Taylor & Francis
Taylor & Francis Group

Ichnos
An International Journal for Plant and Animal Traces

ISSN: 1042-0940 (Print) 1563-5236 (Online) Journal homepage: http://www.tandfonline.com/loi/gich20

The Oldest Beetle and Bee Ichnofossils from Mexico and their Paleoenvironmental Implications

Rosalía Guerrero-Arenas, Eduardo Jiménez-Hidalgo & Jorge F. Genise

To cite this article: Rosalía Guerrero-Arenas, Eduardo Jiménez-Hidalgo & Jorge F. Genise (2017): The Oldest Beetle and Bee Ichnofossils from Mexico and their Paleoenvironmental Implications, Ichnos, DOI: 10.1080/10420940.2017.1386184

To link to this article: https://doi.org/10.1080/10420940.2017.1386184

ICHNOS
https://doi.org/10.1080/10420940.2017.1386184

The Oldest Beetle and Bee Ichnofossils from Mexico and their Paleoenvironmental Implications

Rosalía Guerrero-Arenas[a], Eduardo Jiménez-Hidalgo[a], and Jorge F. Genise[b]

[a]Laboratorio de Paleobiología, Campus Puerto Escondido, Universidad del Mar, Oaxaca, Mexico; [b]CONICET, División Icnología, Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina

ABSTRACT

Specimens of *Fictovichnus gobiensis, Celliforma curvata, Celliforma rosellii, Celliforma germanica* and *Celliforma* isp. were collected from paleosol horizons in a fluviolacustrine succession near Santiago Yolomécatl town, in northwestern Oaxaca, southern Mexico. These ichnofossils represent the oldest evidence of beetles and bees in Mexican localities. K–Ar ages and the record of the equid *Miohippus assiniboiensis*, an index fossil, indicate that the age of the deposits is late Eocene. Based on the presence of the insect ichnofossils, pedogenic carbonate isotopes and mammal proxies, the inferred type of vegetation present in the study area was scrubland/woodland, within subhumid to subarid conditions.

KEYWORDS

Eocene; Oaxaca; *Fictovichnus gobiensis*; *Celliforma* ispp.; *Celliforma Ichnofacies*

Introduction

There are significant gaps in the insect fossil record in tropical North America. Within the Mexican territory, Coleoptera and Hymenoptera are two widely distributed taxa nowadays; however, their evolutionary history is poorly known because of their scarce body fossil record and scantly studied continental formations.

The main reason of the scarce record is that insects lack mineralized tissue and their preservation usually requires extraordinary circumstances (Karr and Clapham 2015); also, there are many unexplored continental areas in Mexican territory. Fortunately, ichnofossils produced by insects can compensate the scarcity or absence of body fossils of a particular taxon, contributing to our knowledge of its evolutionary history.

The objectives of this contribution are as follows: 1) to report the oldest record of bees and beetles from Mexico for the late Eocene evinced by the presence of pupation chambers of beetles and bee cells from deposits of Oaxaca, southern Mexico, 2) to discuss the implications of this evidence for the Mexican insect fossil record, and 3) to preliminarily propose paleoenvironmental conditions of these ichnofossiliferous beds.

Geological setting

The study zone is located within the municipality of Santiago Yolomécatl, in the Tlaxiaco Basin, northwestern Oaxaca, southern Mexico. The region is included in the Sierra Madre del Sur physiographic province (Ortiz-Pérez, Hernández-Santana, and Figueroa Mah-Eng 2004).

The specimens have been collected in ichnofossiliferous beds of the Yolomécatl unit, a fluviolacustrine succession with several paleosol horizons. The lower part of the Yolomécatl unit consists of partially silicified limestone, which changes upward to a succession of about 200 m in thickness of thinly-to-thickly bedded mudstones with occasional coarse lenses and some beds of volcanic and limestone pebble, cobble and boulder conglomerate. Thinly bedded chert layers are also intercalated with the fine-grained strata (Jiménez-Hidalgo et al. 2015).

