). In spite of geographic and taxonomic sampling issues, however, an emerging picture suggests Arikareean through Barstovian LMA lizard communities were still in many ways unlike those observed today.

Paleokarst deposits from the medial Arikareean (the Brooksville 2 LF) and early Hemingfordian (the Miller LF) of northern Florida preserve undescribed herpetofaunal remains that collectively span the Oligocene/Miocene transition. This thesis characterizes the taxonomic diversity of non-anguimorph lizards from both sites in an effort to gain a better understanding of lacertofaunal succession and evolution from a poorly understood time and from a poorly sampled part of the continent.

By outlining exactly which lacertilian groups inhabited Florida in the late Oligocene and early Miocene, I seek to address two main problems. Broadly, I revisit the concept of “modernization” originally explored by Tihen (1964) and Estes (1970) as it pertains to North American lizards. Their ideas remain inadequately tested by the fossil record, and this new material fills specific temporal and geographic gaps acknowledged by both. Anguimorphs will be covered elsewhere, but lineages identified here have important implications for their early observations as well as those discussed later by Smith (2006; 2009a; 2011b).

An ancillary motivation for this study is to test for patterns of regional and latitudinal provincialism already demonstrated for other contemporaneous vertebrate clades. Albright (1998) argued that the Gulf Coast was biogeographically distinct (at least for mammals) from more northern latitudes during the Arikareean and Hemingfordian and that these differences were the result of more “tropical” habitats. More recently Rincón et al. (2012) provided evidence suggesting this provincialism extended south to Panama. As temperature-sensitive ectotherms, it would be surprising if squamates did not exhibit a similar trend. The addition of new lizards from Florida invites comparison, however tentative, with those already known from the Great Plains.

Among squamates only snakes and anguimorph lizards are not treated here. Whether one favors the classic iguanian/scleroglossan dichotomy of morphological analyses (Estes et al. 1988; Gauthier et al. 2012) or the novel rearrangement suggested by nuclear genes (Vidal and Hedges 2004; Townsend et al. 2004; Wiens et al. 2010; Pyron et al. 2013), the exclusion of those 2 clades is more a reflection of historical considerations than of biological reality. “Non-anguimorph lizards” is a decidedly paraphyletic group under either scheme but one that bears strongly on the notion of modernization given their past underrepresentation in older sediments.

The taxonomy employed here draws primarily from that of Estes et al. (1988). As in Smith (2006; 2009a; 2011a; 2011b) and Smith and Gauthier (2013), however, iguanian relationships follow Schulte et al. (2003). Pleurodont iguanians have historically been treated as a singular Iguanidae, but Frost and Etheridge (1989) failed to recover them as a monophyletic group and subsequently divided them into 8 families. Schulte et al. (2003) later provided strong evidence for pleurodont monophyly and resurrected the traditional hierarchy with a few modifications. Their classification recognizes 8 subfamilies: Corytophaninae, Crotaphytinae, Hoplocercinae, Iguaninae, Oplurinae, Phrynosomatinae, Polychrotinae*, and Tropidurinae*. In their analysis the latter 2 are metataxa designated with an asterisk (*) to denote their questionable monophyly. I have made an effort to discuss such caveats wherever alternative relationships proposed in the literature are relevant to my results.

The relationships of fossil taxa described here are inferred on the basis of disarticulated material recovered from screenwashing. Some are represented by a single element (often tooth-bearing), but wherever possible I have assembled a composite of as many elements as possible. To do so, I follow the association criteria (size, relative abundance, complementary articulations, and apomorphies) established by Smith (2009a); the reader is directed there for a more articulate consideration of the merits of each. Some associations are necessarily more tenuous than others, and I do my best to indicate them as such. In other instances, the rarity or fragmentary nature of individual bones frustrated attempts to assign them to any particular taxon. Identifications were aided by the extensive osteological collection at ETSU; a list of modern specimens examined for this study is on file in the Department of Geosciences. Anatomical terminology follows Evans (2008) unless otherwise indicated.

CHAPTER 2

NON-ANGUIMORPH LIZARDS OF THE BROOKSVILLE 2 LOCAL FAUNA

Introduction

The Brooksville 2 Local Fauna (LF) comprises the most diverse mammalian assemblage known from the Arikareean of Florida (Hayes 2000), but its reptilian component has received considerably less attention. Bourque (2013) described the kinosternid turtle *Xenochelys floridensis*, and Mead (2013) reported the occurrence of an indeterminate scolecophidian snake. A preliminary faunal list provided by Hayes (2000) included 3 indeterminate species of lizards (an iguanian, a helodermatid, and an anguid); none have been described in detail, and an in-depth survey of lacertofaunal remains from Brooksville 2 is lacking. This chapter remedies this, in part, by detailing the non-anguimorph lizards from the site. Anguimorphs are currently under study by myself and others at ETSU.

Fossils from Brooksville 2, recovered from karst fissure-fillings in the Suwannee Limestone near Brooksville, Florida (Hernando County), were originally dated to the “medial” Arikareean between 26 and 28 Ma (Hayes 2000). Tedford et al. (2004) later suggested the fauna was slightly younger (between 25 and 26 Ma), but a more recent study of the chiropteran fauna corroborates an older age assignment (26 to 28 Ma; Morgan and Czaplewski 2012). Hayes (2000) discussed the geology and taphonomy of the Brooksville 2 deposits; the abundance of lizard remains reported here is consistent with his interpretation of the presence of cave-like karstic features serving as small carnivore dens.

Anolis sp.

Morphotype A

(Figures 1-9)

Referred Material

UF 274039 (partial dentary), 274041 (partial dentary), 274061 (frontal), 274073 (partial dentary), 274074 (partial dentary), 275606 (partial maxilla), 275608 (partial dentary), 275611 (partial dentary), 275620 (partial dentary), 275627 (left postorbital), 275629 (partial dentary), 275645-275647 (partial dentaries), 275649-650 (partial dentaries), 275653 (partial left maxilla), 275667 (braincase), 275677-275681 (frontals), 275682-275684 (left quadrates), 275685-275686 (frontals), 275693-275694 (partial maxillae), 275697 (partial dentary), 275699-275701 (partial dentaries), 278727 (left prefrontal), 278745 (left prefrontal)

Description

Dentary. Seventeen dentary specimens are associated with this taxon, far more than for any other at the site. None preserve the bone in its entirety, but well-preserved posterior and anterior fragments provide for a satisfactory reconstruction of its morphology when considered together. UF 275620 (Fig. 1) is a posterior fragment of a left dentary. It preserves 10 teeth spaced among 11 loci; all are tricuspid and taper towards the crown. The Meckelian groove is closed and fused for most of its length but is perforated posteriorly by a small, incompletely encircled foramen extending below the last 3 teeth in the tooth row. Presumably, this opening represents the combined alveolar-mylohyoid foramen (hereafter, CAMF) of Castañeda and de Queiroz (2013). Looking through the foramen in lingual view, the terminus of an elongate intramandibular septum (IMS) is visible below the penultimate tooth. The septum is tall and nearly vertical (viewed posteriorly), with a dorsal limb that is continuous with a weakly developed intramandibular lamella (IML; see Smith 2009a) behind it. Posterior (and somewhat ventral) to the tooth row, an extension of the supra-Meckelian lip (sML; see Bhullar and Smith 2008) bears an elongate, external facet for the anteromedial process of the coronoid. Viewed labially, the surface of the bone immediately surrounding the dental parapet is notably wrinkled. There is a facet for an anterolateral extension of the coronoid posteriorly, but it does not appear to have extended below the tooth row.

UF 275645 (Fig. 1) is the anterior portion of a right dentary. There are spaces for 22 teeth, with complete teeth occupying positions 8, 9, 10, 12, 21, and 22. The first 4 preserved teeth are unicuspid and gently recurved, but the last 2 are tricuspid and taper apically. The bone is long and slender; it does not increase in height significantly posteriorly. The Meckelian groove is smoothly fused for its entire length, with an anterior opening at the symphysis in the form of a small, pinhole foramen. Posteriorly, the fused subdental face bears a weak depression extending anteriorly from where the bone is fractured. Comparison with associated posterior fossil fragments and modern *Anolis* suggests this impression emanated from an opening (interpreted here as the CAMF) that would have immediately followed. Assuming the succeeding CAMF occupied a space under the last 3 teeth (see above), this species probably had around 25 teeth. Viewed dorsally, a shallow subdental gutter is developed anteriorly. It begins to fade around the

12th tooth position and is absent posteriorly. Towards the symphysis, the dentary curves abruptly medially. Ventrally, a genioglossus scar (Wellstead, 1982) extends to about the 12th tooth that gives the bone a “stepped” appearance in labial view. A nearly vertical IMS, as in UF 275620 above, is visible posteriorly.

Taken together, these and other specimens suggest a shallow dentary with a high (~25) tooth count, an extensively fused Meckelian groove, and an elongate IMS. The anterior half of the tooth row is never well preserved, but collectively the available material suggests the transition to tricuspid tooth crowns took place between the 10th and 14th tooth positions. A facet for an anterolateral expansion of the coronoid is always present on specimens that are intact far enough posteriorly to record one, but its extent varies. In some specimens (e.g., UF 275620) it does not reach the end of the tooth row. In others (e.g., UF 275697) it extends as far as below the last 2 teeth. The CAMF never reaches further anteriorly than the last 4 teeth, but in some specimens (as in UF 275697) it is bordered dorsally by a lingually projecting ridge of bone that continues for several additional tooth spaces.

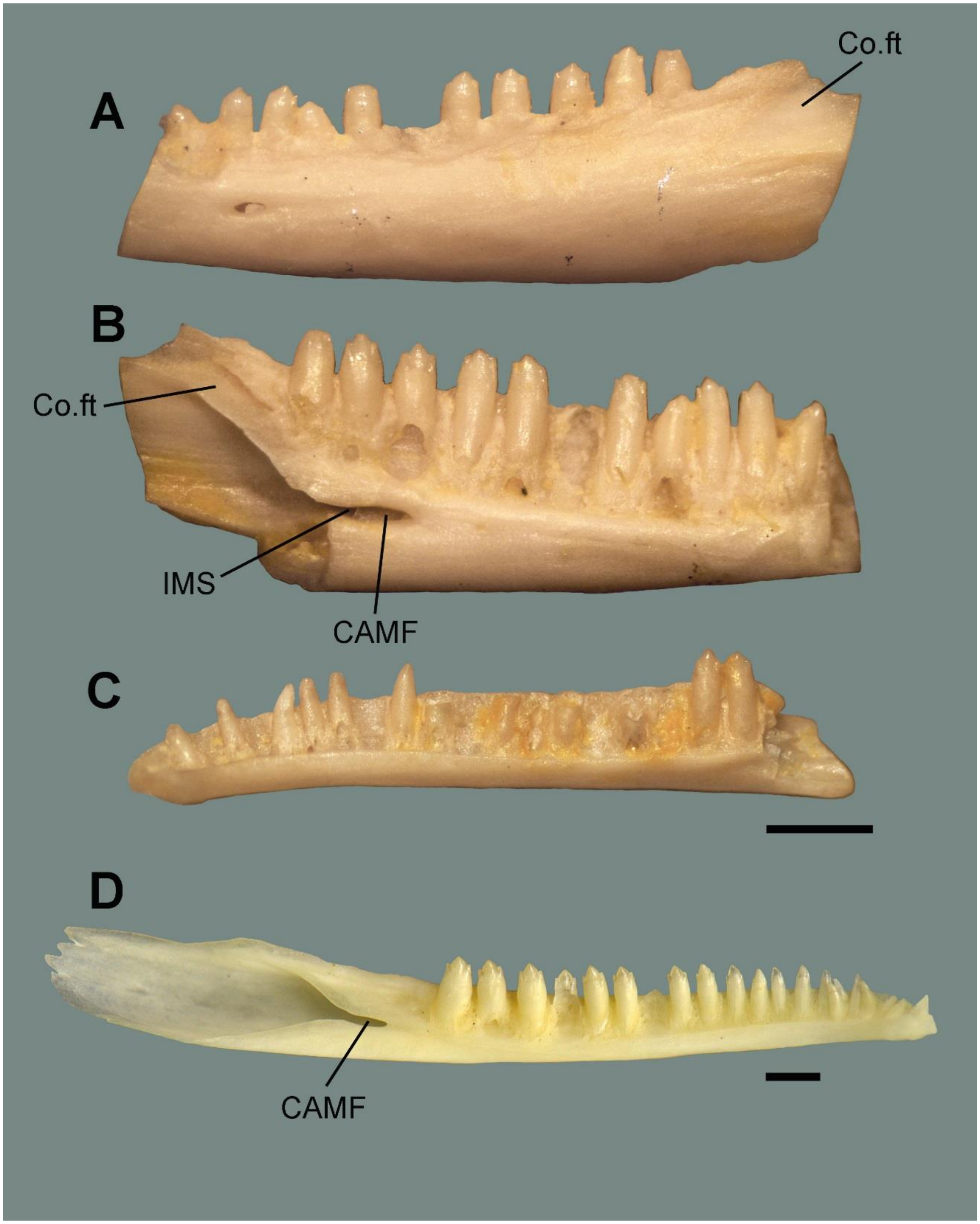

Figure 1. Dentaries of *Anolis* sp. morphotype A. **A, B**, Left dentary of *Anolis* sp. morphotype A, UF 275620, in labial and lingual views, respectively. **C**, Right dentary of *Anolis* sp. morphotype A, UF 275645, in lingual view. **D**, Dentary of *Anolis carolinensis* ETVP 2893 in lingual view. Abbreviations: CAMF, combined alveolar-mylohyoid foramen; Co.ft, coronoid facet; IMS, intramandibular septum. Scale bar equals 1 mm.

Maxilla. Maxillary specimens are associated here based on size, relative abundance, similarity in tooth form, and *Anolis* characters. The most complete specimen, UF 275653 (Fig. 2), is a left maxilla with spaces for 20 teeth. The end of the tooth row is preserved, but the bone is damaged anteriorly. A few tooth spaces may be missing where part of the premaxillary process has broken away. Fully developed mesial and distal accessory cusps do not appear until the ninth preserved tooth position; even without a precise tooth count, this transition evidently did not take place until relatively late in the tooth row. The palatine process is weak but inflected dorsally. This inflection gives the palatal shelf somewhat of a "folded" appearance. The superior alveolar foramen (SAF) is roofed (Smith 2006) but opens into a deep groove that is continuous posteriorly with a facet for the jugal. This morphology is more exaggerated in UF 275606 (Fig. 2), and both specimens retain only a small articular surface posteromedially for the ectopterygoid that is dwarfed by the space for the jugal. Viewed labially, the facial process has a wrinkled, irregular surface. It is not rugose *per se* but lacks the smooth exterior observed for many other iguanids. Anteriorly the facial process bends medially to form a low-angle canthal crest (Smith 2011a) that imparts an elongate appearance to the preorbital portion of the bone. There is only a single foramen at its base where it rises from the premaxillary process. Immediately posterior to the facial process, an additional foramen pierces the dorsal surface of the palatal shelf.

Other material provides additional information and reinforces the interpretation of features described above. UF 275606 and 275693 both preserve a small foramen posterior to the facial process on the palatal shelf. In UF 275606, the portion of the palatal shelf between this foramen and the opening for the SAF is deeply excavated to form a short groove. UF 275693 (Fig. 1) is an anterior fragment and preserves more of the premaxillary and vomerine processes than other specimens. The vomerine process is elongate, and the crista transversalis that rises from it dorsally is well developed. Just as in UF 275653 above, the base of the facial process bears only one foramen anteriorly rather than separate openings for the AIAF and SNAF. Tooth crowns taper noticeably in most specimens, but UF 275694 is exceptional in this regard. In it, a posterior fragment, the bases of the ultimate and penultimate teeth appear mesiodistally expanded.

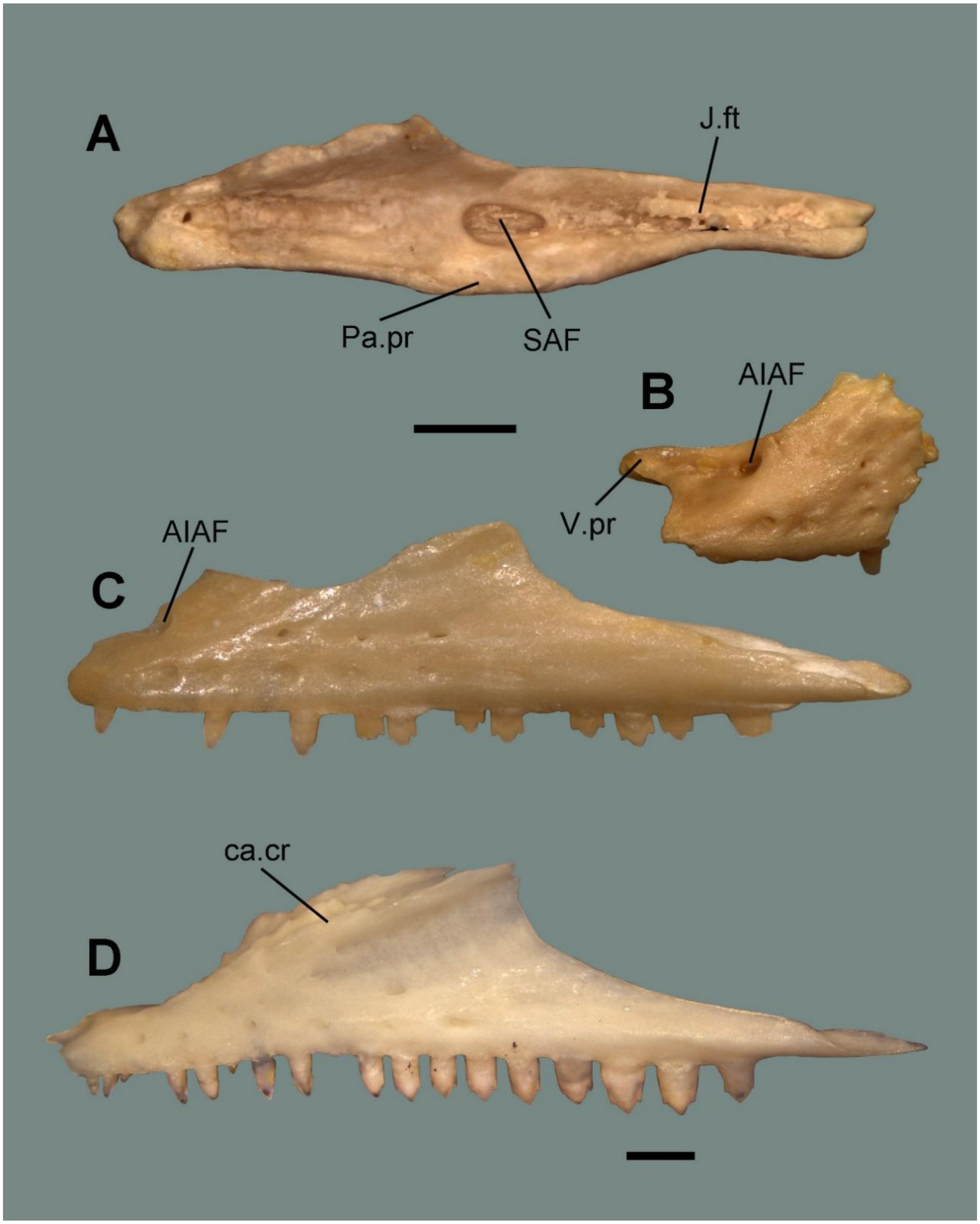

Figure 2. Maxillae of *Anolis* sp. morphotype A. **A,** Right maxilla of *Anolis* sp. morphotype A, UF 275606, in dorsal view. **B,** Left maxilla of *Anolis* sp. morphotype A, UF 275693, in oblique labial view. **C,** Left maxilla of *Anolis* sp. morphotype A, UF 275653 in labial view. **D,** Maxilla of *Anolis carolinensis* ETVP 2893 in labial view. Abbreviations: AIAF, anterior inferior alveolar foramen; ca.cr, canthal crest; J.ft, jugal

facet; Pa.pr, palatine process; SAF, superior alveolar foramen; V.pr, vomerine process. Scale bar equals 1 mm.

Braincase. UF 275667 (Figs. 3-4), an exceptionally preserved braincase, is associated here based on size, relative abundance, and the presence of *Anolis* apomorphies. The sphenoid, basioccipital, supraoccipital, paired prootics, and paired otooccipitals are all present and intact. Most bones are imperceptibly fused, but the contact between the sphenoid and basioccipital maintains a distinctly visible suture. This suture is broadly U-shaped; the posterior border of the sphenoid is convex, and the bone lacks the posterolateral processes present in most other iguanids. The cristae ventrolaterales are confined entirely to the sphenoid, terminating at approximately the same transverse level as the posterior openings for the vidian canal. Anteriorly, the sphenoid bears a strong crista sellaris overhanging the dorsum sella. The parasphenoid rostrum has broken away, and only the ossified bases of the trabeculae cranii remain. The latter do not produce strong cristae trabeculares laterally that, when present in other lizards, form the dorsal roof of the anterior openings of the vidian canal. In the case of UF 275667 these openings lie somewhat dorsal to the horizontal level of the trabeculae cranii rather than ventral to it. The basipterygoid processes are short and neither ventrally nor laterally extensive. The dorsal margins of their distal articular surfaces curve upwards to approach, but not meet, ventrally directed alar processes descending from either side of the crista sellaris. The resulting semicircular invagination would have channeled the lateral head vein (Evans 2008).

The prootic lacks either a supratrigeminal process or an anteriorly directed alar process; its anterodorsal margin is instead formed by the prominent swellings of the anterior semicircular canals. The posterior semicircular canals are similarly distinct; their visibly protruding, vasiform outline can be traced from the dorsal apex of the supraoccipital to a point immediately posterior to the recessus scalae tympani on the otooccipital. The dorsal margins of the posterior semicircular canals are pinched to form a dull crest as they approach each other near the sagittal midline of the bone. This crest is single and continuous and may or may not have been topped by an ossified processus ascendens. If one was present, it has broken away. Viewed posteriorly the crest lends the supraoccipital a superficially tall appearance; the resulting posterodorsal surface, bounded on either side by the semicircular canals, is divided medially by a low ridge of bone. Viewed dorsally the anterior and posterior semicircular canals meet to form a conspicuously X-shaped juncture.

The distal ends of the paraoccipital processes are broken, but enough is preserved to infer their general shape and extent. They are short and do not reach far laterally or posteriorly. Viewed from behind their dorsal margins evince a marked concavity. In dorsal view each otooccipital bears a small but deep depression between the paraoccipital process and the posterior semicircular canal. Both pits are pierced by a small foramen. The ventral bases of the paraoccipital processes produce a strong crista interfenestralis that passes between the fenestra ovalis and the lateral aperture of the recessus scalae tympani (LARST) and continues to a point near the basal tuber. The crest maintains a sharp edge for most of its length but lacks an angular lateral projection observed for some other iguanids. Posterior to the crista interfenestralis, the LARST is divided into rough dorsal and ventral halves by the medial aperture of the recessus scalae tympani above and a moderately deep occipital recess below. A weak, laterally projecting crest separates the two. The crista tuberalis isolating the LARST from the occiput is invaded dorsally by the posterior semicircular canal. Dorsal to the fenestra ovalis, a moderately developed crista prootica spans the distance between the paraoccipital process and the anterior inferior process of the prootic. There is a small facial foramen anterior to the fenestra ovalis, but a prominent bulge occupies the space between them.

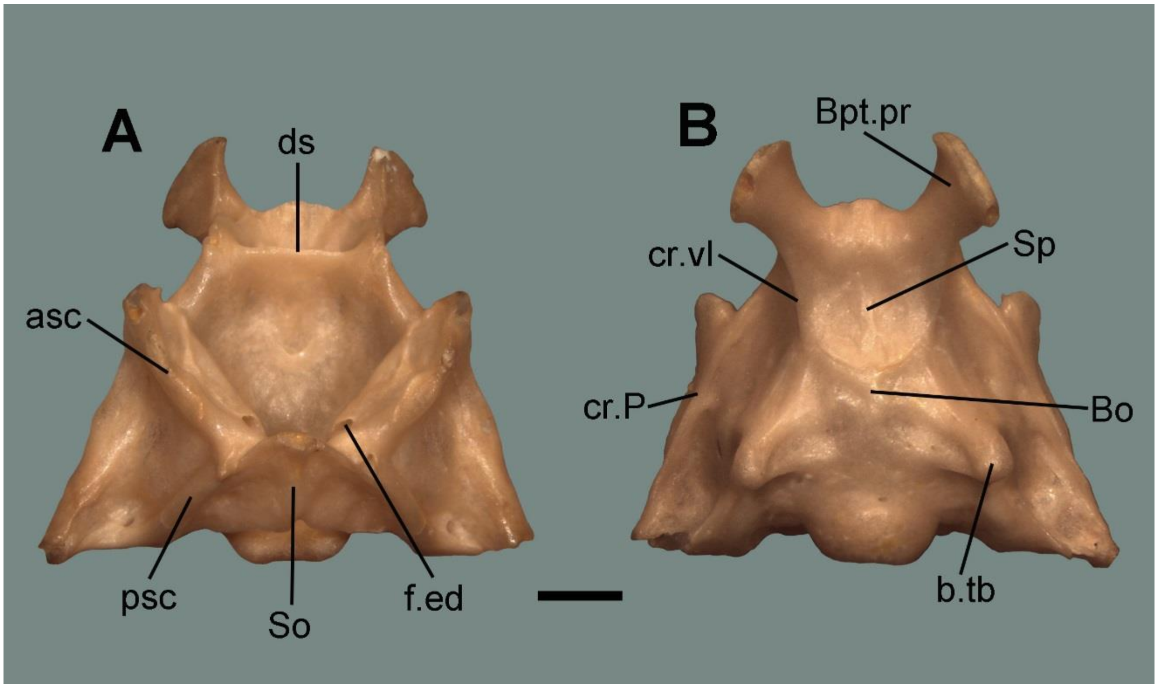

Figure 3. **A, B,** Braincase of *Anolis* sp. morphotype A, UF 275667, in dorsal and ventral views, respectively. Abbreviations: asc, anterior semicircular canal; Bo, basioccipital; Bpt.pr, basipterygoid process; b.tb, basal tuber; cr.P, crista prootica; cr.vl, crista ventrolateralis; ds, dorsum sellae; f.ed, foramen for endolymphatic duct; psc, posterior semicircular canal; So, supraoccipital; Sp, sphenoid. Scale bar equals 1 mm.

