Acta Palaeontologica Polonica 50 (3): 545–548, 2005

Ankle structure in Eocene pholidotan mammal *Eomanis krebsi* and its taxonomic implications

INÉS HOROVITZ, GERHARD STORCH, and THOMAS MARTIN

Georges Cuvier (1798) established the classical concept of Edentata which included sloths, anteaters, armadillos, aardvarks, and pangolins. With the growing body of comparative morphological data becoming available during the nineteenth century, it was evident that Cuvier's "Edentata" was an artificial group (e.g., Huxley 1872). In his classical textbook, Weber (1904) excluded aardvarks and pangolins from the Edentata and put them in separate orders, Tubulidentata and Pholidota. Later on, fossil taxa were repeatedly added to and removed from Edentata, such as various xenarthran groups, taeniodonts, palaeanodonts, and gondwanatheres, but the South American Xenarthra always was considered as their core group. Even the living order Pholidota has been cited again as ?Edentata *incertae sedis* many years after Weber's work (Romer 1966). The validity and extent of a higher taxon Edentata are still in dispute. In this discussion, the Middle Eocene pholidotan *Eomanis* and the putative xenarthran *Eurotamandua* from Grube Messel near Darmstadt (Germany) play an important role (Storch 1978, 1981, 2003; Rose and Emry 1993; Gaudin and Branham 1998; Rose 1999). *Eomanis krebsi* and *Eurotamandua joresi* have been subject to some discussion regarding their taxonomic distinction. It has been suggested that the only specimen known of *Eo. krebsi* might actually be a juvenile representative of the senior species *E. joresi*. A reexamination of the type specimen of *Eo. krebsi* has yielded some new observations regarding the identity of some of its ankle elements. An element that was previously identified as a navicular, is here reidentified as a partial distal tibia, whereas a partially exposed calcaneus had gone unnoticed. These two elements display several differences in morphology between *Eo. krebsi* and *E. joresi*, indicating that these are in fact distinct species.

Introduction

An almost complete skeleton of a juvenile mammal, deemed to be a member of the mammalian order Pholidota (which includes living pangolins), was discovered in the middle Eocene deposits of Grube Messel near Darmstadt in Germany and was named *Eomanis krebsi* Storch and Martin, 1994. Two other species with similar postcranial characteristics were previously described from the same deposits: *Eomanis waldi* Storch, 1978 and *Eurotamandua joresi* Storch, 1981. Storch and Martin (1994) based their generic assignment of *Eomanis krebsi* on a series of characteristics they found it shared with *Eo. waldi*. On the other hand, *E. joresi* was considered to be a myrmecophagid anteater, order Xenarthra, becoming the only representative of this order outside of the Americas, and the oldest anteater in the fossil record. Alternative hypotheses for the evolutionary affinities of *E. joresi* have been proposed by other authors, and some of the more detailed analyses have suggested a sister group relationship with Pilosa (a subgroup of Xenarthra consisting of anteaters and sloths) (Gaudin and Branham 1998), or a position outside of Xenarthra, such as a close relationship with the extinct Palaeanodonta (Rose 1999), or indeterminate (Szalay and Schrenk 1998).

Szalay and Schrenk (1998) contended that similarities between *Eomanis krebsi* and *Eurotamandua joresi* were larger in number and importance than those between *Eo. krebsi* and *Eomanis waldi*. This led them to consider the type and only specimen of *Eo. krebsi* as a juvenile exemplar of *E. joresi*, and to propose *Eo. krebsi* a junior synonym of *E. joresi*.

A recent reexamination of *Eomanis krebsi* has revealed additional information concerning its taxonomic distinction. A fragment of the distal epiphysis of the right tibia was previously misidentified as a navicular and the distal end of the right calcaneus had been unnoticed. The morphology of these elements yields new insights into the taxonomic identity of this specimen, since the same elements are also preserved in the type specimen of *Eurotamandua joresi*. As shown below, comparison of the skeleton of *Eo. krebsi* with that of *E. joresi* incorporating this new information, contradicts the interpretation given by Szalay and Schrenk (1998).

