

Limb elements of *Cervus* sp. from lower Karewa Formation of Jammu and Kashmir, India, comments on functional morphology and palaeobiogeography

RAMAN PATEL, SYED YAFIT ALI SHAH, AAMIR AHMAD KHANDAY, MOHD WAQAS & RAJENDRA SINGH RANA*

JPSI



Limb bones of *Cervus* sp. have been recovered for the first time from the lower Karewa Formation (Hirpur Formation) exposed along the River Romushi, Khaigam, Pakharpora, Budgam District, Jammu and Kashmir, India. The 28 main morphological characters of present fossil tibia, astragalus, calcaneus, cubionavicular, ectomesocueiform and metatarsal have been selected to compare with the fossils and recent limb bones of eleven species of Cervidae, including *Cervus elaphus* (red deer), *Odocoileus hemionus* (mule deer), *O. virginianus* (white-tail deer), *Dama dama* (fallow deer), *Capreolus capreolus* (roe deer), *Muntiacus reevesi* (Reeve's muntjak), *Hydropotes inermis* (Chinese water deer), *Alces alces* (moose deer), *Megaloceros giganteus* (Irish elk deer), *Cervalces* sp. (Elkmoose deer), *Arvernocrous ardei*, and three outgroup taxa, such as Giraffidae, Bovidae and Camelidae. It shows that the maximum characters of limb bones have close affinities with the *Cervus elaphus* and presumably, these bones refer to *Cervus* sp. The study also suggests that the Cervidae originated from Eastern Eurasia/ Asia in the late Oligocene or early Miocene and migrated to Europe and the Indian subcontinent during the middle Miocene. The functional morphology (ecomorphology) of limb bones supports the hypothesis that the *Cervus* sp. have had a cursorial habitat and lived in an open forest (forest and grassland).

ARTICLE HISTORY

Manuscript received 27/01/2021
Manuscript accepted 06/05/2021

Keywords: Karewa Formation, Plio-Pleistocene, Cervidae, Limb bone, Jammu and Kashmir

Department of Geology, HNB Garhwal University, Srinagar Garhwal, Uttarakhand, India
*Corresponding author's e-mail: rajendra.rana1@gmail.com

INTRODUCTION

The Kashmir Valley is bounded in the north by the Main Great Himalayan Range and the southern sides by the Pir Panjal Range, which evolved during the late Cenozoic time uplift of the Pir Panjal Range. The ancient drainage system has been blocked due to the uplift of the Pir Panjal Range, resulting in the development of a large basin (Karewa Basin). The basin received by the thick sequence of glaciolacustrine sediments of the Karewa Group, which came from the higher Himalayan ranges (Godwin-Austin, 1859; Wadia, 1941; Farooqui and Desai, 1974; Burbank and Johnson, 1982, Agrawal *et al.*, 1985, 1989; Kusumgar *et al.*, 1985; Agrawal and Agrawal, 2005).

The initial geological investigation was done by De Terra and Paterson, 1939, followed by several workers and divided Karewa into two lithological units, which are lower Karewa (Hirpur Formation) and Upper Karewa (Nagum Formation), separated by an angular unconformity (Bhatt, 1976; Singh, 1982; Burbank and Johnson, 1982, 1983; Pant *et al.*, 1978; Burbank, 1983; Agrawal *et al.*, 1989). Later, Bhatt (1989) divided the Karewa Group into three formations: Hirpur,

Nagum, and Dilpur formations. The Hirpur Formation consists of green to bluish grey mud, light grey sandy clay, fine to coarse-grained sand, conglomerate, thin bands of lignite and lignitic clay. The Nagum Formation is made up of fine to coarse-grained sand and ochre sandy clay, ochre and cream coloured marl and gravel. The Dilpur Formation mainly consists of a brown silt (Fig. 1).

De Terra reported the initial vertebrate fauna from the Karewa Group, 1934 (in Pasco, 1973) followed by others Hora, 1937; Badam, 1968, 1972; Tripathi and Chandra 1972; Tiwari and Kachroo, 1977; Sahni, 1982; Bhat, 1982; Sahni and Kotlia, 1985; Kotlia, 1990; Kotlia *et al.*, 1982. The invertebrate fauna, such as ostracodes, bivalve and gastropods, as well as the plant fossils such as charophytes, pollens, spores and diatoms, were described by several workers (Bhargava, 2015, reference therein).

