The family Chalicotheriidae, a group of rare, clawed perissodactyls, had a geographic distribution that spanned North America (Oligocene–Miocene), Eurasia (Oligocene–Pleistocene), and Africa (Miocene–Pliocene), with the greatest taxonomic diversity reported from Eurasia (Coombs, 1989). The two included subfamilies, Schizotheriinae and Chalicotheriinae, are distinguished primarily by postcanial differences, but in terms of dental morphology, Coombs (1978a) diagnosed Schizotheriinae as exhibiting relatively higher crowned, anteroposteriorly elongate molars and consistently separated metaconids and metastylids (i.e., twinned metaconids) on lower molars. Only schizotherine chalicotheres are known to have reached North America, first appearing sometime during the Arikareean North American Land Mammal Age (NALMA; Coombs et al., 2001), potentially as early as the latest Oligocene (Coombs, 1978a, 1998; Albright et al., 2008). Here, we report an isolated lower molar of a chalicotherium from the early Miocene of the Panama Canal Basin in southern Central America. Discovery of this specimen in Panama extends the geographic range of New World chalicotheres south by nearly 2000 km and 20° latitude and, with comparisons with other North American chalicotheres, suggests an undetermined diversity of small-bodied chalicotheres in subtropical and tropical regions during the early Miocene.

Abbreviations—APL, anteroposterior length; Mi, Miocene isotopic event; Oi, Oligocene isotopic event; TW, transverse width; UF, Vertebrate Paleontology Collection, Florida Museum of Natural History, University of Florida, Gainesville, Florida, U.S.A.

GEOLOGIC, BIOSTRATIGRAPHIC, AND GEOCHRONOLOGICAL CONTEXT

The Panama chalicotherium was discovered in the Lirio Norte region of the Gaillard (Culebra) Cut of the Panama Canal (Fig. 1) preserved within the early Miocene Las Cascadas Formation, a sequence of volcanic agglomerates, lapilli tuffs, and tuffaceous sedimentary rocks (Montes et al., 2012). The upper Las Cascadas Formation provides definitive evidence for the earliest terrestrial paleoenvironments in the Panama Canal Basin, including fluvially deposited lenticular conglomerates and sandstones (Montes et al., 2012; Rincón et al., 2012), subaerially exposed volcanioclastics (Kirby et al., 2008), and in situ root structures. The chalicotherium tooth was found as float near the contact of a lapilli tuff and an overlying subaerially exposed red ash with centimeter-scale volcanic lithic fragments.

Recently described species of floridatraguline camels and a bovidodontine thoracothere found in association with protoceratids, equids, and amphiiconids in the upper Las Cascadas Formation indicates the presence of a late Arikareean mammalian assemblage with North American affinities (Rincón et al., 2012, 2013). Geochronological analyses of the overlying Culebra Formation (Kirby et al., 2008; Montes et al., 2012) and underlying Bas Obispo Formation (Rooney et al., 2010) constrain the age of the Las Cascadas mammalian assemblage to the latest Oligocene to earliest Miocene (~25–19 Ma). The fossiliferous horizons, however, are restricted to the uppermost Las Cascadas Formation, suggesting that the mammalian assemblage likely existed during the younger end of this age range.

DESCRIPTION AND COMPARATIVE MORPHOLOGY

The tooth, UF 280165, is a relatively unworn, partial right lower molar discovered in two pieces as float. The anterolingual portion of the trigonid, including the paraconid and part of the paralophid, is broken and missing as is the apex of the entoconid. No roots are preserved on the specimen. The estimated APL, measured from the anterior-most preserved portion of the anterior cingulid to the posterior-most portion of the complete posterior cingulid, is 22.5 mm, whereas the measured TW is 11.4 mm.

The tooth is similar in size and crown height to anchitherium horses, particularly Anchitherium clarencei, a taxon found in the stratigraphically younger Centenario Fauna (MacFadden, 2009; MacFadden et al., 2014), yet exhibits features distinguishing it as a chalicotherium: relatively broader trigonid and talonid basins, an anteroposteriorly oriented metaconid-metastylid complex (Fig. 2B), and discontinuous buccal cingulids separated into anterobuccal, buccal, and posterior regions (Fig. 2C, D). UF 280165 also lacks a hypoconulid and exhibits shallow vertical incisures on the posteroemedial surfaces of the protoconid and hypolophid (Fig. 2C). The lingually oriented metaconid clearly distinguishes UF 280165 from rhinocerotoids and tapiroids.