The purpose of this note is to describe the distal tibia and calcaneus of *Eomanis krebsi*, compare them to and point out the differences with those of *Eurotamandua joresi* and solve the controversy surrounding the taxonomic status of *Eo. krebsi* at the "alpha" level. Relevant features are also described in *Patriomanis americana* to offer a separate point of comparison and facilitate an understanding of the morphology of *Eo. krebsi* and *E. joresi*. *P. americana* was the taxon of choice because of its completeness and its relatively primitive-looking ankle, especially compared to that of other pholidotans and "edentates" in general. The ankle structure of *Eomanis waldi* is barely visible and unfortunately none of the features we describe here can be verified in that species. Any similarities or differences between *P. americana* and *E. joresi* and/or *Eo. krebsi* are not presented here as phylogenetic indicators: a much broader analysis would be needed to interpret their characteristics in a phylogen-

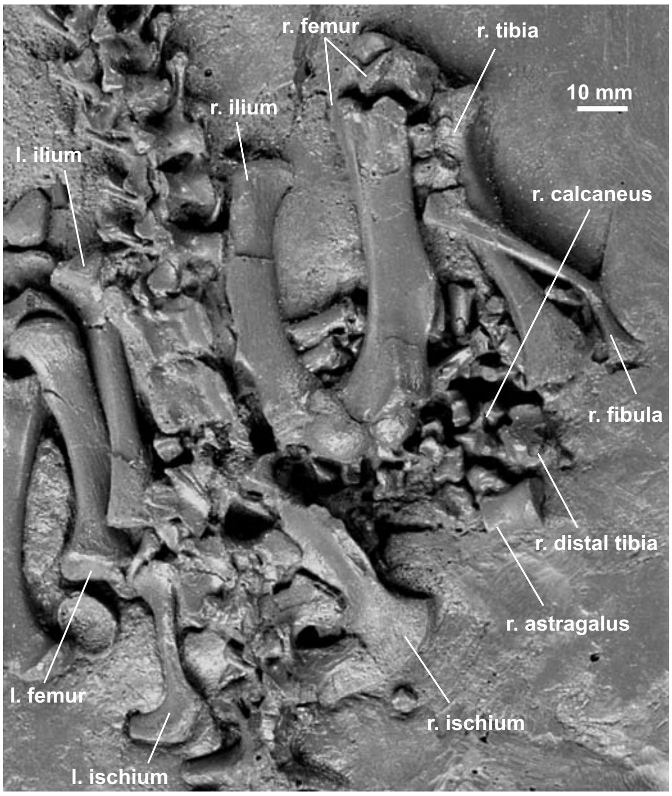

Fig. 1. *Eomanis krebsi*, cast (SMF 94/1, Grube Messel, Germany, middle Eocene), portion of type specimen; l, left; r, right.

etic context. Therefore this note does not seek to test the higher level affinities of *Eo. krebsi*, at the generic level or above.

Institutional abbreviations.—HLMD Me, Hessisches Landesmuseum Darmstadt, Messel-collection, Germany; SMF, Senckenbergmuseum Frankfurt am Main, Germany; USNM, United States National Museum,Washington, DC, USA.

Descriptions

Distal epiphysis of tibia in *Eomanis krebsi*.—The type and only known specimen displays the medial half of the distal epiphysis of the right tibia in distal view, which we will call "element A". Element A is separate from its corresponding diaphysis (Figs. 1 and 2), as are most bone epiphyses in this specimen. It is located near the distal end of the diaphysis of the right tibia, and is lying on top of the posterior area of the right calcaneus, next to the right astragalus which is exposed in dorsal view (Fig. 1). Although element A was previously identified as a navicular (Storch and Martin 1994; Szalay and Schrenk 1998), reexamination indicates that this element does not reflect mammalian navicular anatomy (Fig. 2). First, the articular surface of element A is too large for the head of the astragalus of the same individual. Second, although element A displays a concave articular surface on its body and on a process next to it, the latter is not in line with the major axis of that surface, as would be expected in a navicular. Third, the articular surface of this process is at an angle of about 90 degrees relative to the articular surface of the body. In contrast, an almost continuous curvature matching the corresponding astragalonavicular facet of the astragalus, would be expected in a navicular for this individual, instead of a sharp angle.

