Tarsal morphology of the pleuraspidotheriid mammal *Hilalia* from the middle Eocene of Turkey

GREGOIRE METAIS, OZAN ERDAL, KORHAN ERTURAÇ, and K. CHRISTOPHER BEARD

Pleuraspidotheriids are a group of primitive ungulate mammals that, until recently, were thought to be restricted to the late Paleocene of Western Europe. It has been hypothesized that this family actually survived in Central Anatolia until at least the middle Eocene. However, these anachronistically young Anatolian "survivors", including the genus *Hilalia*, were previously documented mainly by dental remains. Here, we describe the previously unknown astragalus of *Hilalia saribeya*, which confirms the pleuraspidotheriid affinities of the genus, and supports phylogenetic reconstructions that place *Hilalia* as the sister group of *Pleuraspidotherium*. The morphology of the astragalus suggests sub-cursorial plantigrade locomotion for *H. saribeya*, although its tarsal morphology remains generalized enough that scansorial capabilities cannot be ruled out. The evolution of *Hilalia* is addressed in the context of the apparent geographic isolation of Central Anatolia during the Eocene. The endemic character of the mammalian fauna of Central Anatolia during the middle Eocene emphasizes how the complex paleogeography of the northern margin of Neotethys impacted local biotas in a region situated at the crossroads of very distinctive biogeographic zones.

Key words: Mammalia, Pleuraspidotheriidae, paleogeography, Eocene, Turkey, Anatolia.

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Introduction

The early Cenozoic mammalian group "Condylarthra" was originally described by Cope (1881, 1884) on the basis of several postcranial features, including a distally convex astragalar head and the nature and extent of its contact with the navicular. It is now widely recognized that Cope's conception of "Condylarthra" includes a highly diverse and paraphyletic or even polyphyletic assemblage of early eutherian herbivores and omnivores (e.g., Archibald 1998). Nevertheless, tarsal morphology has often been used to interpret the systematics and locomotor behavior of primitive ungulate mammals, including many of the taxa that have conventionally been considered as "condylarths" (Matthew 1937; Schaeffer 1947; Cifelli 1983; Rose 1985, 1996). During the late Paleocene in Western Europe, the family Pleuraspidotheriidae, represented by the genera *Orthaspidotherium* and *Pleuraspidotherium*, was a particularly abun-

dant group of medium-sized basal ungulates or "condylarths" (e.g., Russell 1964). The youngest known record of pleuraspidotheriids in Western Europe occurs in the latest Paleocene Rivecourt local fauna from the north-central part of the Paris Basin (Smith et al. 2014). While pleuraspidotheriids apparently became extinct in Western Europe at or near the Paleocene–Eocene boundary, the family persisted at least until the middle Eocene in Central Turkey, where it is documented by several species of the genus *Hilalia*. Maas et al. (2001) first described *Hilalia* as an indeterminate "condylarth", but *Hilalia* has more recently been interpreted as a pleuraspidotheriid on the basis of its dental morphology (Ladevèze et al. 2010). Likewise, *Parabunodon*, from the ?early Eocene Çeltek Formation, Amasya Province, Central Anatolia, was first described as a choeropotamid artiodactyl (Ducrocq and Sen 1991), but has since been re-interpreted as a bunodont pleuraspidotheriid by Métais et al. (2012).
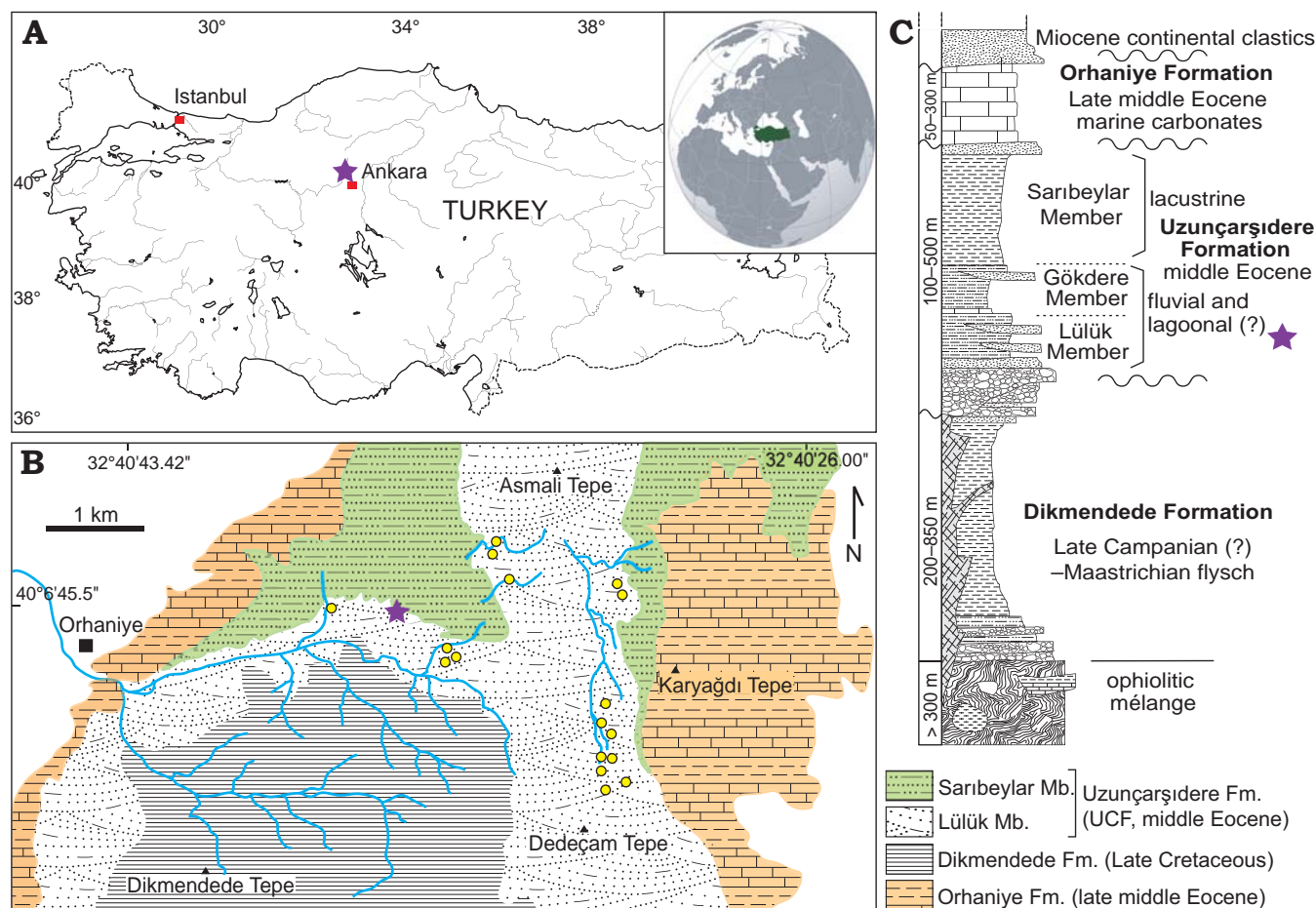
Fig. 1. Map of Turkey with the location of the Orhaniye Basin in Central Anatolia (**A**), geological map of the Orhaniye Basin (**B**) showing the fossil locality that yielded the astragalus described here, and a synthetic log (**C**) showing the succession of lithological units exposed in the Orhaniye Basin. Purple stars indicate the location of the fossil site that yielded EOU-UCF-1.