The age of the Hirpur Formation has been suggested to be early Pliocene-Pleistocene by Bhatia *et al.* (1998) based on diagnostic charophyte flora such as *Nitelopis megarensis*, *Lychnothammus brbatus*, *Chara globularis*, and *C. vulgaris*. The palaeomagnetic and fission track dating of volcanic ash beds of different sections have carried out by several workers and suggested an age of 2.4 ± 0.3 Ma (Burbank and Johnson,

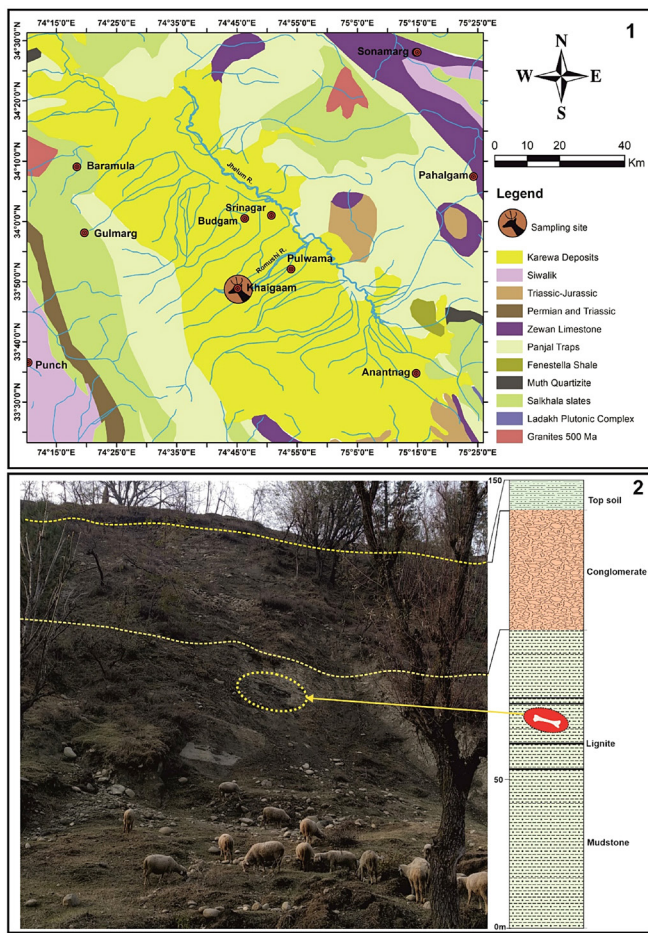


Fig. 1. (1) Geological map of Kashmir Basin (after Thakur and Rawat, 1992); (2) Field photograph of sampling site with yellow circle denote where is the sample from and Litholog of sampling site, bar scale in Meters.



Fig. 2. Right limb of *Cervus* sp. (1) Lateral view; (2) Medial view; (3) Posterior view; (4) Anterior view; (1. Tibia; 2. Calcaneus; 3. Astragalus; 4. Navicular cuboid; 5. Ectomesocuneiform; 6. Metatarsal); bar scale = 2 cm

1982; Kusumgar *et al.*, 1985) and the base layer is 2.48 Ma (Agrawal *et al.*, 1989; Kotlia, 1990, 1992, 1994; Kotlia and Koenigswald, 1992).

The present paper describes detailed morphology and comparison *Cervus* sp. limb bones recovered for the first time from the lower Karewa (Hirpur Formation), Khaigam, Pakharpora, Budgam District, Jammu and Kashmir, India; situated about 59 km south of Srinagar (latitude 33°48'45.49": longitude 74°45'17.37", Fig. 1). The limb elements represent the distal part of the tibia, astragalus, calcaneus, cubonavicular, ectomesocuneiform and metatarsal, which belong to the same animal (Fig. 2). Although, cervids are known from the Indian subcontinent by the antlers and dentition mainly from Miocene to Pleistocene sequence of Siwalik and Karewa (Lydekker, 1876, 1884; Brown, 1926; Colbert, 1935; Azzaroli, 1954; Nanda, 2002; 2008; Kotlia, 1990; Arif and Shah, 1991; Akhtar *et al.*, 1999; Gaffar, 2005; Ghaffar *et al.*, 2004, 2006, 2010, 2011). The present finding is the first detailed description of the tibia, tarsus and metatarsal from the Indian subcontinent. In Indo-Pakistan, the cervids are represented by five species, viz. *Cervus simplicidens*; *C. triplidens*, *C. sivalensis*, *C. punjabiensis* and *C. rawati*.