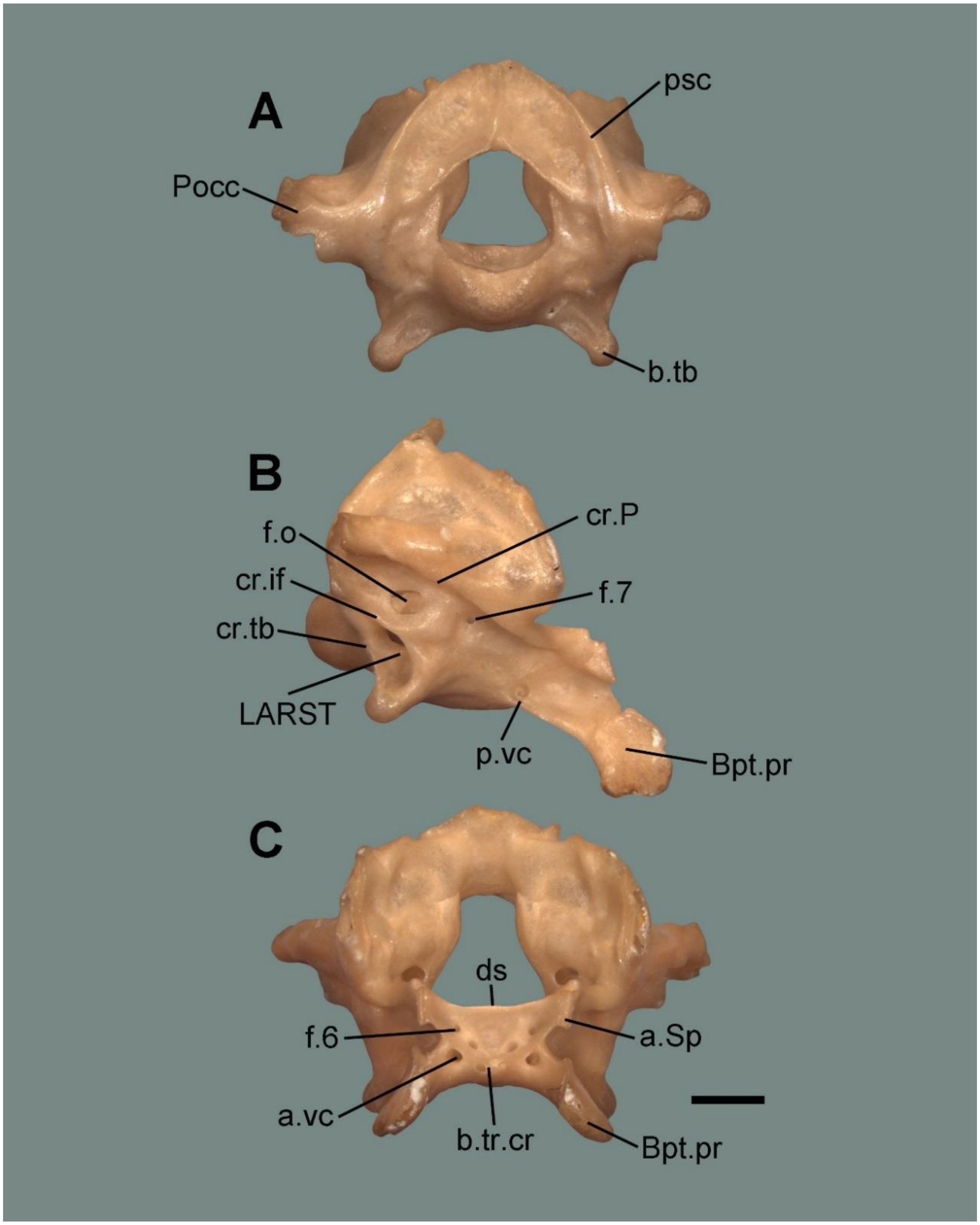

Figure 4. **A, B, C,** Braincase of *Anolis* sp. morphotype A, UF 275667, in posterior, right lateral, and anterior views, respectively. Abbreviations: a.Sp, alar process of sphenoid; a.vc, anterior opening of vidian canal; Bpt.pr, basipterygoid process b.tb, basal tuber; b.tr.cr, base of trabecular cranii; cr.if, crista interfenestralis; cr.P, crista prootica; cr.tb, crista tuberalis; ds, dorsum sellae; f.o, fenestra ovalis; f.6, foramen for abducens nerve (cranial nerve 6); f.7, foramen for facial nerve (cranial nerve 7); LARST, lateral aperture of recessus scalae tympani; Pocc, paroccipital process; psc, posterior semicircular canal; p.vc, posterior opening of vidian canal. Scale bar equals 1 mm.

Frontal. Eight frontals are referred to this taxon, several of which are well preserved and nearly complete. They do not differ substantially in size or morphology. One of the best preserved specimens, UF 275679 (Fig. 5), serves here as an adequate representative for the rest. The bone is gently concave in transverse cross section and has a weakly rugose dorsal surface. This rugosity increases along the length of the bone; the dorsum is pocked with minute pits posteriorly, but shallow grooves and an incipiently pustulate texture develop anterior to the midorbital constriction. The posterior margin of the bone is nearly straight but with a small projection along the midline. Even if a parietal foramen was situated at the frontoparietal suture (a parietal is unknown for this taxon), it did not invade the frontal. Not all of the referred frontals display a posterior projection (even in UF 275679 it is weak), but none show any indication of a foramen. The posterolateral corners of the frontal each bear an elongate, ventrolaterally directed tab of bone that would have underlapped the parietal and made contact with the postorbital. These extensions are clearly visible when the bone is set on a flat surface. Anteriorly the posterolateral corners show articular surfaces for a small postfrontal.

Ventrally UF 275679 is flanked on either side by moderately developed supraorbital flanges. These flanges are always present on other specimens but only weakly so in UF 274061. The crista cranii are well developed and maintain a relatively uniform thickness for their entire length. They nearly meet where the bone is most strongly constricted.

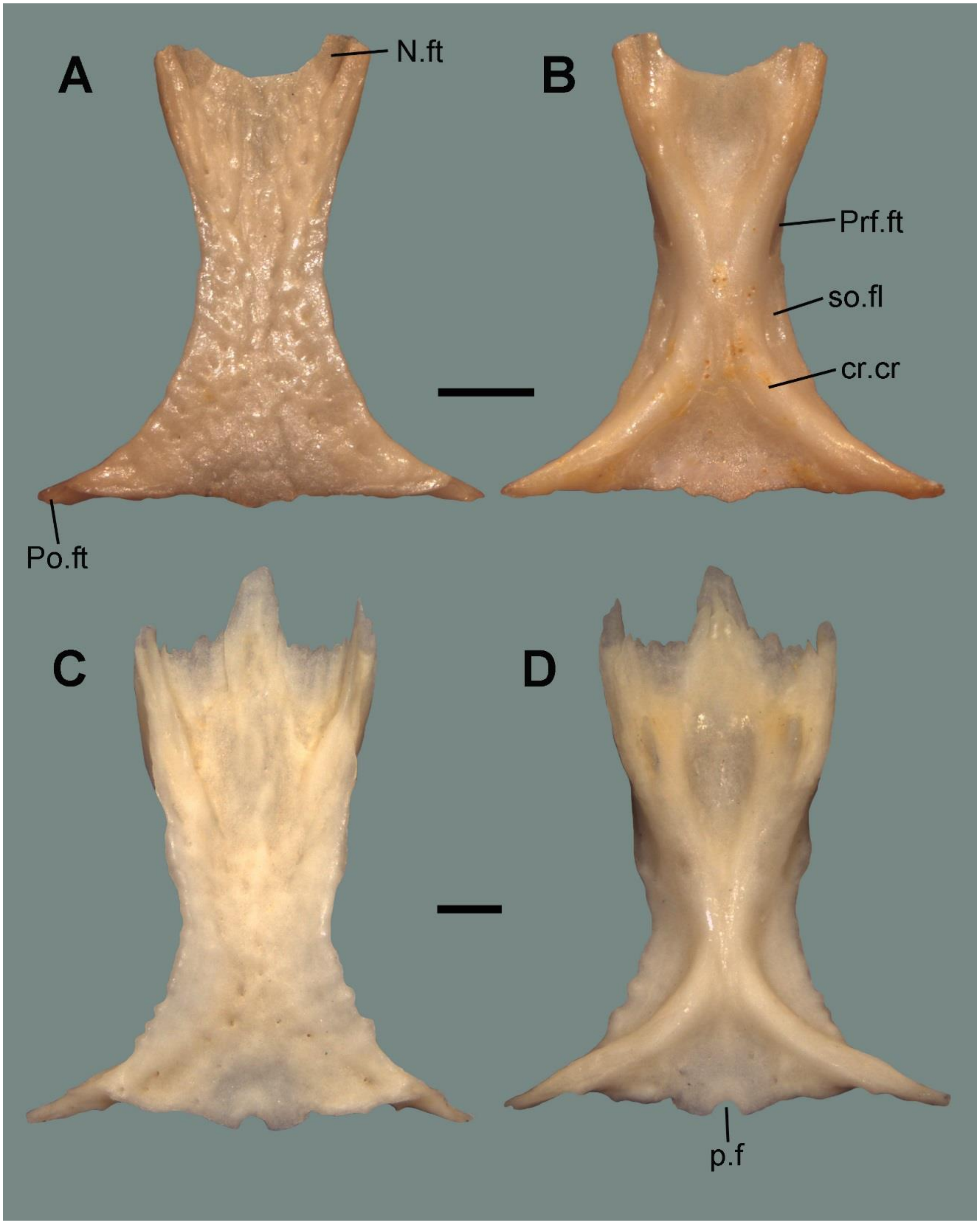

Figure 5. Frontal of *Anolis* sp. morphotype A. **A, B,** Frontal of *Anolis* sp. morphotype A, UF 275679, in dorsal and ventral views, respectively. **C, D,** Frontal of *Anolis carolinensis* ETVP 2893 in dorsal and ventral views, respectively. Abbreviations: cr.cr, crista cranii; N.ft, nasal facet; p.f, parietal foramen; Po.ft, postorbital facet; so.fl, supraorbital flange. Scale bar equals 1 mm.

Prefrontal. UF 278727 (Fig. 6) and UF 278745 are left prefrontals that share a similar size and morphology. The dorsal surface (of both) is coarsely pustulate, and the posterolateral corner of the bone extends laterally to form a strong canthal ridge (sensu Smith 2009b). Based on what is preserved of the articular surfaces, it is unclear if the element would have contacted the nasal anteromedially.

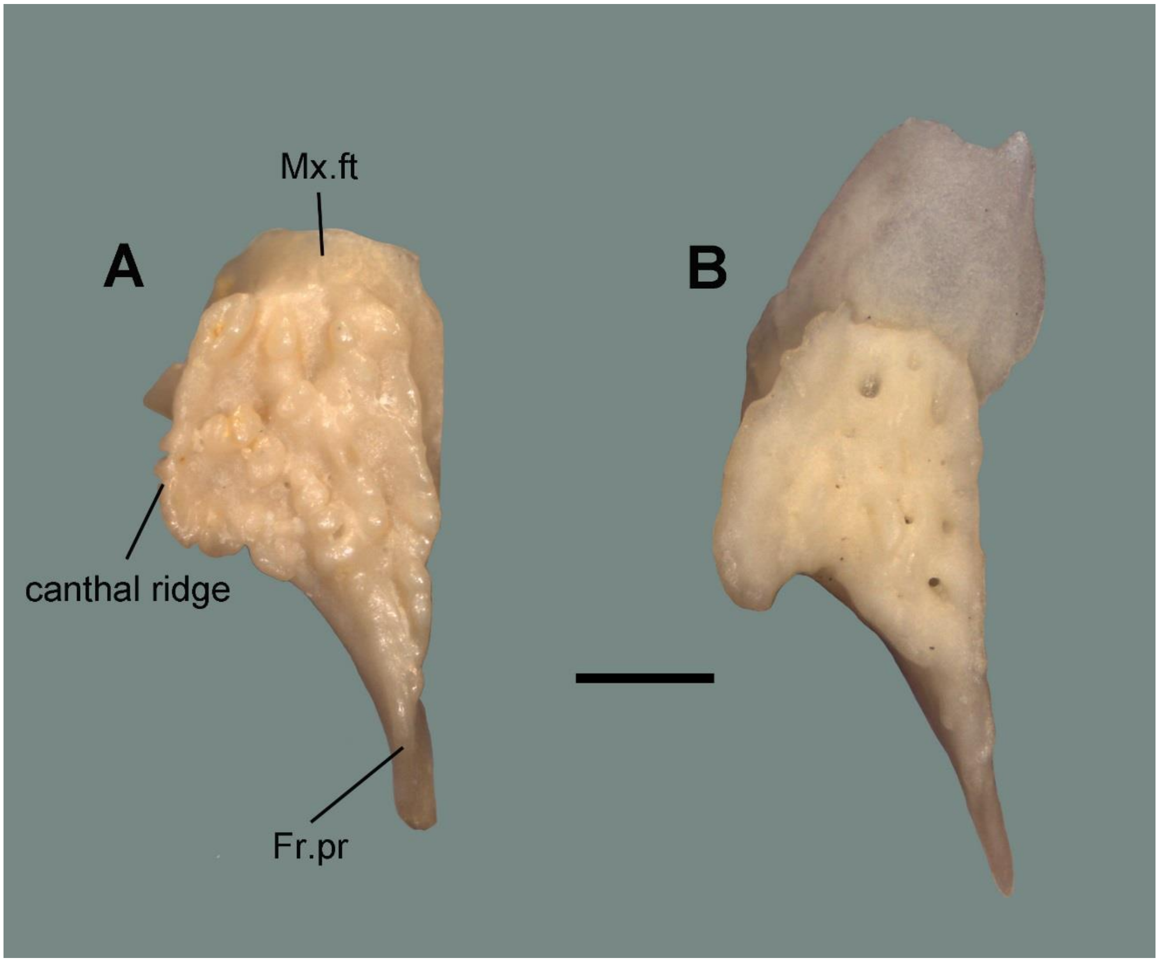

Figure 6. Prefrontal of *Anolis* sp. morphotype A. **A,** Left prefrontal of *Anolis* sp. morphotype A, UF 278727, in dorsal view. **B,** Left prefrontal of *Anolis carolinensis* ETVP 2893 in dorsal view. Abbreviations: Fr.pr, frontal process; Mx.ft, maxillary facet. Scale bar equals 1 mm.

Postorbital. A small postorbital (UF 275627; Fig. 7) is associated with this taxon based on size, relative abundance, and *Anolis* characters. It is a triradiate bone with dorsal, anterior, and posterior rami. The dorsal and anterior rami are approximately equal in length, but the posterior ramus is elongate. The dorsal ramus bears a large, flat frontal/postfrontal facet anteriorly, the ventral extent of which is marked by a weak, laterally projecting knob of bone. The dorsal margin of the posterior ramus is convex. Ventrally a tongue-and-groove facet for the jugal (Oelrich 1956) extends from the tip of the anterior ramus to the transverse level of the posterior margin of the dorsal ramus. Posterior to this a facet for the squamosal is only faintly discernible laterally; it is not clear if the jugal and squamosal would have contacted each other.

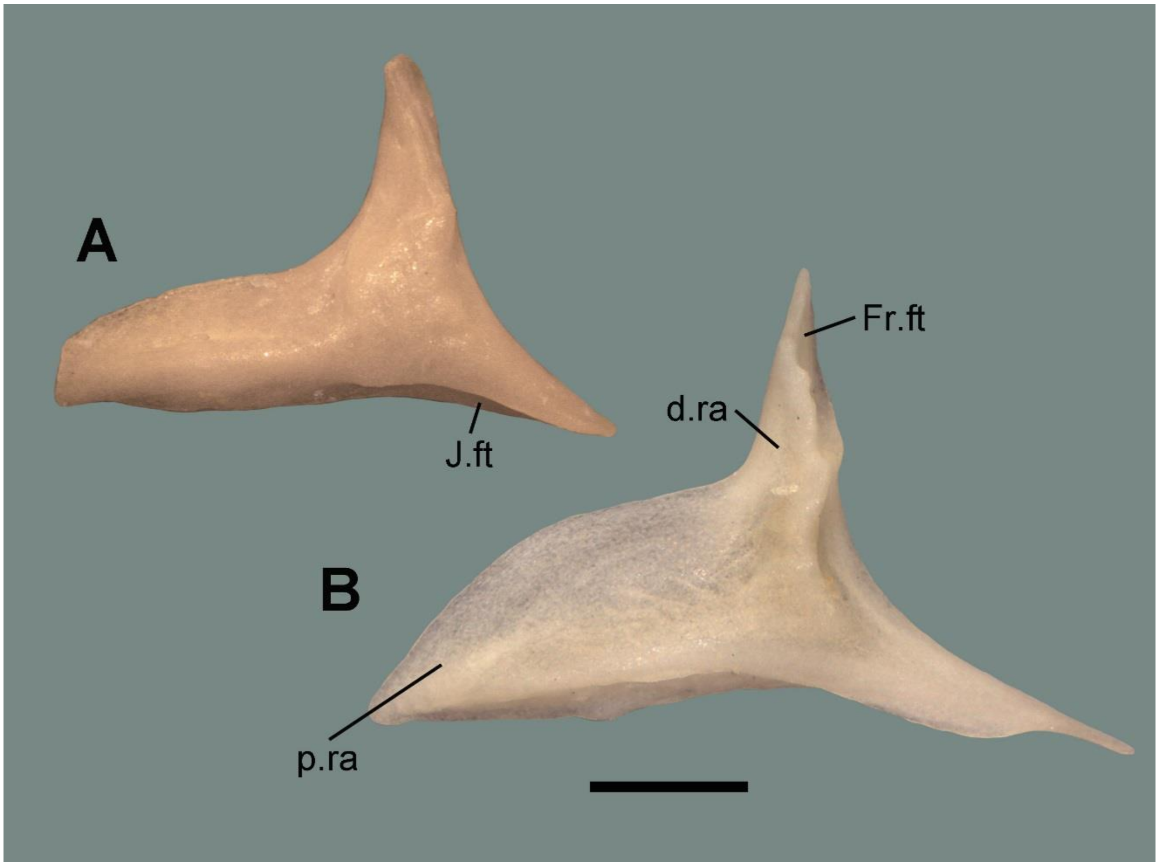

Figure 7. Postorbital of *Anolis* sp. morphotype A. **A,** Right postorbital of *Anolis* sp. morphotype A, UF 275627, in lateral view. **B,** Right postorbital of *Anolis carolinensis* ETVP 2893 in lateral view. Abbreviations: a.ra, anterior ramus; d.ra, dorsal ramus; Fr.ft, frontal facet; J.ft, jugal facet; p.ra, posterior ramus. Scale bar equals 1 mm.

Quadrate. Three complete quadrates are associated here based on size, relative abundance, and *Anolis* characters. The medial concha is highly reduced, and the tympanic crest bounding the lateral concha is formed by a thick, rounded ridge of bone. The lateral concha is not deep, and the posterior crest curves only weakly. Consequently, the element appears straight and thin in lateral view. Viewed posteriorly it is roughly rectangular. The posterior crest is not quite vertical but is not as strongly inclined medially as in many iguanids. The lateral concha extends as far dorsally as the cephalic condyle, and the tympanic crest is continuous medially with the ventral condyle. A small foramen penetrates the boundary between the posterior crest and the reduced medial concha in the ventral half of the bone; it exits somewhat ventrally and laterally on the anterior side. UF 275682 and UF 275684 both bear a small, cannular ridge on the lateral concha (the lateral ridge of Smith 2009b).

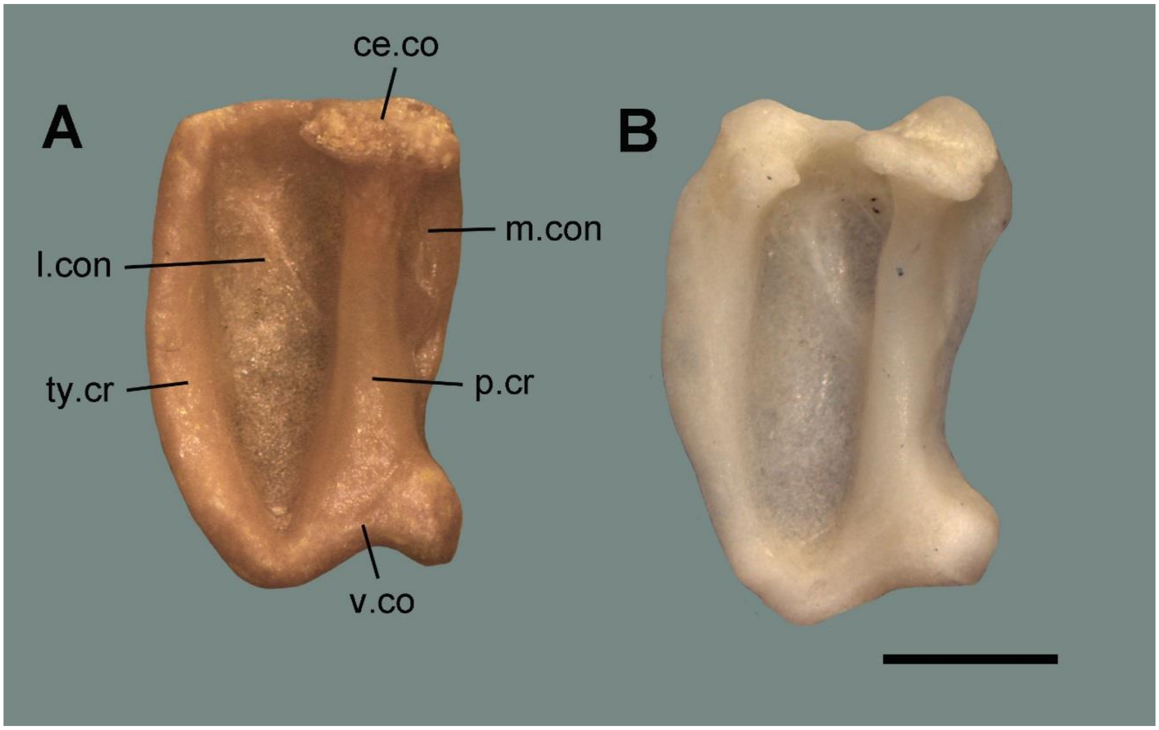

Figure 8. Quadrate of *Anolis* sp. morphotype A. **A,** Left quadrate of *Anolis* sp. morphotype A, UF 275682, in posterior view. **B,** Left quadrate of *Anolis carolinensis* ETVP 2893 in posterior view. Abbreviations: ce.co, cephalic condyle; l.con, lateral concha; m.con, medial concha; p.cr, posterior crest; ty.cr, tympanic crest; v.co, ventral condyle. Scale bar equals 1 mm.

Remarks

Associated material referred to the most abundant lizard at Brooksville 2 all suggests a close relationship with extant *Anolis*. The early Eocene stem anoles *Anolbanolis* (Smith 2009a) and *Paranolis* (Smith 2011a) are known well enough to afford some instructive evolutionary context, and a consideration of character succession in the lineage indicates a number of features that would place the Brooksville species somewhere among the exceptional crown radiation. *Anolbanolis*, *Paranolis*, and the Brooksville anole are known only from isolated cranial elements, and representative bones are not always common to all 3 taxa. Those that are shared mutually, though, provide a useful starting point for a discussion of the phylogenetic position of the Brooksville taxon.