In addition to the relatively abundant teeth and jaws of *Hilalia* reported by Maas et al. (2001), these workers also described a partial calcaneum as pertaining to *Hilalia saribeya*, which is the genotypic (and most common) species. Maas et al. (2001) found that this calcaneum lacks derived features of artiodactyl, perissodactyl or hyracoid calcanea. In contrast, they noted several features in which the partial calcaneum of *Hilalia* resembles those of the "condylarths" *Meniscotherium* and (especially) *Pleuraspidotherium*. However, with the notable exception of the transverse orientation of the cuboid facet, which *Hilalia* shares with *Pleuraspidotherium* but not with *Meniscotherium*, these calcaneal features were interpreted as symplesiomorphies, and thus of little significance for systematics.

Here, we describe an isolated astragalus of *Hilalia* from the Lülük Member of the Uzunçarşıdere Formation or UCF (Fig. 1), the same lithological unit that has yielded all other known specimens of *Hilalia* (Maas et al. 2001). More than half of all fossil mammal specimens collected so far from the UCF belong to *Hilalia*, and the size and morphology of the new astragalus are fully consistent with an attribution to this taxon. Likewise, no other placental mammal taxon currently documented from the UCF fauna is appropriate in size

to be a potential candidate for this astragalus (Kappelman et al. 1996, Maas et al. 1998). The specimen was collected by surface prospecting during the 2011 field season.

Institutional abbreviations.—AÜJM, Ankara University Science Faculty Geology Museum, Ankara, Turkey; EOU, Eskişehir Osmangazi University, Eskişehir, Turkey

Other abbreviations.—IAES, İzmir-Ankara-Erzincan Suture; UCF, Uzunçarşıdere Formation.

Geological setting

The Neotethyan realm within the extent of the modern eastern Mediterranean region can be considered as a flexible collage of interconnected small ocean basins, microcontinents and carbonate platforms (Şengör and Yılmaz 1981; Robertson and Dixon 1984). Within this collage, five different tectonic zones are recognized for modern Turkey. These include the Pontides, Sakarya continent, Kırşehir Block, Taurides (sometimes Anatolides-Taurides) and Menderes Block (Okay and Tüysüz 1999; Bozkurt and Mittwede 2001). Three separate ocean basins are recognized within the
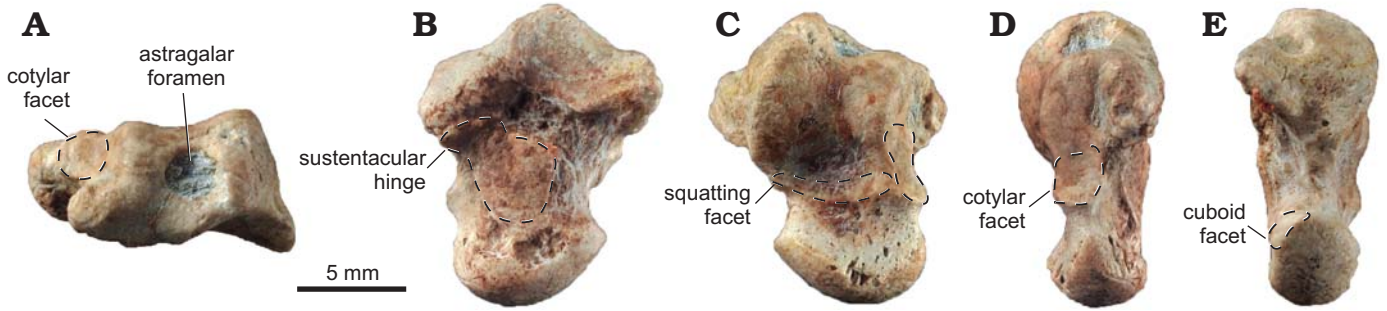
Fig. 2. *Hilalia saribeya* Maas, Thewissen, Sen, Kazanci, and Kappelman, 2001 from the middle Eocene Uzunçarşıdere Formation, Central Turkey; right astragalus (EOU-UCF-1) in proximal (**A**), plantar (**B**), dorsal (**C**), medial (**D**), and lateral (**E**) views. Each homologous articular facet is marked by dashed line.