We also throw light on the hind limb element functional morphology because the bones belong to the same animal. The hock (ankle) joint mechanism works to transform rotational motion to linear motion by three major joints, such as the tibia- astragalus, astragalus –calcaneum and astragalus-cubonevicular (Schaeffer, 1947). The calcaneum functions as a lever arm for the distal rear limb (metatarsal and phalange), due to the gastrocnemius muscle contraction with them in leaving conditions and extended the forward movement of the limb at the parasagittal plane, but, the distal condyle part of the metatarsal is missing. The calcaneum anterior process is missing, articulating with the malleolus and at several places with the astragalus, especially sustentaculum tali. Schaeffer (1947) suggested that the hock joint motion is relatively restricted at the parasagittal plane. The hock joint function depends on the tarsus motion, which indicates the speed and saltatorial to save from the carnivore predators.

In the present paper, we proposed the type of habitat from the functional morphology, adaption for running fast and straight over the level of uneven and plane terrain. So the use of functional morphology to predict palaeo habits in the limited sense and for this method does not require taxonomic identification of the fossil used beyond the family level (DeGusta and Vrba, 2003).

The 28 morphological characters of tibia, astragalus, calcaneus, cubonavicular, ectomesocuneiform, and metatarsal were used for morphological comparison with the Pliocene to the Recent cervids. The data analyses and the relationship between 11 species of Cervidae, including *Cervus elaphus*, *Odocoileus hemionus*, *Odocoileus virginianus*, *Dama dama*, *Capreolus capreolus*, *Muntiacus reevesi*, *Hydropotes inermis*, *Alces alces*, *Megaloceros giganteus*, *Cervalce* sp., *Arvernocrous ardei*; three outgroup taxa took for comparisons such as giraffe (*Decennatherium pachecoi*), sheep (*Sinocapra willdownsi*) and camel (*Camelops hesternus*). The resulting morphological data shows (Table 1) that the present limb elements have close affinities with *Cervus elaphus*, and presumably, this refers to *Cervus* sp. The general morphological terminology is given in Fig. 3.

Table 1: Morphological characters for the comparison

S.N	Characters	<i>Cervus</i> sp.	<i>C. elaphus</i>	<i>D. Dama</i>	<i>C. capreolus</i>	<i>M. reeverse</i>	<i>H. inermis</i>	<i>A. ardei</i>	<i>Cervace/Alee</i>	<i>M.giganteus</i>	<i>O.hemionus</i>	<i>O.virginianus</i>	<i>D. pachecoi</i>	<i>C. hesternus</i>	<i>Capra</i>
o	“+” symbol showing present character. “?” symbol showing missing or not observe character. “←●” marking the characters in figure plate by arrow.														
Tibia															
1.	Surface (lateral edge) of tibial cochlea (Figure no. 4 a1- a6; ←●) Presence of bulge				+				+	+	?	?	+		+
	Absence of bulge	+	+		+	+	+		+		?	?		+	
2.	Medial malleolus ligament (Figure no.4 b1- b6; ←●) curved upward				+	+		+	+	+	?	?		+	+
	nearly straight	+	+							+	?	?	+		
3.	Latero-anterior and Latero-posterior malleolus divided by (Figure no.4 e1-e6; ←●) Deep and narrow				+			+	+	+	?	?	+	+	?
	Shallow and wide	+	+		+	+				+	?	?			?
4.	Edge of Malleolus facet (Figure no.4 b1- b6; ←●) U shape				+	+	+	+	?	+	?	?		+	+
	L shape	+	+					?		?	?	+			
5.	Distal epiphysis more laterally wide, with respect to diaphysis and a postero-medial surface covered by longitudinal ridges (Figure no.4 c1- c6; ←●) Presence	+	+		+			?		+	?	?	?	?	?
	Absence				+	+		+	+						
6.	Anterior-medial side of the diaphysis bulge (Figure no.4 a1- a6; ←●) Pronounced bulge	+	+					+		+	?	?	?	?	?
	Absence of bulge				+	+	+	+	+						
7.	Latero-posterior edge of main articular surface to the astragalus (Figure no. 4 e1 - e6) More rounded right angle	+	+					+	?	+	?	?	?	?	?
	More acute angle				+	+	+			+					
8.	Latero-posterior edge of the distal epiphysis is (Figure no. 4 d1 – d6) Well distally elongated/ rounded				+	+		+	?	+	?	?	?	?	?
	Rises as a wedge between the main articular surface to the lateral malleolus	+	+			+			+						
Calcaneus															
9.	Sustentaculum tali and articular facet of calcaneal shaft (Figure no.6 b1- b6; ←●) With small step				+			+	+	+	?	?	+	+	+
	Without step	+	+		+	+				+	?	?			
10.	Tuber sulcus (Figure no.6 c1 – c6; ←●) narrow/ small				+	+	+	+	?	?	?	?	?	?	?
	large/ broad	+	+						?	?	?	?	?	+	?
Astragalus															
11.	In Posterior view, Lateral and medial edges of trochlea (Figure no.5 a1- a6; ←●) flat bottom				+	+	+	?	+	+		+	+	+	+
	narrow bottom	+	+		+			?			+				
12.	Medial edge of trochlea is (Figure no.5 b1 – b6; ←●) more steeply inclined				+	+	+	+	?	+	+				
	less steeply inclined	+	+							+		+	+	+	+
13.	Lateral extension of ridge (Figure no.5 a1- a6, ←●) distal > proximal				+										
	distal < proximal	+	+		+				+			+			+
	distal = proximal							+	+	+		+	+		