Many vertebrate fossils have been recovered from these beds. The assemblage was described as the Iniyoo Local Fauna (Jiménez-Hidalgo et al. 2015), which includes turtles, lizards, caniforms, rodents, perissodactyls and several artiodactyls. The age of the faunal assemblage is middle-late Chadronian North American Land Mammal Age (35–33.9 Ma) because of the presence of the equid *Miohippus assiniboiensis*. This index equid species has been recorded in Saskatchewan, Wyoming and North and South Dakota (Prothero and Shubin 1989). The mammal age agrees with the radiometric dates of 32.9 ± 0.9 Ma and 35.7 ± 1.0 Ma, from the concordantly overlying Cañada María Andesite (Martini et al. 2000; Santamaría-Díaz, Alaniz-Alvarez, and Nieto-Samaniego 2008). Thus, the minimum age of the ichnofossiliferous beds is late Eocene (Jiménez-Hidalgo et al. 2015).

CONTACT Rosalía Guerrero-Arenas rosaliaga@zicatela.umar.mx Universidad del Mar, Campus Puerto Escondido, Km. 2.5 Carretera Sola de Vega-Puerto Escondido, San Pedro Mixtepec, C.P. 71980, Oaxaca, Mexico.

Besides vertebrate specimens, several insect ichnofossils were discovered in the study area. Secondary components in Yolomécatl paleosols are rizoliths and large vertebrate burrows of geomyid rodents.

One hundred and three specimens were collected in eight different paleosols from three localities. Many ichnofossils were detached from the rock matrix on the floor of the outcrops, and several were found *in situ*.

All the specimens were measured with a digital Vernier caliper for submillimetre precision. Specimens are housed in the Colección de Icnología, Laboratorio de Paleobiología, Universidad del Mar, campus Puerto Escondido, under the acronym UMPLIC-.

Systematic ichnology

Ichnofamily Celliformidae Genise, 2000
Ichnogenus *Celliformа* Brown, 1934
Celliformа curvata Sarzetti et al. 2014

Material: UMPLIC-002, −003, −087, −088, −111, −114, and −115.

Description: Seven specimens were identified as *C. curvata* (Fig. 2). They are internal moulds of vertical cells showing rounded bottoms and a curved neck. The specimens range from 0.89 cm to 3.11 cm in height, the neck diameter ranges from 0.29 cm to 1.18 cm, and the maximum diameter from 0.54 cm to 1.44 cm.

Comments: Curved cells are attributable to Diphaglossinae bees (Sarzetti et al. 2013).

Celliformа germanica Brown, 1935

Material: UMPLIC-057 and −070.

Description: Height of the specimens ranges from 1.22 cm to 1.28 cm and the maximum diameter from 0.61 cm to 0.72 cm. The specimens show a short neck (Fig. 1I).

Celliformа rosellii Genise and Bown, 1994

Material: UMPLIC-085.

Description: Internal mould of a stout cell with a cylindrical shape and rounded bottom and a flat top, with a rind. Its height is 3.1 cm and its maximum diameter is 1.59 cm (Fig. 1H).

Celliformа ispp.

Material: UMPLIC-031 and −082.

Description: Two specimens with a capsule shape are identified as *Celliformа* ispp. (Figs. 1J and K) because the lack of diagnostic features. The height of these specimens ranges from 1.54 cm to 2.14 cm and the maximum diameter from 0.73 cm to 0.86 cm.

Ichnofamily Pallichnidae Genise 2004
Ichnogenus *Fictovichnus* Johnston et al. 1996
Fictovichnus gobiensis Johnston, Eberth and Anderson 1996

Material: UMPLIC-007 to −030; UMPLIC-032 to −052; UMPLIC-055 and −056; UMPLIC-058 to −069; UMPLIC-071 to −081; UMPLIC-083 and −084; UMPLIC-090 to −095; UMPLIC-097 to −101; UMPLIC-103 to −107; UMPLIC-110; UMPLIC-117 to −119.