Eastern Mediterranean: Intra-Pontide, northern Neotethys, and southern Neotethys. A portion of the southern Neotethys still survives as the modern Eastern Mediterranean, in contrast to the two former oceanic basins, which are no longer in existence. The northern branch of Neotethys was closed by a terminal collision and sutured during the Late Cretaceous–early Paleogene between the Pontides and the Tauride-Anatolides platform along the İzmir-Ankara-Erzincan Suture (IAES). The Orhaniye Basin, within which fossiliferous outcrops of the UCF occur, is a retroarc foreland basin that developed immediately north of the IAES zone during the early Paleogene (Licht et al. in press). A thick sequence of marine and continental rocks in the Orhaniye Basin including the fluviolacustrine UCF records the sub-aerial and marine episodes that occurred locally during the Paleogene (Fig. 1). The best outcrops and the type section of the UCF occur in the N-S trending valley excavated by the Uzunçarşı stream, originating from Dedeçam Hill (Fig. 1). The thickness of the UCF approximates 500 m, but the thickness varies laterally. The basal Lülük Member of the UCF consists of braided river deposits alternating with fossiliferous reddish paleosols developed on abandoned fluvial bars. The Lülük Member is conformably overlain by off-white lacustrine limestone and green/gray mudstone that have been dated as Lutetian (~43 Ma; Licht et al. in press).

Systematic palaeontology

Class Mammalia Linnaeus, 1758
Order "Condylarthra" Cope, 1881
Family Pleuraspidotheriidae Zittel, 1892
Genus *Hilalia* Maas, Thewissen, Sen, Kazanci, and Kappelman, 2001

Hilalia saribeya Maas, Thewissen, Sen, Kazanci, and Kappelman, 2001

Material.—EOU-UCF-1, right astragalus from late middle Eocene East Orhaniye locality 1, Lülük Member of the Uzunçarşıdere Formation, central Anatolia (Fig. 1B).

Description.—EOU-UCF-1 is a right astragalus (Fig. 2) that is comparable in size (Table 1) to that of *Pleuraspidotherium*

aumonieri from Cernay (France, MP6). The astragalar neck is proximodistally short and mediolaterally broad compared to the astragali of *Orthaspidotherium* and *Pleuraspidotherium* (Ladevèze et al. 2010: figs. 9, 10). The relatively deep astragalar body bears a moderately grooved tibial trochlea with well-defined and asymmetrical medial and lateral crests. The tibial trochlea is shallow, without sharp crests, and it forms an angle of only 12° with the neck, roughly half the value found in *Pleuraspidotherium* and *Orthaspidotherium*. The astragalar foramen superior is present, suggesting the presence of a large astragalar canal for passage of a branch of the peroneal artery. However, the astragalar foramen inferior, if present, is obscured by diagenetic micrite.

In dorsal view, the distal edge of the tibial trochlea displays a transversely elongated squatting facet that extends slightly onto the astragalar neck as in *Pleuraspidotherium* and *Orthaspidotherium*. The astragalar head is mediolaterally broader than in *Pleuraspidotherium* and (especially) *Orthaspidotherium*, and it is moderately rounded and much wider transversely than dorsoplantarly. The navicular facet occupies most of the distal side of the astragalar head, and it extends far onto the medial side of the neck to approximate the cotylar fossa. A small articular facet for the cuboid occurs on the planto-lateral side of the astragalar head in EOU-UCF-1, thus resembling the astragali of *Pleuraspidotherium* (Thewissen, 1991) and apheliscine "condylarths" such as *Apheliscus* and *Haplomylus* (Zack et al. 2005: fig. 2). On the distomedial side of the bone, a marked facet is present for the medial collateral ligament like in *Pleuraspidotherium*.

Table 1. Measurements (in mm) for the EOU-UCF-1 astragalus of *Hilalia saribeya* from the middle Eocene Uzunçarşıdere Formation, Central Turkey.