We have identified the process on element A as a tibial medial malleolus. This malleolus is rather slender mediolaterally, ends distally in a pointed process, and displays no articular facet on its distal surface. The articular surface adjacent to this process is identified as the medial area of the articular facet for the astragalar trochlea (or medial area of the lateral tibioastragalar facet). It displays a slightly concave area running anteroposteriorly next to the medial malleolus, which would articulate with the medial ridge of the astragalar trochlea in life. A raised central area corresponding to the trochlear groove of the astragalus is well preserved and no distal tibial process is present posteriorly.

Distal epiphysis of tibia in *Eurotamandua joresi*.—The distal end of the left tibia remains articulated with the astragalus, and is exposed in posteromedial view (Fig. 3). It displays a rather short and squarish medial malleolus, which encases the astragalus medially to a limited extent, leaving the medial side of the astragalar body exposed; no distal articular facet is present on the medial malleolus.

A prominent posterior process is also present and it protrudes distally beyond the medial malleolus. The distal tip of this process is located on the medialmost area of the posterior side of the distal epiphysis.

Distal epiphysis of tibia in *Patriomanis americana*.—The right tibia of specimen USNM 299960 is virtually complete (Fig. 4A). The distal articular surface is slanted, in such a way that it is more proximal on the lateral side and more distal medially. The medial side ends gradually at the tip of the medial malleolus, making this structure virtually indistinct in the posterior area. The medial malleolus makes contact with the ectal facet of the calcaneus, along a distomedially oriented facet. There is no posterior process as in *Eomanis krebsi* and in contrast with *Eurotamandua joresi*.

Calcaneus in *Eomanis krebsi*.—The right calcaneus is exposed in distomedial view and is partially obscured by the distal epiphysis of the tibia described above, by an unidentified element, and by the fact that the posterior part of the calcaneus is still embedded in the matrix (Figs. 1 and 2). The sustentaculum astragali and facet are well exposed, whereas the distal facet for the cuboid and the anterior plantar tubercle are only partially visible. The sustentaculum astragali is located a short distance from the distal end of the calcaneus and it measures 4.3 mm anteroposteriorly and 5.4 mm mediolaterally. The distal and proximal edges of the sustentaculum astragali run diagonally to the anteroposterior axis of the calcaneus and converge in a pointed end. This is the medialmost point of the sustentaculum astragali. The sustentacular facet covers the entire dorsal surface of the process.

The distal facet for the cuboid is generally exposed being slightly concave and oriented almost directly distally and very slightly medially. It is nearly circular in outline being 4.6 mm dorsoventrally and approximately 4.7 mm mediolaterally.