UF 280165 is molariform with a high length-to-width ratio and could potentially represent either a dp4 or any of the permanent lower molar positions. Coombs (1978a) described the dp4 of Moropus elatus as having a trigonid slightly smaller than the talonid. No differences in the relative trigonid and talonid proportions relative to M. elatus were reported in the dp4 of Tylocephalonyx skinneri (Coombs, 1979) or in the Aquitanian species of Moropus from France (Coombs, 1974). The widths of the trigonid and talonid in UF 280165, measured as the TW between the bases of the protoconid/metaconid and entoconid/metastylid, respectively, are equal at 11.4 mm. The estimated length of the trigonid, measured either by doubling the APL between the protoconid and metaconid (6.3 mm) or measuring
from the anterior-most edge of the anterior cingulid to the metaconid (7.5 mm), is considerably less than the APL of the talonid (12.7 mm). The m3 of Moropus elatus, M. merriami, and Tylocephalonyx skinneri all exhibit posteriorly displaced hypoconids and entoconids and disproportionately longer metalophids relative to the hypolophids (Coombs, 1978a, 1979, 2004). The metalophid and hypolophid lengths of UF 280165 are comparable at 10.2 and 9.5 mm, respectively. Based on these proportions, UF 280165 most likely represents an m1 or m2.

Upon considering UF 280165 as an m1 or m2, it is similar in size to the smallest chalicotheriid from the Oligocene and Miocene (Table 1), more specifically Butleria rusingense, Chalicotherium salinum, Schizotherium avitum, and S. priscum. Coombs et al. (2001) referred isolated chalicotherium lower molars from the late Arikareean Toledo Bend Local Fauna (Albright, 1999) and a chalicotherium mandible (UF cast 180233) from the St. Mark’s River in Florida to Moropus oregonensis. These specimens from the Gulf Coast are also similar in size to UF 280165.

Chavasseau et al. (2010) and Liu and Zhang (2012) used lower molar width-to-length ratios to identify chalicotherium mandibular fragments without associated upper dentitions or postcrania to the subfamily level. Their use of this metric was based on the observations by previous authors that schizotherine chalicotheres typically have more elongate lower molars relative to chalicotherines (e.g., Coombs, 1989, 2009; Anquetin et al., 2007). Ratios of width to length for the m1 and m2 positions within Chalicotheriinae range from 0.56 to 0.64 and 0.52 to 0.66, respectively, whereas these ratios within Schizotheriinae range from 0.50 to 0.68 and 0.50 to 0.58. The ranges reported here are based on data from Liu and Zhang (2012), available in the online supplemental data. The width-to-length ratio exhibited by UF 280165 (0.51) falls below the range expected for chalicotherines, suggesting that the specimen from Panama is a schizotherine chalicotherium like all other known North American chalicotheres. This subfamily identification for UF 280165 is highly tentative given the large overlap in ratios for the two subfamilies.

UF 280165 lacks a well-developed metastylid on the posterior surface of the metaconid as is typically seen in the lower molars of schizotherine chalicotheres. Two small cuspsids are present instead, separated from each other and the metaconid by short lingual fissures that would not be apparent after moderate dental wear (Fig. 2A, E). The metalophid ends lingually between these two small cuspsids, whereas the metacristid is confluent with the posterior cuspid (Fig. 2B). The lophids of UF 280165 are slightly curved, similar to the condition exhibited in species of Moropus.