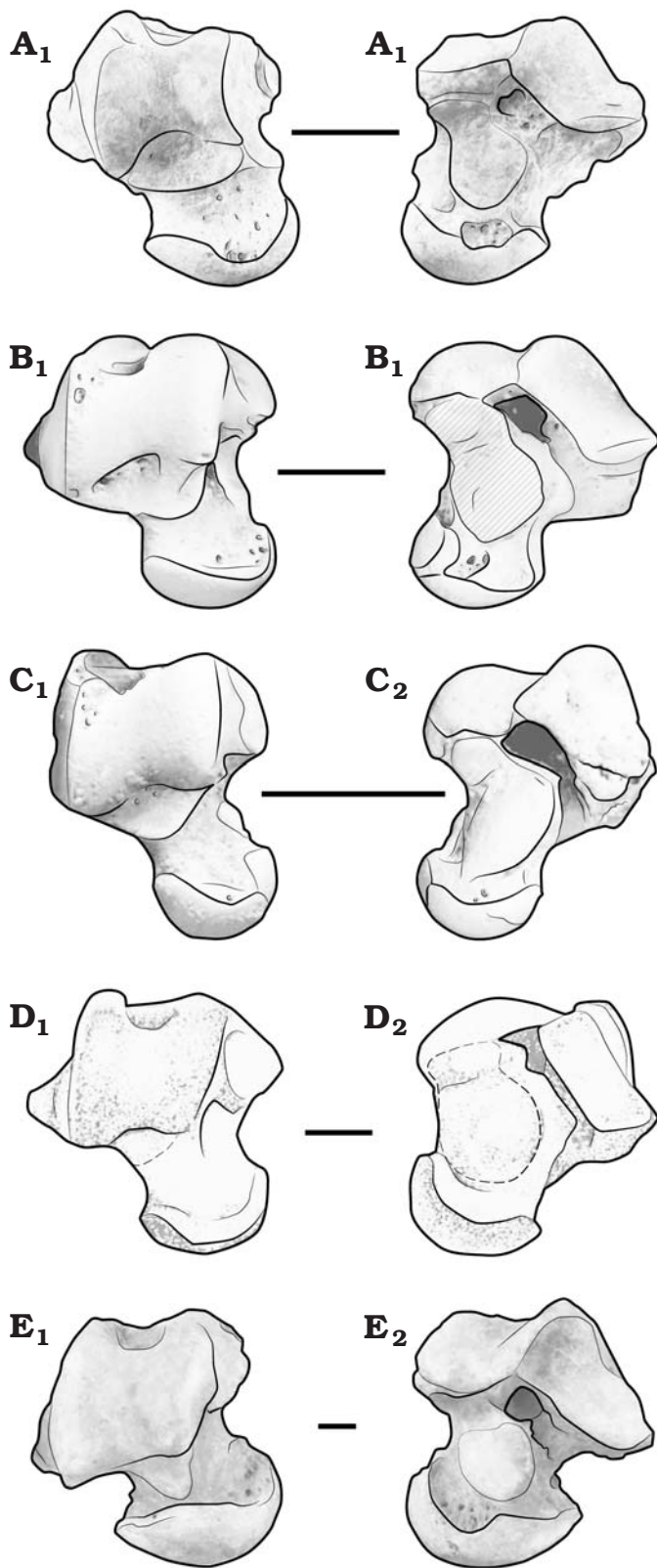|	
Proximal width of astragalar body	7.1
Lateral length of astragalar body	8.9
Maximum width of astragalar body	11.4
Proximal width of astragalar trochlea	6.6
Length of neck parallel to long axis	1.4
Maximum width of neck	6.1
Maximum length of astragalar parallel to long axis	14.0
Long axis of astragalar head	3.2
Long axis of astragalar head (transverse)	7.2

Fig. 3. Comparison of right astragali of Paleocene and Eocene "condylarths": *Hilalia saribeya* (**A**), *Pleuraspidotherium aumonieri* (**B**), *Orthaspidotherium edwardsi* (**C**), *Meniscotherium* sp. (**D**), *Arctocyon primaevus* (**E**), in dorsal (A₁–E₁) and plantar (A₂–E₂) views. Adapted from Argot (2013), Ladevèze et al. (2010), Williamson and Lucas (1992). Scale bars 5 mm.

In medial view, the articular surface for the medial malleolus of the tibia extends distally to form a distinct cotylar fossa. This concave surface is delimited by a sharp bony ridge and is dorsoventrally taller than its homologue in *Pleuraspidotherium*. The cotylar facet is present but even smaller in *Orthaspidotherium*. The distal calcaneal facet is not visible.

In plantar view, the sustentacular facet is proximodistally longer than its transverse dimension, and its outline is similar to that of *Pleuraspidotherium*. The sustentacular facet is distally connected to the navicular facet by two very thin bony bridges. A wide and deep interarticular sulcus intervenes between the ectal facet and a proximomedial extension of the sustentacular facet. The latter structure, which also occurs in *Pleuraspidotherium* and *Orthaspidotherium*, was designated as the sustentacular hinge by Ladevèze et al. (2010). The sustentacular hinge is gently concave and has a rounded proximomedial edge. The sustentacular facet, which occupies the inferior surface of the astragalar neck, is slightly concave along an oblique axis parallel to the long axis of the ectal facet. The latter occupies about half of the plantar side of the body, is concave, and obliquely oriented with respect to the long axis. The long axis of the ectal facet forms an angle of ~58° with the neck; this angle is 52° in *Pleuraspidotherium*, and 42° in *Orthaspidotherium* (Ladevèze et al. 2010). The navicular facet occupies the entire width of the astragalar head, but there is a small trapezoidal facet for the cuboid plantarly.