Smith (2009a; 2011a) allied *Anolbanolis* with *Anolis* based on the common possession of a low-angle canthal crest on the maxilla, a well-developed crista transversalis, a transversely concave frontal with supraorbital flanges, and the development of a canthal ridge on the prefrontal. The Brooksville anole shares all of these characters with both taxa. In noting a close relationship between *Anolbanolis* and *Anolis*, however, Smith (2011a) highlighted a few key differences that would serve to exclude the former from the latter: *Anolbanolis* lacks the fused Meckelian groove, mesiodistally expanded posterior teeth, anterolateral coronoid process, continuity of the opening of the SAF with a deep jugal facet, and unification of the anterior inferior alveolar and subnarial arterial foramina that all characterize *Anolis*. Smith and Gauthier (2013) also argued that the invasion of the frontal of *Anolbanolis* by the parietal foramen (confined primarily or entirely to the parietal in *Anolis*) bars it from the crown of the clade. The dentary, maxilla, and frontal of the Brooksville anole share all of these features with *Anolis* to the exclusion of *Anolbanolis*.

Maxillary specimens are not known for *Paranolis*, but its dentary, postorbital, and frontal document novel transformations that unite it more closely with *Anolis* than

Anolbanolis. Like *Anolis*, it has a shallow, elongate dentary with a fused Meckelian groove, high tooth count (≥ 25), and tapering tooth crowns (Smith 2011a). The two also share a postorbital with a convex dorsal expansion of the posterior ramus and frontal that is not invaded significantly by the parietal foramen (Smith and Gauthier 2013). The Brooksville anole exhibits all of these characteristics as well, but its dentary is more similar to that of *Anolis* for having a more extensively fused Meckelian groove and for bearing a labial facet for an anterolateral extension of the coronoid. Even if *Paranolis* did have an anterolaterally expansive coronoid (its corresponding facet on the dentary is often difficult to discern even on modern disarticulated *Anolis* specimens when it does not incise deeply into the surface of the bone), the nature of its Meckelian groove is fundamentally different from that of observed *Anolis*.

In *Paranolis*, the Meckelian groove is open both anteriorly and posteriorly for a length of about 6 or 7 teeth (Smith 2011a). The posterior opening comes in the form of an anteriorly tapering, V-shaped space that Smith (2011a) suggested might have been filled by the splenial. Etheridge and de Queiroz (1988) identified two synapomorphies of *Anolis* (sensu Poe 2004; the "anoles" of their analysis) that are potentially of some relevance here: the possession of a reduced splenial that does not extend as far anteriorly as the ultimate tooth and the reduction of the angular to a splint. Although the splenial does actually reach the level of the last tooth in some *Anolis* (Poe 1998: fig. 14C), the extreme reduction (or in some cases, loss [Etheridge 1959]) of these two bones manifests itself in a way that is evident even on isolated dentaries. In *Anolis* the Meckelian groove is fused farther posteriorly (sometimes beyond the end of the tooth row) than in most other observed iguanids. Only tropidurines, which also have reduced angulars and splenials (Etheridge and de Queiroz 1988; Frost 1992; Pregill 1992), are similar in this regard. A peculiarity of the *Anolis* mandible, though, is that the anterior inferior alveolar and anterior mylohyoid foramina — separate in other iguanid taxa — merge to form a common opening confined primarily to the dentary. This combined alveolar-mylohyoid foramen (Castañeda and de Queiroz 2013) typically takes shape as a small oval almost fully circumscribed by the supra- and infra-Meckelian lips. Its exact position can vary, even intraspecifically, but the presence of a comparable opening in the Brooksville species (as well as the fusion of its Meckelian groove anteriorly to the symphysis and the anterolateral extension of its coronoid) unites it with *Anolis* to the exclusion of *Paranolis*.

Additional characteristics (either individually or in combination) of the Brooksville taxon ally it exclusively with *Anolis* among living iguanids but admittedly cannot yet be evaluated in *Paranolis*. The *Anolis* maxilla is derived for having only a single foramen anteriorly at the base of the facial process (Smith 2009a; 2009b) and a SAF that opens into a deep jugal groove (Smith 2011a), 2 features shared by the Brooksville anole but not *Anolbanolis*. On the dentary Smith (2009b) found an elongate IMS to be synapomorphic for polychrotines. An exact ratio was not obtainable for the Brooksville specimens, but the termination of the septum under the penultimate tooth in posterior fragments surely affirms its extensive nature. A wrinkled labial parapet and extensive external facet for the coronoid on the supra-Meckelian lip were common among observed *Anolis* but have not been analyzed exhaustively for other iguanids.

The *Anolis* quadrate can generally be distinguished by its reduced medial concha, nearly vertical posterior crest (viewed posteriorly), roughly rectangular shape, and thick tympanic crest. A reduced medial concha is also known for *Polychrus*, some corytophanines, *Phymaturus*, and some phrynosomatines (Lang 1989; Smith 2009b), but I have only observed such a thick tympanic crest for *Anolis* and some tropidurines. In tropidurines, though, the ridge of bone that forms the tympanic crest turns medially and terminates before reaching the ventral condyle, leaving a small notch between the two. This discontinuity is often marked even in taxa that lack a swollen tympanic crest. In most observed *Anolis*, as in the Brooksville taxon, the tympanic crest is smoothly continuous with the ventral condyle.

The fossil braincase shares 2 important features with *Anolis*, namely the raised semicircular canals and the lack of posterolateral processes of the sphenoid. Etheridge (1959) first brought attention to the conspicuous canals of some iguanids and noted their distribution primarily among arboreal taxa. The presence of raised canals has been coded as a derived character state in subsequent phylogenetic analyses of iguanids (Etheridge and de Queiroz 1988; Frost and Etheridge 1989; Lang 1989) but without further mention of any consistent ecomorphological pattern. A recent study of CT-generated endocasts of the vestibular system in a number of squamates found measurable differences in taxa capable of controlled aerial descent (Boistel et al. 2011) but did not discuss how such changes would be expressed skeletally on the surface of the braincase. Curiously, significantly raised canals are present in the “flying” non-iguanid taxa *Ptychozoon* (a gekkotan) and *Draco* (an agamid)(pers. obs.). *Anolis* is known experimentally to be capable of controlled aerial descent (Oliver 1951), but it is easy to imagine how a greater command of airborne roll, pitch, and yaw (cf. Boistel et al. 2011) would be advantageous to any highly mobile lizard in a tree. Besides being phylogenetically informative, then, the conspicuous semicircular canals of the Brooksville anole may provide direct evidence for an arboreal mode of life.

The reduction of the posterolateral processes of the sphenoid is less common. Such processes are reduced in *Anolis*, some *Polychrus*, and at least some *Liolaemus* (Smith 2009b). They are also reduced in some crotaphytines (Norell 1989). Frost et al. (2001) suggested they are present in *A. equestris*, but they are absent in specimens available to me. In most iguanids I have observed that lack extensive processes, the sphenoid and basioccipital meet in a roughly straight transverse suture; only in *Anolis* is this junction normally U-shaped. *Anolis* is not unique for having raised semicircular canals or a modified sphenoid, but a derived combination of both is otherwise present (to my knowledge) only in some species of *Polychrus* (Frost et al. 2001). Observed *Polychrus*, though, have a reduced crista prootica, a reduced occipital recess, and anterior semicircular canals that reach significantly further dorsally than the corresponding posterior semicircular canals. Both pairs of canals are roughly subequal in height in *Anolis*, and meet to form a large “X” on the dorsum of the supraoccipital. The *Anolis* braincase is further characterized by the deeply excavated dorsal pits found at the base of the paraoccipital processes. Many iguanid taxa bear shallow impressions here but never as conspicuously as in *Anolis*.

The frontal of *Anolis*, in addition to features already discussed above, is notable for its form of articulation with the parietal and postorbital. The posterolateral corners of the bone each produce a spine-like projection that extends ventrolaterally to secure the parietal posteriorly and to brace the postorbital anteriorly (Fig. 9). These processes tend to be less exaggerated in species with comparatively squat frontals (e.g., *A. biporcatus* and *A. equestris*), but barring such exceptions I have not observed such laterally extensive projections in other iguanids besides *Anolis*.

The Brooksville taxon, aside from possessing synapomorphies discussed above for clades bracketed successively by *Anolbanolis* and *Paranolis*, displays a number of features not known for either that would ally it exclusively with *Anolis* among known taxa. Assuming all elements are associated correctly, it shares the following additional features with examined members of the extant genus: SNAF and AIAF combined on maxilla; SAF opens into deep jugal groove; anterolateral extension of coronoid; Meckelian groove fused anteriorly to the symphysis; Meckelian groove fused almost to the end of the tooth row, diverging posteriorly only to accommodate a small foramen; lingually projecting ridge of bone dorsal and anterior to CAMF (some); labial parapet notably wrinkled (some); mesiodistally expanded posterior teeth (some); quadrate roughly rectangular with a reduced medial concha and a thick tympanic crest that is continuous medially with the ventral condyle; prefrontal with pustulate rugosities; sphenoid with reduced posterolateral processes and a convex posterior margin; otooccipitals deeply excavated dorsally; outlines of anterior and posterior semicircular canals distinctly visible, forming a large X-shaped juncture dorsally on supraoccipital; frontal with laterally extensive postorbital facets. Even allowing for the possibility that some elements may be associated in error, dentigerous dentaries and maxillae alone may be sufficient for its allocation to *Anolis*.

There are nearly 400 extant species of *Anolis* (Uetz 2014), and to hazard an attempt to place the Brooksville species even among any of its most inclusive subclades is well beyond the scope of this study. Importantly, however, the Brooksville anole bears little resemblance to *A. carolinensis* or to any of its close Caribbean relatives (the *carolinensis* series of Poe 2004). That group is derived for having a combined alveolar-mylohyoid foramen generally positioned posterior to the tooth row (Poe 2004), and members analyzed for this study never had such a strongly vertical IMS (or attendant IML) as in the Brooksville taxon. Smith (2009a) identified at least one potential synapomorphy of the maxilla of the *carolinensis* series that would exclude the Brooksville species, namely a dorsally concave premaxillary process and multiple anterodorsal foramina. Even more generally, though, the canthal crest of observed members of the *carolinensis* series is extremely well defined and often strongly rugose; the medial bend is formed by a sharp angle that is obvious even in living specimens. The canthal crest of the Brooksville species, although apparent, is more subtle. In this way, it is more comparable to the morphology seen for *A. roquet*. Even if the relationships of the Brooksville anole cannot be precisely determined, it is not closely related to the only *Anolis* species native to the United States today.

Other pre-Pleistocene fossil *Anolis* are known only as amber inclusions from the early to middle Miocene of the Dominican Republic (Rieppel 1980; de Queiroz et al., 1998; Polcyn et al. 2004) and Mexico (Lazell 1965; Carbot-Chanona and Milani 2008). Those specimens preserve articulated partial skeletons (often with soft tissue, and usually of juveniles) that did not warrant extensive comparison here. Given the most current age estimates of the amber from the Dominican Republic (15 to 20 Ma; Iturralde-Vinent and MacPhee 1996) and Mexico (early to middle Miocene; Perrilliat et al. 2010), the occurrence of *Anolis* at Brooksville predates all such specimens, minimally, by 3-5 million years.

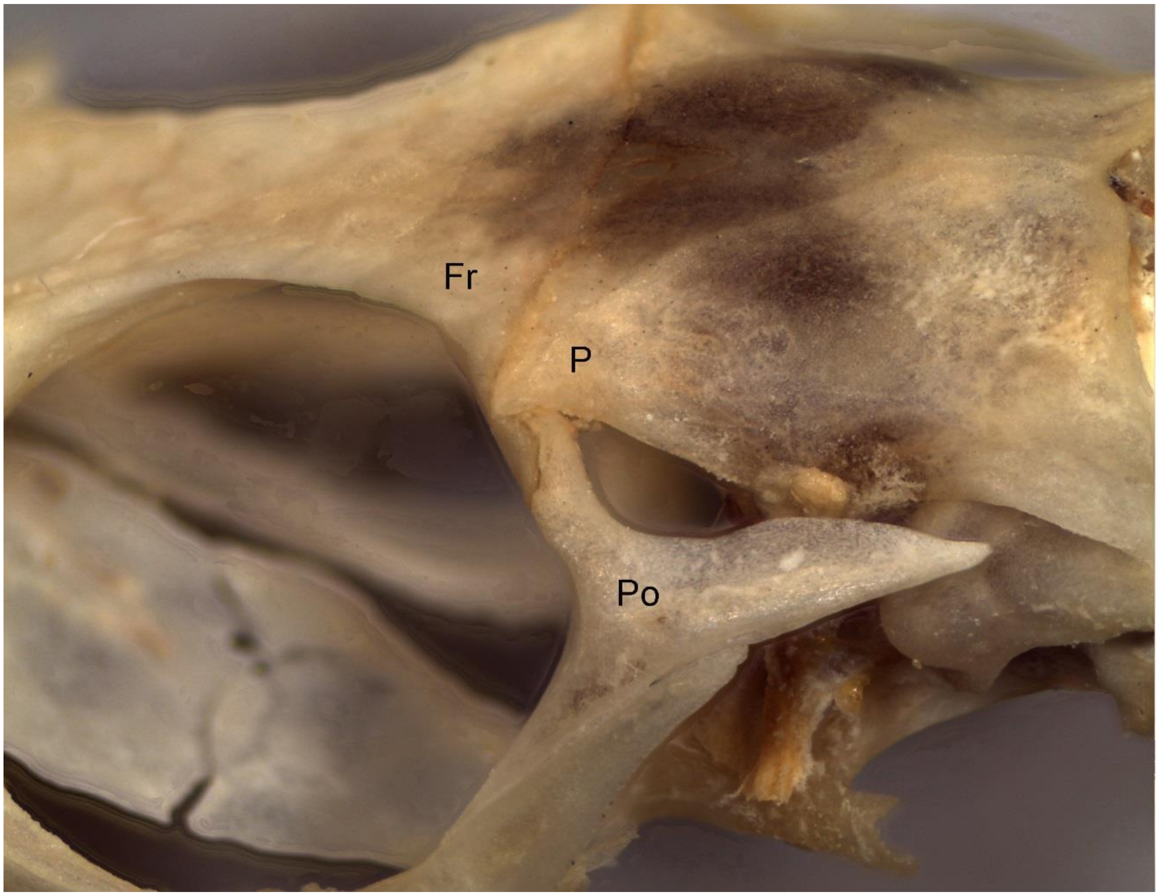

Figure 9. Oblique left lateral view of skull of *Anolis carolinensis* JIM 0266. Abbreviations: Fr, frontal; P, parietal; Po, postorbital. Scale bar equals 1 mm.

cf. *Anolis* sp.

Morphotype B

(Figure 10)

Referred Material

UF 275662 (partial right dentary), UF 275695 (partial right dentary), UF 275696 (partial right dentary), UF 275619 (partial left dentary), UF 275665 (partial left dentary)

Description

Dentary. UF 275696 (Fig. 10) is the posterior portion of a right dentary. There are spaces for 10 teeth, 8 of which are occupied. All preserved teeth are tricuspid with gently tapering crowns. The Meckelian groove is closed and fused but is invaded posteriorly by a small oval foramen at a level below the antepenultimate tooth. The supra-Meckelian lip (sML) descends to nearly contact the infra-Meckelian lip (iML) again immediately afterwards (see Bhullar and Smith 2008), but the foramen remains incompletely encircled by bone. A short dorsal process rises from the dentary posterior to the tooth row to receive the coronoid. Labially, a roughly triangular facet for an anterolateral extension of the coronoid extends to, but not under, the last tooth. The dentary looks to have been posteriorly extensive; the end of the bone is broken but reaches well beyond the end of the tooth row. Looking through the dentary tube posteriorly, there is no IMS or IML.

The anterior end of the bone is best preserved in UF 275695 (Fig. 10). It is long and slender, and the transition to tricuspid teeth occurs around the 12th tooth. A faint subdental gutter is discernible far anteriorly but fades quickly. The Meckelian groove is closed and fused. Anteriorly it opens ventrally as a narrow slit from the symphysis to a level below the sixth tooth. A weak *genioglossus* scar is visible labially. Posteriorly, there is no visible IMS.

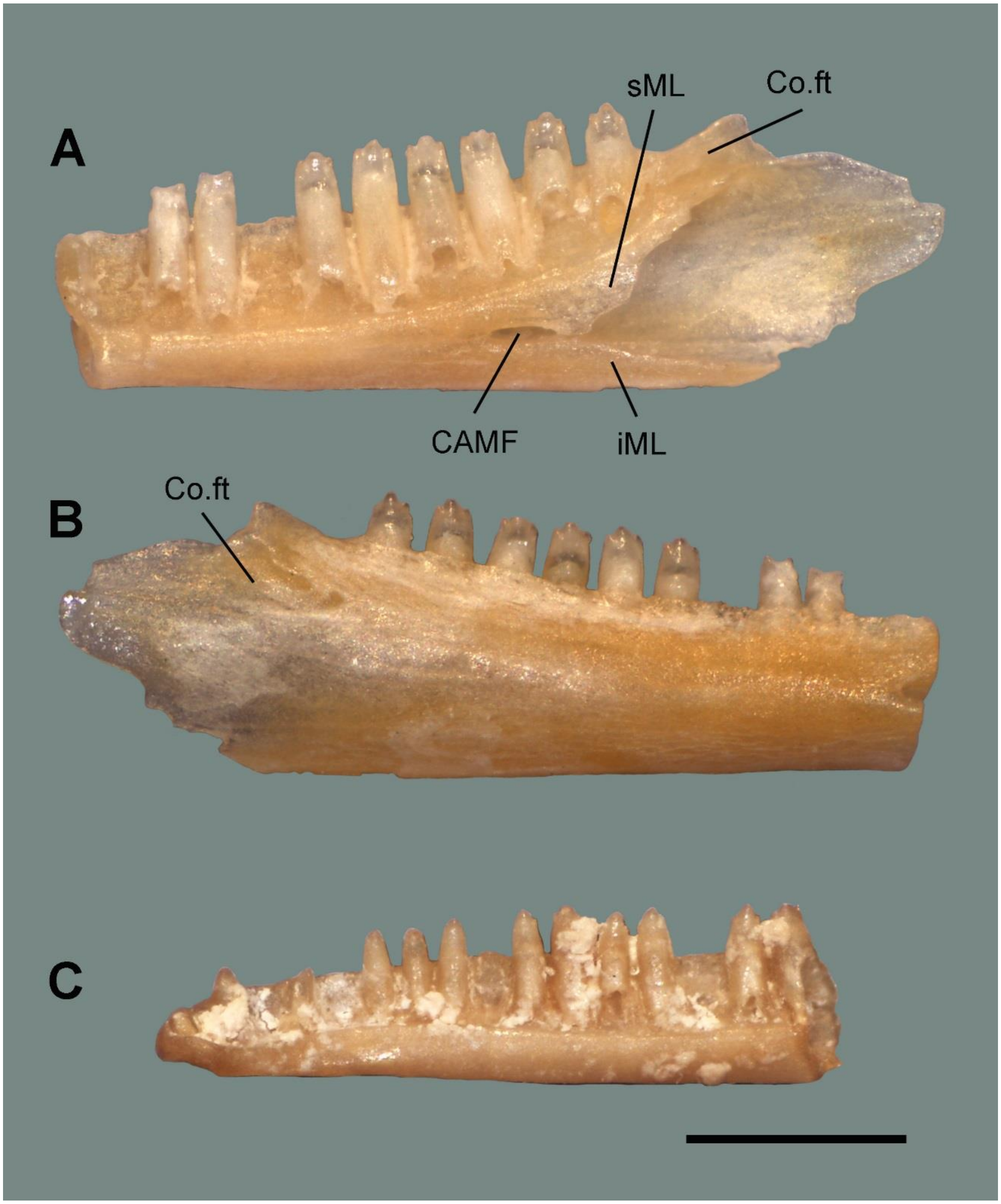

Figure 10. Dentaries of *Anolis* sp. morphotype B. **A, B,** Right dentary of *Anolis* sp. morphotype B, UF 275696, in lingual and labial views, respectively. **C,** Right dentary of *Anolis* sp. morphotype B, UF 275695, in lingual view. Abbreviations: CAMF, combined alveolar-mylohyoid foramen; Co.ft, coronoid facet; iML, infra-Meckelian lip; sML, supra-Meckelian lip. Scale bar equals 1 mm.

Remarks

These specimens are tentatively referred to *Anolis* for having a slender dentary with an extensively fused Meckelian groove, tapering tooth crowns, an anterolaterally expansive coronoid, and for the development of a small foramen (possibly a CAMF) confined primarily to the dentary (see discussion above for morphotype A). Given the morphology of the bone and the position of the foramen, the angular and splenial were necessarily reduced. The posterior end of the dentary almost certainly would have reached beyond the level of the dorsal apex of the coronoid, at least supporting an *Anolis* relationship (Etheridge and de Queiroz 1988). An anterior opening for the Meckelian groove typically does not extend further than the first 2 teeth in *Anolis* (Smith 2006; Smith and Gauthier 2013), and its elongate nature here (to the sixth tooth) might argue against such a relationship.

This taxon differs from morphotype A for having a longer anterior opening for the Meckelian groove, for the development of a dorsal coronoid process posteriorly, for lacking an IML, for its much smaller size (~50%), and for the seeming absence of any indication of an IMS. An alternative explanation for perceived differences among the two could be related to ontogeny; it is possible that these 5 dentaries belonged to immature individuals of morphotype A that lacked a fully developed IMS. An ossified IMS, though, is already present in the smallest available specimens of *A. carolinensis* (FB 274; SVL=38 mm) and *A. porcatus* (JIM 0258; SVL=20 mm), and their Meckelian grooves are fused smoothly to the symphysis.

The recognition of an additional *Anolis* (or *Anolis*-like) species at Brooksville admittedly jeopardizes the association of isolated elements to either. Dentaries of both taxa are easily discriminated by the presence or absence of an IMS, and specimens were not referred to either if this feature could not be evaluated. The much greater size of morphotype A, though, as well as the significantly greater relative abundance of its dentaries, arguably provide a reliable litmus test for the association of nondentigerous material to one taxon or the other. By that metric, of all elements referred to morphotype A, perhaps only the association of frontals is equivocal; all are smaller than would be expected (by comparison with modern *Anolis* individuals) given the relative sizes of the fossil braincase, postorbital, maxillae, prefrontals, and quadrates. The association of those same frontals with morphotype B here would bolster a case for its relationship with *Anolis* but would not significantly alter the interpretation of morphotype A above.

Iguanidae gen. et sp. indet.

(Figure 11)

Referred Material

UF 275612 (partial left dentary), UF 274077 (partial right dentary), UF 275644 (partial right dentary)

Description

Dentary. The most complete dentary, UF 275644 (Fig. 11), measures 5.32 mm in length. It has 16 tooth spaces, with teeth missing from positions 6, 10, 12, 14, and 16. The specimen is broken anteriorly and posteriorly, so a total tooth count or tooth row length is unknown. The dorsal curvature of the tooth row in the posterior half of the specimen suggests it could not have continued much further, but the anterior extent of the bone cannot be estimated. An accurate dentary depth/tooth row length ratio (Smith 2006) is impossible, but it does not appear to have been exceptional at either extreme in this regard.

Anteriorly the teeth are short, recurved, and unicuspid. Posterior teeth are taller, straighter, and bear weak mesial and distal cusps by the seventh preserved tooth position. Such cusps are not strongly defined, even by the last tooth. This may be at least partially attributable to wear; a replacement crown filling the resorption pit at the base of the eighth preserved tooth has more obvious grooves separating the cusps. The teeth are regularly spaced with roughly parallel-sided or gently tapering crowns. A moderately developed subdental shelf is present as far posteriorly as the specimen is preserved. The Meckelian groove is closed for a space of about 4 teeth between the sixth and ninth preserved tooth positions. It opens gently and remains restricted for the length of approximately 2 tooth spaces anterior to this, but thereafter the infra-Meckelian lip is broken and the nature of the groove is uncertain. The infra-Meckelian lip is likewise broken posterior to the level of ninth tooth position, and it is not clear how far posteriorly the closure would have persisted. Under the 11th tooth the supra-Meckelian lip is notched and may have delineated the AIAF dorsally. Just anterior to this the lingual face of the lip is marked by a faintly discernible oval-shaped impression. Lateral to the supra-Meckelian lip the IMS extends to a transverse level between the 10th and 11th teeth. It is displaced somewhat dorsally such that it cannot be seen in lateral view. The IML posterior to this is only very weakly expressed and is almost functionally absent.

The labial surface of the dentary is predominantly flat. Four labial foramina are present, the last at the level of the eighth tooth. Posteriorly, a V-shaped notch is incised into the bone just below the last 2 tooth spaces that would have articulated with an anterolateral extension of the coronoid.

UF 275612 is more fragmentary and less informative. It is similar in size, suggesting this was a small lizard. The (broken) supra- and infra-Meckelian lips approach each other closely but never make contact. Although inconclusive as preserved, UF 275612 indicates the Meckelian groove may not have always fully closed in this taxon.