The morphology of the metaconid region and lophids of UF 280165 distinguishes it from other North American species of schizotherine chalicotheres. Moropus elatus and M. merriami each exhibit strongly developed metastylids on the dp4 and all lower molars (Coombs, 1978a, 2004). Similarly, the metastylid of UF 280165 is highly tentative given the large overlap in ratios for the two subfamilies.
and metaconid are clearly separated in the unworn m3 of *M. cf. oregonensis* from the Toledo Bend Local Fauna (Albright, 1999). Although well preserved, the lower dentition of the St. Mark’s River *M. cf. oregonensis* is in a private collection and will not be discussed further. In *Tylcephalonyx skinneri*, the metastylid of the m1 is lower and barely distinct from the metaconid (Coombs, 1979), but the lophids in *T. skinneri* are distinctively curved in contrast to the slightly curved lophids of UF 280165. Weak metastylid development or variability in metastylid development on lower molars has been reported in species of *Schizotherium* (Coombs, 1978b), *Butleria rusingese* (Butler, 1965), and in Miocene schizotheriines and chalicotheriines from Eurasia and Africa, including *Metaschizotherium bavaricum* (Coombs, 2009), *Anisodon* (Aquetin et al., 2007; Chavasseau et al., 2010; Fahlke et al., 2013), *Chalicotherium* (Coombs, 1989; Khan et al., 2009; Chavasseau et al., 2010; Fahlke et al., 2013), and *Anyclyotherium cheboitense* (Guérin and Pickford, 2005). The condition of having paired cusps posterior to the metaconid, however, has not been described in any of these taxa.

**DISCUSSION**

UF 280165 may represent a new small-bodied genus of schizotheriine endemic to tropical Central America during the late Arikareean. The Panamanian chalicothere lacks a well-developed metastylid and highly curved lophids and consequently cannot be assigned to either of the two known schizotherine genera (*i.e.*, *Moropus* and *Tylcephalonyx*) from North America as they are currently defined. Discovery of chalicotheriote postcrania in the Las Cascadas Formation will be integral to understanding the taxonomy of this species, because many diagnostic features of both schizotherine and chalicotherine taxa are restricted to the postcranial skeleton.

Coombs et al. (2001) hypothesized that the small body sizes of *Moropus oregonensis* from the John Day Formation and the Gulf Coast *M. cf. oregonensis* reflect the primitive condition exhibited by the first immigrant *Moropus* from Eurasia. Furthermore, small body size and weakly or variably developed metastylids are characters of *Butleria*, the basal-most genus within Chalicotheriinae (Anquetin et al., 2007), and *Schizotherium*, the oldest schizotheriine genus (Coombs, 1978b). These characters in UF 280165 suggest that the Las Cascadas chalicothere represents one of the most primitive chalicothereids in the western hemisphere, maintaining the lower dental morphology exhibited by the first chalicothere immigrants.

Hunt (2004) hypothesized that first appearances of Eurasian mammals in North America during the late Arikareean were associated with glacioeustatic sea-level changes and opening of Beringian dispersal routes. The earliest, well-documented occurrences of North American chalicotheres (*i.e.*, *Moropus oregonensis*) are from the Kimberly Member (lithostratigraphic unit M) of the John Day Formation in Oregon (Coombs et al., 2001; Albright et al., 2008). Albright et al. (2008) correlated lithostratigraphic unit M to magnetochrons C7r and C7n, establishing a minimum age of 24.9 Ma for the first chalicothere immigrants. The chron C7 correlation of Albright et al. (2008) and the minimum age of chalicothere immigration to North America are coincident with the 25.2–24.8 Ma Oi2c δ18O event (Miller et al., 1998; Pekar et al., 2006) and concurrent drop in global sea levels (~20 m below modern sea level; Miller et al., 2005; Komizn et al., 2008). This evidence suggests that the first appearance of primitive, small-bodied chalicothereids in North America can be linked to a specific global paleoclimate event (*i.e.*, the Oi2e Antarctic ice sheet expansion/sea-level lowstand) with some confidence.

As noted above, the age of the Las Cascadas Formation is constrained to roughly 25–19 Ma, spanning the Oligocene–Miocene
boundary and several of the Oi2 and Mi1 δ18O glaciation events and related sea-level lowstands (see Bouilla et al., 2011: table 1 for the ages of these events). In addition, trace element analyses indicate that the intense volcanic activity preserved in the Las Cascadas Formation may mark the transition from arc magmatism to local extensional magmatism in the Panama Canal Basin during the initial collision with South America (Farris et al., 2011). The combination of intensive volcanic activity, basin extension, and repeated sea-level lowstands (i.e., changes in base level) may explain the repeated volcanic to sedimentary sequences recorded in the Las Cascadas Formation (Montes et al., 2012).