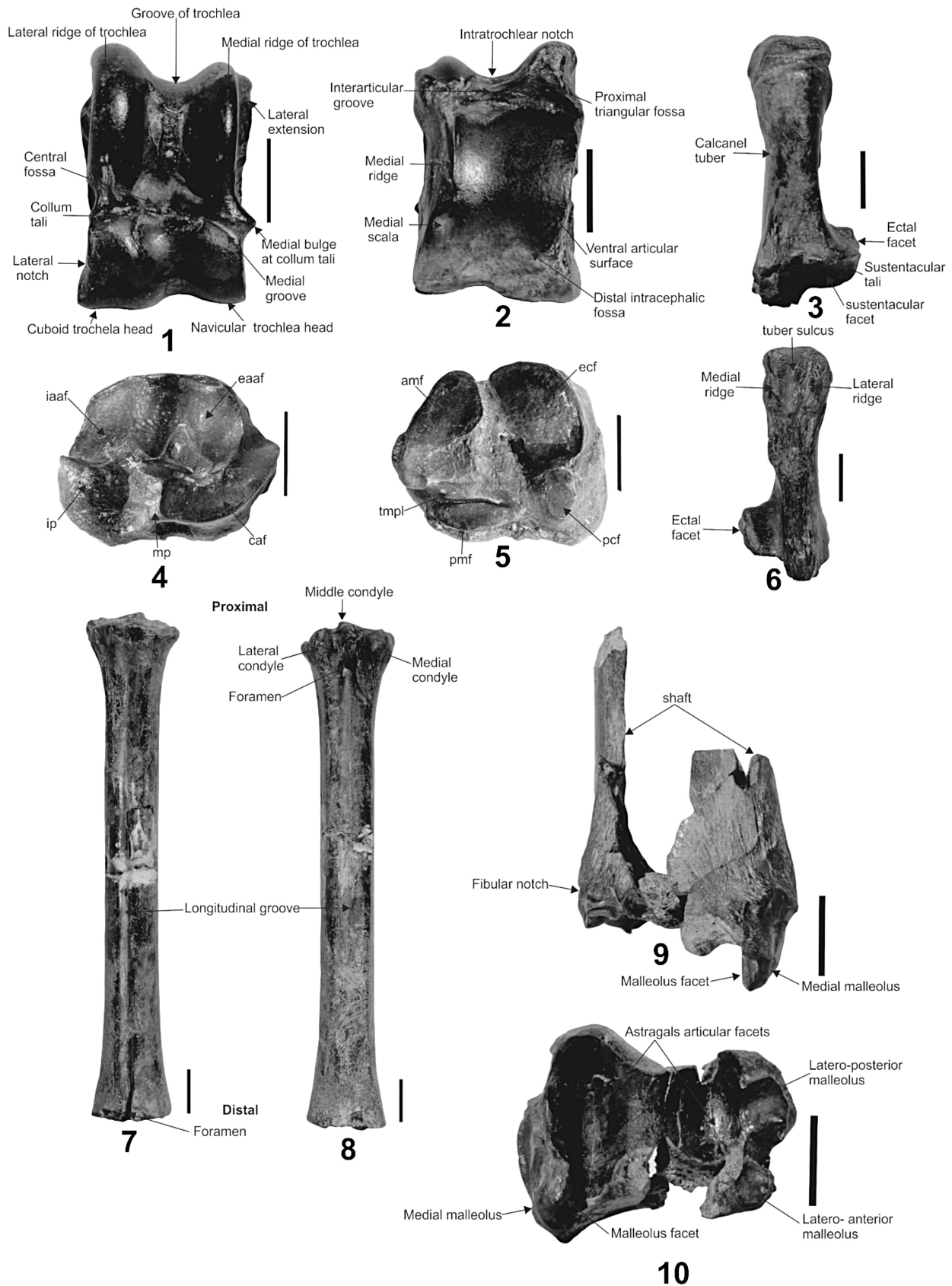


Fig. 3. Representative terminology of (1) Astragalus anterior view; (2) Astragalus posterior view; (3) Calcaneus anterior view; (4) Cubonavicular dorsal view; (5) Cubonavicular ventral view; (6) Calcaneus posterior view; (7) Metatarsal anterior view; (8) Metatarsal posterior view; (9) Tibia Anterior view; (10) Tibia distal end; bar scale = 2 cm

