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Unique anatomy of lagomorph calcaneus

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The mammalian order Lagomorpha (hares, rabbits, pikas) comprises two families (Ochotonidae and Leporidae; McKenna and Bell 1998; Nowak 1999), and Recent members have a nearly world-wide distribution (Hoffman 1993; Nowak 1999). Detailed examination of the pedal morphology of extant and fossil lagomorphs revealed a unique channel (the "calcaneal canal") running diagonally through the lagomorph calcaneus. The ancientness, ubiquity, and appearance of the calcaneal canal in all, including the earliest recognized lagomorph calcanea, and its absence from the pedes of other mammalian taxa, may indicate a long evolutionary separation of lagomorphs from other, previously suggested lagomorph relatives.

While living members of this ubiquitous group are familiar to specialist and non-specialist alike, many features of their skeletal anatomy are not as easily recognized. There are several analyses of skeletal morphology of extant lagomorphs (Bensley 1945; Crabb 1946; Rowett 1957; Barone et al. 1973; McLaughlin 1977; Lewis 1989), as well as some of fossil members (Dice 1933; Camp and Borell 1937; Wood 1940; Dawson 1958, 1979; Bleefeld and McKenna 1985). Most studies concerning lagomorphs, nevertheless, concentrate on phylogeny or faunal descriptions (e.g., Wood 1940; McKenna 1982).

In this paper we set forth the calcaneal anatomy of a Recent ochotonid *Ochotona princeps*. We also present the results of an analysis of lagomorph tarsal features, including dissection of a pika (Ochotonidae) hind foot. These results, described below, emphasize salient features of the lagomorph pes, with respect to lagomorph systematics.

Institutional abbreviations.—AMNH-M, Department of Mammalogy, American Museum of Natural History; AMNH-VP, Division of Paleontology, American Museum of Natural History.

Material

The following specimens of extant and fossil lagomorphs were used in this study (all from AMNH-M collections). The letters after the specimen number indicate the condition of the calcaneal canal: L, large; R, reduced; M, minute (greatly reduced); A, absent (lost); MO, multiple openings; the first letter refers to the proximal opening of the calcaneal canal, the second letter refers to the distal calcaneal canal opening.

Leporidae.—Africa: *Lepus supercelearis* (23569 L,R), *Lepus crawshayi* (80840; R,R), (80841; M,M), (80854; M,M), (168933; A,A), *Lepus saxatilis* (90358; R,R), (169247; A,R), (169248; R,R), (169250; R,L), *Lepus capensis* (187425; R,L), *Poelagus marjorita* (216260; R,R), (216262; R,R).
The Americas: *Lepus californicus* (38875; A,R), (131874; R,R), *Lepus americanus* (99110; R,R), (99132; R,R), *Lepus europaeus* (262662; L,MO), (205750; R,R), *Lepus europaeus* (205731; MO,MO), (205746; R,MO), (205747; R,R), *Sylvilagus brasiliensis* (134267; A,A), (134208; A,A), (134233; A,A), (134248; A,A), (262661; R,R), *Sylvilagus floridanus* (242665; A,L), (290532; A,L), (187038; R,MO), (245055; R,R), (146570; R,R), (123803; R,R), (187037; R,R), *Sylvilagus palustris* (237430; R,R), (252707; R,R), (242800; R,R).
Greenland: *Lepus arcticus* (19169; L,L).
Siberia, Russia: *Lepus grichiganus* (18033; L,L), (18304; L,L).

Ochotonidae.—*Ochotona pallasi* (55981; L,L), *Ochotona princeps* (AWBB100; L,L).

The studied specimens of fossil lagomorph calcanei (all from AMNH-VP collections; proximal and distal calcaneal canal openings are large (L,L) on all specimens):

Leporidae.—Hsanda Gol Formation (Oligocene), Mongolia: Specimens 700, 701, 702, 1257, 1270, 2485, 2486, 2487, 2489, 2490, 2491. White River Formation (Oligocene), N.A.: *Palaeolagus haydeni* (5696). Kamyk, Poland (Pleistocene): *Hypolagus brachygnathus* (39526).

Ochotonidae.—Hsanda Gol Formation (Oligocene), Mongolia: Specimens 5, 10, 21, 24, 114, 221, 701, 1258, 1280, 1281, 1282, 1283, 1284, 2500, 2501. Ossis Breccia (Pleistocene), Mt. St. Giovanni, Sardinia, Italy: "Ochotonid" (168226).

Description

Calcaneus of *Ochotona princeps* (AMNH-M AWBB 100; Fig. 1). —This diminutive tarsal element is elongate and bilaterally compressed. The ectal prominence, consisting of the ectal and fibular facets, is situated at approximately the longitudinal midpoint of the bone. The circular fibular facet is oriented proximally. Anteriorly, the narrow ectal facet rises higher above the calcaneal neck than the fibular facet, at an angle of 90°. On its convex posterior side, the ectal facet slopes gradually and finally merges with the dorsum of the calcaneal tuber. A prominent sustentaculum extends from the medial side of the calcaneal body, bearing a shallow, circular sustentacular facet. Sustentacular and ectal facets are separated by a wide trough. Distally, the cuboid facet is crescent-shaped and obliquely aligned at a low angle to the calcaneal long axis. Consequently, the cuboid facet has a distomedial orientation with respect to the calcaneal long axis. The ochotonid calcaneus is unremarkable on its plantar side, except for a plantar tubercle, which consists of a small, blunt bony projection on the distal edge of the bone.