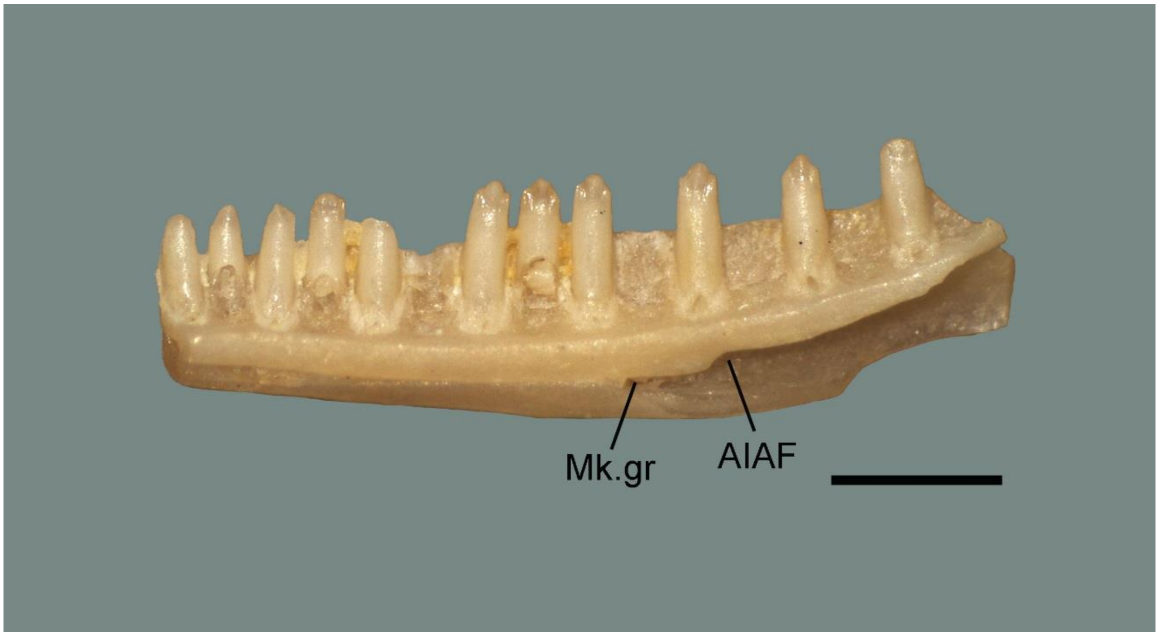

Figure 11. Right dentary of Iguanidae gen. et sp. indet., UF 275644, in lingual view. Abbreviations: AIAF, anterior inferior alveolar foramen; Mk.gr, Meckelian groove. Scale bar equals 1 mm.

Remarks

The sparse material attributable to this taxon presents a mosaic of features that do little to constrain its relationships. I have assigned it to the Iguanidae based on its pleurodont, tricuspid teeth and form of tooth replacement.

Partial closure of the Meckelian groove without fusion occurs among phrynosomatines, crotaphytines, oplurines, some corytophanines, and some *Liolaemus* (Smith 2006). It is also known for the early Eocene stem anole *Anolbanolis* (Smith 2009a; 2011a; Smith and Gauthier 2013), the problematic late Eocene *Cypressaurus* (Holman 1972; Smith 2006), and the problematic Oligocene *Aciprion* (Estes 1983a). Brief constriction, if not closure, is a consistent feature of Eocene and Oligocene fossil corytophanines from both Europe and North America. It is restricted (and sometimes closes) in early Eocene species of *Suzanniwana* (Smith 2009a; 2011a; Smith and Gauthier 2013), restricted in the late Eocene *Oreithyia oaklandi* (Smith 2011b; 2011c), and variably restricted or closed (interspecifically) in the Eocene-Oligocene European *Geiseltaliellus* (Smith 2009b; Augé and Pouit 2012). The groove is briefly restricted in the Eocene taxon *?Crotaphytus oligocenicus* (Holman 1972; Estes 1983a), a species of uncertain ancestry (Estes 1983a; Sullivan and Holman 1996) that may be related to corytophanines (Rossman 1999; but see Smith 2009b).

An anterolateral extension of the coronoid is known for iguanines, hoplocercines, *Anolis*, *Leiocephalus*, and liolaemins (Etheridge and de Queiroz 1988; Smith 2011b); it has also been reported for *Geiseltaliellus* and some specimens of *Suzanniwana* (Smith 2011a). A less common feature, perhaps, of the Brooksville taxon is the presence of a posteriorly extensive subdental shelf. Smith (2009a) commented on its rarity among iguanids, noting its presence primarily among modern and fossil corytophanines. It is also evidently prominent in *?Crotaphytus oligocenicus* (Holman 1972; Rossman 1999). In having a briefly closed Meckelian groove, a coronoid facet on the dentary that extends below the tooth row, and a conspicuous subdental shelf, the specimens referred here fit a relatively consistent morphological pattern for better known stem-members of Corytophaninae. The absence of a well-developed IML, however, would argue against such an assignment (Smith 2009a; 2009b). Additional material is desirable for a firmer diagnosis, but at present I propose that the fossil species represents neither taxon (*Anolis* or *Sceloporus*) inhabiting Florida today.

Iguaninae gen. et sp. indet.

(Figure 12)

Referred Material

UF 274049 (partial right dentary), UF 275635 (partial left dentary)

Description

Dentary. UF 274049 and UF 275635 (Fig. 12) are roughly the same size and preserve similar features. They are broken anteriorly, but both appear to include the posterior extent of their respective tooth rows. The tooth shafts are tall, straight, and cylindrical in cross-section. Tooth crowns are flared and tricuspid. The teeth of UF 275635 are somewhat worn, but the better-preserved crowns of UF 274049 exhibit a general trend in which the anterior accessory cusp tends to be slightly elevated relative to the posterior accessory cusp. Many of the tooth crowns gently overlap; this seems to be just as much of a product of tooth density (the teeth are closely-spaced) as of the degree of flaring. Neither specimen displays a subdental gutter. If present anteriorly, it evidently was not extensive. A weakly developed subdental shelf is present but fades posteriorly.

The Meckelian groove is closed and fused for the majority of the length of the specimens. The resulting fused lingual face is flat and dorsoventrally tall, contributing to an overall deep appearance of the dentary. This surface increases in height posteriorly to where it opens at the Meckelian reentrant (Wellstead 1982). The Meckelian reentrant is a rounded, U-shaped opening that is somewhat dorsally displaced. Its apex extends anteriorly to a level under the last 4 to 5 teeth. Posteriorly, a moderately well developed IML is present. Looking down through the dentary in posterior view, a reduced IMS is visible only in UF 275635. Its exact limit is unknown, but it appears to end several tooth spaces anterior to opening of the last labial foramen. Dorsal to the IMS, an additional flange of bone bounds an even smaller opening of uncertain homology.

The labial surface of the dentary is fairly convex. Posteriorly there is a broad, rounded facet for an anterolateral extension of the coronoid that extends below the last 3 to 4 teeth. The facet is demarcated dorsally by a ridge of bone that may indicate the presence of a small dorsal process posterior to the tooth row. Both specimens preserve 2 small labial foramina anteriorly and a third that is considerably larger. In UF 275635, the ultimate foramen is teardrop-shaped and opens primarily anteriorly.

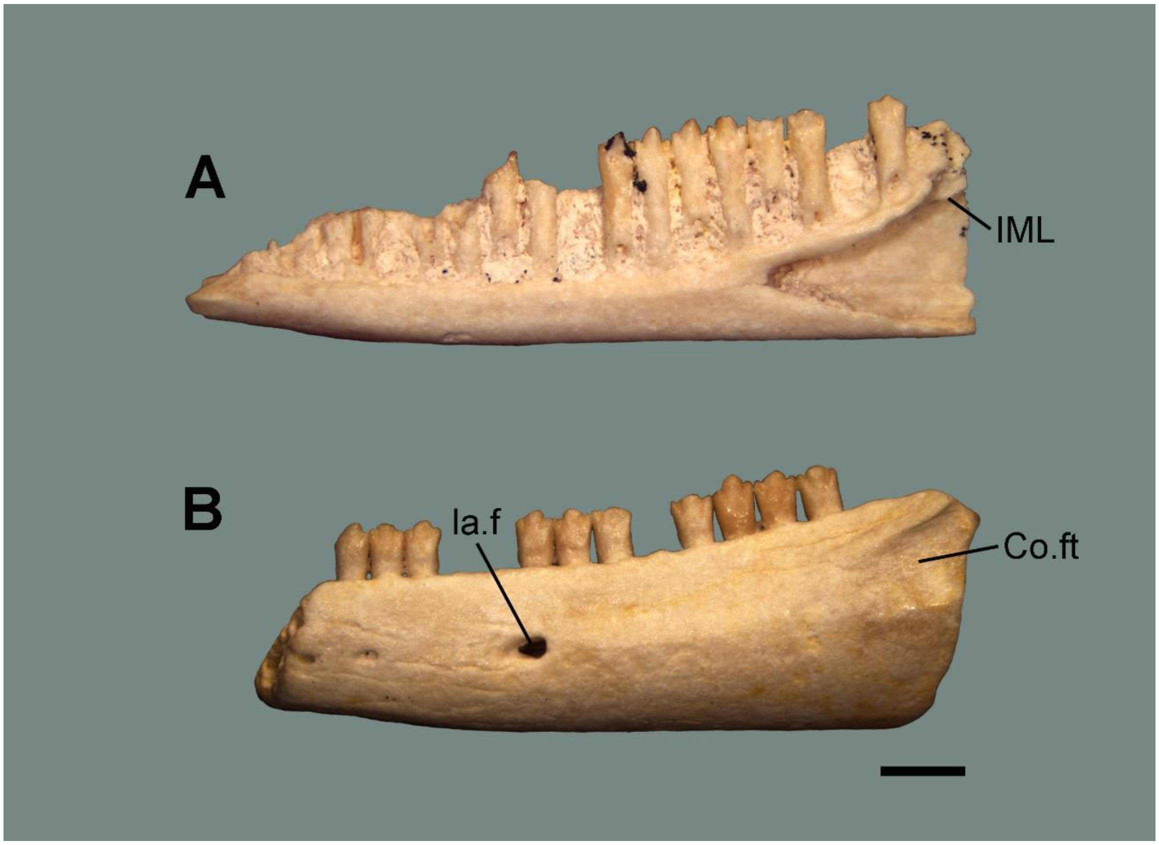

Figure 12. Dentaries of Iguaninae gen. et sp. indet. **A,** Right dentary of Iguaninae gen. et sp. indet., UF 274049, in lingual view. **B,** Left dentary of Iguaninae gen. et sp. indet., UF 275635, in labial view. Abbreviations: Co.ft, coronoid facet; IML, intramandibular lamella; la.f, labial foramen. Scale bar equals 1 mm.

Remarks

A derived combination of flared tooth crowns, an anterolateral extension of the coronoid, and a fused Meckelian groove is common to iguanines and some tropidurines (Norell 1989; Pregill 1992), but additional characters of the referred dentaries favor a relationship with the former. The presence of a dorsoventrally short, posteriorly extensive intramandibular lamella in both specimens is noteworthy. Smith (2009a) originally drew attention to this structure as a functional feature of the iguanid dentary; a small flange of bone develops to secure the coronoid and splenial against the lateral surface of the supra-

Meckelian lip in some taxa. He noted its presence primarily among corytophanines, but also in crotaphytines, some hoplocercines, some oplurines, some *Anolis*, and the iguanine *Sauromalus*. I have observed a similar feature in *Brachylophus*, *Ctenosaura*, *Cyclura*, *Dipsosaurus*, *Iguana*, and *Sauromalus* – every iguanine genus for which disarticulated specimens were examined. The lamella of iguanines, however, differs from other taxa in being more dorsally, laterally, and often posteriorly displaced. In this way its structural significance seems to emphasize support of the surangular instead. Indeed, the anterior end of the compound bone of observed iguanines typically bears an exaggerated groove that sheathes the base of the lamella and minimizes its contact with either the coronoid or the splenial. Although the mandible of the Brooksville taxon is represented only by dentaries, the placement and morphology of the intramandibular lamella most closely matches what is seen in iguanines. An intramandibular lamella was not observed for tropidurines.

In many ways the Brooksville species resembles figured specimens of *Leiocephalus nebraskensis* (Wellstead 1983: fig. 1; = *L. septentrionalis* of Wellstead 1982) from the Barstovian of Nebraska. That taxon is represented by more abundant material (primarily maxillae and postdentary bones), and Norell (1989) and Pregill (1992) made convincing arguments for its close relationship with the monotypic *Dipsosaurus dorsalis* rather than with *Leiocephalus*. Some of their more salient points regarding its taxonomic reallocation are relevant here as well.

The Brooksville dentaries are similar to those described for *L. nebraskensis* based on tooth morphology (Pregill 1992), the anterior extent of the coronoid (Norell 1989), the broad Meckelian reentrant (Pregill 1992), the flat subdental lingual face (Norell 1989), and the reduction of the IMS (Wellstead 1982). Flared tooth crowns bearing 4 or more cusps are common, but not ubiquitous, among iguanines (de Queiroz 1987); the presence of only 3 cusps does not exclude either fossil taxon from that clade (Norell 1989; Pregill 1992). Pregill (1992) suggested the crowns of *L. nebraskensis* are not as broad or labiolingually compressed as those of *Dipsosaurus dorsalis*, and his brief description of them approximates what is observed for the Brooksville specimens. The crowns of UF 274049 (which are better preserved) have taller, more pointed cusps than those of modern and fossil *D. dorsalis* (see Norell 1989: fig. 8), but their morphology would serve only to exclude them from that species. Stem dipsosaurs are known from the Eocene and Miocene; the crowns of the Barstovian *Armandisaurus explorator* (Norell and de Queiroz 1991) from New Mexico are exposed only labially (hindering comparison), and those of the Chadronian *Queironius praelapsus* (Smith 2011b) lack a distal flare altogether. Olson (1937) described the quadricuspid *Tetralophosaurus minutus* from the Arikareean of Nebraska, a species Norell (1989) later united with *Dipsosaurus*. It is known from a single fragmentary dentary but demonstrates that the addition of a fourth cusp had evolved in at least some members of the iguanine lineage by the late Oligocene.

The broad, dorsally displaced Meckelian reentrant of the Brooksville dentaries is reminiscent of that figured for *Leiocephalus nebraskensis* and observed for *Dipsosaurus dorsalis*, and at the very least would serve to exclude it from *Leiocephalus*. The splenial of *Leiocephalus* is reduced, necessitating a smaller notch in the dentary to accommodate it (Pregill 1992). Even in the absence of a fossil splenial, it is clear that the Brooksville taxon did not share this character. Anterior to the reentrant, the fused subdental face of the Brooksville specimens has a flat, nearly vertical lingual surface that, as for *L.*

nebraskensis, is inconsistent with the shallow and rounded morphology shared among species of *Leiocephalus* (Norell 1989).

Of the groups that share a fused Meckelian groove, an anterolateral extension of the coronoid, and flared tooth crowns, process of elimination leaves the assignment of the Brooksville fossils to the Iguaninae as the most defensible option. Although admittedly based primarily on plesiomorphy (i.e., it merely lacks derived characters of tropidurines), the morphology of its intramandibular lamella (possibly synapomorphic) reinforces this conclusion. At least superficially the fossil dentaries most closely resemble *Dipsosaurus*. Ultimately, however, the preserved material lacks characters that would ally it with any particular genus. Among fossil iguanines the Brooksville species is predated only by the late Eocene *Queironius praelapsus* (Smith 2011b).

Eublepharidae gen. et sp. indet.

(Figures 13-14)

Referred Material

UF 275603 (partial left maxilla), UF 274247 (partial right dentary), UF 278770 (partial left dentary)

Description

Maxilla. UF 275603 (Figs. 13-14) is a relatively complete maxilla measuring 7.59 mm in length. There are spaces for 27 teeth, with empty loci positioned at roughly equal intervals between every 3 to 4 teeth. A portion of the tooth row is missing anteriorly, and perhaps posteriorly as well. Most of the teeth that remain are broken; only the 13th tooth retains an intact crown. The crown is weakly striated lingually, and its apex bears a longitudinal “valley” separating distinct labial and lingual cusps. Replacement crowns at the base of the 20th, 24th, and 26th tooth positions exhibit a similar morphology. The teeth are small, cylindrical, and densely spaced. They sit in a wide, deep supradental trough that spans the preserved length of the tooth row. Teeth are fairly uniform in size in the anterior portion of the maxilla but become progressively shorter towards the posterior end. Most of the premaxillary process is missing anterior to the AIAF, which opens at approximately the same horizontal level as the palatal flange. Posterior to the AIAF, the ascending portion of the facial process rises steeply. Much of the facial process is broken dorsally. Posteriorly the descending portion of the facial process continues as a sharp, vertical lateral wall to the end of the bone. Viewed dorsally, this posterior section turns slightly laterally relative to the anterior half of the maxilla. The palatine process is present as a weak medial bulge that roughly divides the palatal flange into anterior and posterior halves. Anteriorly the medial margin of the palatal flange is fairly straight (i.e., it lacks the conspicuous laterally-directed concavity common to many gekkotans). Posteriorly the flange tapers only gently in width; its medial and lateral borders are nearly parallel for a short distance where the jugal would have articulated. The SAF opens posterolaterally at about the same transverse level as the palatine process. Posterior to the SAF, there is a long, low, obliquely oriented ridge of bone. It arises in the middle of the palatal flange but soon after becomes confluent with its medial margin and continues posteriorly. By comparison with extant gekkotans this ridge would have bordered the prefrontal and/or jugal. The lateral face of the maxilla is nearly flat with 7 labial foramina. A ventral row has 5 foramina. The last is the largest and is positioned at nearly the same transverse level as the SAF. There are 2 additional foramina dorsally.

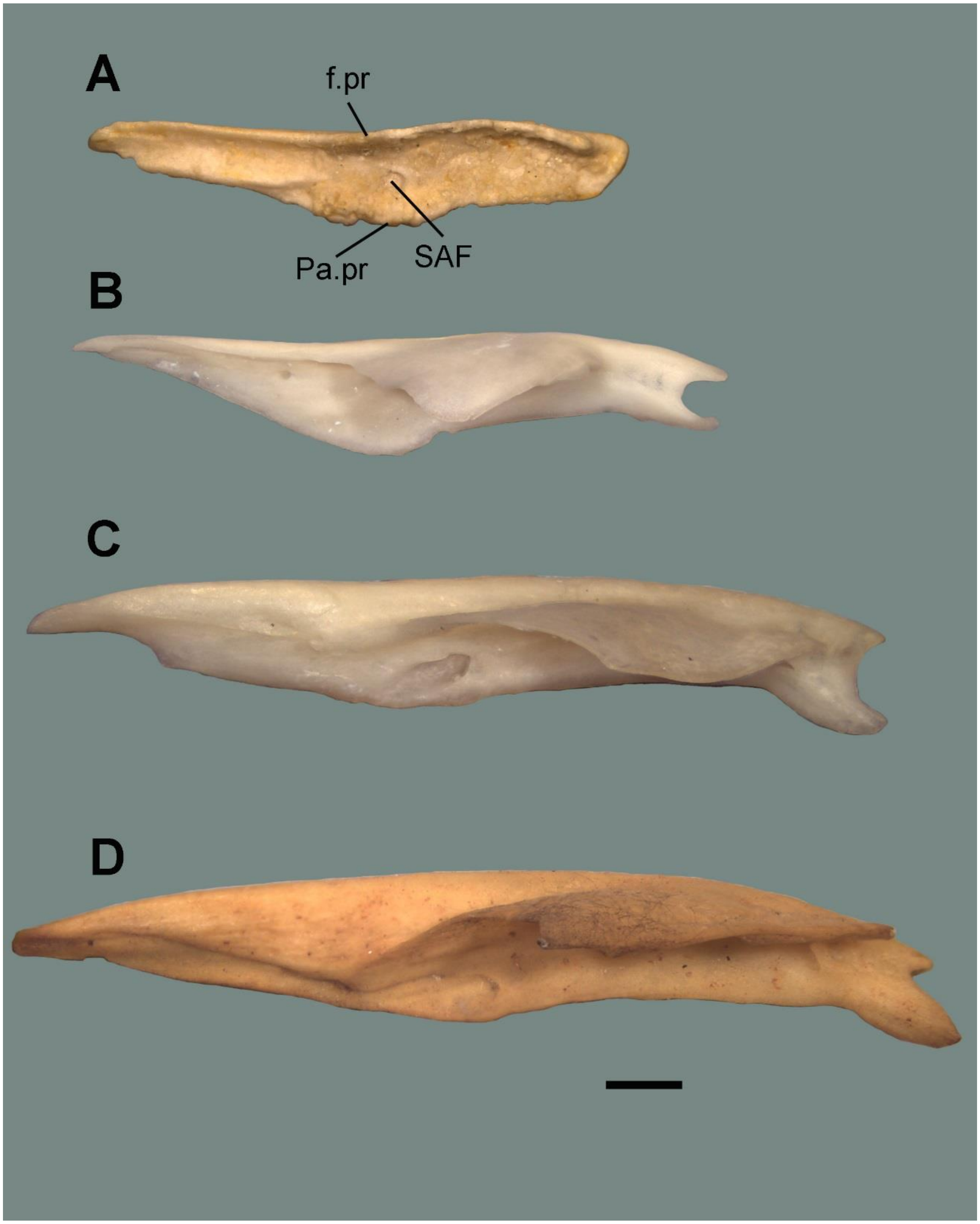

Figure 13. Comparative maxillae of gekkotans in dorsal view. **A,** Left maxilla of Eublepharidae gen. et sp. indet., UF 275603. **B,** Left maxilla of *Coleonyx mitratus* (Eublepharidae) FB 2296. **C,** Left maxilla of *Aristelliger praesignis* (Sphaerodactylidae) UF 21740. **D,** Left maxilla of *Thecadactylus rapicauda* (Phyllodactylidae) JIM 1664. Abbreviations: f.pr, facial process of maxilla; Pa.pr, palatine process; SAF, superior alveolar foramen. Scale bar equals 1 mm.

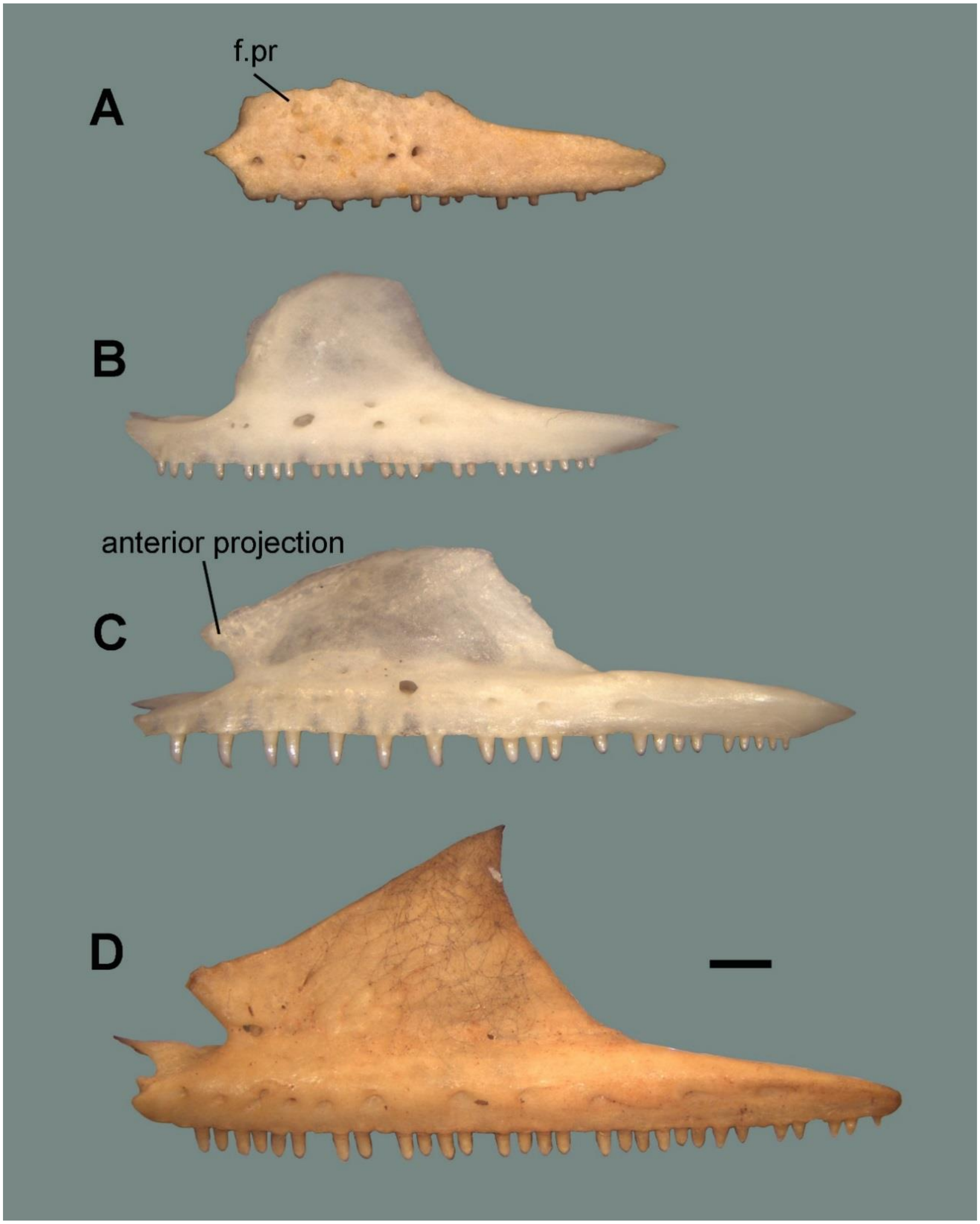

Figure 14. Comparative maxillae of gekkotans in labial view. **A,** Left maxilla of Eublepharidae gen. et sp. indet., UF 275603. **B,** Left maxilla of *Coleonyx mitratus* (Eublepharidae) FB 2296. **C,** Left maxilla of *Aristelliger praesignis* (Sphaerodactylidae) UF 21740. **D,** Left maxilla of *Thecadactylus rapicauda* (Phyllodactylidae) JIM 1664. Abbreviations: f.pr, facial process of maxilla. Scale bar equals 1 mm.