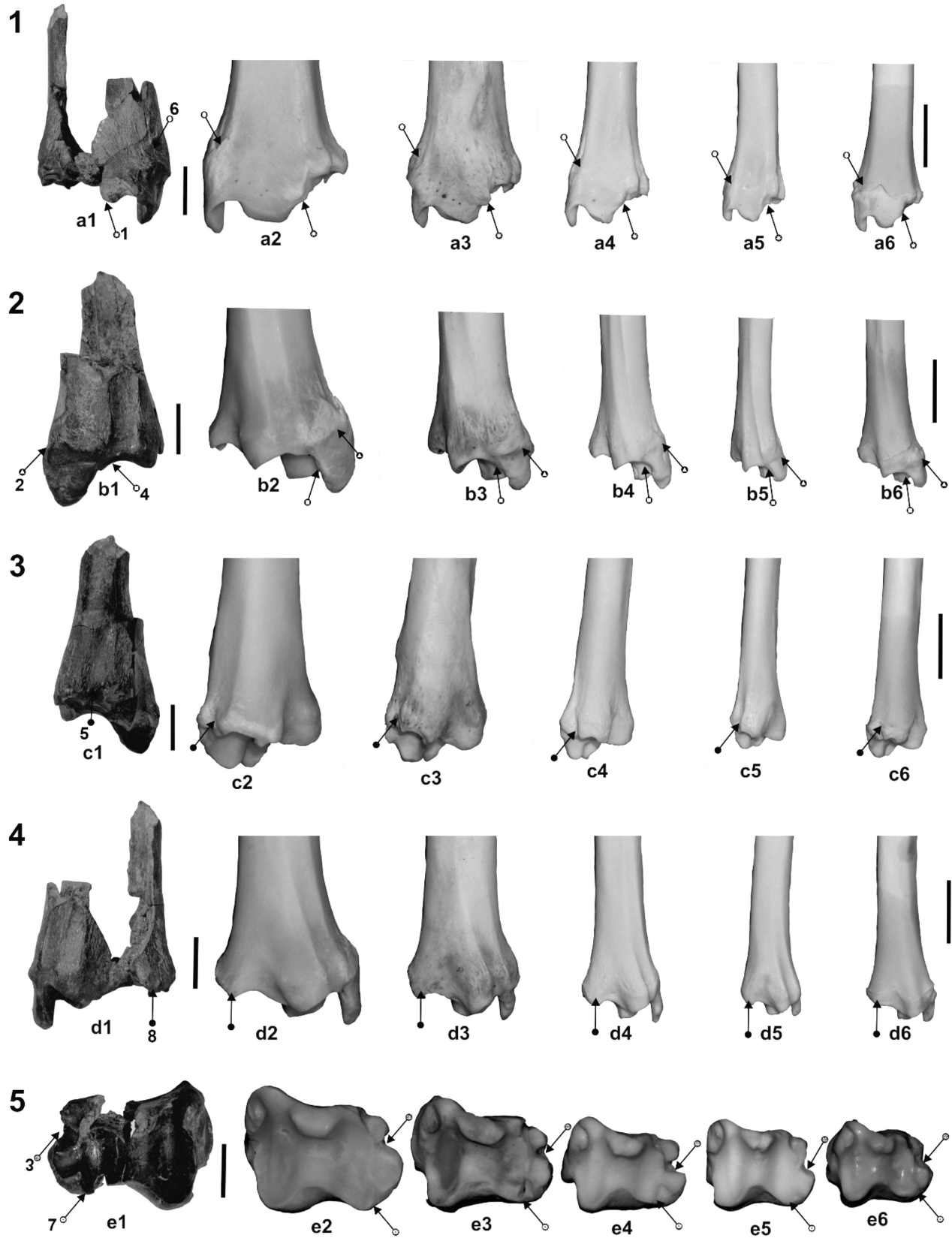


Fig. 4. Tibia (1) Anterior view; (2) Lateral view; (3) Posterior- medial view; (4) Posterior view; (5) Distal end of tibia; right tibia of *Cervus* sp. (a1, b1, c1, d1, e1); left tibia of *Cervus elaphus* (Red deer) (a2, b2, c2, d2, e2); *Dama dama* (Fallow deer) (a3, b3, c3, d3, e3); *Capreolus capreolus* (Roe deer) (a4, b4, c4, d4, e4); *Muntiacus reevesi* (Reeve's muntjuk) (a5, b5, c5, d5, e5) and *Hydropotes inermis* (Chinese water deer) (a6, b6, c6, d6, e6); bar scale= 2 cm; arrow and number show that morphological characters (see table 1; characters no. 1, 2, 3, 4, 5, 6, 7, 8)

MATERIALS AND METHODS

The specimens were recovered from the bluish-grey mud of the lower Karewa (Hirpur Formation), Khaigam, Pakharpora, Budgam District, Jammu and Kashmir, India by handpicking during the field investigation in January 2019 by A.A. Khanday and S.Y.A. Shah. The photographs have been taken with a Nikon DSLR- 5200 camera with 1855 mm lens. The photograph quality and color were enhanced in different types of the colour filter in Microsoft Office, and bone plates were edited using CorelDRAW 17 software. All the specimens are placed at the palaeontology laboratory, Department of Geology, HNB Garhwal University, Srinagar Garhwal, and catalogue no. GU/K- 900 where GU –Garhwal University and K –Karewa.

The recent bone specimens photographs have been taken from the collection on John Rochester link, <https://www.flickr.com/photos/jrochester/albums/72157644273190148>.

Order **Artiodactyla** Owen, 1848

Family **Cervidae** Gray, 1821

Subfamily **Cervinae** Goldfuss 1820

Genus **Cervus** Linnaeus, 1758

Cervus sp.

(Figs. 4 – 9)

