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The occurrence of metatarsal splint bones in ruminants and their potential use in establishing phylogenetic relationships

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Abstract

The occurrence of metatarsal splint bones was examined in 21 ruminant species. Lateral metatarsal splint bones were found in 75% of metatarsal specimens from mature moose (*Alces alces*) on Isle Royale, MI, USA, and 95% of specimens from Alaska and other North American locations. Lateral splints were found in 94% of fossil specimens of *A. alces* from Alaska and in 100% of fossil specimens of *Cervalces scotti*. Thus, it is common feature in the Alceini. Medial metatarsal splints were also found commonly in *A. alces* (69%). Lateral splints are also common in the extant Capreolinae examined (84% of specimens from five species) and Cervinae (88% of specimens from two species). Medial metatarsal splints are less common in the Cervidae (Capreolinae, 23%; Cervinae, 19%). The occurrence of metatarsal splints was examined in nine species from family Bovidae. Only 70% of the specimens had lateral splints, fewer than in the Cervidae ($P=0.14$). The occurrence of medial splints (51%) tended to be greater than in the Cervidae (22%, $P=0.09$). The occurrence of lateral splints in the two extant species of Giraffidae (*Giraffa camelopardalis*, 0%; *Okapia johnstoni*, 40%) was low. In contrast, the occurrence of medial splints in the giraffids was high (*G. c.*, 89%; *O. j.*, 100%). Neither lateral (40%) nor medial splints (0%) were common in *Antilocapra americana*. Overall, there is considerable variation among species in the percent occurrence of metatarsal splint bones. Detailed comparison of splint bone occurrence may provide information that is useful in resolving some phylogenetic relationships among ruminant species. While there appear to be general patterns of occurrence of metatarsal splint bones that typify and distinguish Cervidae and Bovidae, the Giraffidae and Antilocapridae do not follow either of these patterns. We conclude that each ruminant family has followed an independent pathway in the reduction of metatarsi II and V, resulting in different patterns of occurrence of metatarsal splint bones. Thus, the usefulness of these as characteristics for resolving phylogenetic relationships among families is questionable.

Key words: Ruminant, metatarsus, phylogeny.

1. Introduction

The highly derived nature of ruminant limbs has provided us with a rich source of characters that can be used to assist in phylogenetic analyses (Brooke 1878; Heintz 1963; Janis and Scott 1987; Gentry 1992; Gatesy & Arctander 2000; Hernández Fernández & Vrba 2005). Characteristics of the metapodials have been the subject of extensive investigation in this regard. The presence and structure of metacarpal II and V have been reported in the descriptions of most ruminants. Descriptions of metatarsi II and V are conspicuously absent for ruminant species outside of the Tragulidae in which complete metatarsi II and V are present. Recently, a lateral metatarsal splint bone was described in a population of North American moose (*Alces alces*) from Isle Royale National Park, USA (Silvia et al. 2011). One objective

of this research was to describe the presence of the lateral metatarsal splint bone in other populations of moose and extend these observations more broadly in cervids and other ruminants. The second objective of this research was to document and characterize the occurrence of the medial metatarsal splint bone from a diverse group of ruminants. The potential utility of these characters in delineating phylogenetic relationships among ruminants is examined.

2. Material and Methods

The presence of lateral and medial metatarsal splint bones was evaluated in 21 species of ruminants. The most extensively studied species, both in numbers and subpopulations, was North American moose (*Alces alces*). The occurrence of the lateral

Table 1: Taxa (in addition to *Alces alces* described in text) in which the presence of metatarsal splint bones was examined. The sources of metatarsals and numbers of specimens observed are also indicated. AMNH: American Museum of Natural History, New York, USA. MCZ: Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA. NHM: Natural History Museum, London, United Kingdom. NMLN: Naturhistorisches Museum Landessammlung für Naturkunde Rheinland-Pfalz, Mainz, Germany. NJSM: New Jersey State Museum, Trenton, NJ, USA. OHS: Ohio Historical Society, Columbus, OH, USA. SMNK: Staatliches Museum für Naturkunde di Karlsruhe, Germany. UKAFS: University of Kentucky, Department of Animal and Food Sciences Collection, Lexington, KY, USA. UKNHM: University of Kansas, Natural History Museum, Lawrence, KS, USA.

