

Oligocene mammals from Ethiopia and faunal exchange between Afro-Arabia and Eurasia

John Kappelman¹, D. Tab Rasmussen³, William J. Sanders⁴, Mulugeta Feseha², Thomas Bown⁵, Peter Copeland⁶, Jeff Crabaugh⁷, John Fleagle⁸, Michelle Glantz⁹, Adam Gordon¹, Bonnie Jacobs¹⁰, Murat Maga¹, Kathleen Muldoon³, Aaron Pan¹⁰, Lydia Pyne¹, Brian Richmond¹¹, Timothy Ryan¹², Erik R. Seiffert¹², Sevket Sen¹³, Lawrence Todd⁹, Michael C. Wiemann¹⁴ & Alisa Winkler^{10,15}

- ¹Department of Anthropology, and ²Department of Geological Sciences, University of Texas, Austin, Texas 78712, USA
- ³Department of Anthropology, Washington University, St Louis, Missouri 63130, USA
- ⁴Museum of Paleontology, University of Michigan, Ann Arbor, Michigan 48109, USA
- ⁵2300 Arapahoe Avenue, no. 236, Boulder, Colorado 80302, USA
- ⁶Department of Geosciences, University of Houston, Houston, Texas, 77204-5503, USA
- ⁷Department of Geology and Geophysics, University of Wyoming, Laramie, Wyoming 82071-3006, USA
- ⁸Department of Anatomical Sciences, State University of New York, Stony Brook, New York 11794-8081, USA
- ⁹Department of Anthropology, Colorado State University, Fort Collins, Colorado 80523-1787, USA
- ¹⁰Department of Geological Sciences, Southern Methodist University, Dallas, Texas 75275-0395, USA
- ¹¹Department of Anthropology, George Washington University, Washington DC 20052, USA
- ¹²Department of Biological Anthropology and Anatomy, Duke University, Durham, North Carolina 27708-0383, USA
- ¹³Museum National d'Histoire Naturelle, Laboratoire de Paléontologie, 8 rue Buffon, 75005 Paris, France
- ¹⁴Center for Wood Anatomy Research, USDA Forest Service, Forest Products Laboratory, One Gifford Pinchot Drive, Madison, Wisconsin 53705-2398, USA
- ¹⁵Department of Cell Biology, University of Texas Southwestern Medical Center, Dallas, Texas 75390, USA

Afro-Arabian mammalian communities underwent a marked transition near the Oligocene/Miocene boundary at approximately 24 million years (Myr) ago. Although it is well documented that the endemic paenungulate taxa were replaced by migrants from the Northern Hemisphere, the timing and evolutionary dynamics of this transition have long been a mystery because faunas from about 32 to 24 Myr ago are largely unknown¹. Here we report a late Oligocene fossil assemblage from Ethiopia, which constrains the migration to postdate 27 Myr ago, and yields new insight into the indigenous faunal dynamics that preceded this event. The fauna is composed of large paenungulate herbivores and reveals not only which earlier taxa persisted into the late Oligocene epoch but also demonstrates that one group, the Proboscidea, underwent a marked diversification. When Eurasian immigrants entered Afro-Arabia, a pattern of winners and losers among the endemics emerged: less diverse taxa such as arsinotheres became extinct, moderately species-rich groups such as hyracoids continued into the Miocene with reduced diversity, whereas the proboscideans successfully carried their adaptive radiation out of Afro-Arabia and across the world.

The newly discovered fossils are from the Chilga region of Ethiopia's northwestern plateau at an elevation of about 1,950 m (Fig. 1). Sedimentary rocks total at least 130 m and are exposed in a series of stream and gully cuts²⁻⁵. The channel and floodplain deposits include reworked volcanoclastics, common but usually thin lignites², and claystones and siltstones that often represent

palaeosols with varying degrees of maturity. Fossils have been found in each of these settings. Earlier work with a rich pollen assemblage³ suggests that the sediments were deposited at an elevation of about 1,000 m.