Remarks.—According to Ladevèze et al. (2010), diagnostic tarsal features of pleuraspidotheriids include: a transversely oriented cuboid facet on the calcaneum and the presence of a squatting facet (sensu Szalay and Decker 1974), a cotylar fossa, and a sustentacular hinge on the astragalus. EOU-UCF-1 displays all three of these astragalar features and is thus regarded as an astragalus of *Hilalia*, the only "condylarth" known so far from the UCF. The partial calcaneum (AÜJM99-5), described previously by Maas et al. (2001) from the UCF as pertaining to *Hilalia*, likewise bears a transversely oriented cuboid facet. Accordingly, *Hilalia* appears to retain all of the known diagnostic pleuraspidotheriid tarsal features. Assignment of EOU-UCF-1 to *H. saribeya* is based on size. With regard to its overall morphology and proportions, EOU-UCF-1 more closely resembles astragali of *Pleuraspidotherium* than those of *Orthaspidotherium* (Lemoine 1891; Ladevèze et al. 2010). The astragalus of *Orthaspidotherium* is much smaller, the neck is more gracile, and the ectal facet is oriented more proximodistally (Fig. 3), suggesting a different locomotor adaptation than in *Hilalia* and *Pleuraspidotherium*. EOU-UCF-1 differs from astragali of *Pleuraspidotherium* in having a more robust astragalar neck and head that are less medially deviated, and a dorsoventrally wider and more strongly delimited cotylar fossa that articulates with the tibial malleolus on the medial aspect of the astragalar body. In both of the latter respects, EOU-UCF-1 diverges even more from the astragalar morphology of *Orthaspidotherium*. Although we have not per-

formed a formal phylogenetic analysis that includes the new tarsal data for *Hilalia*, the strong phenetic similarities between EOU-UCF-1 and astragali of *Pleuraspidotherium* observed here are consistent with the phylogenetic results reported by Ladevèze et al. (2010), who recovered *Hilalia* and *Pleuraspidotherium* as sister taxa, with *Orthaspidotherium* as the sister group of the former clade.

The pleuraspidotheriids are currently known by four genera, and their origin remains unknown. Ladevèze et al. (2010) provided an historical overview of the proposed systematic affiliations of pleuraspidotheriids as well as a comprehensive analysis of the family and its phylogenetic position with respect to other "condylarths" and some modern ungulates. The strict consensus trees yielded by their analyses do not definitively resolve the affinities of pleuraspidotheriids, although a possible relationship with *Chriacus* is supported by two postcranial features, including the presence of a squatting facet on the astragalus of *Chriacus*. Afrotheres were not included in the analysis of Ladevèze et al. (2010). Louisinids, including *Paschatherium* and *Teilhardimys* (formerly *Microhyus*; Hooker and Russell 2012), are another group of "condylarths" restricted to the Paleocene and early Eocene of Europe. *Paschatherium* and *Teilhardimys* are considerably smaller than known pleuraspidotheriids. The astragalus of *Paschatherium* bears a well-developed cotylar fossa (Godinot et al. 1996), but this structure is much weaker in *Teilhardimys* (Tabuce et al. 2006). Both of these louisinid taxa lack the squatting facet and sustentacular hinge on the astragalus that are characteristic features of pleuraspidotheriids. Moreover, unlike the condition seen in pleuraspidotheriids, the calcanei of *Paschatherium* and *Teilhardimys* display a proximodistally elongated ectal facet (it is more tranversely oriented in *Pleuraspidotherium* and *Orthaspidotherium*).

The presence of a cotylar fossa has been proposed as a key character linking various afrotheres with some Holarctic apheliscine "condylarths" (Zack et al. 2005) and South American "native ungulates" (Agnolin and Chimento 2011), but this structure also occurs in pleuraspidotheriids, casting some doubt on the phylogenetic significance of this feature. Comparisons between the astragalus of *Hilalia* and those of other "condylarths" such as *Protungulatum*, *Arctocyon*, or *Hyopsodus* reveal that the proximal tarsus of *Hilalia* is distinctive in having the following combination of features: astragalar neck relatively short, transversely wide, and weakly constricted, and the presence of a squatting facet and a sustentacular hinge. During our comparisons with astragali of other "condylarths", we noticed some similarities between EOU-UCF-1 and the astragalus of *Meniscotherium* (Fig. 3): the tibial trochlea is shallow and the sustentacular facet tends to extend proximomedially. However, the interarticular sulcus for the interosseous ligament remains continuous in *Meniscotherium*, unlike the condition in *Hilalia* and other pleuraspidotheriids, in which the sustentacular hinge obliterates the interarticular sulcus. Moreover, in dorsal view, the slight development of a distal extension of the tibial trochlea on the astragalus of *Meniscotherium* tends to mimic the squatting facet found in pleuraspidotheriids, although the structure is much less extensive in *Meniscotherium*.

Stratigraphic and geographic range.—Middle Eocene, Lülük Member of the Uzunçarşıdere Formation, Orhaniye Basin, central Turkey.