The Las Cascadas chalicotherium along with the rest of the mammalian fossil assemblage were found in the uppermost volcanogenic-sedimentary sequence and are likely synchronous with one of the several Mi1 ice sheet expansions/sea-level lowstands between 23 and 19 Ma. The implication here is that the occurrence of a chalicotherium in the late Arikareean New World Tropics could be significantly younger than the first North American immigration of chalicotheriids during the latest Oligocene. In addition, the primitive, small-bodied Las Cascadas chalicotherium is likely contemporaneous with the large-bodied Moropus elatus from the Harrison Formation of Nebraska with a minimal age of 22.9 ± 0.08 (Coombs, 2004; Tedford et al., 2004).

These observations led to two alternative hypotheses concerning the origin of the Las Cascadas chalicotherium. First, primitive, small-bodied chalicotheriids similar to the first North American immigrants persisted in tropical Central America during the late Arikareean as large-bodied taxa became more prevalent at higher latitudes. The taxon represented by the Las Cascadas chalicotherium may have been ecologically excluded from these higher latitudes due to changes in vegetation and habitat structure in the earliest Miocene (Strömberg, 2002, 2006), a situation similar to that of the late Arikareean Gulf Coast Moropus reported by Frailey (1979), and Albright III, and Coombs et al. (2001). The second hypothesis is that the Las Cascadas chalicotherium represents a second immigration of Eurasian chalicotheriids into North America. Multiple dispersals of mammalian carnivores into North America during the latest Oligocene and earliest Miocene (e.g., Hunt, 2004) set a precedent for more than one migration event in this interval, indicating the plausibility of two chalicotheriid dispersals from Eurasia. Additional material of the Las Cascadas chalicotherium along with a rigorous phylogenetic analysis of Eurasian and North American chalicotheres will be necessary to test these hypotheses.

ACKNOWLEDGMENTS

We thank J. Bloch, J. Bourque, R. Hulbert Jr., C. Manz, P. Morse, and A. Rincón for helpful discussions during preparation of the manuscript. C. Manz provided comments on an earlier version of the manuscript that greatly improved its quality, and the constructive comments of our reviewers, B. Albright and J. Fahlike are much appreciated. Thanks to C. Jaramillo and L. Londón for logistical support conducting field work in Panama and to S. Moran for photographing the cast of UF 280165. Special thanks go to the Autoridad del Canal de Panamá for access to important fossil localities along the Panama Canal. This work was supported by NSF project 0966884 (OISE, EAR, DRL). This is University of Florida Contribution to Paleobiology number 667.

LITERATURE CITED

Albright, L. B., III. 1999. Ungulates of the Toledo Bend local fauna (late Arikareean, early Miocene), Texas coastal plain. Bulletin of the Florida Museum of Natural History 42:1–80.

Albright, L. B., III, M. O. Woodburne, T. J. Fremd, C. C. Swisher III, B. J. MacFadden, and G. R. Scott. 2008. Revised chronostratigraphy and biostratigraphy of the John Day Formation (Turtle Cove and Kimberly members), Oregon, with implications for updated calibration of the Arikareean North American land mammal age. Journal of Geology 116:211–237.

Anquetin, J., P.-O. Antoine, and P. Tassy. 2007. Middle Miocene Chalicotheriidae (Mammalia, Perissodactyla) from France, with a discussion on chalicotheriine phylogeny. Zoological Journal of the Linnean Society 151:577–608.

Bouilla, S., B. Galbrun, K. G. Miller, S. F. Pekar, J. V. Browning, J. Laskar, and J. D. Wright. 2011. On the origin of Cenozoic and Mesozoic “third-order” eustatic sequences. Earth-Science Reviews 109:94–112.

Butler, P. M. 1965. Fossil mammals of Africa. No. 18. East African Mioocene and Pleistocene chalicotheres. Bulletin of the British Museum Natural History Geology 10:165–237.

Chaveaou, O., Y. Chaimanee, P. Coster, E.-G. Emonet, A. N. Soe, A. A. Kyaw, A. Maung, M. Rugubumung, H. Shwe, and J.-J. Jaeger. 2010. First record of a chalicotherium from the Miocene of Myanmar. Acta Palaeontologica Polonica 55:13–22.

Coombs, M. C. 1974. Ein Vertreter von Moropus aus dem europäischen Aquitanien und eine Zusammenfassung der europäischen postoli- gozänen Schizotheriinae (Mammalia, Perissodactyla, Chalicotheriidae). Sitzungsberichten der Österreichischen Akademie der Wissenschaften, Mathematik-Naturwissenschaftliche Klasse 182:273–288.