The sediments conformably overlie the uppermost Ethiopian plateau flood basalts. A basalt sample from the base of the section (Fig. 2) provides a whole-rock K–Ar date of 32.4 ± 1.6 Myr (see Supplementary Information) and offers a maximum age for the sediments. Duplicate ⁴⁰Ar–³⁹Ar analyses of K-feldspar⁶ from a tuff within the fossiliferous portion of the sedimentary section yield ages with a weighted average of 27.36 ± 0.11 Myr (see Supplementary Information). These data, along with the results from palaeomagnetic studies⁷, support a correlation of the Chilga section with Chron C9n (ref. 8) (see Methods and Fig. 2). Our dates are consistent with new dates for the Ethiopian plateau flood basalts in both Ethiopia⁹⁻¹¹ and Yemen¹². Previous work³ reported that the Chilga sediments were no older than late Miocene in age, but the basalt that was dated by the whole-rock K–Ar technique at 8.0 ± 1.2 Myr is not conformable with the sediments.

There are now over 70 localities at Chilga with vertebrates, invertebrates, plant macrofossils and trace fossils (burrows, termitaria and rhizoliths). Vertebrate remains are usually fragmentary and represent medium- to large-sized herbivores. A possible preservational bias against small mammals may be due to diagenetic leaching of bone before fossilization. Vertebrates and plant macrofossils are often found together, with some leaf impressions preserved in clays that drape fossil vertebrates. Such occurrences are usually rare; the Chilga finds are significant in proving that these plants and animals were contemporaneous. Details of the macroflora will be provided elsewhere.

The Chilga mammals provide evidence for the continued evolution and diversification of some of the most common elements of the endemic Fayumian fauna (Table 1). One of the most distinctive taxa is a new species of *Arsinoitherium* (order Embrithopoda), well known for its distinctive horns and high-crowned molars. This new species (Fig. 3a–c) is the largest yet known of the genus. *Arsinoitherium* is best known from Palaeogene deposits of Egypt, Libya, Oman, and Angola¹³⁻¹⁷ and its occurrence at Chilga is the last

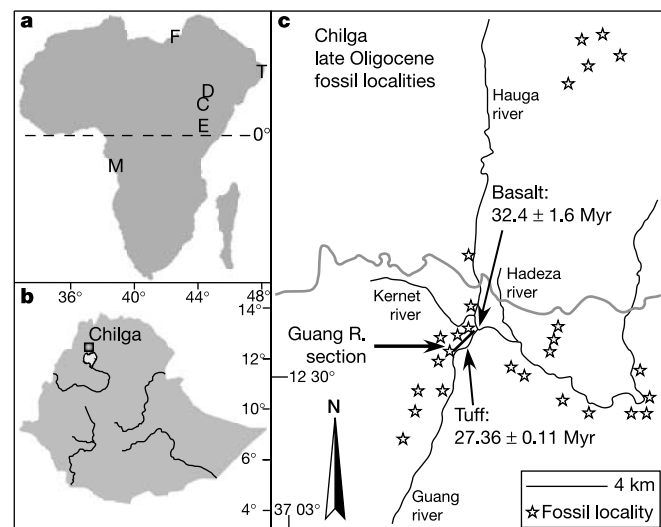


Figure 1 Map of Chilga and surrounding area containing the fossil localities. **a**, Map of Afro-Arabia with several important Palaeogene localities including Chilga (C; Ethiopia), Dogali (D; Eritrea) (ref. 27), Eragaleit (E; Kenya) (ref. 29), Fayum (F; Egypt) (ref. 13), Malembe (M; Angola) (ref. 16) and Thaytini and Taqah (T; Oman) (ref. 17). **b**, Location of Chilga in Ethiopia and north of lake Tana. **c**, Detailed map of the Chilga area showing the fossil localities, geological section (see Fig. 2) and dated rock samples (see Supplementary Information) along the Guang and Hauga rivers.

known for the order Embrithopoda.

Hyracoids are moderately diverse at Chilga and document the continued presence of two well known but conservative Fayumian taxa. *Pachyhyrax crassidentatus* and *Megalohyrax eocaenus* are the most common large hyracoids from the early Oligocene^{18,19}, with the latter first appearing in the late Eocene and changing little over its duration of several Myr. The new Chilga taxa are distinct from these at the specific level, with *Pachyhyrax* sp. nov. being smaller than *P. crassidentatus* and differing from it in its relatively higher, sharper and more delicate crests, whereas *Megalohyrax* sp. nov. (Fig. 3d) is remarkably close in size and structure to *M. eocaenus* but differs in premolar proportions. A third, larger hyracoid at Chilga is a new genus probably related to *Pachyhyrax*, whereas a fourth is closely related to *Bunohyrax*.