Discussion

Locomotion of *Hilalia*.—The EOU-UCF-1 astragalus and the fragmentary calcaneum referred to *Hilalia* by Maas et al. (2001) illuminate some functional aspects of the locomotion of *Hilalia*. The functional implications of pleuraspidotheriid tarsal morphology have been debated. Thewissen (1991) concluded that *Pleuraspidotherium* was a generalist terrestrial taxon with plantigrade feet, lacking the supination ability and the wide range of mobility at the ankle joint that has been described in the arctocyonid *Chriacus* (Rose 1987, 1996). By contrast, Ladevèze et al. (2010) noted a number of similarities between the tarsus of Pleuraspidotheriidae and that of *Chriacus*. Body mass estimates for *Pleuraspidotherium* vary from 3 to 5 kg depending on the anatomical element and metric (e.g., femoral length versus femoral midshaft diameter) employed in the analysis (Thewissen 1991). Assuming the absence of unusual allometric scaling, a similar body mass estimate can be proposed for *Hilalia*. The astragalar morphology of *Hilalia* differs from that of *Pleuraspidotherium* in having a wider and less medially deviated astragalar neck and head, yielding a reduced angle between the tibial trochlea and the long axis of the astragalus. These characters favor parasagittal movements and may indicate a reduced capacity for inversion and eversion in *Hilalia*, consistent with a terrestrial and sub-cursorial mode of locomotion. This is consistent with the moderately grooved tibial trochlea, which suggests enhanced stability at the proximal tarsal joint. The tibial trochlea is almost flat transversely in the arctocyonid *Chriacus*, which is interpreted to have had arboreal capabilities (Rose 1987). Likewise, the relatively transverse orientation of the ectal facet of the calcaneum in *Pleuraspidotherium* and *Orthaspidotherium* (this feature is not observable on the damaged calcaneum of *Hilalia* reported by Maas et al. 2001) suggests terrestrial locomotion. The ectal facet is proximodistally elongated in more scansorial/arboreal taxa such as the extant hyracoid *Dendrohyrax* or the arctocyonid *Chriacus* (Szalay and Lucas 1996: fig. 17), and the European louisinid "condylarths" *Paschatherium* and *Teilhardimys* (Godinot et al. 1996). The distal extension of the trochlear articular surface onto the dorsal side of the astragalar neck (or "squatting facet") in *Hilalia* and other pleuraspidotheriids suggests that these animals frequently maintained dorsiflexed postures at the upper ankle joint, which may indicate a generalized "ambling" type of terrestrial locomotion (probably more adapted for walking on variable substrates than for running). The ranges of movement interpreted for a joint are based upon the osteological structure of the joints themselves and do not in-

clude limitations to movement imposed by soft tissue. Further data from the appendicular skeleton of *Hilalia* are needed in order to elucidate its locomotor adaptations and movement capabilities. It is worth noting that the posture and locomotion of primitive ungulates are often difficult to infer from skeletal morphology, mostly because there are no modern analogues, and thus biomechanical and functional hypotheses are difficult to test.

Paleobiogeography and paleoecology.—The close similarities in tarsal and dental morphology shared by *Hilalia* and Paleocene pleuraspidotheriids known from Western Europe make it clear that this clade persisted at least until the middle Eocene on the Pontide terrane in what is now Central Anatolia. The apparently relictual occurrence of pleuraspidotheriids in Central Anatolia highlights the endemic nature of the mammalian fauna of this region during the middle Eocene. This high level of faunal endemism presumably reflects the strong paleogeographic isolation of the Pontide terrane from Africa to the south, Europe to the north and west, and Asia to the north and east. Nevertheless, the apparent proximity of the Pontide terrane to adjacent tectonic blocks, and the high potential for emergent Tethyan island arcs due to N-S convergence in the region, made the Pontides a potential locus for mammalian dispersal from the Late Cretaceous through the Eocene. Pleuraspidotheriids must have dispersed onto the Pontide terrane sometime prior to the Paleocene–Eocene boundary, based on their documented stratigraphic distribution in Western Europe. However, the paleogeographic linkages that allowed pleuraspidotheriids to colonize the Pontide terrane must have been severed by the earliest Eocene, because there is no evidence of such common Eocene Laurasian mammal taxa as artiodactyls, perissodactyls, and rodents in the UCF fauna.

The persistence of pleuraspidotheriids on the Pontide terrane for roughly 15 Ma after their extinction in Western Europe raises many questions as to the date of their extinction in the region. The spotty Paleogene fossil record of Central Anatolia precludes attempts to track their persistence locally later in the Eocene. The late Eocene Süngülü fauna of easternmost Anatolia, although documented exclusively by small mammals, clearly displays typical Eurasian taxa (de Bruijn et al. 2003). However, paleogeographic continuity between the Süngülü fauna, from what is now the Caucasus area near Turkey's border with the Republic of Georgia, and the Pontide terrane bearing the UCF fauna has not yet been demonstrated. In any case, the late Oligocene faunas of the Kızılırmak Formation in the Çankırı-Çorum Basin of Central Anatolia clearly show that the endemic UCF fauna was replaced by a typical Eurasian fauna by the end of the Paleogene (Antoine et al. 2008; Métais et al. 2016).