Dentary. A fragmentary dentary is associated here based on similar tooth form. There are 11 tooth spaces with 5 complete, if worn, teeth. The Meckelian groove is completely fused, and the teeth sit in a wide, deep subdental gutter.

Remarks

The size, shape, and spacing of the teeth are sufficient for the assignment of these specimens to Gekkota. Grismer (1988) noted the presence of a supradental "trough" in the maxilla of *Aeluroscalabotes*; I find this feature, also observed in UF 275603, to be exaggerated in almost all observed gekkotans relative to other lizards. The unique "bicuspid" crown morphology of the teeth in the fossil maxilla would likewise unite it with most other geckos (Sumida and Murphy 1987; Grismer 1988), as would the closure and fusion of the Meckelian groove and the tubular morphology of the dentary (Estes et al. 1988).

Two features of the maxilla potentially link this taxon exclusively with eublepharids: the absence of a triangular anterior projection (see Müller and Mödden 2001 on this term) and the near-vertical continuation of the facial process posteriorly. In most gekkotans the ascending portion of the facial process of the maxilla curves parabolically to contact the nasal anteromedially and to contribute significantly to the posterior border of the external naris. This curvature results in a distinctive triangular protrusion that overhangs the premaxillary process. In eublepharids the anterior margin of the nasal widens (Grismer 1988), and there is no anterodorsal projection on the maxilla. Although much of the facial process of the fossil is missing, the slope of the preserved ascending portion (viewed laterally) suggests it would have continued posterodorsally without turning back on itself to form a projection.

The descending portion of the facial process of UF 275603 also indicates a eublepharid relationship. In most observed gekkotans the posterior half of the facial process curves strongly medially and either terminates abruptly without continuing far onto the orbital process or else decays into a low, wide, and rounded section of bone that extends further posteriorly. In observed eublepharines (sensu Grismer 1988; i.e., to the exclusion of *Aeluroscalabotes*) the facial process maintains a sharp dorsal edge and a (relatively) vertical position to the end of the bone. In this way the fossil approaches the condition seen in comparative specimens of *Coleonyx*, *Eublepharis*, and *Hemitheconyx* (representatives of *Goniurosaurus* and *Holodactylus* were not examined).

Among eublepharids only *Coleonyx* occurs in the Americas today. Seven species are distributed from Central America to the southwestern United States, and their ancestors are presumed to have migrated from Asia sometime in the early Cenozoic (Grismer 1988; Gamble et al. 2011). Unfortunately, pre-Pleistocene fossil geckos are rare from North America. Estes (1963) identified a single fragmentary dentary from Thomas Farm as an indeterminate gekkotan, and 3 incomplete dentaries are known from the Eocene of California (Schatzinger 1975). Hirsch (1996) named the oospecies *Gekkoolithus columnaris* based on fossilized gekkotan eggshells from the Eocene Wind River Basin, but skeletal remains were not recovered. Even higher-level relationships of all 3 taxa are uncertain. *Coleonyx* fossils are reported from the Holocene (Van Devender and Mead 1978) and late Pleistocene (Van Devender et al. 1977; 1991) of Arizona and the late Pleistocene of California (Norell 1986), but a detailed treatment of diagnostic characters for the identification of isolated fossil remains is lacking. Although the Brooksville 2 material cannot be assigned to any particular genus, the morphology of the maxilla seems to minimally place it somewhere among the Eublepharidae.

Rhineuridae gen. et sp. indet.

(Figure 14)

Referred Material

UF 268989-94 (vertebrae), UF 274047 (vertebra), UF 275673 (partial right dentary)

Description

Dentary. UF 275673 is a partial right dentary measuring 1.94 mm in length. It is broken posteriorly and ventrally, but the symphysis and a partial tooth row remain. There are 4 subpleurodont teeth, the first 3 of which bear a small nutritive foramen posteriorly at each of their respective bases. The teeth appear short and stout, but the crowns look to have suffered some form of taphonomic corrosion. It is not clear how tall they may have been or if they were recurved. The teeth are roughly oval in cross-section and sit on a weak subdental shelf. Judging from the circumference of their bases, the first and third teeth are enlarged relative to the other two. The mandibular symphysis is well developed. It is flat, dorsoventrally tall, and has a weakly reniform outline. A small foramen, presumably an anterior opening of the Meckelian canal, exits its anteromedial face. The nature of the Meckelian groove is ambiguous posteriorly where the bone is broken.

Because it is encircled by bone anteriorly at the symphysis, however, I tentatively suggest it was closed and fused in this taxon.

Vertebrae. The 7 vertebrae assigned here vary in relative proportions and represent different positions along the vertebral column. They are small with exaggerated prezygapophyses, strong interzygapophysial ridges, and wide, dorsoventrally compressed cotyles and condyles. Centra are parallel-sided and ventrally flattened; only a single specimen, UF 268994, shows a low, sharp haemal keel. The synapophyses are well developed, oval in shape, and ventrally displaced. Subcentral foramina are variably (and sometimes only asymmetrically) present but are typically developed along the lateral margins of the centrum just posterior to the synapophyses. The anterior openings for the neural canal are subtriangular, with a dorsal apex that continues posteriorly as a low neural spine. Three vertebrae (UF 268991, UF 268992, and UF 274047) are dorsoventrally short and anteroposteriorly elongate. Following Hoffstetter and Gasc (1969), these presumably occupied more posterior positions in the vertebral series. The remaining specimens are relatively wider, bear a well-developed neural spine posteriorly, and often have wrinkled posterodorsal surfaces.

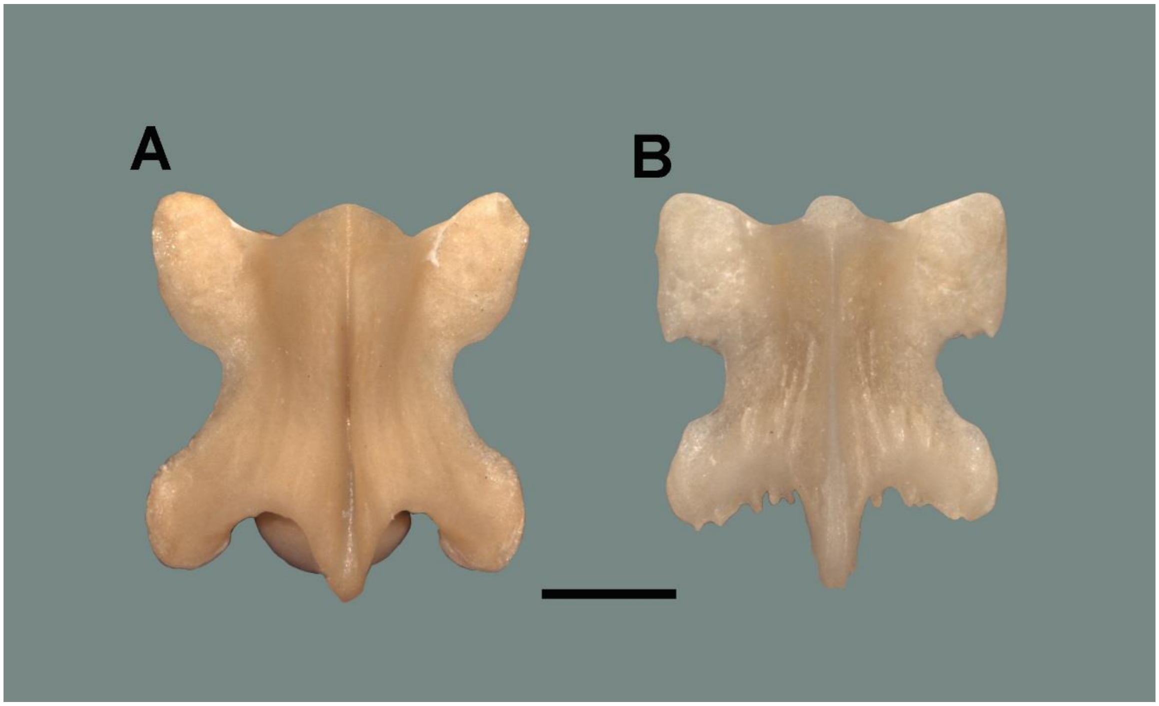

Figure 15. Vertebrae of rhineurids. **A,** Vertebra of Rhineuridae gen. et sp. indet., UF 268993, in dorsal view. **B,** Vertebra of *Rhineura floridana* ETVP 7223 in dorsal view. Scale bar equals 1 mm

Remarks

The record of rhineurid amphisbaenians in North America extends to the Paleocene (Sullivan 1985), but they are especially common in Eocene-Miocene faunas (reviewed in Hembree 2007). Genera and species have typically been diagnosed on the basis of relatively complete skulls, and none of the material preserved at Brooksville 2 would suggest affinities with one particular group or another. Vertebral characters for rhineurids are given by Holman (1958) and Smith (2006). Yatkola (1976) noted subtle differences in the placement of the synapophyses in the Hemingfordian taxon *Rhineura marslandensis* as compared to the modern *Rhineura floridana*, a character that Holman (1979) later suggested was intraspecifically variable in the latter. Instead, in describing the Hemingfordian *Rhineura sepultura*, Holman (1979) remarked on the overall similarity of its vertebrae with those of the extant species. Rhineurid vertebrae are clearly morphologically conservative, and specimens here do not warrant identification below the family level. They do not differ considerably, in size or otherwise, from *Rhineura floridana* living in the area today.

The single partial dentary described here is only tentatively associated with the vertebrae (on the basis of its overall amphisbaenian morphology) and does not factor into their taxonomic allocation. A full tooth count is desirable, but the apparent enlargement of the first and third teeth is potentially significant. Most known rhineurids are characterized by the enlargement of the first and fourth dentary teeth (Smith 2006), and the enlargement of the third tooth instead in UF 275673 would be a notable deviation from this pattern. The closure and fusion of the Meckelian groove, if interpreted correctly, would suggest a rhineurid relationship (Smith 2009a). Additional material is necessary to confirm if the specimen is even properly assigned.

The only living rhineurid, *Rhineura floridana*, is confined to the extreme southeastern United States. Previous records of the family east of the Mississippi River are known only from the Pliocene (Meylan 1982) and Pleistocene (Holman 1958; 1959; 1962) of Florida, and the Brooksville 2 specimens extend their known temporal range from their modern center of endemism by approximately 26 million years.

Scincidae gen. et sp. indet.

(Figure 16)

Referred Material

UF 274043 (partial right dentary with splenial), UF 274063 (partial right dentary), UF 274239 (partial right dentary), UF 274240 (partial right dentary), UF 274252 (right premaxilla)

Description

Dentary. UF 274043 (Fig. 16) is the middle portion of a right dentary. It is 4.43 mm long and bears 12 tooth spaces with 10 preserved teeth. The teeth are moderately low-crowned and sit in a well-developed subdental gutter that extends the entire length of the preserved portion of the dentary. The crowns are slightly bulbous, labially convex, and lingually striated. The Meckelian groove is open and increases in height posteriorly where it is invaded by a partially preserved splenial. The splenial has a U-shaped, posteriorly concave anterior margin formed by dorsal and ventral anterior extensions that continue along the supra- and infra-Meckelian lips, respectively. Presumably, this margin would have partially bound the AIAF. Part of the anterior mylohyoid foramen can be made out posterior to this but has mostly been broken away. An additional partial dentary, UF 274063, lacks a preserved splenial. Viewed ventrally a wedge-shaped facet for that bone is formed just lateral to the supra-Meckelian lip. It tapers anteriorly to an apex just under the 10th tooth position from the symphysis. The symphysis is relatively weak in lingual view, but the anterior-most portion of the dentary assumes a precociously deep appearance when viewed labially.

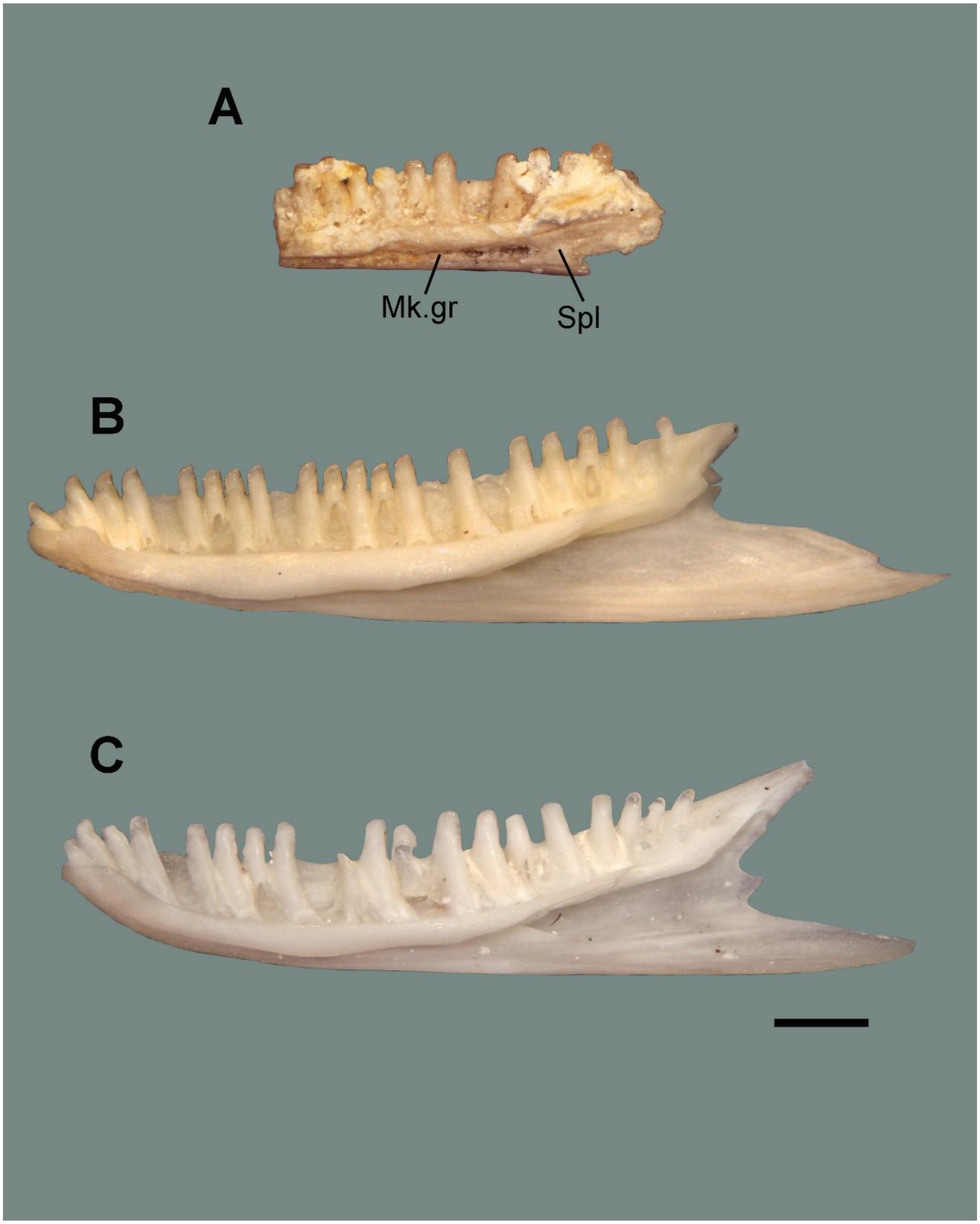

Figure 16. Comparative dentaries of scincids. **A,** Right dentary of Scincidae gen. et sp. indet., UF 274043, in lingual view. **B,** Right dentary of *Plestiodon fasciatus* ETVP 2892 in lingual view. **C,** Right dentary of *Mesoscincus managuae* FB 1131 in lingual view. Abbreviations: Mk.gr, Meckelian groove; Spl, splenial. Scale bar equals 1 mm.

Premaxilla. A single right premaxilla, UF 274252, is associated here based on similar tooth morphology, its unfused nature, and size. It bears three medial teeth, but the broken lateral portion of the dental shelf suggests the presence of a partial fourth locus.

Remarks

Beginning in the Oligocene a number of geographically and temporally disparate North American fossils (mostly dentaries) have been assigned to extinct, extant, or indeterminate species of the genus *Eumeces* (reviewed in Estes 1983a). For the purposes of this discussion, I hereafter assume that previous mention of *Eumeces* in the North American fossil literature should be taken to mean *Plestiodon* (Smith 2005) unless otherwise noted. Such assignments are in fact made to living species now allocated to *Plestiodon*, and the description of extinct species typically involves modern comparisons that are exclusive to members of that genus (e.g., Holman 1977, 1981; Taylor 1941).

The morphology of the Brooksville specimens agrees strongly with dental characters reviewed by Estes (1963), Norell (1989), and Bell (1993) for *Plestiodon*. Estes and Tihen (1964) remarked on the anteriorly deep dentary of the genus, a feature that also characterizes the fossils. Unfused premaxillae are known to occur only in some scincids and gekkotans among squamates (Estes et al. 1988), and the splenial morphology seen here is also suggestive of a scincomorph relationship (pers. obs.). Kingman (1932) and Olson et al. (1986) both noted a consistent asymmetry in premaxillary tooth counts for *Plestiodon*: 4 teeth on the right side, and 3 teeth on the left side (Kingman's [1932] study also included a specimen of *E. schneiderii*, a member of *Eumeces sensu stricto*). A left premaxilla is not known here, but the presence of 4 tooth spaces on the corresponding right element in the fossil taxon is notable.

Five extinct species of *Eumeces* (now *Plestiodon*) have been described: *E. antiquus* from the Arikareean of Nebraska (Holman 1981), *E. miobsoletus* from the Barstovian of Texas (Holman 1977), *E. hixonorum* from the Clarendonian of Kansas (Holman 1975), *E. striatulus* from the Blancan of Kansas (Taylor 1941), and *E. carri* from the Irvingtonian of Florida (Meylan 1982). Estes (1963), Wilson (1968), and Wellstead (1982) have all remarked on the difficulty of ascribing fossil material to any particular species of *Plestiodon* given their diversity and overall morphological similarity. I likewise find no reliable, objective metric for the identification of isolated tooth-bearing elements, even for more inclusive subclades indicated by molecular phylogenies (Brandley et al. 2012). I have not seen any of the type material, but extinct fossil species appear to be insufficiently diagnosed.

Eumeces antiquus is known from a single dentary and is diagnosed primarily by the presence of flattened tooth crowns in the posterior half of the tooth row. Holman (1981) notes that at least some of the posterior teeth are worn, so additional and better-preserved material is desirable to more confidently assess the importance of such a character. *Eumeces miobsoletus* (Holman 1977) is known from a maxilla, a premaxilla, and a retroactively referred dentary (from the same locality) originally described and figured in Holman (1966). Holman (1977) argues that pigmentation in the maxillary and premaxillary tooth crowns of *E. miobsoletus* (not described for the dentary) is indicative of a close relationship with extant *P. obsoletus*. Pigmented tooth crowns were only observed in 2 of 12 modern skeletons of *P. obsoletus* available for this study. They are also present in a specimen of *P. laticeps*, suggesting it may be a more widespread feature for the group with little taxonomic utility. The Brooksville fossils lack apical pigmentation. *Eumeces hixonorum* (Holman 1975) and *E. striatulus* (Taylor 1941) are diagnosed primarily based on size and tooth spacing, characters that display too much intraspecific variation and interspecific overlap to be of much value. Estes (1983) suggests that diagnostic features given by Meylan (1982) for the extinct *E. carri* are taphonomically artifactual or otherwise occur elsewhere in *Plestiodon*.

The relatively recent recognition of a paraphyletic *Eumeces* (Brandley et al. 2005, 2012; Griffith et al. 2000; Schmitz et al. 2004) has 2 important zoogeographic implications for the early fossil record of North American scincines: 1) Assuming a single invasion by the genus, there is little reason to expect North American fossil members of the *Plestiodon* lineage to fall outside the crown of the clade. North American members are nested well within East Asian *Plestiodon*, suggesting an Asian origin for the genus (Brandley et al. 2012; Macey et al. 2006). Despite an estimated 18-30 Ma divergence date (Brandley et al. 2011), morphological analysis (skeletal and external) indicates they remain very similar (Griffith et al. 2000). Indeed, Estes (1963) commented on his inability to tell apart modern Asian and North American forms based on cranial skeletal elements. Even the earliest New World immigrants, then, would be expected to look much like living species if molecular hypotheses are correct. 2) *Mesoscincus* (3 species; also formerly *Eumeces*) from southern Mexico and Central America does not appear to be the sister taxon of *Plestiodon* (Brandley et al. 2005, 2012; Pyron et al. 2013; Schmitz et al. 2004). Such a scenario would necessitate an independent dispersal event that is thus far unaccounted for in the fossil record.

The single specimen of *Mesoscincus managuae* examined for this study shares with examined members of *Plestiodon* (and the fossil specimens) an open Meckelian groove that is directed ventrally anteriorly and turns lingually posteriorly, labially convex tooth crowns with lingual striae, an AIAF that is anteriorly displaced relative to the splenial (and an overall similar splenial morphology), and unfused premaxillae with 4 tooth spaces on the right and 3 on the left (incompletely known for the fossil). Tooth-bearing elements of the 2 genera are remarkably similar, but I tentatively suggest closer affinities of the fossils with *Plestiodon* for sharing slightly bulbous tooth crowns (not present in all observed *Plestiodon*) that are more strongly striated and the possession of a well-developed subdental gutter. The crowns of *M. managuae* are parallel-sided and only very weakly striated, and the teeth sit on a narrower, shallower dental shelf. Tooth apices also appear more angular. The postdentary articulations of *M. managuae* differ from at least some examined *Plestiodon*, but a broader survey of this character was not undertaken because none of the fossils preserve the posterior portion of the dentary. A greater sample size of comparative specimens of all 3 species of *Mesoscincus* is desirable, but preliminary analysis suggests closer morphological affinities of the fossils to *Plestiodon*.

Among extant species of *Plestiodon*, only the anomalously derived (Telford 1959) *P. reynoldsi* (formerly *Neoseps*; a Florida endemic) can be reasonably excluded from consideration as a candidate for the fossil species. An adult (SVL= 56 mm) male specimen (JIM 1624) has fewer (15) teeth that are more widely spaced, slimmer, and have a markedly different, blade-like shape. An exact tooth count for the fossils is unknown, but almost certainly would have exceeded 15.

Conclusions

At least 7 species of non-anguimorph lizards are present in the Brooksville 2 LF. Taxonomic resolution varies, but the assemblage includes the earliest record of *Anolis*, an additional "anole" that may or may not fall within the crown radiation, an iguanid of uncertain phylogenetic affinities, an iguanine, a eublepharid gekkotan, a rhineurid amphisbaenian, and a scincid. The fossil species of *Anolis* is disproportionately common relative to other taxa, and an argument for the generic-level identification of abundant dentaries is strengthened by the association of additional cranial elements displaying *Anolis* characters. It does not share a close relationship with *A. carolinensis*, the only species of anole native to the southeastern United States today. A second *Anolis*-like taxon is distinguished by its small size and highly reduced IMS but cannot confidently be referred to the extant genus. Even allowing for some taxonomic uncertainty, the early co-occurrence of a species of *Anolis* with such a close relative is noteworthy given the extensive sympatry that characterizes many modern *Anolis* communities (Losos 2009). The relationships of 2 additional iguanids are less precise (one is likely an iguanine), but neither has a close living relative native to Florida. A eublepharid gekkotan could not be identified to any particular genus. Regardless, its occurrence is extralimital; the family is represented in the New World today only by *Coleonyx* in tropical Mesoamerica and the desert southwest. In contrast, new records of rhineurid amphisbaenians significantly extend their temporal range within their modern, relictual center of endemism. A scincid closely resembles species of *Plestiodon* inhabiting the region today, but a relationship instead with the tropical genus *Mesoscincus* cannot be ruled out.