Family	Subfamily/tribe	Genus/species	Housing Institution*	Number of specimens examined
Cervidae	Capreolinae	<i>Odocoileus hemionus</i>	AMNH	17
Cervidae	Capreolinae	<i>Odocoileus virginianus</i>	AMNH NHM OHS UKAFS	12 2 1 23
Cervidae	Capreolinae	<i>Capreolus capreolus</i>	NHM SMNK NMLN	12 1 8
Cervidae	Capreolinae	<i>Rangifer tarandus</i> (caribou)	AMNH NMLN NHM UKAFS	9 1 2 2
Cervidae	Capreolinae	<i>Rangifer tarandus</i> (reindeer)	AMNH NHM UKAFS	2 4 12
Cervidae	Capreolinae	<i>Cervalces scotti</i>	AMNH NJSM OHS UKNHM	1 1 2 1
Cervidae	Capreolinae	<i>Cervalces latifrons</i>	SMNK NMLN	7 22
Cervidae	Cervinae	<i>Cervus canadensis</i>	AMNH UKAFS	20 10
Cervidae	Cervinae	<i>Cervus elaphus</i>	AMNH SMNK	23 5
Bovidae	Bovini	<i>Bos taurus</i>	UKAFS	30
Bovidae	Bovini	<i>Bison bison</i>	MCZ UKAFS NHM	1 4 4
Bovidae	Bovini	<i>Bison bonasus</i>	NMLN NHM	2 2
Bovidae	Boselaphini	<i>Boselaphus tragocamelus</i>	NHM UKAFS	4 3
Bovidae	Caprini	<i>Budorcas taxicolor</i>	NHM	5
Bovidae	Caprini	<i>Ovis aries</i>	UKAFS	7
Bovidae	Caprini	<i>Ovibos moschatus</i>	NHM NMLN	3 1
Bovidae	Tragelaphini	<i>Tragelaphus oryx</i>	NHM	5
Bovidae	Aepycerotini	<i>Aepyceros melampus</i>	NMLN NHM	1 5
Giraffidae		<i>Giraffa camelopardalis</i>	MCZ NHM	1 8
Giraffidae		<i>Okapia johnstoni</i>	MCZ NHM	2 3
Antilocapridae		<i>Antilocapra americana</i>	MCZ UKAFS	6 1

splint bone and its morphology has been previously described in great detail for a population of *Alces alces* from Isle Royale National Park, USA (Silvia et

al. 2011; see Fig. 1). The precise origin of the moose on Isle Royale is not known. The island is located in Lake Superior, approximately 30 km from the Onta-



Figure 1: Three views of the lateral metatarsal splint bone (arrow points to the distal end) in a specimen from *Alces alces* (UKAFS 2100 013).