Four, and perhaps five, species of *Hilalia* (mostly differentiated by size) have been reported from the UCF (Maas et al. 2001), suggesting a local radiation of the genus in ecological niches occupied elsewhere in Eurasia by artiodactyls and perissodactyls. Although *H. saribeya* was probably a terrestrial mammal, the locomotion and ecological preferences of the other species remain unknown. Smaller species such as *H. sezerorum* and another unnamed tiny species mentioned by Maas et al. (2001) possibly retained some climbing capabilities, as Ladevèze et al. (2010) hypothesized for the European pleuraspidotheriid *Orthaspidotherium*. In any case, these closely related Turkish pleuraspidotheriids must have practiced some form of ecological niche partitioning in order to coexist, even if they maintained a very similar dental morphology.

Conclusions

The astragalar morphology of the middle Eocene "condylarth" *Hilalia saribeya* from central Turkey shows clear affinities with that of the late Paleocene pleuraspidotheriid *Pleuraspidotherium aumonieri*, a species known only from the Paris Basin. This is consistent with dental evidence suggesting that *Pleuraspidotherium* is more closely related to *Hilalia* than it is to the contemporary and sympatric genus *Orthaspidotherium* (Ladevèze et al. 2010). The tarsal morphology of *Hilalia* suggests a generalist terrestrial locomotion, although its tarsal morphology remains generalized enough that some scansorial capabilities cannot be ruled out. The endemic character of the UCF mammalian fauna emphasizes how the complex paleogeography of the northern margin of Neotethys impacted local biotas, in a region situated at the crossroads of very distinctive biogeographic zones during the Eocene.

Acknowledgements

References

Agnolin, F.L. and Chimento, N.R. 2011. Afrotherian affinities for endemic South American "ungulates". *Mammalian Biology* 76: 101–108.

Antoine, P.-O., Karadenizli, L., Saraç, G., and Sen, S. 2008. A giant rhino-

cerotoid (Mammalia, Perissodactyla) from the late Oligocene of north-central Anatolia (Turkey). *Zoological Journal of the Linnean Society* 152: 581–592.

Archibald, J.D. 1998. Archaic ungulates ("Condylarthra"). *In*: C.M. Janis, K.M. Scott, and L.L. Jacobs (eds.), *Evolution of Tertiary Mammals of North America*, 292–331. Cambridge University Press, Cambridge.

Argot, C. 2013. Postcranial analysis of a carnivoran-like archaic ungulate: The case of *Arctocyon primaevus* (Arctocyonidae, Mammalia) from the late Paleocene of France. *Journal of Mammalian Evolution* 20: 83–114.

Bozkurt, E. and Mittwede, S.K. 2001. Introduction to the geology of Turkey—a synthesis. *International Geology Review* 43: 578–594.

Cifelli, R.L. 1983. The origin and affinities of the South American Condylarthra and early Tertiary Litopterna (Mammalia). *American Museum Novitates* 2772: 1–49.

Cope, E.D. 1881. On some Mammalia of the lower beds of New Mexico. *Proceedings of the American Philosophical Society* 19: 484–495.

Cope, E.D. 1884. The Condylarthra. *American Naturalist* 18: 790–805, 892–905.

de Bruijn, H., Ünay, E., Saraç, G., and Yïlmaz, A. 2003. A rodent assemblage from the Eo/Oligocene boundary interval near Süngülü, Lesser Caucasus, Turkey. *Coloquios de Paleontología, Volumen Extraordinario* 1: 47–76.

Ducrocq, S. and Sen, S. 1991. A new Haplobunodontidae (Mammalia, Artiodactyla) from the Eocene of Turkey. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* 1991 (1): 12–20.

Godinot, M., Smith, T., and Smith, R. 1996. Mode de vie et affinités de *Paschatherium* (Condylarthra, Hyopsodontidae) d'après ses os du tarse. *In*: M. Godinot and P.D. Gingerich (eds.), *Paléobiologie et évolution des mammifères paléogènes*, 225–242. Palaeovertebrata, Montpellier.

Hooker, J.J. and Russell, D.E. 2012. Early Palaeogene Louisinidae (Macroscelidea, Mammalia), their relationships and north European diversity. *Zoological Journal of the Linnean Society* 164: 856–936.

Kappelman, J.W., Maas, M.C., Sen, S., Alpagut, B., Fortelius, M., and Lunkka, J.-P. 1996. A new early Tertiary mammalian fauna from Turkey and its paleobiogeographic significance. *Journal of Vertebrate Paleontology* 16: 592–595.

Ladevèze, S., Missiaen, P., and Smith, T. 2010. First skull of *Orthaspidotherium edwardsi* (Mammalia, "Condylarthra") from the late Paleocene of Berru (France) and phylogenetic affinities of the enigmatic European family Pleuraspidotheriidae. *Journal of Vertebrate Paleontology* 30: 1559–1578.

Lemoine, V. 1891. Etude d'ensemble sur les dents de mammifères fossiles des environs de Reims. *Bulletin de la Société géologique de France* 19: 263–290.