Material: The limb elements (GU/KB-900, Fig. 2), metatarsal, cubonavicular, astragalus, and calcaneus are well-preserved and a fragmentary distal end of the tibia.

Horizon and locality: Bluish-grey mud bed of lower Karewa Formation, Khaigam, Pakharpora, Budgam District, Jammu and Kashmir, India.

DESCRIPTION

Tibia: The fragmentary distal part of the right tibia (Fig. 4 a1-e1) consists of the well preserved medial malleolus, tibial cochlea, and posterior process, distal fibula syndesmosis (fibula notch), sulcus for the tendon of flexor digitorum longus, and astragal facets. The distal end of the tibia anteroposteriorly is deeper while mediolaterally wider. The astragal articular facets are covered by the variable size of anterior and posterior processes with well pronounced tibial medial malleolus. They are represented by two nearly straight and parallel grooves, which connect with the astragal trochlea ridges (Fig. 4 e1). The medial side groove is deep, narrow, and more crescentic in shape than the lateral side groove, which is slightly smaller, shallow, and subrounded. The astragal facets or ridges are articulated with the astragal trochlea grooves, which helps to move anterior and posterior processes at the margin of the connecting surface. In lateral view (Fig. 4 b1), a shallow, wider straight furrow is well pronounced where the fibula distal part is connected. The medial malleolus is larger than the anterior and posterior processes, while the anterior process is missing and might have been projecting toward distally. The tibial cochlea has an asymmetrical tip, robust and rugose surface without a bulge at the margin, similar to *Cervus elaphus* (Fig. 4 b2), whereas the bulge is prominent in *Arvernoceros ardei* (Pfeiffer,