rio, Canada coastline. The founding animals for this population could be from either *A. alces americana* or *A. alces andersoni* subspecies; however, the Isle Royale moose are morphologically different from either of these subspecies (Peterson et al. 2011). These metatarsal specimens are currently housed at Michigan Technological University's (MTU) Ford Center in Alberta, MI, USA. Recognizing that the Isle Royale population has descended from a very small number of founder animals, the occurrence of this splint bone has now been examined in three other North American moose populations. One population consisted of modern Alaskan moose (subspecies *A. alces gigas*). Included in this set are specimens housed at 1) the Museum of the North, University of Alaska, Fairbanks, AK, USA (collected from Denali National Park; $n = 65$), 2) MTU's Ford Center in Alberta, MI, USA (collected in the Kenai National Wildlife Refuge (KNWR); $n = 95$), 3) the American Museum of Natural History (AMNH), New York, NY, USA (collected throughout Alaska; $n = 6$) and 4) the Field Museum of Natural History (FMNH), Chicago, IL, USA (collected throughout Alaska; $n = 3$). Another group of metatarsi was from late Pleistocene age, fossil material collected in an area 10–35 km north of Fairbanks, AK (Frick 1930; Wilkerson 1932), part of the Frick collection at the AMNH ($n = 49$). These are presumed to be from subspecies *A. alces gigas* as well. The last set of *A. alces* specimens was collected from a variety of sites in Canada and the United States (excluding Alaska) and included subspecies *A. alces americana*, *A. alces andersoni* and *A. alces shiras*. This population will be referred to as mainland moose throughout the rest of the manuscript. These specimens are housed at 1) MTU's Ford Center in Alberta, MI (collected by the Michigan and Minnesota Departments of Natural Resources ($n = 20$), 2) the AMNH ($n = 7$), 3) the FMNH ($n = 1$), 4) Brown University ($n = 1$), 5) Harvard University ($n = 2$) and 6) the

University of Kentucky ($n = 3$). Only 13 metatarsi from *Alces alces* (Isle Royale, $n=3$; mainland, $n=10$) were examined for the presence of medial splint bones.

As noted above, we have extended our observations on the occurrence of metatarsal splint bones to other ruminants. The species and the sources of skeletal materials are listed in Tab. 1. Data used in this study were from skeletally mature animals only. Skeletal maturity was defined as having a distal metatarsal epiphyseal growth plate that was no longer visible as a suture. The morphology of metatarsal splint bones in other adult ruminants was assumed to be similar to *Alces alces* in that the splint bones are fused to the corresponding cannon bone (fused metatarsi III and IV). Splint bones can be physically removed during preparation, as is commonly observed in *Alces alces*, but a break at the point of fusion is typically visible.

The percent of specimens displaying lateral and medial metatarsal splint bones was calculated for each species and for each of the four specific subpopulations within *Alces alces*. Differences in the percent occurrence of the metatarsal splint bones within specific populations of *Alces alces* were determined by Chi-square using the FREQ procedure of SAS (SAS, 1985). The effect of subfamily within the Cervidae (Capreolinae versus Cervinae) on the percentage of specimens with metatarsal splint bones was determined by analysis of variance using the GLM procedure of SAS (SAS, 1985). The effect of family (Cervidae versus Bovidae) was determined in a similar manner.

3. Results and Discussion

A lateral metatarsal splint bone is quite common in North American moose (*Alces alces*). As reported previously, approximately 75% of adult moose from Isle Royale have this splint bone (Silvia et al. 2011). The splint bone is more common in the Alaskan subspecies (*Alces alces gigas*, 95%) and the mainland moose (95%, Fig. 2) ($P < 0.01$). The Isle Royale population is clearly a unique population. The Isle Royale animals are the descendants of a relatively small number of moose that first colonized the island in the early 1900s (Peterson 1977). They have been genetically isolated for over 70 years. It is not surprising that the occurrence of the lateral metatarsal splint in this group differs from other North American moose. The metatarsus of moose from Isle Royale is shorter and less sexually dimorphic (Peterson et al. 2011). A much smaller subset of metatarsi was examined for the presence of the medial metatarsal splint bone. The medial splint is quite prevalent (69%) in this subset.

Based on preliminary observations, the lateral metatarsal splint bone appears to be quite common in European moose (100%, $n=5$). The lateral splint bone is also common in fossil *Alces alces* from Alaska (94%) and in fossil *Cervalces*. It was present in