The Proboscidea has ancient Afro-Arabian roots^{20,21} and is the most diverse order of mammals at Chilga, represented by three families and five new species. Three of the Chilga proboscideans belong to the Palaeomastodontidae, a primitive family previously known from the late Eocene and early Oligocene of Afro-Arabia²². Two of these new species have close taxonomic ties to the genus *Palaeomastodon*, but are larger than the Fayum *Palaeomastodon* (Fig. 3e, f). The larger has some molar features that anticipate the morphology of the early Miocene mammutid *Eozygodon* (Fig. 3f). A

third new species (Fig. 3g) is closely aligned with the palaeomastodont *Phiomia*; its molars equal or exceed the uppermost size range of Fayum specimens of this genus and it has an outsized mandibular symphysis considerably longer than those of its Fayumian congeners. The Chilga palaeomastodonts represent the youngest-known record for this family.

Chilga also documents the oldest occurrence of deinotheres (Fig. 3h, i). This distinctive family of proboscideans was previously known from the early Miocene through to the early Pleistocene epoch but its origins are poorly understood²³. The new taxon clearly differs from other deinotheres, particularly in the nascent development of a third loph(id) in deciduous fourth premolars and first molars. The occlusal morphology of its cheek teeth suggests independent derivation from a bunolophodont form such as *Moeritherium*^{23,24}, rather than sharing an earlier ancestry with barytheres and numidotheres in the lophodont barytherioid group. The recovery of deinotheres at 27 Myr ago extends the temporal range of this group by 7 Myr.

A third Chilga proboscidean family, Gomphotheriidae, is represented by a rare species with molars closely resembling those of primitive *Gomphotherium* (Fig. 3j), which previously had an earliest appearance of approximately 20–18 Myr ago in Africa and Eurasia^{25–27}. A similarly ancient but undescribed proboscidean with possible affinity to the Chilga gomphotheres is known from Dogali, Eritrea (Fig. 1a)²⁸. The Chilga specimens are among the smallest to be attributed to Elephantoidea and markedly extend the known duration of this family back into the late Oligocene.

The recovery of these fossils from Ethiopia enlarges our understanding of some of the ecological attributes of Afro-Arabia's Oligocene fauna. For example, arsinotheres, hyracoids, and palaeomastodonts are best known from Palaeogene sites in Egypt, Libya, Oman and Angola^{13–17} (Fig. 1), and the shared continental margin setting suggested that their habitat preferences were limited to coastal and estuarine environments. The discovery of these taxa in