Coombs, M. C. 1978a. Reevaluation of early Miocene North American Moropus (Perissodactyla, Chalicotheriidae, Schizotheriinae). Bulletin of the Carnegie Museum of Natural History 41:1–62.

Coombs, M. C. 1978b. Additional Schizotherium material from China, and a review of Schizotherium dentitions (Perissodactyla, Chalicotheriidae). American Museum Novitates 2647:1–18.

Coombs, M. C. 1979. Tylacephalax, a new genus of North American dome-skulled chalicotheres (Mammalia, Perissodactyla). Bulletin of the American Museum of Natural History 164:1–64.

Coombs, M. C. 1989. Interrelationships and diversity in the Chalicotheriidae: pp. 438–457 in D. R. Prothero and R. M. Schoch (eds.), The Evolution of Perissodactyla. Oxford University Press, New York.

Coombs, M. C. 1998. Chalicotherioidea; pp 560–568 in C. M. Janis, K. M. Scott, and L. L. Jacobs (eds.), Evolution of Tertiary Mammals of North America. Cambridge University Press, Cambridge, U.K.

Coombs, M. C. 2004. Moropus merriami in the early Barstovian Lower Snake Creek fauna of Nebraska, with comments on biogeography of North American chalicotheres. Bulletin of the American Museum of Natural History 285:191–208.

Coombs, M. C. 2009. The chalicotherium Muytwchichtherium bavarium (Perissodactyla, Schizotheriidae, Schizotheriinae) from the Miocene (MNS) Lagerstätte of Sandelhausen (Germany): description, comparison, and palaeoecological significance. Paläontologische Zeitschrift 83:85–129.

Coombs, M. C., R. M. Hunt Jr., E. Stepleton, L. B. Albright III, and T. J. Fremd. 2001. Stratigraphy, chronology, biogeography, and taxonomy of early Miocene small chalicotheres in North America. Journal of Vertebrate Paleontology 21:607–620.

Fahlike, J. M., M. C. Coombs, and G. M. Semprebon. 2013. Anisodon sp. (Mammalia, Perissodactyla, Chalicotheriidae) from the Turolian of Dorn-Dürkheim 1 (Rheinhesse, Germany): morphology, phylogeny, and palaeoecology of the latest chalicotherium in Central Europe. Palaeodiversity and Palaeoenvironments 9:S151–170.

Farris, D. W., C. Jaramillo, G. Bayona, S. A. Restrepo-Moreno, C. Montes, A. Cardona, A. Mora, R. J. Speakman, M. D. Glascok, and V. Valencia. 2011. Fracturing of the Panamanian Isthmus during initial collision with South America. Geology 39:1007–1010.

Frailey, D. 1979. The large mammals of the Buda Local Fauna (Arikareean: Alachua County, Florida). Bulletin of the Florida Museum of Natural History 24:123–173.

Guerin, C., and M. Pickford. 2005. Ancylotherium cheboitense (Perissodactyla, Chalicotheriidae) from the uppermost Miocene: Alachua County, Florida). Bulletin of the Florida Museum of Natural History 24:123–173.

Hunt, R. M., Jr. 2004. Global climate and the evolution of large mammalian carnivores during the later Cenozoic of North America. Bulletin of the American Museum of Natural History 285:139–156.

Janis, C. M., G. F. Gunnell, and M. D. Uhen (eds). 2008. Evolution of Tertiary Mammals of North America, Volume 2. Cambridge University Press, Cambridge, U.K., 795 pp.
Janis, C. M., K. M. Scott, and L. L. Jacobs (eds.). 1998. Evolution of Tertiary Mammals of North America, Volume 1. Cambridge University Press, Cambridge, U.K., 691 pp.

Khan, M. A., M. Iqbal, M. Akhtar, and M. Hassan. 2009. Chalicotheres in the Siwaliks of Pakistan. Pakistan Journal of Zoology 41:429–435.

Kirby, M. X., D. S. Jones, and B. J. MacFadden. 2008. Lower Miocene stratigraphy along the Panama Canal and its bearing on the Central American peninsula. PLoS ONE 3:e2799.

Kominz, M. A., J. V. Browning, K. G. Miller, P. J. Sugarman, S. Mizintseva, and C. R. Scotese. 2008. Late Cretaceous to Miocene sea-level estimates from the New Jersey and Delaware coastal plain coreholes: an error analysis. Basin Research 20:211–226.