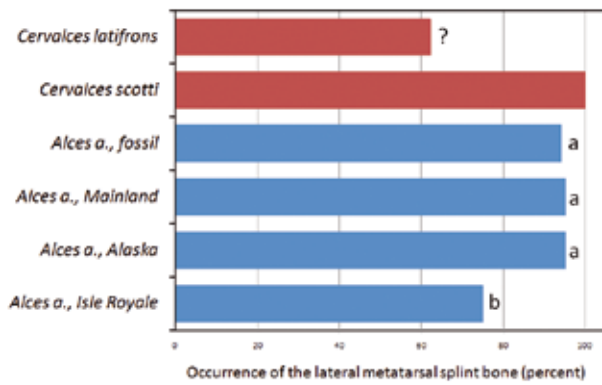


Figure 2: The occurrence of lateral metatarsal splint bones (% of specimens with the splint bone) in four populations of *Alces alces* (blue bars) and 2 species of *Cervalces* (red bars). *A. a.*, Isle Royale (n=366); *A. a.*, Alaska (n=132); *A. a.*, mainland (n=22); *A. a.*, fossil (n=49), *C.s.* (n=7); *C.l.* (n=29). a, b: *A. a.* subgroups with different superscripts are different (P<0.01).

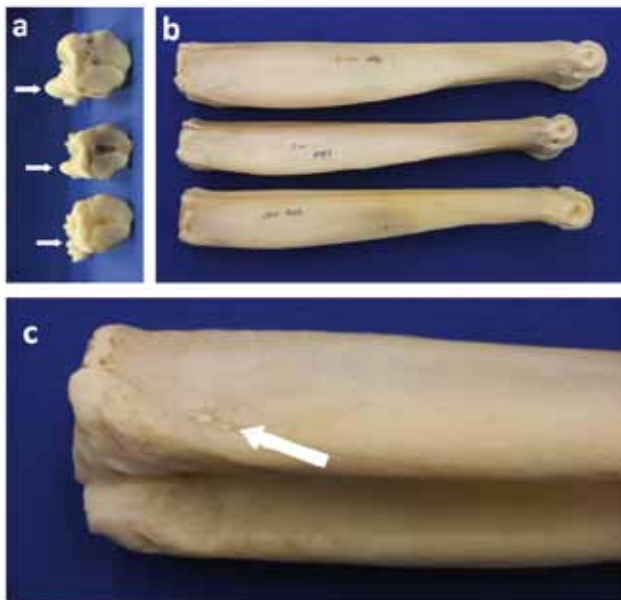


Figure 4: The morphology of three right metatarsals in *Rangifer tarandus*. (a) View of the proximal articular surface, plantar surface to left. Arrows point to the plantar extension of the lateral margin for each specimen. (b) View of the lateral side of the same three metatarsals with the plantar surface down, distal end to the right. The plantar extension of the lateral margin is clearly evident. The top specimen has a lateral metatarsal splint bone. The splint is shown in greater detail in (c). The other two specimens do not have lateral splint bones. (UKAFS 2100 041, UKAFS 2100 046, UKAFS 2100 068).

all North American specimens of *Cervalces scottii* collected from peat bogs (100%, n=5; Fig. 2). Lateral splint bones were not commonly observed in metatarsals from *C. scottii* that were collected from river-deposited, gravel beds (25%, n=4). These ‘river’ specimens were severely worn, particularly on the plantolateral edge, where the lateral metatarsal splint bone is found. We believe that the specimens recovered from the peat bogs are more completely preserved and represent the distribution of the la-