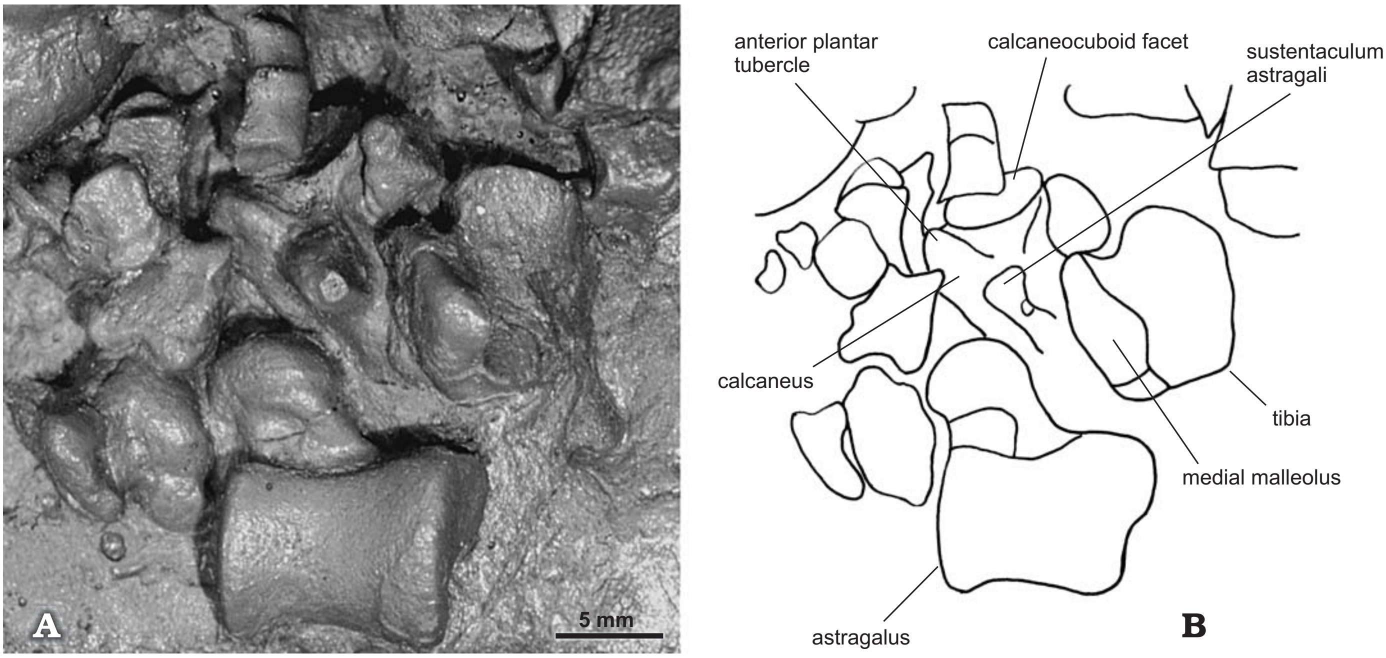

Fig. 2. *Eomanis krebsi*, cast (SMF 94/1), close-up of Fig. 1 showing right ankle elements (**A**); and explanatory drawing of the same (**B**), not to scale.