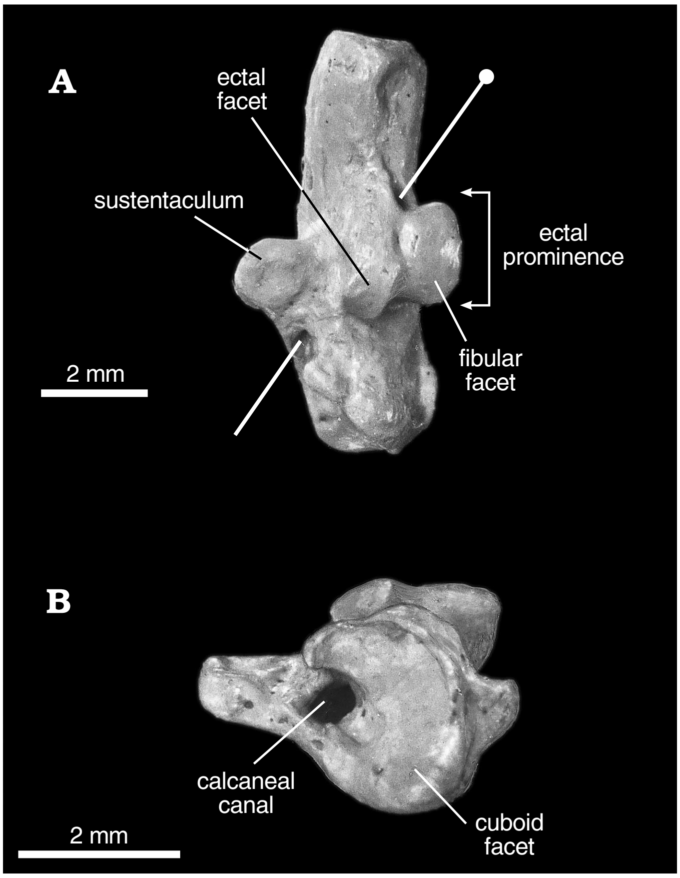

Fig. 1. Calcaneus of *Ochotona princeps* (AMNH AWBB100) in dorsal (**A**) and distal (**B**) views. Hatpin shows direction of calcaneal canal.

The calcaneal canal.—On the lateral side of the calcaneal tuber lies a narrow furrow which enters a circular foramen. This foramen serves as an entry way into a tunnel that traverses the calcaneal body, diagonally. This passageway (here termed the "calcaneal canal") exits the calcaneus *via* an aperture situated between the sustentaculum and the cuboid facet (see also Wood 1940).

Discussion

In an effort to discover what, if anything, is housed within the calcaneal canal, we dissected an ankle of *Ochotona princeps*, and found that passing through the canal is a vessel of the circulatory system. The vessel enters the bone via the proximal entryway on the lateral side of the calcaneal tuber, and exits the bone via the large, distomedial opening. After exiting the canal, the vessel passes to the anterior portion of the foot by passing along the plantar side of the cuboid.

Diagonal transverse histological sections were prepared at the midpoint of the ectal prominence of a decalcified ochotonid calcaneus, which was embedded in epoxy. As seen on Fig. 2, the circulatory vessel is circular in cross-section and lies wholly within the almost completely bony channel. A dark, amorphous material fills the vessel and no red or white blood cells are visible. Three to five layers of thin squamous epithelial cells comprise the vessel walls which are thin and fragile.

A variety of vessels traverse the crus, tarsus and foot of mammals including: distal trunks of the saphenous vein, artery and

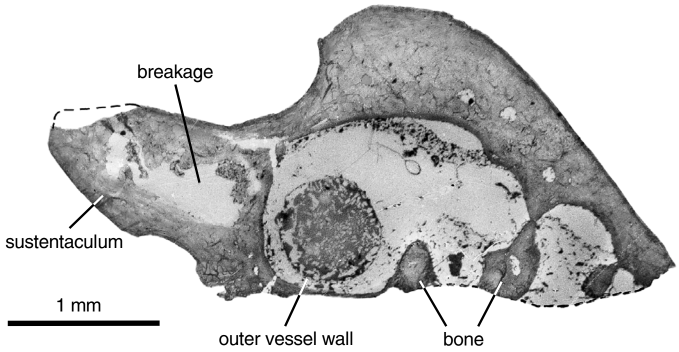

Fig. 2. Histological cross-section through the ectal prominence of a calcaneus (AMNH AWBB100) of *Ochotona princeps* (figure reversed for comparison).

nerve, as well as trunks of the posterior tibial artery (Crabb 1946); the lateral plantar artery (McNally et al. 1992) and a variety of lymphatic trunks arising from the popliteal and sacral lymph nodes (Pflug and Calnan 1968; Barone et al 1973; Evans and Christensen 1979). From the structure of the walls of the vessel that passes through the pika calcaneus, and the lack of erythrocytes, we infer that the vessel represents a branch of the lymphatic system, although the possibility of a blood vessel should not be ruled out.