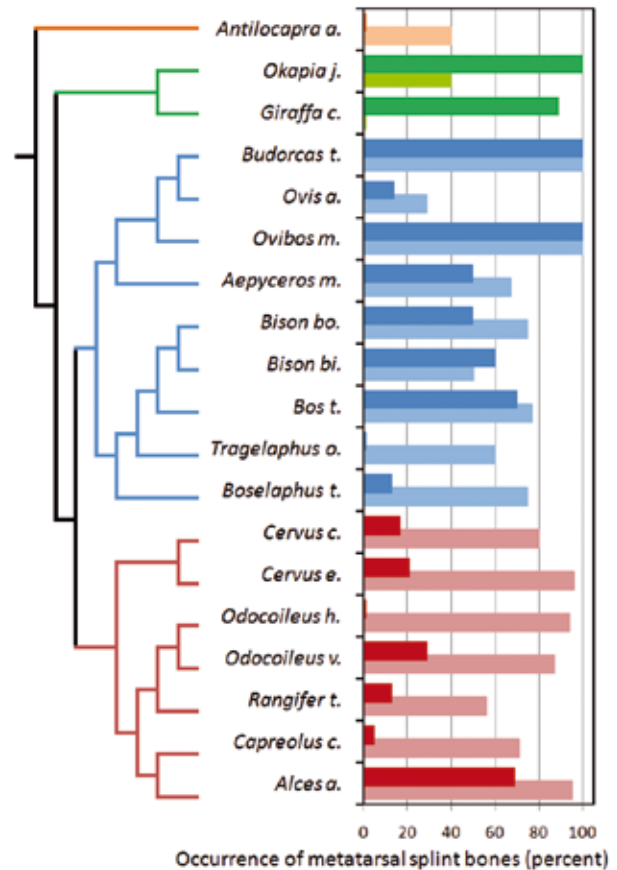


Figure 3: The occurrence of lateral (lighter shaded bars) and medial (darker shaded bars) metatarsal splint bones (% of specimens with the splint bone) in extant Cervidae (7 species, red line/bars), Bovidae (9 species, blue line/bars), Giraffidae (2 species, green line/bars) and Antilocapridae (1 species, orange line/bars). The phylogeny is based on Hassanin et al. (2012), with the placement of *Bison bonasus* modified based on Buntjer et al. (2002), Verkaar et al. (2004), Nijman et al. (2008) and Hassanin et al. (2013).

teral metatarsal splint bone more accurately. Fossil specimens from the European *Cervalces latifrons* (n=29) were also examined. All of these were recovered from river-deposited, gravel beds. As with the specimens of *C. scottii*, many of these were severely worn. Despite the poor condition, 62% of the specimens showed clear traces of the lateral metatarsal splint bone. Undoubtedly, the percentage would be higher in specimens collected from peat bogs but none have been examined at this point in time. Thus, the lateral metatarsal splint bone appears to be an extremely common feature throughout the tribe Alceini. None of the fossil *Alces* or *Cervalces* metatarsals were specifically examined for the presence of a medial metatarsal splint bone.

We examined metatarsals of four other extant species from the subfamily Capreolinae. The lateral metatarsal splint bone was very common in *Odocoileus hemionus* and *Odocoileus virginianus* (Fig. 3). It was also common in *Capreolus capreolus*. The splint bone was not quite so common in *Rangifer tarandus*. This was true for both forms within the species, North American caribou (64%) and European reindeer (50%). The low percentage of expression in *R.*

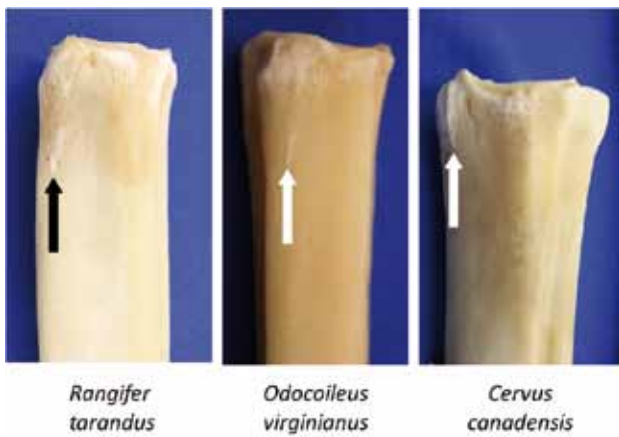


Figure 5: The typical morphology of the lateral metatarsal splint bones in specimens of three species from the Cervidae. Splint bones are indicated by arrows. (*Rangifer tarandus*: UKAFS 2100 043; *Odocoileus virginianus*: UKAFS 2100 0009; *Cervus canadensis*: UKAFS 2100 062).