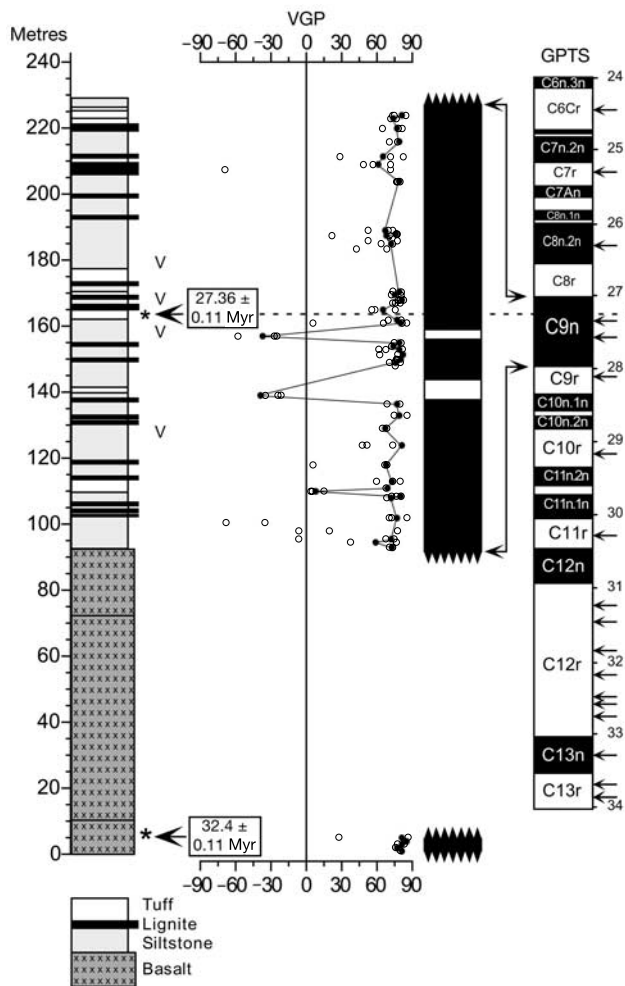


Figure 2 The Chilga section preserves volcanics and fluvial sediments. Vertebrate fossils date to around 27 Myr ago (see Methods for details). Ages along right of the GPTS panel are in Myr. V, vertebrate localities. VGP, virtual geomagnetic pole. White circles, samples; black circles, site means. Black bars, normal polarity; white bars, reversed polarity. Arrows, tiny wiggles.

Table 1 Taxonomy and temporal occurrence of Chilga mammals

Taxonomic group	Fayumian Eocene/Oligocene	Chilga late Oligocene	Rusingan early Miocene
Proboscidea			
Palaeomastodontidae	X	X	–
<i>Palaeomastodon beadnelli</i>	X	–	–
<i>Palaeomastodon parvus</i>	X	–	–
<i>Palaeomastodon intermedius</i>	X	–	–
aff. <i>Palaeomastodon</i> sp. nov. A	–	X	–
aff. <i>Palaeomastodon</i> sp. nov. B	–	X	–
<i>Phiomia wintoni</i>	X	–	–
<i>Phiomia minor</i>	X	–	–
<i>Phiomia osborni</i>	X	–	–
<i>Phiomia</i> sp. nov.	–	X	–
Gomphotheriidae	–	X	X
cf. <i>Gomphotherium</i> sp. nov.	–	X	–
<i>Gomphotherium angustidens</i>	–	–	X
Deinotheriidae	–	X	X
Gen. et sp. nov.	–	X	–
<i>Prodeinotherium hobleji</i>	–	–	X
Hyracoidea			
Saghatheriidae	X	X	–
<i>Pachyhyrax crassidentatus</i>	X	–	–
<i>Pachyhyrax</i> sp. nov.	–	X	–
Gen. et sp. nov., aff. <i>Pachyhyrax</i>	–	X	–
<i>Megalohyrax eocaenus</i>	X	–	–
<i>Megalohyrax</i> sp. nov.	–	X	–
<i>Bunohyrax fajumensis</i>	X	–	–
<i>Bunohyrax major</i>	X	–	–
<i>Bunohyrax</i> sp.	–	X	–
Titanohyracinae*	X	–	X
Embrithopoda			
Arsinotheriidae	X	X	–
<i>Arsinotherium zitteli</i>	X	–	–
<i>Arsinotherium</i> sp. nov.	–	X	–

Taxonomic groups include order (in bold font), family/subfamily, genus and species. X, family or subfamily present; x, genus and species present; –, not present.

*Although this subfamily does not occur at Chilga, titanohyracines are known from either side of the transition but have much reduced diversity in the early Miocene.

the highlands of northwestern Ethiopia instead suggests that they were widespread herbivores in Afro-Arabia, and occupied generalist niches with broad ecological tolerances. This observation is especially interesting in light of their overall low specific diversities.

Before the discovery of the Chilga fauna many aspects of Afro-Arabia's Oligocene/Miocene faunal transition were matters of speculation. It is now clear that the success of the invading northern immigrants was not a consequence of their movement into an

ecological vacuum created by a much earlier extinction of the Afro-Arabian endemics; instead, the new fossils provide evidence that they evolved and diversified through the late Oligocene. Some taxa, such as arsinotheres and hyracoids, continued a conservative evolutionary trajectory with size changes and slight morphological innovation, whereas others, such as the proboscideans, underwent a radiation that resulted in the origin of new families including the gomphotheres and deinotheres. At present, there is no indication