Perforations of the mammalian calcaneus that provide channels for small blood vessels, and investments of the bone by ligamentous or muscular attachment, are common. Indeed, these foramina are depicted in nearly every morphological study of this tarsal element, in mammals (e.g., Wood 1940; Barone et al. 1973; Szalay 1985; Lewis 1989). Whereas these minute openings are numerous and infiltrate the calcaneus at various sites, none are known to traverse the calcaneus completely, except for the calcaneal canal of lagomorphs, described above.

It is of interest that, although the proximal and distal calcaneal canal openings are large in all recognized fossil lagomorph calcanea, the calcaneal canal is greatly reduced, or lost, in extant leporids (see "Materials," above). On some leporid calcanea (e.g., *Sylvilagus floridanus*, AMNH-M 242665), the proximal foramen is nearly obliterated, while the distal foramen remains large. On other specimens (e.g., *Lepus arcticus* AMNH-M 19169), both openings are large. Interestingly, some calcaneal specimens of extant forms bear multiple openings (e.g., *Sylvilagus floridanus*, AMNH-M 187038; *Lepus europaeus*, AMNH-M 205731). (To our knowledge, this feature does not occur on any fossil lagomorph calcaneal specimens.) Finally, we regard the reduction in the size of the calcaneal canal in extant leporids as a derived lagomorph feature (see Fong et al. 1995).

Functional morphology.—Rotations of the lagomorph upper and lower tarsal articulations occur along an axis that is perpendicular to the long axis of the crus and foot (Bleefeld and McKenna 1985; Szalay 1985). Moreover, the distal crus is fused (tibiofibula), and there is little, if any, cruropedal or intratarsal space. Thus, passage of any vessel across or between the osseous elements of the ankle is precluded. A passageway within the calcaneus (calcaneal canal) therefore, permits the vessel to span the cruropedal region without bearing the brunt of compressive forces during locomotion. Consequently, the flow of lymph (or blood) is not impeded, even as the bones of the ankle and crus rotate in relation to one another. Moreover, since the vessel exits the calcaneus via an opening that is oriented toward the sole of the foot, the vessel is further protected from any calcaneocuboid rotations that may occur.

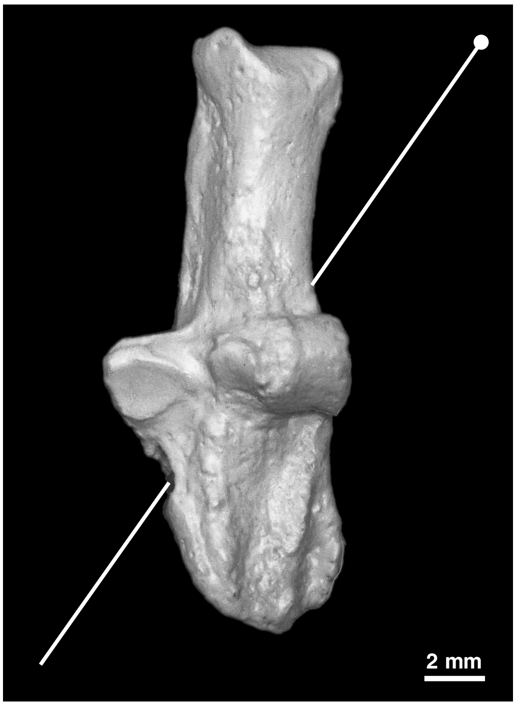

Fig. 3. Leporid calcaneus (AMNH-VP 1257; Hsanda Gol Fm. (Oligocene), Mongolia, in dorsal view. Hatpin shows direction of calcaneal canal.

Conclusions

The calcaneal canal is a feature that is unique to lagomorphs that appeared early in the history of this order, and occurs in all recognized Recent and fossil lagomorph calcanea (e.g., Figs. 1 and 3). As such it increases the store of information from which to draw morphological comparisons among mammalian taxa. With respect to lagomorph phylogeny, both the ancientness of the calcaneal canal and its ubiquity among lagomorphs further emphasize the monophyly of the order. Moreover, no similar feature has been described for any calcaneus recognized as that of a rodent, or other suggested Recent or fossil lagomorph relatives (e.g., macroscelidids, anagalids). Consequently, the morphological distinctiveness of the earliest recognized pedes of lagomorphs from those of macroscelidids and anagalids may indicate a long evolutionary separation of those mammalian orders, including taxa currently considered members of Glires (Lagomorpha, Rodentia).

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