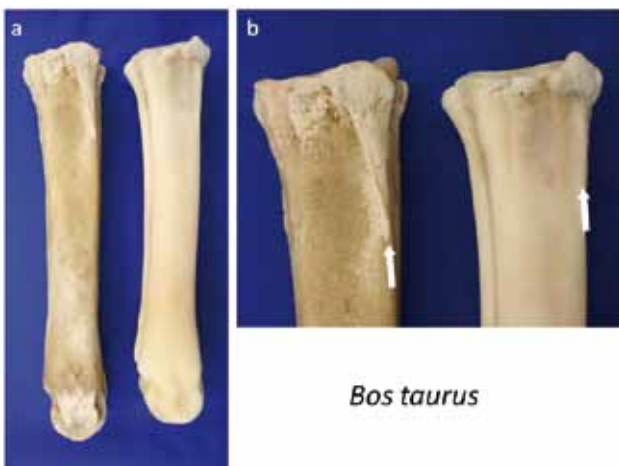


Figure 6: The morphology of two left metatarsi in *Bos taurus*. (a) View of the lateral side. The specimen on the left (UKAFS 2100 083) has a distinct lateral metatarsal splint showing the typical morphology in bovids. The specimen on the right (UKAFS 2100 030) does not have a lateral metatarsal splint bone. The area where the splint is found is shown in more detail in (b).

tarandus may be explained by its unique metapodial structure. Throughout the length of the diaphysis, the lateral and medial margins extend in the plantar direction, creating a very deep plantar gully (Fig. 4). These extended margins may facilitate movement of the metapodial portion of the limb through snow. The splint bone may be integrated into this expansion to such a degree that it is no longer visible in many specimens. For all of these species, the lateral metatarsal splint bone is much smaller than it is in *Alces* and *Cervalces* (Fig. 5). The medial metatarsal splint bone is much less common in these other Capreolinae (0-29%) than in the Alceini (Fig. 3).

The only two species from the subfamily Cervinae that we have examined thus far are *Cervus canadensis* and *Cervus elaphus*. The lateral metatarsal splint bone was extremely common in both species (Fig. 3). Overall, the percentage occurrence of lateral

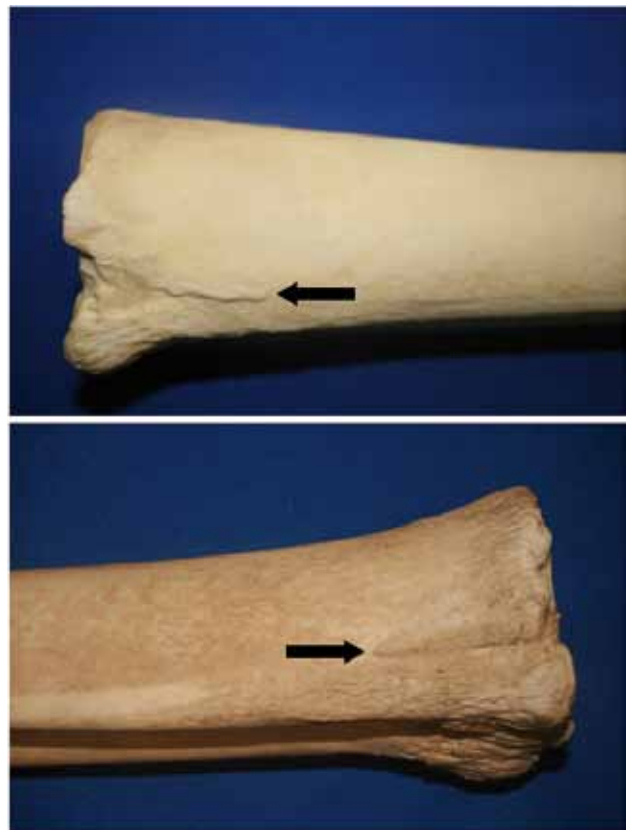


Figure 7: The morphology of two metatarsi in family Giraffidae (top panel: *Okapia johnstoni*, NHM 1971-1738; bottom panel: *Giraffa camelopardalis*, NHM 1950-10-18-3). Both panels are views of the medial side. Both specimens have prominent medial metatarsal splint bones (arrows).