2019, Fig. 10 a, b). The malleolus facet is laterally facing and articulates with a collum tali bulge, which controls the maximum tibia movement. The medial malleolus anterior and medial sides have a shallow sub-elliptical fossa or depression (medial collator ligament fossa) for collator ligament mussels attachment. The medial collator fossa at the posterior side, a shallow and broad sulcus, is well distinct, possibly for the tendon attachment of the flexor digitorum longus muscle. The medial malleolus ligament is bent upwards, forming curved to a straight ridge (Fig. 4 b1), while curved in *A. ardei* and straight and blurred in *C. elaphus* (Pfeiffer, 2019; Fig. 10 c, d). The lateroposterior malleolus is large undulating, subelliptical, and latero-anterior malleolus small subrounded, similar to recent *C. elaphus* and *Odocoileus virginianus* (Fig. 4 e1).

Astragalus: The right astragalus is robust, subrectangular in shape (Fig. 5, a 1 to d 1), about 60.05 mm long and 36.80 mm wide. In anterior view (Fig. 5, a 1), the proximal portion of the astragalus is termed trochlea, which consists of two ridges; the lateral trochlea ridge is long, broad, while the medial trochlea ridge is slightly shorter and narrow than the lateral trochlea ridge. These are separated by a broad, nearly U-shape trochlear groove, which is identical to *C. elaphus*, *D. dama*, *C. capreolus* (Fig. 5, a 2 to a 4), but by the shallow curve in *M. reevesi* and *H. inermis* (Fig. 5, a 5 and a 6). The fibula and calcaneus articulates with the lateral trochlea ridge, while the entire medial ridge is articulated with the tibia. A broad, deep triangular fossa (central fossa) is distinct in the center where the anterior process of the tibia is articulated, due to which the maximum flexion of the foot has taken place during the movement. The central fossa is also nearly rounded as in *C. elaphus* and *A. ardei*, while elliptical in *O. virginianus* (Smart, 2009, Fig. 31; Table 1 and Fig. 5). The trochlea distal side is represented by the astragalus head and separated by collum tali, which are distinct and thin, undulated ridge. The collum tali ridge is longer and well pronounced as in *C. elaphus* while shorter and weaker in *D. dama*, *O. virginianus* and *O. hemionus* (Lister, 1996, Fig. 2.8; Jacobson, 2003, Fig. 6.1 and see Fig. 5 and Table 1). On the medial side of the collum tali, a well-pronounced bulge is distinct (Fig. 5 a1), similar to *C. elaphus* but less pronounced in *D. dama*, *O. virginianus*, *O. hemionus*, *Cervalces* sp. and *Megaloceros giganteus* (Lister, 1996, Fig. 2.8; Jacobson, 2003, Fig. 6.1; Breda, 2005, Fig. 24). The head is divided into two parts: a broad, shallow groove; the lateral head (cuboid trochlea), which is larger, and the medial head (navicular trochlea), is smaller and narrow than the cuboid trochlea. The navicular trochlea and cuboid trochlea are connected with external and internal articular facets of the cubonavicular. The lateral extension of the medial trochlea is broader on its proximal side and narrow on the distal side and further extend at the collum tali ridge (Fig. 5 a1), which is morphologically similar to *C. elaphus*, *O. virginianus*, and *Cervalces* sp., while equal in *A. ardei* and *M. giganteus* but narrow in the proximal side and broader in the distal side in *D. dama* and not reached at collum tali ridge (Pfeiffer, 2019, Fig. 15 a, b; Lister, 1996, Fig. 2.8; Jacobson, 2003, Fig. 6.1; Breda, 2005 Fig. 24). There are two depressions in the medial view (Fig. 5 d1); the proximal side is sinus shape sulcus. It is shallow on the medial ridge of the trochlea, where the movement of tibial malleolus took place, and the second one