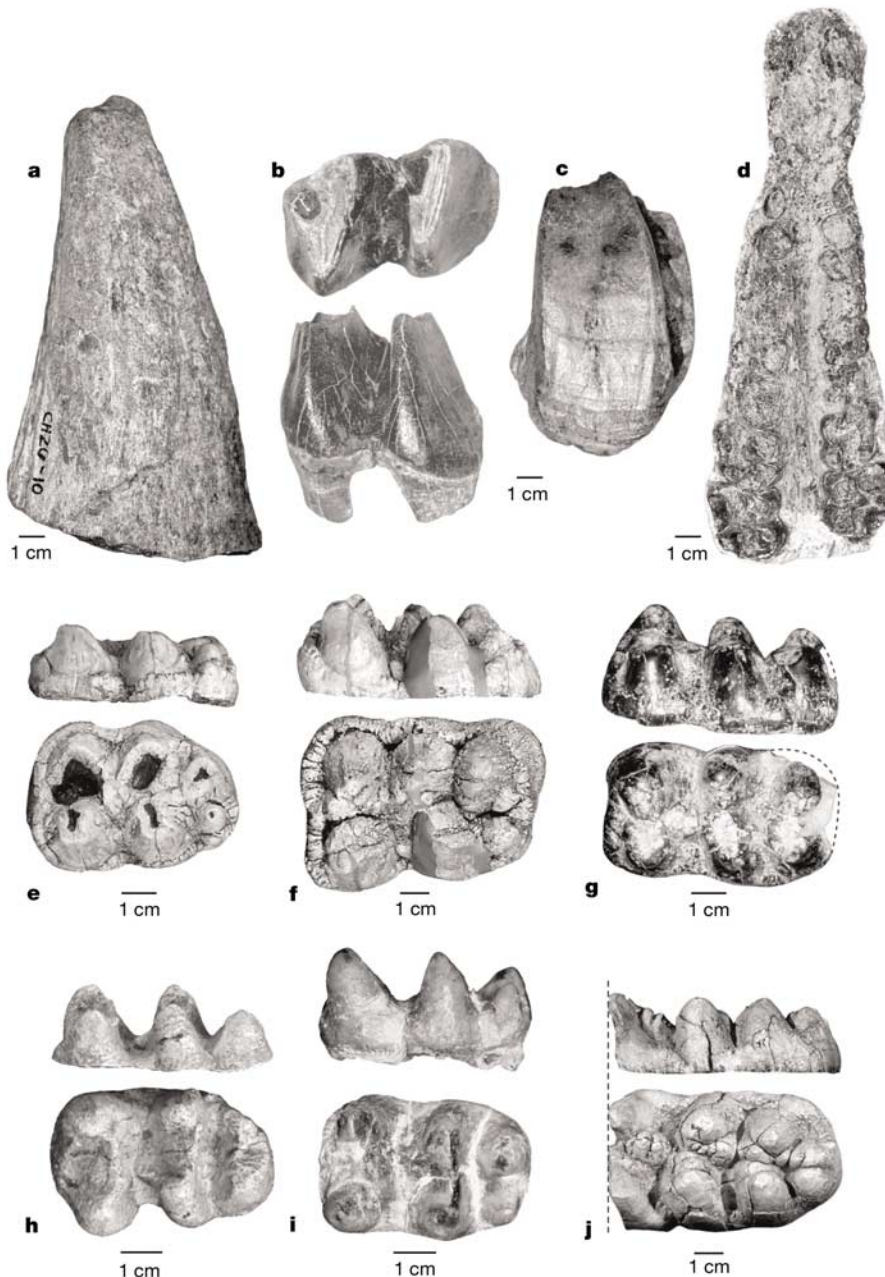


Figure 3 Fossils representing paenungulate taxa from Chilga. **a**, Specimen CH26-10. *Arsinoitherium* sp. nov., partial horn core (left side?), height = 225 mm. **b**, Specimen CH25-17. *Arsinoitherium* sp. nov., lower molar, occlusal and buccal views. **c**, Specimen CH3-95. *Arsinoitherium* sp. nov., upper molar, distal view, height = 131 mm. **d**, Specimen CH18-1. *Megalohyrax* sp. nov., palate, length = 210 mm. **e**, Specimen CH35-23. New species, affinity to *Palaeomastodon* (aff. *Palaeomastodon* sp. nov. A), right third upper molar (M^3), buccal and occlusal views. Note the incomplete trilophodonty of the specimen. **f**, Specimen CH14-11. New species, affinity to *Palaeomastodon* (aff. *Palaeomastodon* sp. nov. B), right M^3 , buccal and occlusal views. Note the incomplete trilophodonty of the specimen and its more rectangular occlusal outline in comparison