CHAPTER 3

NON-ANGUIMORPH LIZARDS OF THE MILLER LOCAL FAUNA

Introduction

Published lacertofaunas from the Hemingfordian LMA are rare; Robinson and Van Devender (1973) and Yatkola (1976) described lizards from the Split Rock and Runningwater Formations (respectively) from the Great Plains, Holman (1998) reported a single species of anguid from the Pollack Farm locality in Delaware, and Estes (1963) and Bhullar and Smith (2008) collectively documented the presence of 8 species of lizard from the Thomas Farm local fauna of Florida. Abundant and well-preserved microvertebrate remains from the Miller local fauna of Dixie County, Florida include a number of squamate taxa that promise to add significantly to our understanding of Hemingfordian herpetofaunas. In this chapter I seek to summarize the non-anguimorph lizard assemblage recovered so far from the site. Anguimorphs will be covered elsewhere by myself and others from the ETSU Department of Geosciences.

Only a select few taxa have been reported from the Miller LF. Fossils come from the Suwannee River (Baskin 2003), but there are no comprehensive discussions of the geology or taphonomy of the fossil-bearing deposits. Wang et al. (1999) reported the borophagine canid *Desmocyon matthewi*, Wang (2003) reported the hesperocyonine canid *Osbornodon scitulus*, Baskin (2003) described the potosin procyonid *Bassaricyonoides phyllismillerae*, and Mead and Schubert (2013) reported the occurrence of the erycine boid *Pterygoboa*. Morgan and Czaplewski (2012) discussed the presence of at least 3 species of bat, and Baskin (2003) mentioned undescribed mustelids. The latter, along with the described canid taxa, suggest an early Hemingfordian age for the fauna (Baskin 2003).

Anolis sp.

(Figure 17)

Referred Material

MLF A1 (partial right dentary), MLF A2-3 (partial left dentaries), MLF A4 (partial right maxilla)

Description

Dentary. MLF A1 (Fig. 17) is the posterior portion of a right dentary with the last 11 spaces of the tooth row. The teeth have tapering, tricuspid crowns dominated by a large central cusp. Accessory cusps are developed on all preserved teeth but remain small throughout. Posterior teeth become gradually and weakly mesiodistally expanded relative to anterior teeth. The Meckelian groove is closed and fused far posteriorly, but eventually opens dorsally as a narrow slit (interpreted here as a CAMF) that extends beneath the last five teeth. Dorsal to the CAMF, the sML is pinched to form a lingually projecting ridge of bone that continues anteriorly for the length of several tooth spaces. Inside the dentary tube, an elongate, subvertical IMS extends to a level below the fourth from last tooth. The dorsal ramus of the IMS is continuous posteriorly with a moderately developed IML that surpasses the end of the tooth row. Immediately posterior to the tooth row there is an elongate external medial notch for the coronoid. Labially a well-developed facet for an anterolateral extension of the coronoid extends below the ultimate tooth.

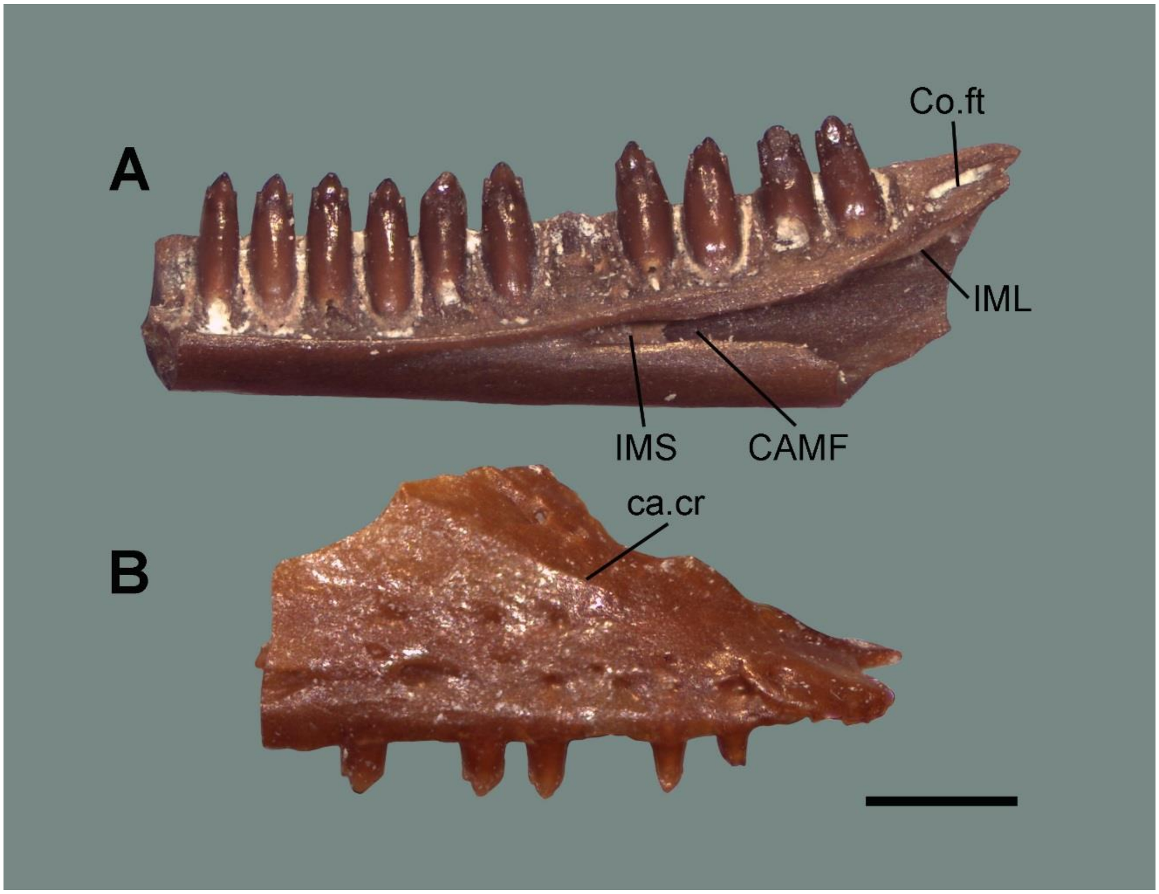

Figure 17. Cranial elements of *Anolis* sp. **A,** Right dentary of *Anolis* sp., MLF A1, in lingual view. **B,** Right maxilla of *Anolis* sp., MLF A4, in labial view. Abbreviations: ca.cr, canthal crest; CAMF, combined alveolar-mylohyoid foramen; Co.ft, coronoid facet; IML, intramandibular lamella; IMS, intramandibular septum. Scale bar equals 1 mm.

<u>Maxilla.</u> A single maxilla, MLF A4 (Fig. 17), is associated here based on similar size and tooth form. It is broken posteriorly but retains the first 10 tooth spaces of the tooth row. Weak accessory cusps are developed by the seventh tooth. The SAF is roofed, and a small foramen pierces the dorsal surface of the palatal flange posterior to the crista

transversalis. Labially the surface of the maxilla is weakly rugose. The anteriormost labial foramen is distinct from the rest for being set on a globular “pedestal” of bone. The ascending portion of the facial process rises from the premaxillary process at a shallow angle and is folded weakly medially to form a subtle canthal ridge. There are not separate openings for the AIAF and SNAF, only a single large foramen at the anterior base of the facial process. Much of the anterior margin of the premaxillary process is broken, but an anteromedially projecting vomerine process is preserved. At its distal end the vomerine process bears an elongate facet for the vomer that is oriented ventromedially. Ventrally a small foramen penetrates the lingual edge of the palatal flange between the transverse level of the first and second teeth.

Remarks

Reasons for the referral of this species to *Anolis* are the same as given for dentary and maxillary specimens of *Anolis* sp. (morphotype A) in Chapter 2. Although less abundant and more poorly represented, material here does not differ significantly in morphology from the Brooksville taxon. Both share a strongly vertical IMS and possess a moderately developed IML posteriorly. The CAMF in the Miller anole is more elongate, but this character is intraspecifically variable in examined comparative material of modern *Anolis*.

Smith (2009a) remarked on the presence of dorsal and ventral foramina on the palatal flange of *Anolis*; one posterior to the crista transversalis dorsally, and another at the base of one of the anteriormost teeth ventrally. While such foramina are perhaps most common among *Anolis*, they evidently have a wider distribution among iguanids. I have observed a dorsal foramen to be variably present among corytophanines, iguanines, phrynosomatines, and tropidurines in addition to *Anolis*. A ventral foramen is less common but occurs with some frequency among phrynosomatines. Both are present in the Miller *Anolis*, but their phylogenetic significance is not clear.

A common feature of observed *Anolis* maxillae, as described for the fossil above, is the tendency for the anteriormost labial foramen to protrude slightly. This may merely be related to the development of rugosities on the external surface of the bone, but its presence here at least supports an *Anolis* relationship.

cf. *Basiliscus* sp.

(Figure 18)

Referred Material

MLF C1 (right dentary), MLF C2 (partial right dentary), MLF C3 (splenial), MLF C4 (ectopterygoid), MLF C5 (coronoid)

Description

Dentary. MLF C1 (Fig. 18) is a nearly complete right dentary with spaces for 22 teeth. The ventral border of the bone is nearly flat in lateral view, turning only at the symphysis. The tooth row, preserved in its entirety, measures 14.9 mm in length. Anterior teeth are short and unicuspid but become taller posteriorly. Weak accessory cusps are developed by the ninth tooth position; fully tricuspid teeth with flared crowns begin by the 13th tooth position and continue for the remainder of the dentary. The Meckelian groove is open anteriorly, highly restricted at the level of the 10th through 12th tooth positions, and widely open posteriorly. The broadly diverging infra- and supra-Meckelian lips in the posterior half of the jaw give the bone a deep appearance. The dentary depth/ tooth row length ratio (Smith 2006) is 0.31. A subdental shelf is present for most of the tooth row, but ends abruptly after the level of the penultimate tooth. The end of the tooth row is marked by a vertical ridge of bone that forms the anterior border of a strong medial coronoid notch (Smith 2009a). The IMS extends to a level between the 16th and 17th tooth positions, giving an IMS/ tooth row length ratio (Smith 2006) of 0.69. Posterior to this, there is a prominent IML that continues beyond the ultimate tooth to form part of the medial coronoid notch. Labially there is no coronoid facet. There are 8 labial foramina, the first 6 of which are roughly paired. The last is at the level of the 16th tooth and opens primarily posteriorly.

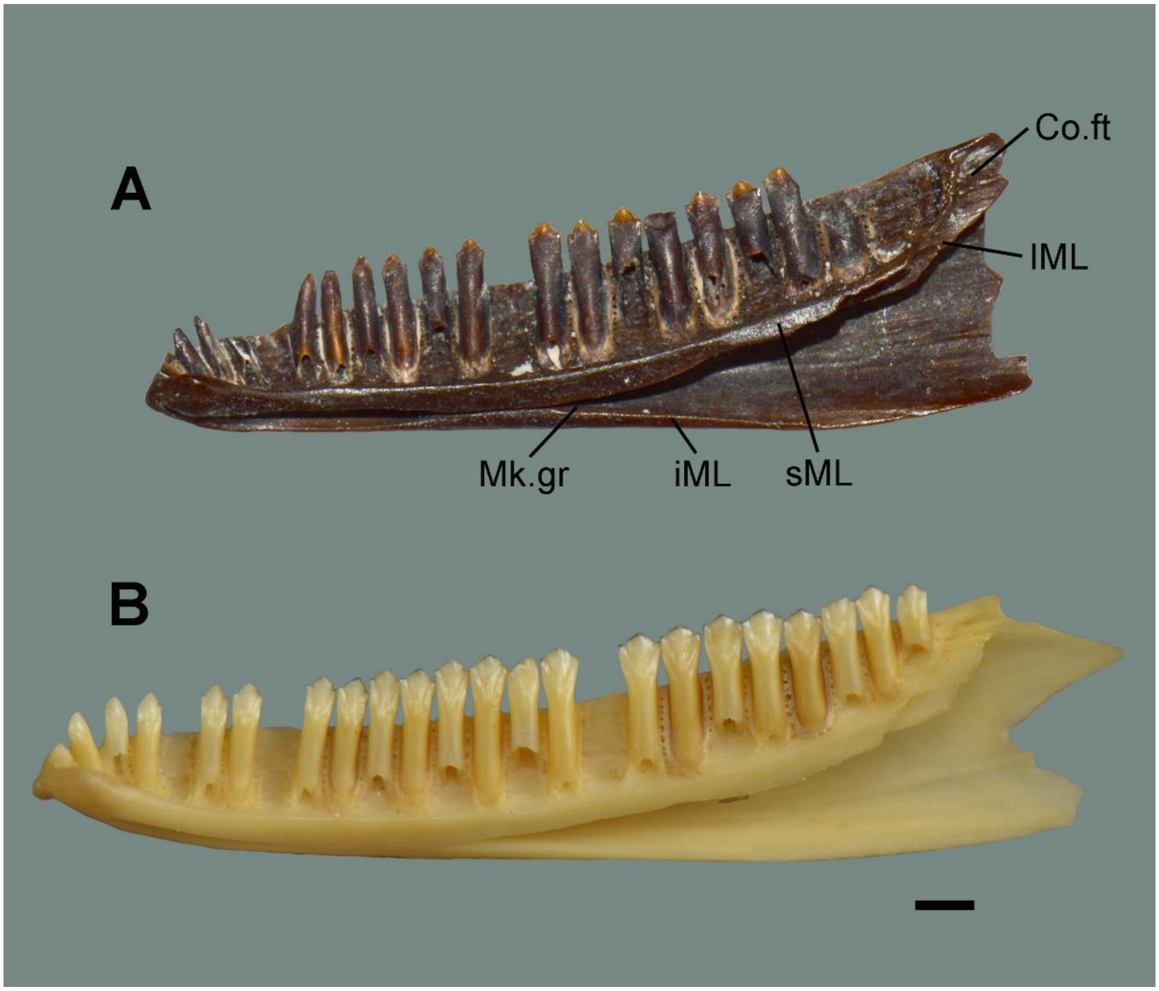

Figure 18. Comparative dentaries of corytophanines. **A,** Right dentary of cf. Basiliscus sp., MLF C1, in lingual view. **B,** Right dentary of *Basiliscus vittatus* JIM 0228 in lingual view. Abbreviations: Co.ft, coronoid facet; iML, infra-Meckelian lip; IML, intramandibular lamella; Mk.gr, Meckelian groove; sML, supra-Meckelian lip. Scale bar equals 1 mm.

Remarks

The posterior development of the subdental shelf, the well-developed intramandibular lamella, and the brief restriction of the Meckelian groove all indicate affinities with Corytophaninae (see Chapter 2 under Iguanid Brooksville A). The length of the intramandibular septum and depth of the dentary are also consistent with what is observed for the clade, but not necessarily to the exclusion of other groups. Smith (2006) considered an IMS ratio greater than 0.7 to be derived in a number of iguanids. An IMS ratio of 0.69 in the MLF C1, while common to corytophanines, is probably plesiomorphic. The depth of MLF C1 (with a ratio of 0.31) is not exceptional for iguanids (some iguanines and phrynosomatines, in particular, have similar ratios), but is roughly equal to values for *Basiliscus* and *Corytophanes* (Smith 2011a). The most telling evidence for a corytophanine relationship comes in the form of strong medial coronoid facet and a well-developed intramandibular lamella. Smith (2009a) first noted the significance of the medial coronoid facet in modern and fossil members of Corytophaninae, and I likewise have observed a comparable feature only in that group.

With the exception of the retention of an open Meckelian groove, MLF C1 is nearly identical to observed specimens of *Basiliscus*; the teeth are remarkably similar. The tooth crowns of fossil corytophanines are typically parallel-sided (Smith 2009a; 2009b; 2011a; 2011b) and flare only infrequently in some specimens (Smith and Gauthier 2013). Consistently flared tooth crowns, then, are probably derived for *Basiliscus* and *Corytophanes* and subsequently lost in *Laemanctus* (Lang 1989). Flared tooth crowns are common among iguanids (Lang 1989) but take on a variety of different forms. Although a detailed morphometric analysis of the variation this character encompasses was beyond the scope of this study, the teeth of MLF C1 are more like those of *Basiliscus* than of *Corytophanes* (see Pregill 1992).

The Meckelian groove is open (but restricted) in stem corytophanines (Smith 2011b), but its closure (and sometimes fusion) may have occurred independently in all 3 extant genera (Smith 2009a; 2011b). It is fused in all species of *Corytophanes*, only closed in some species of *Basiliscus* (but fused in others), and even open in some specimens of *Laemanctus* (Lang 1989). Depending on the evolution of this character, the open groove of the Miller species may or may not exclude if from the crown of *Basiliscus*.

While fossil corytophanines are increasingly common in the Paleogene of North America and Europe, the Miller specimens may be the oldest material referable to an extant genus. Additional representative elements are needed for a stronger diagnosis, but preliminary evidence suggests a relationship with *Basiliscus*. Regardless of its lower-level affinities, the Miller species represents the latest known extra-tropical occurrence of the subfamily.

Iguanine gen. et sp. indet.

(Figure 19)

Referred Material

MLF I1 (partial left mandible), MLF I2-3 (partial left dentaries), MLF I4 (partial right dentary)

Description

Mandible. MLF I1 (Fig.19) is a partial left dentary that retains articulated fragments of the splenial, coronoid, angular, and surangular posteriorly. There are spaces for 16 teeth, and the 5 that remain are tricuspid. The bone is broken anteriorly and posteriorly, so a total tooth count is not possible. There probably were not many additional tooth spaces posteriorly. The Meckelian groove is closed and fused. A weak subdental shelf is present anteriorly but fades to barely accommodate the circumference of the tooth bases posteriorly. Even far back along the length of the bone, the lingual margin of the subdental shelf forms a sharp corner with the sML. The Meckelian reentrant is long, narrowly U-shaped, and extends to a level under the fourth from last preserved tooth space. It is invaded by part of the coronoid posterodorsally, part of the angular posteroventrally, and part of the splenial anteriorly. The AIAF, situated at the anterior apex of the Meckelian reentrant, is divided roughly equally between the dentary anterodorsally and the splenial posteroventrally. A smaller mylohyoid foramen is positioned posteroventral to the AIAF and is contained entirely by the splenial. Viewed lingually, the angular is exposed to a level under the penultimate tooth and the coronoid to under the ultimate tooth. The coronoid almost certainly extends farther anteriorly; it is deep to the splenial and obscured from view. Where the splenial is broken posteriorly, there is an obvious facet on the coronoid where the 2 bones overlapped. A fragment of the surangular previously occupied a position along the inside of the labial wall of the dentary, but became isolated during preparation. There is no obvious facet for an anterolateral extension of the coronoid. If present, it did not extend far anteriorly.

Other dentary specimens provide additional information. The symphysis is fairly robust, and the Meckelian groove is fused far anteriorly. An oval opening for the groove extends only for the length of the first 2 to 3 teeth. Anterior teeth are high-crowned, strongly lingually recurved, and develop accessory cusps early in the tooth row. In one specimen, MLF I4, distinct shoulders (Hotton 1955) are present by the second tooth. Teeth are evenly spaced, and crowns do not overlap. Relatively few crowns are well preserved for any specimen, but there is a tendency for the anterior accessory cusp to be slightly higher relative to the posterior accessory cusp. The IMS, although not directly measurable in any specimen, is not elongate. Looking posteriorly into the dentary tube of MLF I2, the septum does not extend to the level of the last labial foramen. Viewed lingually the ventral margin of the bone is straight and curves only at the symphysis.

Figure 19. Left mandible of Iguaninae gen. et sp. indet., MLF I1, in lingual view. Abbreviations: AIAF, anterior inferior alveolar foramen; AMF, anterior mylohyoid foramen; An, angular; Co, coronoid; Spl, splenial. Scale bar equals 1 mm.

<u>Remarks</u>

These specimens are referred to Iguaninae for having an extensively fused Meckelian groove and flared tooth crowns (see Iguaninae gen. et sp. indet. in Chapter 2). The development of accessory cusps early in the tooth row (Smith 2011b) and the higher relative position of mesial cusps compared to distal ones (pers. obs.) support this assignment. The absence of a preserved labial coronoid facet on the dentary on any specimen is not surprising; all are broken posteriorly where one would (potentially) be found. Even with so many elements of the mandible represented, the Miller iguanine is difficult to place at lower taxonomic levels. The relative positioning of the AIAF and AMF is intraspecifically variable in iguanines (de Queiroz 1987; pers. obs.), so neither is very informative. Based on what is preserved of the postdentary bones in MLF I1, perhaps only *Sauromalus* can be excluded for having a characteristically reduced splenial (de Queiroz 1987).

Tricuspid teeth are found in *Amblyrhynchus*, some *Brachylophus*, and some *Ctenosaura* among iguanines (de Queiroz 1987), but the evolution of polycuspate (here, more than 3) teeth is not well understood (see Chapter 2). The presence of only 3 cusps for some *Brachylophus* and some *Ctenosaura* could potentially represent apomorphic reversals (de Queiroz 1987), in which case an argument for referral of the Miller specimens to either could be made. The tooth crowns of *Amblyrhynchus* have exaggerated accessory cusps and would not be easily mistaken with other taxa (de Queiroz 1987; pers. obs.). Tricuspid teeth are also known for some *Dipsosaurus dorsalis* (Norell 1989) and the Eocene dipsosaur *Queironius praelapsus* (Smith 2011b); this character alone is insufficient for fossil referral. Alternatively, the population at the Miller site may not be adequately sampled. There are only a few specimens, and all are small relative to mature adults of most observed modern taxa. Some iguanines are tricuspid as juveniles, and then add cusps ontogenetically (de Queiroz 1987). Additional material may reveal that not all of the Miller individuals retained only 3 cusps.

The sparse material available for the Brooksville and Miller iguanines is not amenable to extensive comparison, but there are at least 2 apparent differences. Even in the absence of measurable tooth rows, the dentary of the Brooksville iguanine looks to be deeper than that of the Miller taxon. In the Brooksville specimens, the subdental lingual face is tall and nearly vertical; this results in a very “narrow” appearance when viewed posteriorly. In this way, it is similar to the morphology of *Dipsosaurus dorsalis*. In the Miller iguanine the same feature is shorter and more rounded, just as in many other iguanines. The teeth of the Miller specimens also never overlap as they do in the Brooksville iguanine, but the posterior end of the tooth row is admittedly never as well preserved in the former.

Two other fossil taxa deserve mention. Stevens (1977) referred a fragmentary left dentary from the Arikareean of Texas to either *Ctenosaura* or *Sauromalus*. The specimen lacks features that would unite it definitively with either, but its fused Meckelian groove at least supports an iguanine relationship. Estes (1963) described a dentary fragment and single vertebra from Thomas Farm that potentially represent an iguanine (de Queiroz 1987), but again, there is not enough preserved to merit further interpretation. Ultimately, the relationships of all 4 fossil taxa can only be clarified with additional material.

Phrynosomatinae gen. et sp. indet.

(Figures 20-21)

Referred Material

MLF PDr1-10 (partial right dentaries), MLF PDl (partial left dentaries), MLF PMr1 (partial right maxilla), MLF PMl1-2 (partial left maxillae), MLF PF1-2 (partial frontals), MLF PP1-2 (partial parietals) MLF PB1-4 (partial braincase)

Description

Dentary. Dentaries are well represented for this taxon, but only 2 specimens, MLF PDr1 and MLF PDr2, preserve the entire tooth row. They have spaces for 22 and 21 teeth, respectively, and MLF PDr1 is approximately 25% larger than MLF PDr2. MLF PDr1 has an IMS/ tooth row length ratio of 0.75; MLF PDr2 has a slightly higher ratio of 0.798. An exact measurement was unobtainable for other specimens, but the IMS consistently ends at around the level of the fifth (from last) tooth space whenever the posterior end of the bone is preserved. Teeth are high crowned, unicuspid, and gently recurved, especially anteriorly. Tooth shafts are distended lingually at mid-height, extending further medially than both the base and the crown. The shafts are oval in cross section, but the crowns taper conically to a sharp apex. In a few specimens weak accessory cusps are developed on only the posteriormost teeth. In most specimens, however, crowns are uniformly unicuspid throughout. Commonly, all but the last few teeth are weakly recurved. Genioglossus scars (Wellstead 1982) are frequently but not universally present anteriorly. An IML is variably present; it is moderately developed in some (e.g., MLF PDr1) specimens but absent in others. The Meckelian groove is either closed or restricted anteriorly but never fuses. Some individuals bear a distinct, obliquely oriented dorsolabial “shelf” posteriorly (the “dorso-labial concavity” of Wellstead 1982). Two specimens (MLF PDr3 [Fig.20] and MLF PDr4) exhibit a posterior extension of the dentary that continues well beyond the end of the tooth row. Labially the posterodorsal end of the bone is constructed to accommodate a weak invasion by the coronoid that does not reach the tooth row.