metatarsal splint bones in the Cervinae (88%) is not different from the Capreolinae (84%, $P > 0.60$). The occurrence of the medial metatarsal splint bone for these two species of Cervinae can be seen in Fig. 3. Looking more broadly at the cervids, the occurrence of the medial splint was low in the Cervinae (19%) and not different from the Capreolinae (23%, $P = 0.85$). Thus, *Alces alces* seems to be unique among extant cervids examined in the high percentage of specimens with medial metatarsal splint bones.

Nine species from the family Bovidae were also examined. The percentage of specimens in which a distinct lateral metatarsal splint bone was present for each species is shown in Fig. 3. The morphology of metatarsi from *Bos taurus* with and without lateral splints is shown in Fig. 6. There is considerable variation in the percentage of occurrence within the Bovidae. In many cases, the number of specimens examined is relatively low. The bovid species examined come from 5 tribes: Boselaphini ($n = 1$ species), Tragelaphini ($n = 1$ species), Bovini ($n = 3$ species), Aepycerotini ($n = 1$ species), and Caprini ($n = 3$ species) (see Tab. 1 for individual species within tribe). There do not appear to be any obvious differences among tribes. This interpretation may be premature considering the relatively small number of species examined to date. Overall, the percentage occurrence of the lateral metatarsal splint bone tended to be grea-

ter in the Cervidae (85%) than in the Bovidae (70%; $P=0.14$). The percentage of specimens in which a distinct medial metatarsal splint bone was present for each bovid species is shown in Fig. 3. Again, there is considerable variation in the percentage of occurrence within the Bovidae. As with the lateral metatarsal splint bone, there do not appear to be any obvious differences among tribes in the occurrence of the medial metatarsal splint bone. In contrast to the lateral splints, the percentage occurrence of the medial metatarsal splint bone tended to be greater in the Bovidae (51%) than in the Cervidae (22%, $P=0.09$).

The other ruminants examined were from the families Giraffidae (*Giraffa camelopardalis*, *Okapia johnstoni*) and Antilocapridae (*Antilocapra americana*). The giraffe is unique among the ruminants in that none of the nine specimens examined had a lateral metatarsal splint bone (Fig. 3). Only two of the five okapi specimens had lateral splint bones (Fig. 3). Interestingly, the vast majority of both the giraffes (89%) and the okapi (100%) had pronounced medial metatarsal splint bones (Fig. 3). The morphology of the medial splint bone in the two giraffids species is shown in Fig. 7. These observations agree with a previous report on the occurrence of metatarsal splint bones in Giraffidae (Fraser 1951). The lateral metatarsal splint bone is present in just 40% of the *Antilocapra americana* (pronghorn) specimens examined (Fig. 3). None of the specimens showed any evidence of a medial metatarsal splint bone (Fig. 3).

Based on these observations, one can make some generalizations about the presence of splint bones in bovids and cervids. For all cervids and with just a single exception in the bovids (*Ovis aries*), at least 50% of the metatarsal specimens within a species have a lateral metatarsal splint bone. The percentage of specimens within a species with a medial metatarsal splint bone is much lower and more variable. For all cervids and with just a single exception in the bovids (*Bison bison*), the percentage of metatarsal specimens within a species that have a lateral splint bone exceeds the percentage with a medial splint. The percentage of specimens with a lateral splint bone tends to be greater in the cervids than in the bovids. In contrast, the percentage of specimens with medial splint bones tends to be greater in the bovids than in the cervids. Both species from the Giraffidae appear to be quite different from the cervids and bovids in that the lateral metatarsal splint bone is not common while the medial metatarsal splint bone is extremely common. In contrast to the general distribution of metatarsal splint bones in cervids and bovids, fewer than half of the pronghorn specimens had lateral splints and none of them had medial splints. Thus, neither the Giraffidae nor the Antilocapridae can be associated with either the Cervidae or the Bovidae based on the presence of metatarsal splint bones.