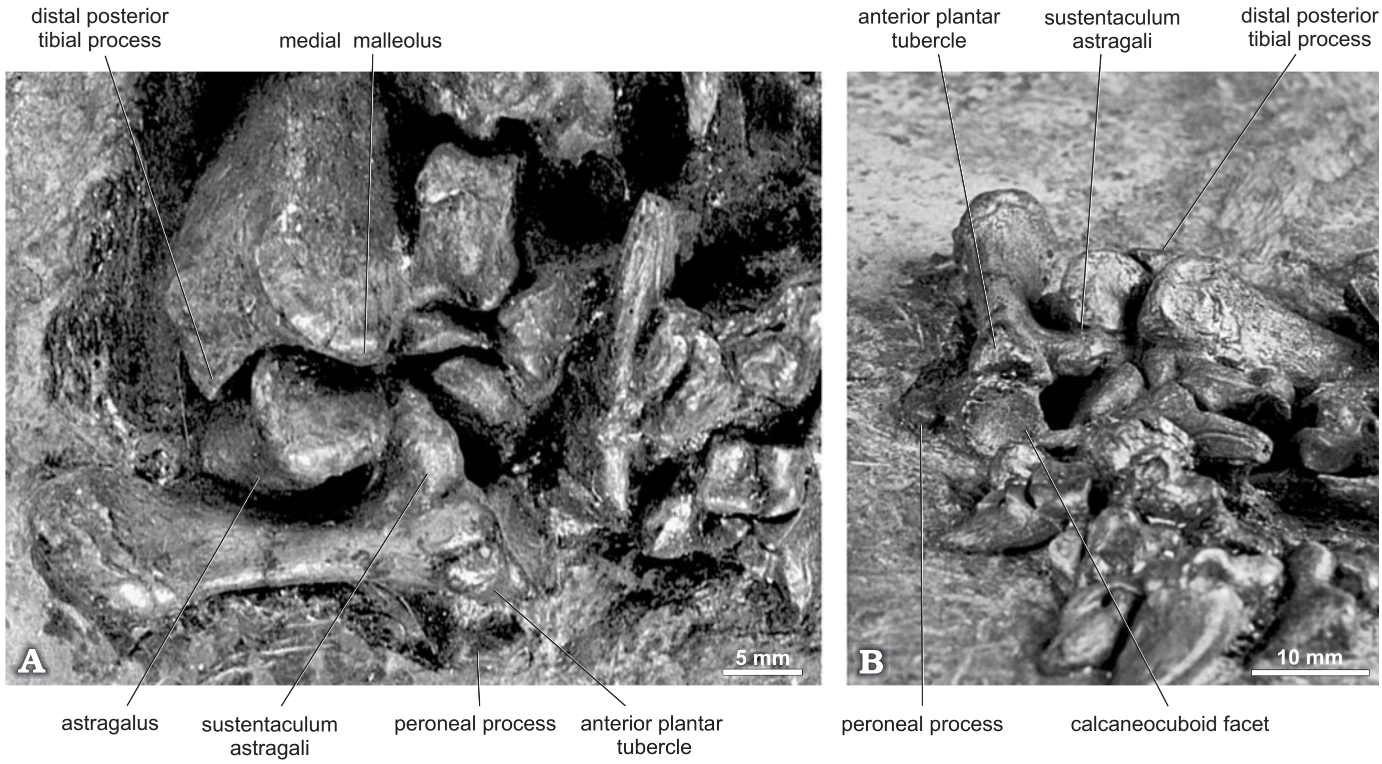

Fig. 3. *Eurotamandua joresi*, portion of type specimen HLMD Me 17000, Grube Messel, Germany, middle Eocene, showing left ankle elements in two different angles. **A**. Calcaneus visible in ventral view. **B**. Calcaneus visible in distoventral view.

The anterior plantar tubercle is located ventral to this facet. It is depressed dorsoventrally and protrudes distally slightly beyond the facet for the cuboid.

Calcaneus in *Eurotamandua joresi*.—Most of the calcaneus is visible and was described by Storch (1981). The right calcaneus of *E. joresi* is only exposed in lateral view, but fortunately the left calcaneus is visible in ventral and partial distal views (Fig. 3). The sustentaculum is partially obscured in its proximal area by the astragalus, however, it is possible to see where the proximal end is located along the medial wall of the body of the calcaneus. Its distal edge almost coincides with the distal end of

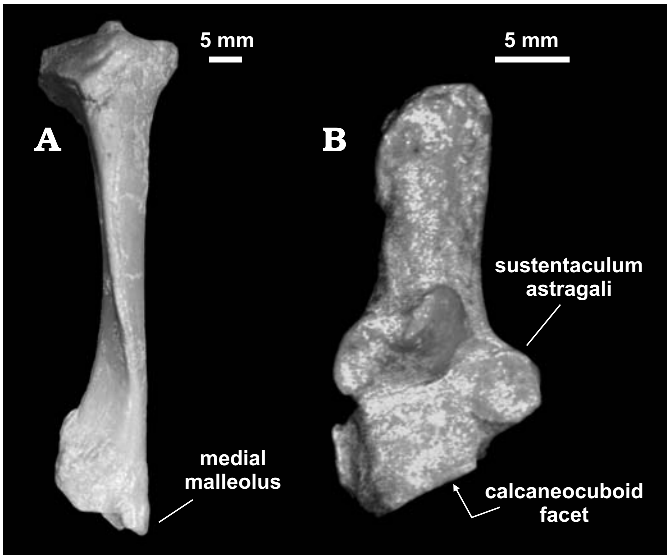

Fig. 4. *Patriomanis americana*, Natrona County, USA, early Oligocene. **A**. Cast of right tibia of USNM 299960 in anterior view. **B**. Cast of right calcaneus of USNM 299960 in dorsal view. The broken arrow indicates that the calcaneocuboid facet is at a right angle to the illustrated view.