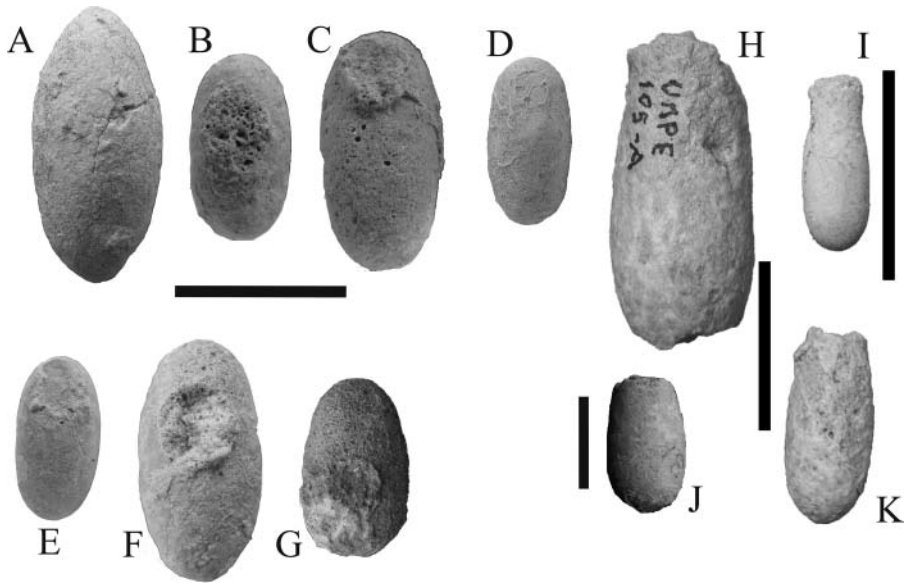

Figure 1. *Fictovichnus gobiensis* (A–G). A, UMPLIC-052. B, UMPIC-008. C, UMPLIC-017. D, UMPLIC-010. E, UMPLIC-18. F, UMPLIC-007. G, UMPLIC-144. Scale: 2 cm. *Celliformа* ispp. (H–K). H, *Celliformа rosellii* (UMPLIC-085). I, *Celliformа germanica* (UMPLIC-057). J, *Celliformа* isp. (UMPLIC-031) and K, *Celliformа* isp. (UMPLIC-082). Scales: 2 cm, except in J and K that is 1 cm.

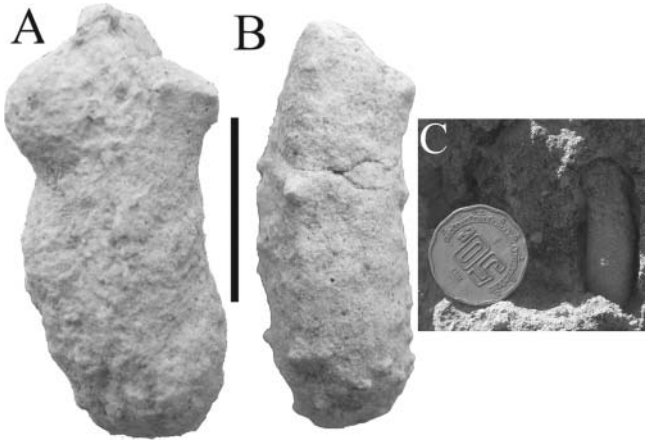

Figure 2. *Celliforma curvata*. A, UMPLIC-088. B, UMPLIC-087. Scale: 2 cm. C, Specimen *in situ*, diameter of the coin is 2.2 cm.

Description: 91 specimens. All are ellipsoid internal casts. The majority with rounded extremes and smooth surface; some specimens show pointed extremes (Fig. 1A). The exit hole appears subequatorial in the majority of the specimens (Figs. 1B, C and F). They range in length from 1.44 cm to 2.97 cm and in maximum diameter from 0.65 cm to 1.34 cm.

Comments: *F. gobiensis* is interpreted as a coleopteran pupation chamber (Johnston et al. 1996; Genise et al. 2007). Johnston et al. (1996) proposed Scarabaeidae, Curculionidae and Tenebrionidae as potential producers. Recently, Alonso-Zarza et al. (2014) modified the original description from Johnston et al. (1996) with the purpose to ease the identification for the ichnospecies.

Discussion

Implications in the Mexican fossil record

Fictovichnus and *Celliforma* collected from Yolomécatl beds are the oldest insect ichnofossils formally reported from Mexico. Previous reports of beetle and bee ichnofossils from the Mexican territory are doubtful or incomplete.

Buck, Lawton, and Brock (2010) mentioned the presence of *Ancorichnus*, a horizontal burrow with distinct walls and discrete backfilled menisci, from the Paleogene Carroza Formation, in La Popa Basin, northeastern Mexico. They mentioned that *Ancorichnus* could be interpreted as the result of a beetle burrowing in upper vadose zone while feeding on organic debris. However, these meniscate burrows can be produced by different organisms in paleosols and *Ancorichnus* is almost exclusive of marine environments (Smith et al. 2008; Bradshaw 2010; Desay and Saklani 2014). Consequently, *Ancorichnus* cannot be considered an indisputable evidence for the presence of beetles in the Carroza Formation.