These major differences among ruminant fami-

lies in metatarsal splint bone occurrence may not be surprising given that the divergence of these families occurred approximately 20 million years ago (Bibi 2013). Common ancestors of these families may have been similar in metatarsal development to late Oligocene/early Miocene stem pecorans like *Gelocus* or *Dremotherium*. Metatarsi III and IV are fused to some degree in these species but regression of metatarsi II and V is incomplete (Webb & Taylor, 1980). For example, in *Gelocus*, metatarsi II and V are reduced in diameter but only the middle portion is completely lost. Both proximal and distal splints remain for both metatarsi II and V (Kowalevsky 1876). Regression of metatarsi II and V appears to have occurred relatively rapidly in the early Miocene radiation of pecoran ruminants. In *Eotragus cristatus*, one of the earliest known bovids from the mid Miocene, metatarsal V is reduced to a short, proximal splint bone (Filhol 1891: plate XLI). The splint bone depicted is similar in length but much more robust than the ones found in extant bovids. There does not appear to be a splint bone on the medial aspect of the metatarsus. In contrast, a very long, thin, lateral splint bone is attached proximally in *Micromeryx flourentianus*, an early moschid recovered from the same locality as *E. cristatus* described above (Filhol 1891: plate XXV). Thus, it appears that these two ruminant families may have differed in the rate at which the lateral metatarsal regressed.

The modern splints may represent differing degrees of regression of these digits that have occurred independently since divergence of the families, as suggested by Janis & Scott (1987). The difference in the occurrence and size of the splint bones could also represent a difference in atavistic expression of previously regressed digits. The large variation within families supports this concept of independent progress in regression and/or atavistic reoccurrence. In some ways, this is similar to the well described differences in the pattern of metacarpal regression in Capreolinae versus Cervinae (Brooke 1878). In Cervinae, proximal splints of metacarpi II and V are retained. This is referred to as the plesiometacarpal condition. These splint bones are typically more substantial than the ones in the hind limb described in this report. They are most commonly separable from the metacarpus, each splint having a distinct articulation surface at the proximal end where it meets the metacarpus. In Capreolinae, the proximal portions of metacarpi II and V regress while the distal portions are retained as splints. This is commonly referred to as the telemetacarpal condition. The distal end of each telemetacarpal splint includes an articulation surface that meets with the proximal phalanx of the corresponding regressed digit. Differences among ruminant families can also be seen in the degree of regression of the phalanges in both the front and hind limbs. In all of the cervids we have examined, digits 2 and 5 are comprised of three complete and distinct phalanges (Hamilton & Silvia, unpublished

observations). Small, keratinized hoofs (dewclaws) are associated with digits 2 and 5, the distal phalanges lying within these hooves. Bovids have either two phalanges (middle and distal) or only a single phalanx (distal) in digits 2 and 5. They also have keratinized dewclaws for both digits. In contrast, the phalanges are completely regressed in digits 2 and 5 of both the giraffids and the pronghorn. Neither group has keratinized dewclaws. Thus, it appears that the ruminant families have pursued independent pathways in reducing the size and occurrence of digits 2 and 5.

In conclusion, both lateral and medial metatarsal splint bones are commonly found in ruminants. These represent the regressed elements or atavistic expression of metatarsi II and IV. There is considerable variation among species in the percent occurrence. Detailed comparison of the occurrence and other attributes of these splint bones may provide information that is useful in resolving some phylogenetic relationships among ruminant species. Based on the limited number of species described thus far, there appear to be distinct patterns of occurrence for the four ruminant families examined in this report. This suggests that independent, convergent patterns of regression may have occurred. Thus, the utility of these structures in resolving phylogenetic relationships among the ruminant families seems questionable.

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