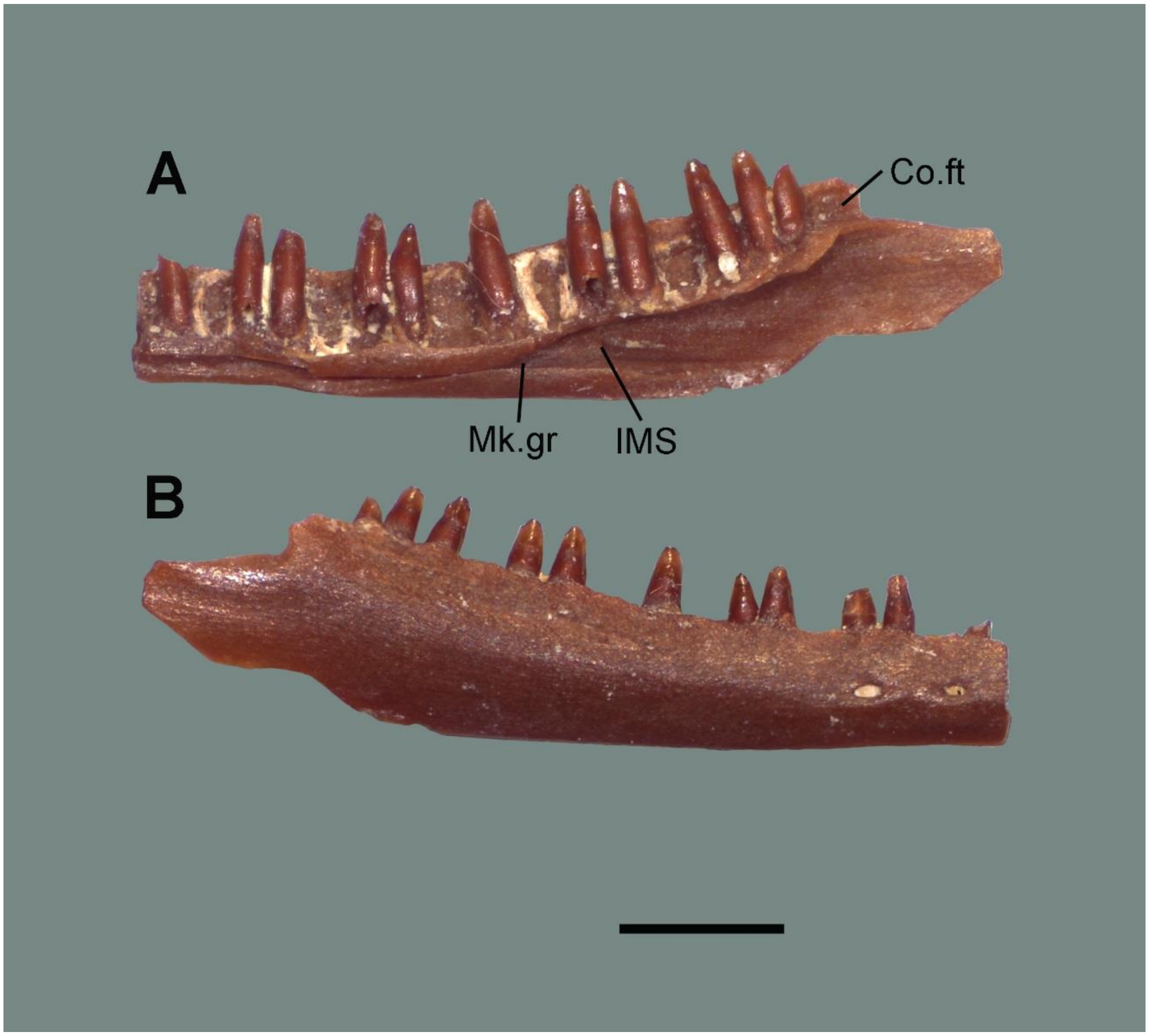

Figure 20. Dentary of Phrynosomatinae gen. et sp. indet. **A, B,** Right dentary of Phrynosomatinae gen. et sp. indet., MLF PDr3, in lingual and labial views, respectively. Abbreviations: Co.ft, coronoid facet; IMS, intramandibular septum; Mk.gr, Meckelian groove. Scale bar equals 1 mm.

<u>Maxilla.</u> Three maxillary fragments are associated here based on tooth form, size, and relative abundance. The most complete fragment, MLF PMl1, is 5.29 mm in length. Nineteen tooth spaces are preserved, but part of the premaxillary process is broken away. One or 2 additional teeth were likely present anteriorly. Teeth are high crowned and unicuspid but lack the lingual distension described for dentary teeth. Maxillary teeth also appear more lingually recurved than those found on the mandible, even posteriorly. The

SAF is roofed. No specimen preserves a complete palatine process, so its morphology is unknown. Immediately posterior to where the palatine process is broken away on MLF PMl1, the lingual edge of the palatal flange bears a smooth, flattened area extending posteriorly for the length of several tooth spaces. At the end of the bone, the palatal flange is divided longitudinally into nearly equal labial and lingual halves by a low ridge of bone that separates the jugal and ectopterygoid facets. Much of the facial process is broken dorsally, but anteriorly it bends medially to join the crista transversalis. The resulting canthal ridge slopes fairly steeply towards a dorsoventrally short premaxillary process. Medially the crista transversalis is very strongly developed. The relationship of the AIAF and SNAF is unclear due to breakage, but they are separate on MLF PMl2. On that specimen the anterior margin of the premaxillary process is asymmetrically concave when viewed dorsally; a medial projection extends further anteriorly than the lateral one. On both MLF PMl2 and MLF PMr1 a small foramen is present ventrally on the palatal flange at the anterior end of the tooth row.

Frontal. Two azygous frontals are associated here based on size, relative abundance, and iguanian morphology. Both are broken anteriorly but were obviously constricted strongly between the orbits. The ratio of the narrowest width to the widest posterior width is 0.214 for MLF PF1 and 0.204 for MLF PF2. Dorsally weak epidermal scale impressions can be made out on both specimens. The crista cranii are individually wide posteriorly but narrow anteriorly where they approach each other. The posterior margin of the frontal is concave, suggesting the presence of a widely open parietal fontanelle. The posterolateral corners of the bone bear postfrontal facets.

Parietal. Two parietal fragments are tentatively associated with this taxon based on size and relative abundance. The parietal table of MLF PP1 is flat and roughly trapezoidal. The left postparietal process is broken, but the right one bears a lateral supratemporal facet posteriorly. The posterior nuchal fossae are widely separated. Ventrally a narrow parietal fossa is situated at the posterior margin of the bone.

Braincase. The right portion of a damaged braincase, MLF PB1 (Fig. 21), is associated on the basis of size, relative abundance, and iguanian morphology. Portions of the basiocciptal, supraoccipital, otooccipital, and prootic are all represented and indistinguishably fused. A dorsal alar process is not developed. Medially, a very weakly developed supratrigeminal process is present. The crista prootica is reduced, and the paraoccipital process is short. The LARST is wider in diameter than the fenestra ovalis. The crista interfenestralis that separates them sweeps up and appears as a weak, angular projection when viewed posteriorly. A well-developed occipital recess is present dorsal to the basal tuber. In lateral view the ventral tip of the basal tuber is directed somewhat anteriorly. It is not clear if the sphenoid contacted the tuber, but there are no obvious facets indicating such an arrangement. The small facial foramen is positioned anterior to the fenestra ovalis. An additional foramen of similar size exits dorsal to the fenestra ovalis just below the crista prootica; its origin is unknown.

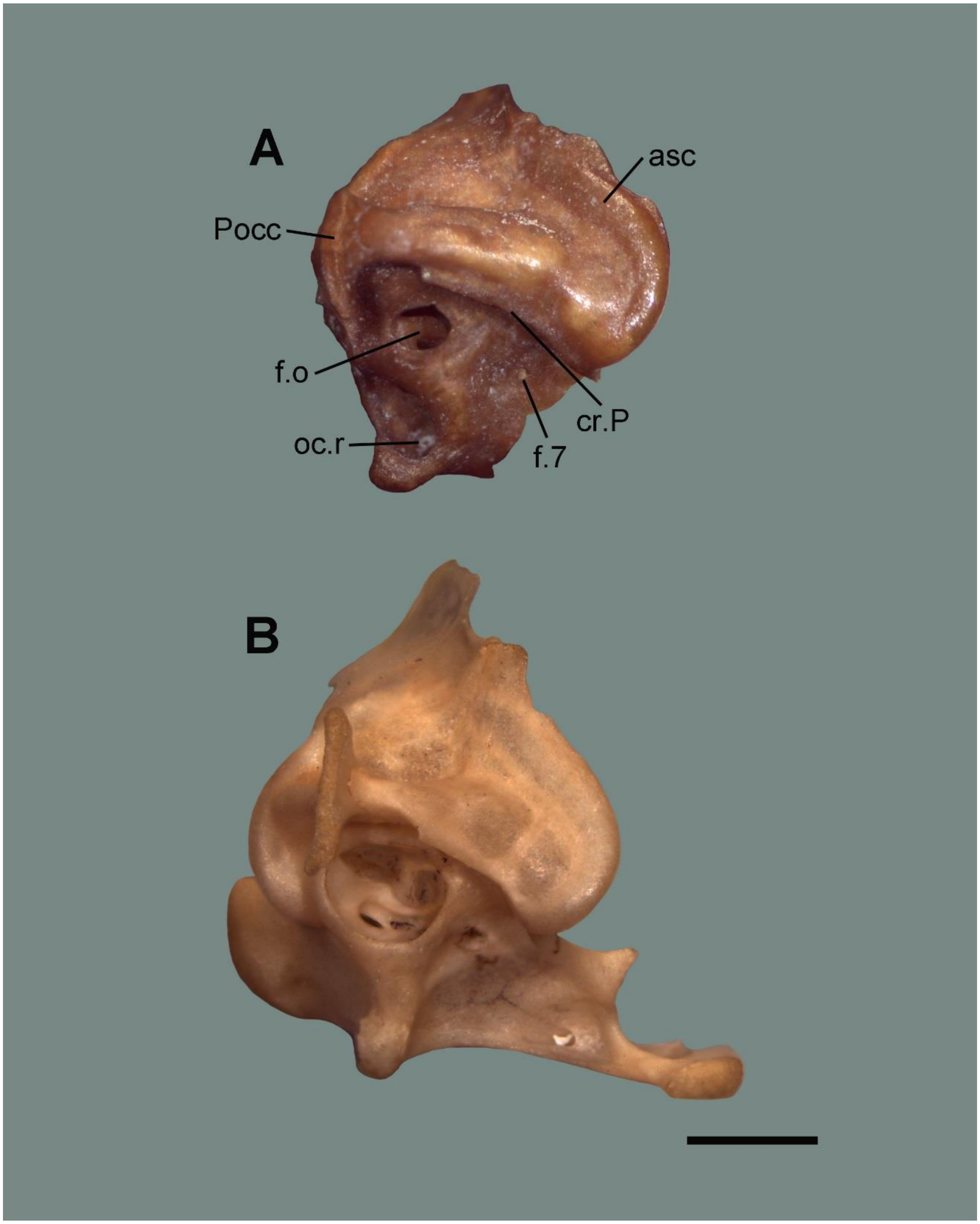

Figure 21. Comparative braincases of phrynosomatines. **A,** Braincase of Phrynosomatinae gen. et sp. indet., MLF PB1, in lateral view. **B,** Braincase of *Holbrookia maculata* ETVP 4038 in right lateral view. Abbreviations: asc, anterior semicircular canal; cr.P, crista prootica; f.o, fenestra ovalis; f.7, foramen for facial nerve; oc.r, occipital recess; Pocc, paroccipital process. Scale bar equals 1 mm.

Remarks

A phrynosomatine relationship is inferred on the basis of the posterior elongation of the dentary (Etheridge and de Queiroz 1988), the slight anteroventral expansion of the coronoid (Etheridge and de Queiroz 1988), extensive closure/restriction of the Meckelian groove without fusion (Etheridge and de Queiroz 1988), the elongate IMS (Smith 2006), and the high-angle medial bend of the facial process of the maxilla (Smith 2011a). Other characters at least consistent with phrynosomatine morphology include the dorsolabial "shelf" of the dentary (Twente 1952; Etheridge 1958; Wellstead 1982), a large parietal fontanelle (see Etheridge 1964: fig. 1), and a highly constricted frontal (pers. obs.); interpretation of the latter 2 characters assumes that nondentigerous elements are associated correctly.

Phrynosomatines are a diverse (>140 spp.) group of iguanids distributed primarily among drier regions of the southwestern United States and Mexico (Uetz 2014). They are composed of 2 main clades: one containing *Phrynosoma* and the "sand lizards" (*Callisaurus*, *Cophosaurus*, *Holbrookia*, and *Uma*), and another containing *Petrosaurus*, *Urosaurus*, *Uta*, and *Sceloporus* (Reeder and Wiens 1996; Wiens et al. 2010). In an early study of the group Etheridge (1964: 612) observed that it was "impossible to arrange all of the species of [phrynosomatines] into neat groups according to dentition." Norell (1989) undertook a more detailed analysis of their dental variation but ultimately used differences in tooth morphology only to delimit sympatric fossil morphotypes rather than to assign his specimens to modern groups. Even in the absence of clear-cut criteria for taxonomic differentiation, the sharp, recurved, and primarily unicuspid teeth displayed by (most of) the Miller sample are noteworthy. They are unlike those found in either of the 2 phrynosomatines inhabiting the eastern United States today (*Sceloporus undulatus* and the Florida endemic *S. woodi*; Krysko et al. 2011) and perhaps most closely match those observed here for *Urosaurus*. Still, there is little evidence linking the Miller species to any particular genus.

Among roughly contemporaneous fossil taxa, the morphology of the Miller specimens draws comparison with *?Holbrookia antiqua* from the Hemingfordian of Nebraska (Yatkola 1976) for sharing a diminutive size and similar tooth morphology. That species was assigned to *Holbrookia* only with reservation and is represented by three broken dentaries and a single fragmentary maxilla.

If the frontals and braincase are associated here correctly, at least 2 characters would exclude the Miller species from *Holbrookia* or other sand lizards: the retention of a small postfrontal and the lack of an enlarged fenestra ovalis. The postfrontal is lost in the sand lizards (Etheridge and de Queiroz 1988), and the Miller frontals bear small facets indicating its presence. In *Callisaurus*, *Cophosaurus*, and *Holbrookia* the diameter of the fenestra ovalis of the braincase is greatly expanded at the expense of the (much smaller) LARST (Evans 2008; pers. obs.). This morphology is taken to an extreme in the earless lizards *Cophosaurus* and *Holbrookia* (Fig. 21), and the tendency to enlarge this opening appears convergently common in other, unrelated burrowing lizard taxa that have lost external ear openings (e.g., *Plestiodon reynoldsi*). The functional significance of this character in eared *Callisaurus* is less clear, but it seems to unite all 3 genera to the exclusion of the Miller phrynosomatine. Because the Miller species lacks derived features of other genera, though, it is not identified below the subfamily level.

Scincidae gen. et sp. indet.

(Figures 22-23)

Referred Material

MLF S1-6 (partial right dentary), MLF S7-9 (partial left dentary), MLF S10 (partial right maxilla), MLF S11-12 (?), MLF S13-16 (right premaxilla), MLF S17-20 (left premaxilla), MLF S21 (left postfrontal)

Description

Dentary. All recovered dentaries are anterior, symphysis-bearing fragments. No specimen preserves an entire tooth row, so a tooth count is unobtainable. Tooth crowns are low, labially smooth and convex, and lingually striated (Fig. 22). The teeth of some specimens are labiolingually expanded and have a more robust appearance than the teeth of others. A moderately developed subdental gutter is always present, and the Meckelian groove is always open (primarily ventrally) as far as the bone is preserved.

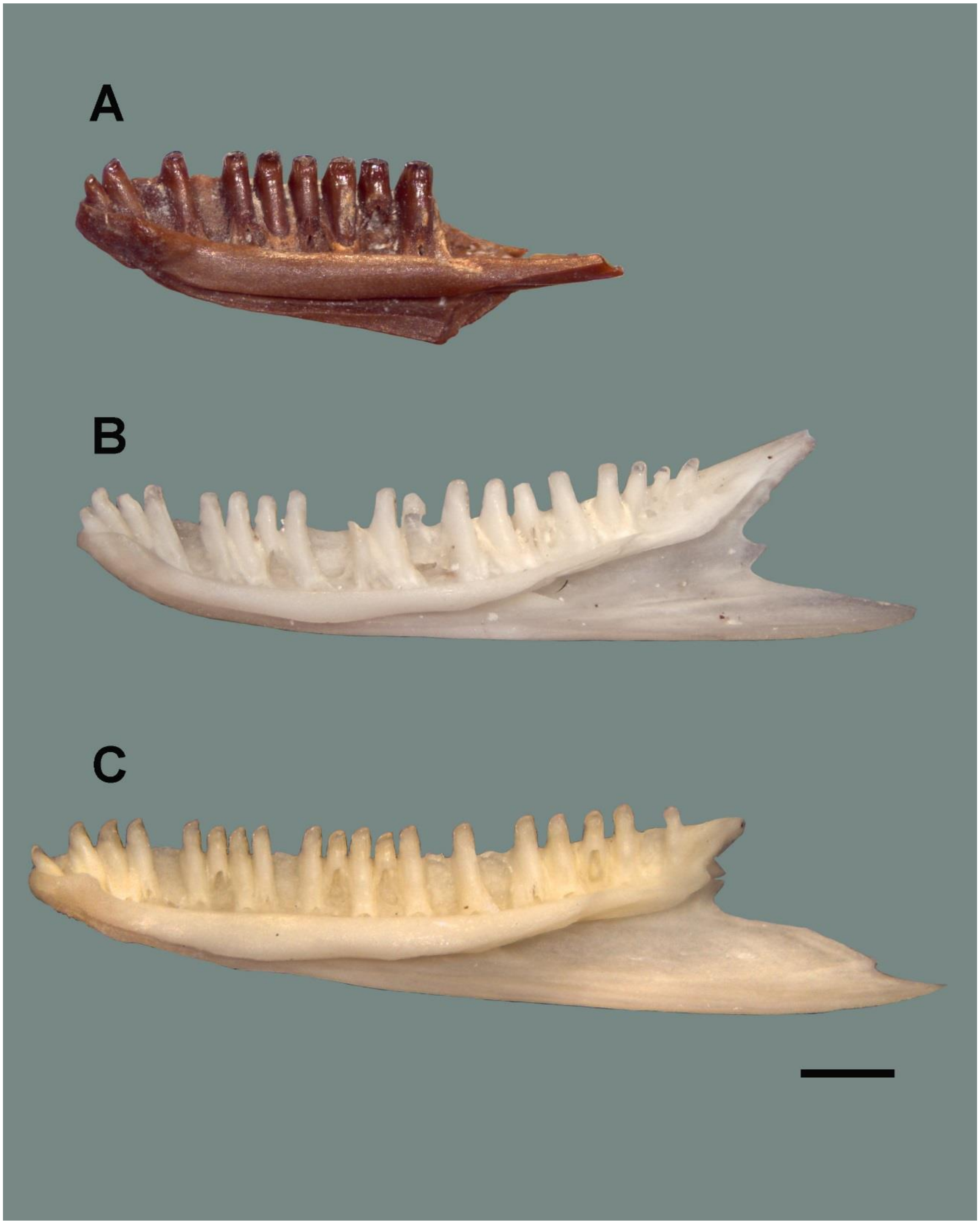

Figure 22. Comparative dentaries of scincids. **A,** Right dentary of Scincidae gen. et sp. indet., MLF S1, in lingual view. **B,** Right dentary of *Mesoscincus managuae* FB 1131 in lingual view. **C,** Right dentary of *Plestiodon fasciatus* ETVP 2892 in lingual view. Scale bar equals 1 mm.

Maxilla. Maxillary fragments are associated here based on similar size and tooth form. Only the posteriormost portion of the bone is known. There are dorsal and medial facets at the end of the palatal flange for the jugal and ectopterygoid, respectively, and the terminus is bifurcated.

Premaxilla. Not all premaxillae preserve a complete palatal flange, but of those that do left elements consistently bear 3 tooth spaces while right elements bear 4.

Postfrontal. The postfrontal (Fig. 23) is triradiate with a long, broad main body posteriorly and smaller lateral and medial processes anteriorly. The posteromedial edge is damaged. The anteromedial process bears a medial facet that would have clasped the frontal dorsally and ventrally. The anterolateral process lacks an obvious facet but presumably would have contacted the jugal. The anterior margin of the bone between the frontal and jugal processes is markedly concave and would have marked the posterodorsal boundary of the orbit. A long facet runs along the dorsal surface of the posterolateral edge. By comparison with other scincids, this facet would have been overlapped by either the postorbital or the squamosal.

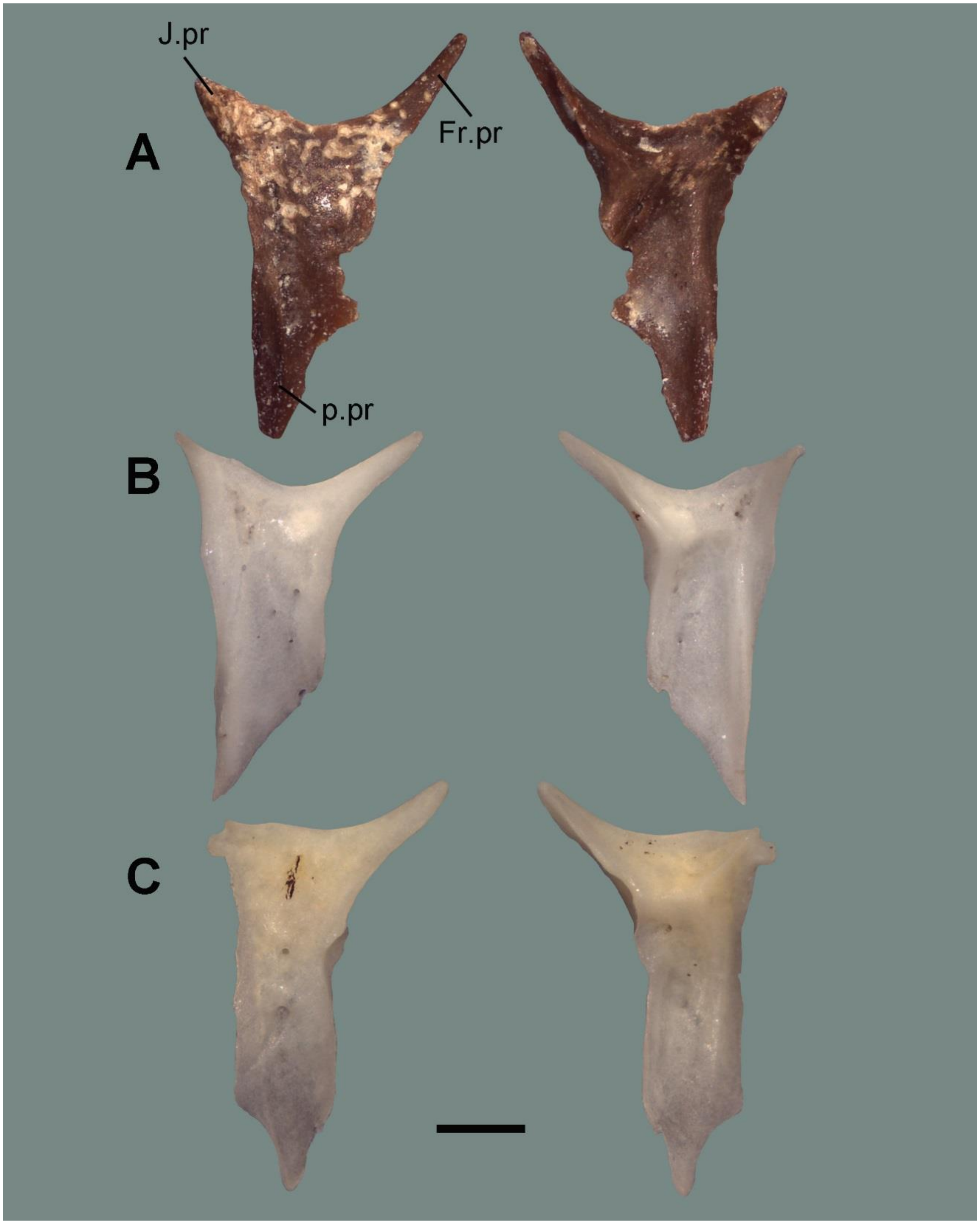

Figure 23. Comparative postfrontals of scincids. **A,** Left postfrontal of Scincidae gen. et sp. indet., MLF S21. **B,** Left postfrontal of *Mesoscincus managuae* FB 1131. **C,** Left postfrontal of *Plestiodon fasciatus* ETVP 2892. **First column,** Dorsal view. **Second column,** Ventral view. Abbreviations: Fr.pr, frontal process; J.pr, jugal process; p.pr, posterior process. Scale bar equals 1 mm.