The only brief report of beetle ichnofossils in Mexico are represented by specimens from Pliocene beds of Jalisco. Morón (2004) named these samples as dung beetle "*bolas-nido*." Considering the original photos, we identified them as *Coprinisphaera* isp.

Regarding *Celliforma*, a dubious record of this ichnogenus was reported by Gardner (1945) in marine Cenozoic deposits of the Gulf of Mexico region. The original figure does not support key features such as spiral closure and shape.

Specimens of *Fictovichnus* and *Celliforma* from Yolomécatl beds represent the oldest ichnofossils attributable to beetles and bees in Mexico, from the late Eocene.

Body fossils of beetles and bees are present in younger formations. The oldest record of beetles in Mexico is represented by remains of an incomplete and unidentified beetle specimen from the Oligocene Coatzingo Formation of Puebla, central Mexico (Cifuentes-Ruiz et al. 2007). *Fictovichnus* specimens from Oaxaca are at least 1.0 Ma older than the body fossil remains of Puebla. Other well-identified and younger beetle specimens (e.g. Erwin 1971; Solórzano-Kraemer 2006) were collected from the early Miocene La Quinta Formation (Calvillo-Canadell et al. 2010).

Specimens of *Celliforma* from Yolomécatl are important because of the lack of records of bee body fossils in Mexico during the Paleogene. The previously known Mexican bee fossil record is younger. It is represented by the Simojovel amber specimens, from Chiapas, southern Mexico, collected from the early Miocene La Quinta Formation (e.g. Engel 2014). The Oaxacan reported *Celliforma* isp. specimens are at least 10 Ma older. The records of *C. curvata* from Yolomécatl represent the earliest evidence of Diphaglossinae (Colletidae) in Mexico. That subfamily is still present along Mexican territory (e.g. Ayala and Engel 2014). Diphaglossinae were widespread from early Eocene to middle Miocene, ranging from southern Utah to extra-Andean Patagonia at 42°S (Sarzetti et al. 2013). The specimens of *C. curvata* in Yolomécatl are in concordance with these previous records.

Paleoenvironmental implications

The Yolomécatl assemblage can be included in the *Celliforma Ichnofacies*, which is represented by associations of insect trace fossils produced by beetles, bees and wasps, such as *Celliforma, Fictovichnus* and *Rebuffoichnus* ichnospecies (Genise et al. 2010). The *Celliforma Ichnofacies* is typical of carbonate-rich paleosols from semiarid to subhumid environments and reflects palustrine, scrubland or dry woodland conditions (Genise et al. 2010). According to the scale of field acid reaction to approximate carbonate content (Retallack 1988), the paleosols of Yolomécatl are very strongly calcareous.

Isotopic values of pedogenic carbonates (range of −8.0‰ to −8.9‰ δ $C13_{PDB}$) from four of the ichnofossiliferous

paleosol horizons indicate open shrubland or woodland vegetation (Wynn 2000; Sikes and Ashley 2007). Several mammalian species of the Iniyoo Local Fauna provide further clues about environmental conditions in Yolomécatl deposits: cursoriality in *Miohippus* is evidence for open vegetation (Retallack 2004), *Trigonias* has been reported close to river habitats (Clark, Beerbower, and Kietze 1967), but recently, Zanazzi and Kohn (2008) suggested that this genus inhabited open plains; *Merycoidodon* has been reported in riparian forests to open plains (Lander 1998) and woodlands (Zanazzi and Kohn 2008) and *Poebrotherium* inhabited open plains (Janis 1982; Zanazzi and Kohn 2008).

Isotopic values suggest a type of vegetation consisting of small- to medium-height wooded vegetation (Wynn 2000); mammalian species and ichnofossil association additionally suggest the presence of open habitats with poor or scanty herbaceous coverage.

Conclusions

1) *F. gobiensis, C. rosellii, C. germanica, C. curvata* and *C.* ispp. are present in the Late Eocene beds of the Yolomécatl Formation, in southern Mexico.
2) These records represent the oldest evidence of bees and beetles for Mexico and the first mention of the *C. Ichnofacies*.
3) Vegetation type inferred from ichnofossils, along with isotopic values of pedogenic carbonates of the study area and the mammalian fauna suggest scrubland/woodland paleoenvironments.