with CH35-23. **g**, Specimen CH 9-1. *Phiomia* sp. nov., left M^2 , lingual and occlusal views; portion of posterior end is missing (dotted line). **h**, Specimen CH35-3c. Deinotheriidae gen. et sp. nov., left first lower molar (M_1), buccal and occlusal views. **i**, Specimen CH35-3a. Deinotheriidae gen. et sp. nov., right fourth lower deciduous premolar (DP_4), lingual and occlusal views. **j**, Specimen CH14-14. Cf. *Gomphotherium* sp. nov., right M_3 , lingual and occlusal views; anterior end is missing (dotted line). Note the rounded conelets, transverse continuity of half-lophids, larger posterior 'heel', and trefoil arrangement of outer main conelets and anterior and posterior accessory conules on the pretrite side.

that contact with the invading migrants spurred on any of these changes; rather, fluctuations in environmental conditions possibly drove their continued evolution⁹. The discovery of new fossil localities dating to the Oligocene/Miocene boundary will be required to test the remaining possibility that competitive exclusion between the Afro-Arabian endemics and the invading immigrants was responsible for the extinction of the former. It seems likely that the phyletic conservatism and perhaps generalized habits of many of the endemic taxa greatly limited their ability to compete with the invaders; other endemics such as the proboscideans, which underwent greater diversification and specialization in the Afro-Arabian Oligocene, ended up on the winning side of the equation. □

Methods

Chronology

The Chilga section has more than 90 m of volcanics at its base that are overlain by at least 130 m of fluvial sediments. The basalt at the base of the section is dated at 32.4 ± 1.6 Myr (see Supplementary Information) and provides a maximum age for the section. Studies of the isothermal remanent magnetism⁷ for a suite of siltstones show a dominance of low-coercivity grains indicating magnetite or maghaematite, an expected result given that basalts form the dominant parent material. All sediments show some evidence of intermediate-coercivity grains indicating specular haematite as well as small amounts of high-coercivity grains suggesting pigmentary haematite and goethite, but these are both minor constituents relative to the low-coercivity fraction. Stepwise alternating-field demagnetization was carried out on 118 samples with generally three samples per stratigraphic level. Palaeomagnetic reversal stratigraphy demonstrates a dominance of normal polarity. Duplicate ⁴⁰Ar–³⁹Ar age spectra analyses of K-feldspar each separated from a tuff at 165 m produced a weighted average of 27.36 ± 0.11 Myr (see Supplementary Information) that provides an absolute tie point to Chron C9n ($27.004\text{--}27.946$ Myr). Small arrows to the far right of the geomagnetic polarity timescale (GPTS)⁸ in Fig. 2 represent “tiny wiggles” and the two brief reversals within Chron C9n may be present at Chilga, thereby providing additional but more indirect support for this correlation. Together these data suggest that this section is probably limited to the duration of Chron C9n (<1 Myr). Vertebrate localities occur primarily through the middle part of the section.

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Correspondence and requests for materials should be addressed to J.K. (jkappelman@mail.utexas.edu).

Ocean currents mediate evolution in island lizards

Ryan Calsbeek¹ & Thomas B. Smith^{1,2}

¹Center for Tropical Research, Institute of the Environment, ²Organismic Biology, Ecology and Evolution, University of California, Los Angeles, California 90065, USA

Islands are considered to be natural laboratories in which to examine evolution because of the implicit assumption that limited gene flow allows tests of evolutionary processes in isolated replicates¹. Here we show that this well-accepted idea requires re-examination. Island inundation during hurricanes can have devastating effects on lizard populations in the Bahamas^{2,3}. After severe storms, islands may be recolonized by over-water dispersal of lizards from neighbouring islands³. High levels of gene flow may homogenize genes responsible for divergence, and are widely viewed as a constraining force on evolution^{4,5}. Ultimately, the magnitude of gene flow determines the extent to which populations diverge from one another, and whether or not they eventually form new species^{6,7}. We show that patterns of gene flow among island populations of *Anolis* lizards are best explained by prevailing ocean currents, and that over-water dispersal has evolutionary consequences. Across islands, divergence in fitness-related morphology decreases with increasing gene flow⁵. Results suggest that over-water dispersal after hurricanes constrains adaptive diversification in *Anolis* lizards, and that it may have an important but previously undocumented role in this classical example of adaptive radiation.