Liu, Y., and Z. Q. Zhang. 2012. New materials of Chalicotherium brevirostris (Perissodactyla, Chalicotheriidae) from the Tunggur Formation, Inner Mongolia. Geobios 45:369–376.

MacFadden, B. J. 2009. Three-toed browsing horse Anchitherium (Equidae) from the Miocene of Panama. Journal of Paleontology 83:489–492.

MacFadden, B. J., J. I. Bloch, H. Evans, D. A. Foster, G. S. Morgan, A. Rincón, and A. R. Wood. 2014. Temporal calibration and biochronology of the Centenario Fauna, early Miocene of Panama. The Journal of Geology 122:113–135.

Miller, K. G., G. S. Mountain, J. V. Browning, M. Kominz, P. J. Sugarman, N. Christie-Blick, M. E. Katz, and J. D. Wright. 1998. Cenozoic global sea level, sequences, and the New Jersey transect: results from coastal plain and continental slope drilling. Review of Geophysics 36:569–601.

Miller, K. G., M. A. Kominz, J. V. Browning, J. D. Wright, G. S. Mountain, M. E. Katz, P. J. Sugarman, B. S. Cramer, N. Christie-Blick, and S. F. Pekar. 2005. The Phanerozoic record of global sea-level change. Science 310:1293–1298.

Montes, C., A. Cardona, R. McFadden, S. E. Morón, C. A. Silva, S. Restrepo-Moreno, D. A. Ramírez, N. Hoyo, J. Wilson, D. Farris, G. A. Bayona, C. A. Jaramillo, V. Valencia, J. Bryan, and J. A. Flores. 2012. Evidence for middle Eocene and younger land emergence in central Panama: implications for isthmus closure. Geological Society of America Bulletin 124:780–799.

Pekar, S. F., and R. M. DeConto. 2006. High-resolution ice-volume estimates for the early Miocene: evidence for a dynamic ice sheet in Antarctica. Palaeogeography, Palaeoclimatology, Palaeocology 231:101–109.

Rincón, A. F., J. I. Bloch, B. J. MacFadden, and C. A. Jaramillo. 2013. First Central American record of Anthracotheriidae (Mammalia, Botheriodontinae) from the early Miocene of Panama. Journal of Vertebrate Paleontology 33:421–433.

Rincón, A. F., J. I. Bloch, C. Suarez, B. J. MacFadden, and C. A. Jaramillo. 2012. New floridatragnulines (Mammalia, Camelidae) from the early Miocene Las Cascadas Formation, Panama. Journal of Vertebrate Paleontology 32:456–475.

Rooney, T., P. Franceschi, and C. Hall. 2010. Water saturated magmas in the Panama Canal region: a precursor to Adakite-like magma generation. Contributions to Mineralogy and Petrology 161:373–388.

Strömberg, C. A. E. 2002. The origin and spread of grass-dominated ecosystems in the Late Tertiary of North America: preliminary results concerning the evolution of hypsodonty. Palaeogeography, Palaeoclimatology, Palaeocology 177:59–75.

Strömberg, C. A. E. 2006. Evolution of hypsodonty in equids: testing a hypothesis of adaptation. Paleobiology 32:236–258.

Tedford, R. H., L. B. Albright III, A. D. Barnosky, I. Ferrusquia-Villafranca, R. M. Hunt Jr., J. E. Storer, C. C. Swisher III, M. R. Voorhies, S. D. Webb, and D. P. Whistler. 2004. Mammalian biochronology of the Arikareean through Hemphillian interval (late Oligocene through early Pliocene epochs); pp. 169–231 in M. O. Woodburne (ed.), Late Cretaceous and Cenozoic Mammals of North America: Biostratigraphy and Geochronology. Columbia University Press, New York.

Submitted December 13, 2013; revisions received May 3, 2014; accepted May 9, 2014.

Handling editor: Marcelo Sanchez-Villagra.

Citation for this article: Wood, A. R., and N. M. Ridgwell. 2015. The first Central American chalicothere (Mammalia, Perissodactyla) and the paleobiogeographic implications for small-bodied schizotherines. Journal of Vertebrate Paleontology. DOI: 10.1080/02724634.2014.923893.