Acknowledgments

We would like to thank academic and administrative teams of Universidad del Mar for logistical support during fieldtrips. We thank K.T. Smith, A. Merlin, K. Ayala, J. Priego, S. Jarquin and M.P. Cruz Olmedo, for their assistance during fieldtrips. Thanks to Tamás Mikes, Andreas Mulch and K.T. Smith for isotopic analyses on paleosol samples. We thank M.A. Morón-Ríos for providing literature. We appreciate the kind help of municipal representatives of Santiago Yolomécatl, especially Yolanda Reyes García. G. Ruelas-Inzunza is thanked for the revision of the written English. We thank two anonymous reviewers for their comments.

Funding

This project was partially funded by Conacyt CB-2008-01, No. 101626 and Conacyt CB-2015, No. 255883.

References

Alonso-Zarza, A. M., J .F. Genise, and M. Verde 2014. Paleoenvironmets and ichnotaxonomy of insect trace fossils in continental mudflat deposits of the Miocene Calatayud-Daroca Basin, Zaragoza, Spain. *Palaeography, Palaeoclimatology, Palaeoecology* 414:342–351.

Ayala, R., and M. S. Engel 2014. A new species of *Ptiloglossa* from Mexico, with new records of *Ptiloglossa cyaniventris* from Panama and Costa Rica (Hymenoptera: Colletidae). *Journal of Melittology* 35:1–13.

Bradshaw, M. A. 2010. Devonian trace fossils of the Horlick Formation, Ohio Range, Antarctica: Systematic description and palaeoenvironmental interpretation. *Ichnos* 17:58–114.

Buck, B. J., T. F. Lawton, and A. L. Brock. 2010. Evaporitic paleosols in continental strata of the Carroza Formation, La Popa Basin, Mexico: Record of Paleogene climate and salt tectonics. *Geological Society of America Bulletin* 122:1011–26.

Calvillo-Canadell, L., S. R. S. Cevallos-Ferriz, and L. Rico-Arce. 2010. Miocene Hymenaea flowers preserved in amber from Simojovel de Allende, Chiapas, Mexico. *Review of Palaeobotany and Palynology* 160:126–34.

Cifuentes-Ruiz, P., F. J. Vega, S. R. S. Cevallos-Ferriz, E. González-Soriano, S. Zaragoza-Caballero, and L. Garibayromero. 2007. Oligocene Scorpion and insects (Plecoptera and Coleoptera) from the Los Ahuehuetes Locality, Puebla, Mexico. *Ameghiniana* 44:673–9.

Clark, J., J. R. Beerbower, and K. K. Kietze. 1967. Oligocene sedimentation, stratigraphy, palaeoecology, and paleoclimatology in the Big Badlands of South Dakota. *Fieldana Geology Memoirs* 5:1–158.

Desay, B. G., and R. D. Saklani. 2014. Ichnofabric analysis of the Tithonian shallow marine sediments (Bhadasar Formation) Jaisalmer, Basin, India. *Journal of Earth System Science* 123:1413–31.

Engel, M. S. 2014. An orchid bee of the genus *Eulaema* in Early Miocene Mexican amber (Hymenoptera: Apidae). *Novitates Paleoentomologicae* 7:1–15.

Erwin, T. L. 1971. Fossil Tachyne beetles from Mexican and Baltic Amber with notes on a new synonymy of an extant group (Col, Carabidae). *Entomologica Scandinavica* 2:233–6.

Gardner, J. 1945. Mollusca of the tertiary formations of Northeastern Mexico. *Geological Society of America Memoir* 11:1–332.

Genise, J. F., R. Melchor, E. S. Belosi, M. González, and M. Krause. 2007. New insect pupation chambers (Pupichnia) from the Late Cretaceous of Patagonia (Argentina). *Cretaceous Research* 28:545–59.

Genise, J. F., R. Melchor, E. S. Bellosi, and M. Verde. 2010. Invertebrate and vertebrate trace fossils in carbonates. In *Carbonates in continental settings. Developments in sedimentology*, eds. A. M. Alonso-Zarza, and L. Tanner, vol. 61, 319–69. Amsterdam: Elsevier.

Janis, C. M. 1982. Evolution of horns in ungulates: Ecology and palaeoecology. *Biology Reviews* 57:261–318.

Jiménez-Hidalgo, E., K. T. Smith, R. Guerrero-Arenas, and J. Alvarado-Ortega. 2015. The first Late Eocene continental faunal assemblage from tropical North America. *Journal of South America Earth Sciences* 57:39–48.