Licht, A., Coster, P., Ocakoğlu, F., Campbell, C., Métais, G., Mulch, A., Taylor, M., Kappelman, J., and Beard, K.C. (in press). Tectonostratigraphy of the Orhaniye Basin, Turkey: Implications for collision chronology and Paleogene biogeography of central Anatolia. *Journal of Asian Eath Sciences*.

Maas, M.C., Thewissen, J.G.M., and Kappelman, J.W. 1998. *Hypsamasia seni* (Mammalia: Embrithopoda) and other mammals from the Eocene Kartal Formation of Turkey. *In*: K.C. Beard, and M.R. Dawson (eds.), *Dawn of the Age of Mammals in Asia. Bulletin of Carnegie Museum of Natural History* 34: 286–297.

Maas, M.C., Thewissen, J.G.M., Sen, S., Kazanci, N., and Kappelman, J.W. 2001. Enigmatic new ungulates from the early middle Eocene of Central Anatolia, Turkey. *Journal of Vertebrate Paleontology* 21: 578–590.

Matthew, W.D. 1937. Paleocene fauna of the San Juan Basin, New Mexico.

Transactions of the American Philosophical Society, New Series 30: 1–510.

Métais, G., Gheerbrant, E., and Sen, S. 2012. Re-interpretation of the genus *Parabunodon* (Ypresian, Turkey): implications for the evolution and distribution of pleuraspidotheriid mammals. *Palaeobiodiversity and Palaeoenvironments* 92: 477–486.

Métais, G., Albayrak, E., Antoine, P.-O., Erdal, O., Karadenızlı, L., Oyal, N., Saraç, G., İslamoğlu, Y., and Sen, S. 2016. Oligocene ruminants from the Kızılırmak Formation, Çankırı-Çorum Basin, Central Anatolia, Turkey. *Palaeontologia Electronica* 19.3.37A: 1–23.

Okay, A.I. and Tüysüz, O. 1999. Tethyan Sutures of northern Turkey. *In*: B. Durand, L. Jolivet, F. Hovarth, and M. Séranne (eds.), The Mediterranean Basins: Tertiary extension within the Alpine Orogen. *Geological Society of London, Special Publication* 156: 475–515.

Robertson, A. and Dixon, J. 1984. Introduction: aspects of the geological evolution of the Eastern Mediterranean. *Geological Society of London, Special Publication* 17: 1–74.

Rose, K.D. 1985. Comparative osteology of North American dichobunid artiodactyls. *Journal of Paleontology* 59: 1203–1226.

Rose, K.D. 1987. Climbing adaptations in the early Eocene mammal *Chriacus* and the origin of Artiodactyla. *Science* 236: 314–316.

Rose, K.D. 1996. On the origin of the order Artiodactyla. *Proceedings of National Academy of Science, USA* 93: 1705–1709.

Russell, D.E. 1964. Les mammifères Paléocènes d'Europe. *Mémoires du Muséum National d'Histoire Naturelle, série C, Sciences de la Terre* 13: 1–324.

Schaeffer, B. 1947. Notes on the origin and function of the artiodactyl tarsus. *American Museum Novitates* 1356: 1–24.

Şengör, A.M.C. and Yilmaz, Y. 1981. Tethyan evolution of Turkey: a plate tectonic approach. *Tectonophysics* 75: 181–241.

Smith, T., Quesnel, F., De Plöeg, G., De Franceschi, D., Métais, G., De Bast, E., Solé, F., Folie, A., Boura, A., Claude, J., Dupuis, C., Gagnaison, C., Iakovleva, A.I., Martin, J., Maubert, F., Prieur, J., Roche, E., Storme, J.-Y., Thomas, R., Tong, H., Yans, J., and Buffetaut, E. 2014. First Clarkforkian equivalent land mammal age in the latest Paleocene basal Sparnacian facies of Europe: fauna, flora, paleoenvironment and (bio)stratigraphy. *PlosOne* 9 (1): 1–19.

Szalay, F.S. and Decker, R.L. 1974. Origin, evolution, and function of the tarsus in Late Cretaceous Eutheria and Paleocene Primates. *In*: F.A. Jenkins, Jr. (ed.), *Primate Locomotion*, 223–259. Academic Press, London.

Szalay, F.S. and Lucas, S.G. 1996. The postcranial morphology of Paleocene *Chriacus* and *Mixodectes* and the phylogenetic relationships of archontan mammals. *Bulletin of the New Mexico Museum of Natural History and Science* 7: 1–47.

Tabuce, R., Antunes, M.T., Smith, R., and Smith, T. 2006. Dental and tarsal morphology of the European Paleocene/Eocene "condylarth" mammal *Microhyus*. *Acta Paleontologica Polonica* 51: 37–52.

Thewissen, J.G.M. 1991. Limb osteology and function of the primitive Paleocene ungulate *Pleuraspidotherium* with notes on *Tricuspiodon* and *Dissacus*. *Géobios* 24: 483–495.

Williamson, T.E. and Lucas, S.G. 1992. *Meniscotherium* (Mammalia, "Condylarthra") from the Paleocene–Eocene of Western North America. *Bulletin of the New Mexico Museum of Natural History and Science* 1: 1–75.

Zack, S.P., Penkrot, T.A., Bloch, J.I., and Rose, K.D. 2005. Affinities of "hyopsodontids" to elephant shrews and a Holarctic origin of Afrotheria. *Nature* 434: 497–501.