the bone. The sustentaculum astragali is 6.6 mm long and about 5.2 mm wide. The distal area displays an anterior edge that is virtually perpendicular to the sagittal axis of the calcaneus. The medial edge of the sustentaculum astragali is parallel to the same axis, at least in the section that is visible. The distal facet for the cuboid (or calcaneocuboid facet) is almost completely exposed. It is slightly concave and almost circular in outline: approximately 6.7 mm dorsoventrally and 6.8 mm mediolaterally. Its orientation is mostly distal with a very slight medial component. The anterior plantar tubercle is located directly ventral to the facet for the cuboid. It is depressed dorsoventrally and it does not protrude distally beyond the facet for the cuboid.

Calcaneus in *Patriomanis americana*.—The sustentaculum astragali in *P. americana* has a rather rounded outline (Fig. 4B), and it differs in shape from the mediolaterally elongated sustentaculum of *Eomanis krebsi* and the squarish one of *Eurotamandua joresi*. There is a plantar tubercle in *P. americana* and as in *E. joresi,* it does not protrude distally beyond the facet for the cuboid, in contrast with that of *Eo. krebsi*. In *P. americana* the facet for the cuboid is distomedially oriented at about 30 degrees from being completely distally oriented, differing from both *E. joresi* and *Eo. krebsi* where it is directed almost completely distally. The outline of this facet in *P. americana* is rather triangular than circular, most wide dorsoventrally on the lateral side and narrowing medially.

Discussion

The morphology of the distal tibia and calcaneus of *Eomanis krebsi* and *Eurotamandua joresi* shows a mosaic of features. The fact that they differ in several respects is significant for the taxonomic status of *Eo. krebsi*. The differences are beyond those one might expect among individuals of a single species. A posterior process is absent from the distal tibia of *Eo. krebsi* whereas it is present and prominent in *E. joresi*. Further, the sustentaculum astragali is wider than its length and pointed medially in *Eo. krebsi*, whereas it is longer than wider, with a squarish distal shape in *E. joresi*. The sustentaculum astragali is located a short distance from the distal end of the calcaneus in *Eo. krebsi*, whereas the distal edge almost coincides with the distal end of this bone in *E. joresi*. Lastly, both species display a medial malleolus that differs in shape: the malleolus is pointed in *Eo. krebsi* whereas it is squarish in *E. joresi*.

In sum, the morphological differences illustrated here indicate that *Eo. krebsi* and *E. joresi* are and should be considered separate taxa. With regard to the higher level affinities of *Eo. krebsi*, many similarities have been listed between it and both *Eomanis waldi* and *E. joresi*. Whether *Eo. krebsi* does indeed belong to the genus *Eomanis,* to Pholidota or to some other group of eutherians (the genus *Eurotamandua* included) remains to be solved with a higher level phylogenetic analysis of Eutheria.

Acknowledgments.—We thank Ann Bleefeld (American Museum of Natural History) and two anonymous reviewers for corrections and feedback on this manuscript and Norbert Micklich and Conny Kurz (Hessisches Landesmuseum Darmstadt) for access to specimens.

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Inés Horovitz [horovitz@ucla.edu], Department of Ecology and Evolutionary Biology, University of California, Los Angeles, 621 Young Drive South, BOX 951606, Los Angeles, CA 90095-1606;

Gerhard Storch [gerhard.storch@senckenberg.de] and Thomas Martin [tmartin@senckenberg.de], Forschungsinstitut Senckenberg, Senckenberganlage 25, D-60325 Frankfurt am Main, Germany.