Johnston, P. A., D. A. Eberth, and P. K. Anderson. 1996. Alleged vertebrate eggs from Upper Cretaceous redbeds, Gobi Desert, are fossil insect (Coleoptera) pupal chambers: *Fictovichnus* new ichnogenus. *Canada Journal of Earth Sciences* 33:511–25.

Karr, J. A., and M. E. Clapham. 2015. Taphonomic biases in the insect fossil record: Shifts in articularion over geologic time. *Paleobiology* 41:16–32.

Lander, B. 1998. Oreodontoidea. In *Evolution of tertiary mammals of North America. terrestrial carnivores, ungulates, and ungulate like mammals*, eds. C. M. Janis, K. M. Scott, and L. L. Jacobs, vol. 1, 402–25. United Kingdom: Cambridge University Press.

Martini, B., R. G. Martínez-Serrano, D. J. Morán-Zenteno, C. Macías-Romo, and R. A. Ayuso. 2000. Stratigraphy, geochemistry and tectonic significance of the Oligocene magmatic rocks of western Oaxaca, southern Mexico. *Tectonophysics* 318:71–98.

Morón, M. A. 2004. *Escarabajos. 200 millones de años de evolución*, 204. Zaragoza, España: Instituto de Ecología A. C.- Sociedad Entomológica Aragonesa.

Ortiz-Pérez, M. A., J. R. Hernández-Santana, and J. M. Figueroa Mah-Eng. 2004. Reconocimiento fisiográfico y geomorfológico. In *Biodiversidad en Oaxaca*, eds. A. J. García-Mendoza, M. J. Ordoñez, and M. Briones-Salas, 43–54. México: Instituto de Biología, UNAM-Fondo Oaxaqueño para la Conservación de la Naturaleza-World Wildlife Foundation.

Prothero, D. R., and N. Shubin. 1989. The evolution of Oligocene horses. In The evolution of Perissodactyls, eds. D. Prothero, and R. M. Schoch, 142–75. New York: Oxford University Press.

Retallack, G. J. 1988. Field recognition of paleosols. In *Paleosols, their recognition and interpretation*, ed. P. V. Wright, 1–57. Oxford: Blackwell.

Retallack, G. J. 2004. Late Oligocene bunch grassland and early Miocene sod grassland paleosols from central Oregon, USA. *Palaeogeography, Palaeoclimatology, Palaeoecology* 207:203–47

Santamaría-Díaz, A., S. A. Alaniz-Alvarez, and A. F. Nieto-Samaniego. 2008. Deformaciones cenozoicas en la cobertura de la falla Caltepec en la región de Tamazulapam, sur de México. *Revista Mexicana de Ciencias Geológicas* 25:494–516.

Sarzetti, L. C., P. A. Dinghi, J. F. Genise, E. Bedatou, and M. Verde. 2013. Curved fossil bee cells as tools for reconstructing the evolutionary history and palaeogeographical distribution of Diphaglossinae (Apoidea, Colletidae). *Palaeontology* 57:1–9.

Sikes, N. E., and G. M. Ashley. 2007. Stable isotopes of pedogenetic carbonates as indicators of palaeoecology in the Plio-Pleistocene (Upper Bed I), western margin of the Olduvai Basin, Tanzania. *Journal of Human Evolution* 53:574–94.

Smith, J. J., S. T. Hasiotis, M. J. Kraus, and D. T. Woody. 2008. *Naktodemasis bowni*: New ichnogenus and ichnospecies for adhesive meniscate burrows (AMB), and paleoenvironmental implications, Paleogene Willwood Formation, Bighorn Basin, Wyoming. *Journal of Paleontology* 82:267–78.

Solórzano-Kraemer, M. M. 2006. The first fossil Paussine (Coleoptera: Carabidae) from Mexican amber. *Paläontologische Zeitschrift* 80:107–11.

Wynn, J. G. 2000. Paleosols, stable carbon isotopes, and paleoenvironmental interpretation of Kanapoli northern Kenya. *Journal of Human Evolution* 39:411–32.

Zanazzi, A., and M. J. Kohn. 2008. Ecology and physiology of White River mammals based on stable isotope ratios of teeth. *Palaeogeography, Palaeoclimatology, Palaeoecology* 257:22–37.