Remarks

Reasons for referral to the Scincidae are the same as for the Brooksville skink above, and there is little about either that would distinguish the two. At least some of the Miller dentaries exhibit a feature not observed in the Brooksville specimens, namely a labiolingual expansion of the tooth shafts. In some specimens of *Plestiodon* (as well as in the single specimen of *Mesoscincus*) tooth shafts are expanded and rotated so that the lingual side of each tooth is directed somewhat posteriorly relative to the labial side. At least for *Plestiodon* this seems to be an ontogenetic transformation; it is more pronounced in larger individuals. Because its expression is tied with size and age, there is little reason to assign any special significance to discrepancies between the Brooksville and Miller specimens in this regard.

The morphology of the Miller postfrontal, however, may be informative. The anterior margin of the postfrontal of *Mesoscincus* is markedly concave (viewed dorsally), just as in the fossil. I have not observed a similar morphology in any examined member of *Plestiodon*, but only a single, immature individual of a single species of *Mesoscincus* was available for comparison. Without a broader osteological sample of *Mesoscincus*, it is difficult to judge the utility of this bone for drawing taxonomic conclusions. A better understanding of the *Mesoscincus* skeleton, as well as additional representative elements of both the Brooksville and Miller skinks, is necessary for a more definitive assignment.

Teiidae gen. et sp. indet.

(Figures 24-25)

Referred Material

MLF T1-7 (7 partial dentaries), MLF T8 (partial left maxilla), MLF T9 (premaxilla), MLF T10 (frontal)

Description

Dentary. Most specimens consist of anterior dentary fragments; the posterior end of the bone is never preserved. The best-preserved specimen, MLF T1 (Fig. 24), is the anterior portion of a left dentary with 12 teeth and 16 tooth spaces. Teeth are heterodont and subpleurodont with basal cementum. Anterior teeth are markedly shorter and smaller than those that follow. The first 6 teeth are unicuspid, but posteriorly the teeth become asymmetrically bicuspid with the addition of a small anterior cusp. The sML is dorsoventrally tall but never extends far enough ventrally to contact the iML. Consequently, the Meckelian groove is open lingually and somewhat ventrally. The dorsal margin of the sML is straight in lingual view, even anteriorly at the weak mandibular symphysis where most lizards evince a notable curvature. Another specimen, MLF T2, stands out for broadening considerably just before the broken posterior end. Viewed dorsally, the labial margin of the bone curves abruptly after the transverse level of the last preserved tooth and presages a significant labiolingual expansion posteriorly.

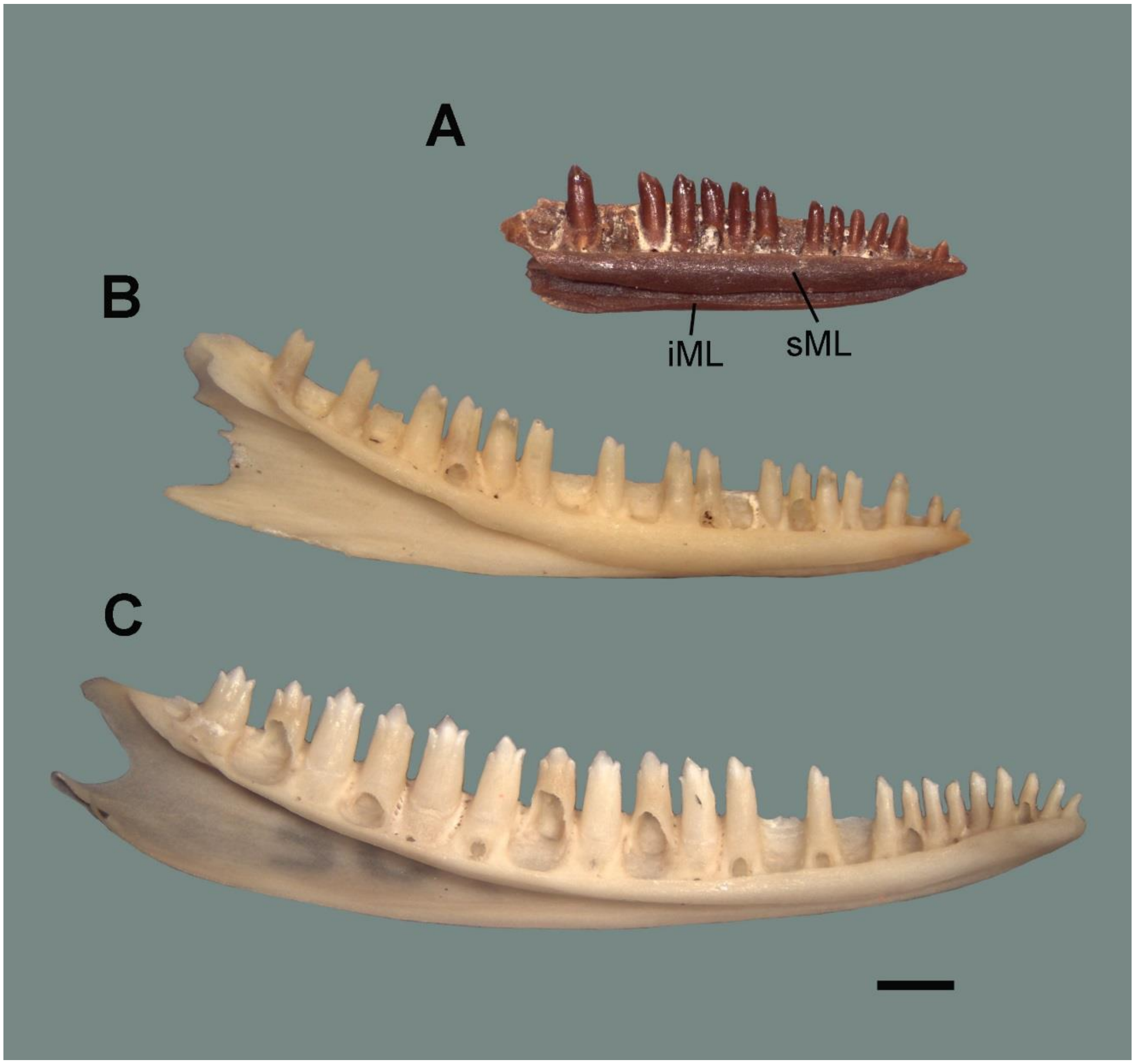

Figure 24. Comparative dentaries of “cnemidophorine” teiids. **A,** Left dentary of Teiidae gen. et sp. indet., MLF T1, in lingual view. **B,** Left dentary of *Aspidoscelis tigris* JIM 0290 in lingual view. **C,** Left dentary of *Kentropyx calcarata* ETVP 3040 in lingual view. Abbreviations: iML, infra-Meckelian lip; sML, supra-Meckelian lip. Scale bar equals 1 mm.

<u>Maxilla.</u> A single posterior maxillary fragment is associated here based on similar tooth form. There are 4 tooth spaces and 3 bicuspid teeth that probably represent the end of the tooth row. A facet for the jugal is developed along the posterolateral edge of the

palatal flange. The SAF opens at the anterior end of the fragment, suggesting it must have been positioned far posteriorly on the maxilla.

Premaxilla. A single premaxilla is associated here based on its overall teiid morphology. Teeth are broken and worn, and part of the left portion of the bone is broken away. Assuming bilateral symmetry of the tooth row (the right side is complete), there were likely 8 teeth. The ascending nasal process rises fairly steeply, and there is no medial incisive process posteriorly. The left and right arms of the palatal flange diverge only gently posteriorly; they form an acute angle where they meet along the midline.

Frontal. MLF T10 (Fig. 25) is a small azygous frontal. It has a weak hourglass shape, reaching its narrowest point in the posterior half of the bone and widening anteriorly and posteriorly. The dorsal surface is rugose, and the boundaries between the paired frontoparietal and single frontal epidermal scales are clearly delineated by grooves in the bone. Viewed laterally, there is a gentle dorsal convexity. Ventrally, the crista cranii are spaced widely enough to accommodate a low midline ridge that arises posteriorly and runs between them before disappearing anteriorly. There is no indication of the distinctive descending processes found on the frontal of other scleroglossans (Evans 2008).

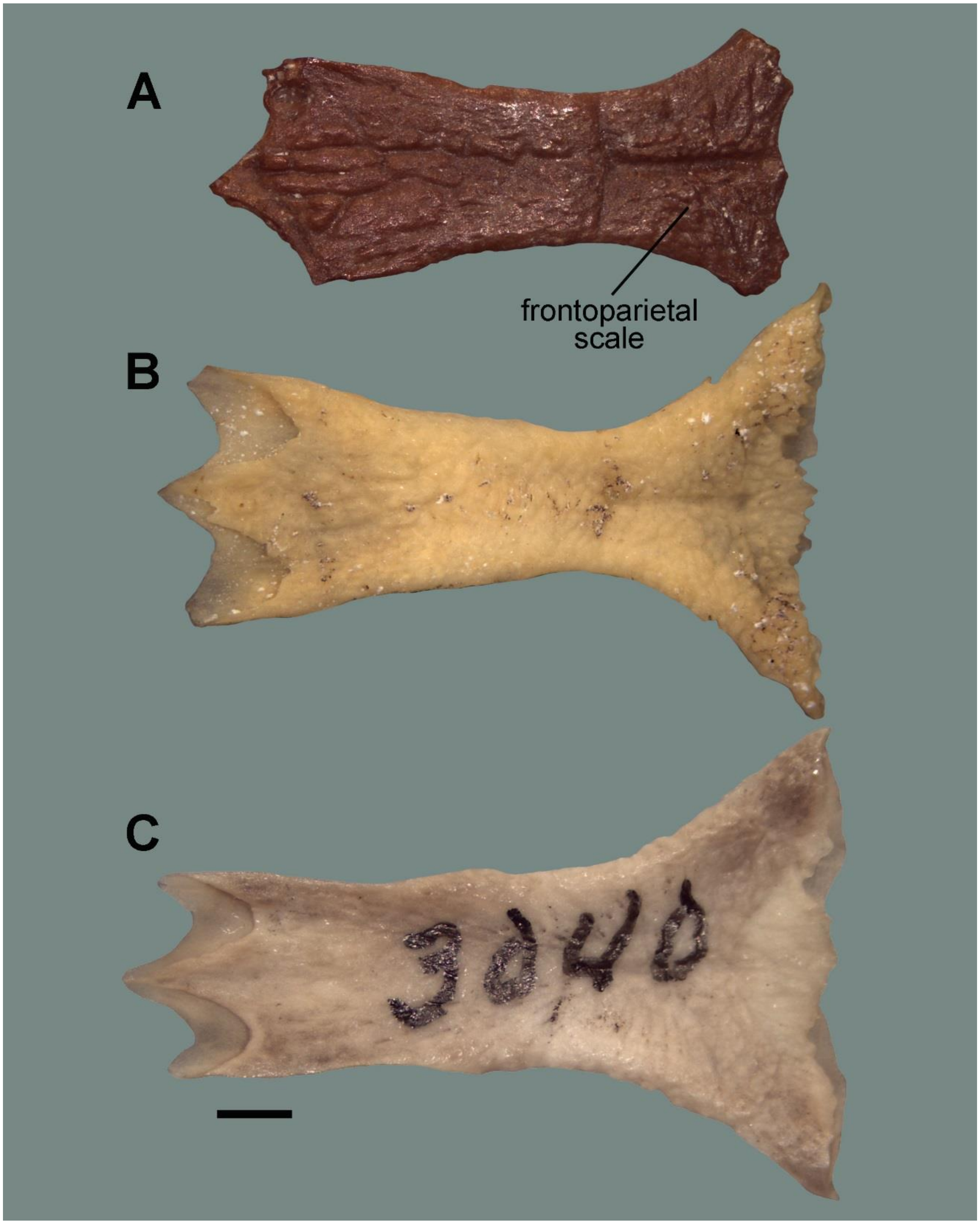

Figure 25. Comparative frontals of “cnemidophorine” teiids. **A,** Frontal of Teiidae gen. et sp. indet., MLF T10, in dorsal view. **B,** Frontal of *Aspidoscelis tigris* JIM 0290 in dorsal view. **C,** Frontal of *Kentropyx calcarata* ETVP 3040 in dorsal view. Scale bar equals 1 mm.

Remarks

Problematic generic-level relationships among at least some teiid lizards have provided an enduring source of uncertainty for the referral of North American fossil material (Estes 1963; Estes and Tihen 1964; Norell 1989; Bell 1993). Historical diagnoses of *Ameiva* and *Cnemidophorus* have relied on soft-tissue differences (Burt 1931) that are not expressed skeletally, and consequently their remains cannot be confidently differentiated. Estes and Tihen (1964) suggested the taxonomy of both might be better served by synonymizing them under the same name, but even the inclusion of genetic characters has yet to fully clarify relationships that Estes (1963: 250) considered “hopelessly snarled.” Reeder et al. (2002) recovered both genera as paraphyletic, but did recover a monophyletic North American clade (all formerly *Cnemidophorus*) for which they resurrected the genus name *Aspidoscelis*. Their analysis also recognized a more inclusive “cnemidophorine” clade comprised of *Ameiva*, *Cnemidophorus*, *Aspidoscelis*, and *Kentropyx*, even while highlighting problems with the former two. In the absence of a stable definition of either *Ameiva* or *Cnemidophorus* (although see Harvey et al. 2012) to inform osteological comparisons, it is simplest at present to identify the Miller specimens only as a “cnemidophorine” teiid (sensu Reeder et al. 2002).

The distinctive bicuspid tooth crown morphology and basal cementum seen in the fossils are characteristic of all cnemidophorines (Estes 1963; Estes and Tihen 1964; Norell 1989; Bell 1993), but additional features of the dentary and frontal may rule out at least *Kentropyx*. Presch (1974) described *Kentropyx* as having a convex parietal-frontal roof, whereas Norell (1989) described it as having a concave parietal. Regardless of how one chooses to interpret this character, the single specimen of *Kentropyx* examined for this study possesses a frontal that is markedly different from other cnemidophorines. It is dorsally concave (viewed laterally and anteriorly) and tapers to its narrowest point in the anterior half of the bone. In other cnemidophorines the frontal is weakly dorsally convex and tapers to its narrowest point in its posterior half. Viewed ventrally the *Kentropyx* frontal bears strong supraorbital flanges that I otherwise only observed as weaker developments on some specimens of *Ameiva*. The dentary of *Kentropyx* also differs from other cnemidophorines in having a more strongly curved (viewed laterally) crista dentalis and in possessing a much shorter (dorsoventrally) and less distinct supra-Meckelian lip. A broader skeletal sample of *Kentropyx* is desirable for a better understanding of the observed deviation in both bones.

The frontal of cnemidophorines becomes increasingly rugose with ontogeny (Norell 1989), suggesting the single frontal here belonged to an older individual. The divided frontoparietal scales inferred from encrustations on MLF T10 are probably primitive for teiids but exclude it from at least some members of *Aspidoscelis*. *Aspidoscelis carmensis*, *A. ceralbensis*, *A. danheimae*, *A. espiritensis*, *A. franciscensis*, *A. hyperythra*, and *A. picta* all have a single, undivided frontoparietal scale (Walker et al. 1966; Walker and Taylor 1968; Reeder et al. 2002). That they are not closely related with the Miller species is not surprising given their distribution; all are found in southern California and on the Baja Peninsula (Grismer 1999).

Cnemidophorine teiids are common in late Neogene fossil herpetofaunas (Norell 1989), but only a single extinct species has been described. Taylor (1941) named *Cnemidophorus* (= *Aspidoscelis*) *bilobatus* from the Pliocene of Kansas. His diagnosis was based mainly on subtle differences in tooth morphology that appear to be too intraspecifically variable in modern specimens to warrant comparison with the Miller material. Previously, the oldest record of teiids in North America was from the Hemingfordian Thomas Farm locality (Estes 1963); the Miller specimens may be slightly older.

Conclusions

Non-anguimorph lizards from the early Hemingfordian Miller LF include a species of *Anolis*, a corytophanine closely resembling *Basiliscus*, an iguanine, a diminutive phrynosomatine, a scincid, and a "cnemidophorine" teiid. Remains of *Anolis* cannot be reliably distinguished from those from Brooksville 2, but they are considerably less abundant. Taken together, both records suggest the continued presence of non-*carolinensis* anoles in Florida across the Oligocene/Miocene boundary. The corytophanine differs from modern species of *Basiliscus* only in retaining an open Meckelian groove but otherwise shares closer affinities with modern taxa than with fossil relatives from the Eocene. The precise relationships of an iguanine could not be determined. Regardless, the record is biogeographically significant because the subfamily does not have native representatives in the southeastern United States today. The small phrynosomatine is the most abundant lizard at the site. Characters of associated frontals and a partial braincase exclude it only from the "sand lizards" among the subfamily. The presence of a scincid, as for Brooksville 2, highlights the need for a better understanding of the *Mesoscincus* skeleton. A "cnemidophorine" teiid is the oldest known from North America. Records are unknown prior to the Hemingfordian, and their appearance in the early Miocene likely documents dispersal from South America.

CHAPTER 4

DISCUSSION AND CONCLUSIONS

In a study of late Eocene lizards from North Dakota, Smith (2006) brought attention to an uncharacteristic assemblage of iguanids that contrasted sharply with the known Paleogene record of the family. Gilmore's (1928) original compendium of North American fossil lizards was dominated by early Cenozoic accounts of anguimorphs and amphisbaenians, and later overviews by Tihen (1964) and Estes (1970) yielded a similar pattern. The latter 2 studies were aided by an improved Neogene record that, considered together with the living herpetofauna, pointed to a dramatic taxonomic reorganization sometime in the Oligo-Miocene involving 1) the extirpation of anguimorphs and amphisbaenians from much of their former range, 2) a substantially increased representation of iguanids, 3) the arrival of scincids from Eurasia, and 4) the appearance of teiids from South America.

That anguimorphs and amphisbaenians were affected by Cenozoic climatic changes is expected. Both groups are well represented in the North American Paleogene, and their modern diversity and distributions speak to conservative environmental preferences that would have hindered their continued occupation of middle latitudes. Modern scincids do not appear in the North American record until the Oligocene (Sullivan and Holman 1996), and teiids are unknown before the Miocene (Estes 1963; this study). The exact timing of their (multiple) respective dispersals is constrained only by negative fossil evidence, but comprehensive molecular phylogenies have mostly upheld early biogeographic hypotheses concerning their external origin (Reeder et al.

2002; Macey et al. 2006; Giugliano et al. 2007; Brandley et al. 2011; Brandley et al. 2012).

In the separate summaries of Tihen (1964) and Estes (1970), iguanids were still poorly represented from the Paleogene. The description of a diverse iguanid community in the late Eocene by Smith (2006) suggested their apparent rise in the Miocene and after was artifactual; taxonomic biases in older faunas stemmed from inadequate sampling techniques that disproportionately favored the recovery of larger lizards (typically anguimorphs). Importantly, however, the iguanids identified by Smith (2006) were unlike those inhabiting the temperate latitudes of North America today. A more detailed reassessment of the same Chadronian fauna (Smith 2011b) and additional records from the early Eocene (Smith 2009a; 2011a; Smith and Gauthier 2013) bore out this notion further: Eocene iguanids included corytophanines, iguanines, and fossil relatives of *Anolis* and *Polychrus* — taxa now confined primarily to the neotropics. None of these groups have a definitive fossil record from middle latitudes in the Oligocene (Sullivan and Holman 1996), and their disappearance coincides with the climatic deterioration that characterizes the beginning of the epoch (Smith 2006).

In some ways iguanid assemblages from Brooksville 2 and Miller are more similar to those from the Eocene than to others reported from the late Oligocene and Miocene. Arikareean, Hemingfordian, and Barstovian iguanids come almost exclusively from Great Plains localities, though, and provincialism in the Gulf Coast region has been demonstrated for mammals at this time (Albright 1998). The taxonomic resolution afforded by fossil squamate remains does not often lend itself to the same kind of between-locality faunal comparison that is possible for mammals (Norell 1989), but a similar pattern for lizards is evident even at broad taxonomic levels at coarse temporal scales. Aside from a ubiquitous phrynosomatine presence at iguanid-bearing sites from the Great Plains (Estes and Tihen 1964; Robinson and Van Devender 1973; Yatkola 1976; Wellstead 1982), several studies include an additional taxon that is invariably aligned with *Leiocephalus* (Estes and Tihen 1964; Robinson and Van Devender 1973; Wellstead 1982). Allowing for the possibility that such taxa may actually represent Iguaninae (Norell 1989; Pregill 1992), the contemporary (broadly-speaking) record from Florida is unique for the presence of anoles and corytophanines (this study).

Comparisons with the Hemingfordian Thomas Farm locality are more difficult. Estes (1963) listed 4 iguanid taxa from the site: *Leiocephalus* sp. and 3 additional indeterminate morphotypes. His record of *Leiocephalus* sp. is insufficiently diagnosed (Pregill 1992), and the fragmentary material for the 3 other species provides few clues about their relationships. Estes (1963) suggests that his “species A” has teeth similar to *Anolis*, and that his “species C” may be an iguanine. “Species B” is differentiated from the others for having an open Meckelian groove, but no potential relationship is proposed.

Ostensibly, regional provincialism observed for lizards in the late Oligocene and early Miocene presages some of the taxonomic disparity between eastern and western herpetofaunas today. Phrynosomatinae is the most speciose clade of lizards in North America, but most of this diversity is concentrated in relatively arid regions (Wiens et al. 2013). Of more than 140 extant species (Uetz 2014), only 2, *Sceloporus undulatus* and *S. woodi*, occur in the eastern United States (Krysko et al. 2011). The presence of a small phrynosomatine at Miller does not necessarily imply strong faunal continuity with western sites in the early Neogene. Great Plains localities often include multiple phrynosomatine taxa (Robinson and Van Devender 1973; Yatkola 1976), and at least 2 preserve the western endemic *Phrynosoma* (Estes and Tihen 1964; Robinson and Van Devender 1973). The paleontological signal for the proliferation of phrynosomatines in western regions in the Neogene is strong (see, for example, Norell 1989), but because other iguanid clades were present in the Eocene, Smith (2006: 37) emphasized the need to make a distinction between modernization and "phrynosomatization."

Tihen (1964) and Estes (1970; 1983) both spoke generally of a gradual "restriction" of tropical lineages to lower latitudes in the Cenozoic, a concept that Smith (2009a; 2011b) later explored in greater detail. *Restriction*, he argued, involved the extirpation of extra-tropical members of widespread clades when climates became unfavorable at higher latitudes. *Retreat*, instead, involved the movement of entire clades from high latitudes to low latitudes as meridional temperature gradients increased through time. The second scenario does not require that a clade had low-latitude representatives in the past to be found in the tropics today and allows for the possibility that modern tropical clades originated elsewhere. The presence of corytophanines and non-*carolinensis* anoles at Brooksville 2 and Miller is consistent with either scenario; both have relatives at higher latitudes in the warmer Eocene, and both are limited to tropical latitudes today.

Either way, the strong extralimital character of lacertofaunas from Brooksville 2 and Miller lend paleontological support to aspects of the Tropical Conservatism Hypothesis of Wiens and Donoghue (2004). They argued that tropical regions are more species-rich for 3 complementary reasons: 1) megathermal (see Smith 2009a) environments have typically been much more extensive than they are now, 2) many modern clades have inhabited megathermal environments for longer than they have temperate ones, allowing them more time to diversify there, and 3) phylogenetic niche conservatism generally prevents tropical organisms from invading temperate habitats. As ectotherms, species richness patterns of reptiles are correlated strongly with temperature (Qian 2010; Jetz and Fine 2012). That entire clades of lizards seem to so closely track the climatic changes of the Cenozoic (Smith 2009a; 2011b; this study) suggests a basic environmental preference that has not changed for tens of millions of years.

Just as for many of Smith's (2009a; 2011b) Eocene taxa, a number of lizards from Brooksville 2 and Miller are limited to the neotropics today. The distributions of *Anolis*, corytophanines, iguanines, and helodermatids are all confined by a common northern boundary along Mexico's Atlantic coast (Vitt and Caldwell 2014; see also Wiens et al. 2006). The eublepharid genus *Coleonyx* has disjunct distributions in North America that reflect phylogenetically progressive adaptations to arid habitats, but basal tropical species have a similar northeastern limit (Dial and Grismer 1992). This trend extends to other Arikareean and Hemingfordian Gulf Coast taxa as well. Albright (1994) reported *Dermatemys* from the Toledo Bend LF of Texas, and Baskin (2003) described a potosin procyonid from Miller.

Only the phrynosomatine iguanid and teiid from Miller, the rhineurid amphisbaenian from Brooksville 2, and possibly the scincid from both sites conform to expectations based on modern distributions. Still, each is significant. The phrynosomatine is the earliest eastern record of the subfamily. The teiid represents the earliest record of "cnemidophorine" teiids in North America. Rhineurid amphisbaenians are endemic to the extreme southeastern United States today, and their presence at Brooksville 2 extends their temporal range in the region by 26 to 27 million years. The significance of the scincid at both sites ultimately depends on whether each represents temperate *Plestiodon* or tropical *Mesoscincus* (or a close relative of either).

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