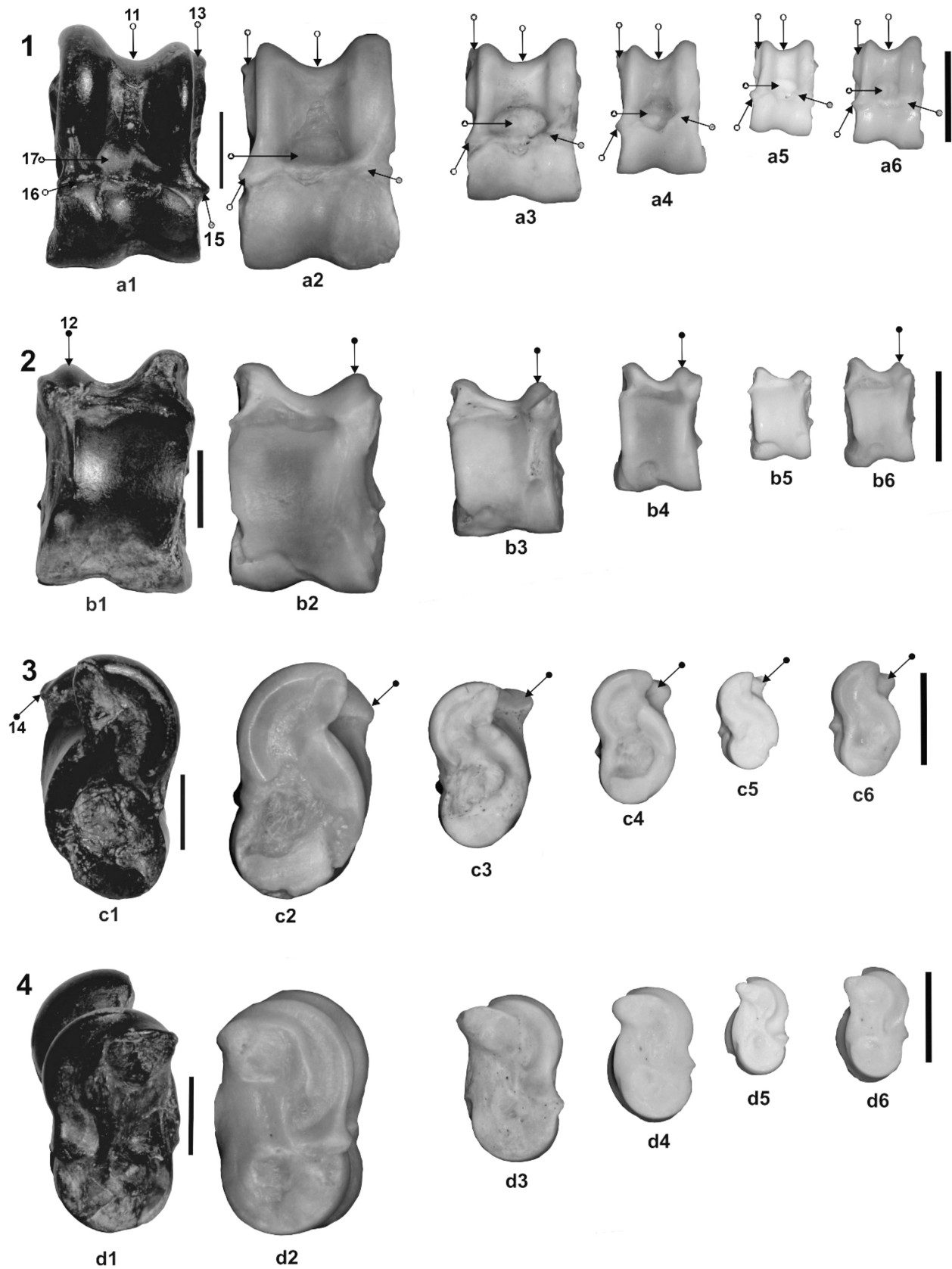


Fig. 5. Astragalus (1) Anterior view; (2) Posterior view; (3) Lateral view; (4) Medial view; right astragalus of *Cervus* sp. (a1, b1, c1, d1); left astragalus of *Cervus elaphus* (Red deer) (a2, b2, c2, d2); *Dama dama* (Fallow deer) (a3, b3, c3, d3); *Capreolus capreolus* (Roe deer) (a4, b4, c4, d4); *Muntiacus reevesi* (Reeve's muntjak) (a5, b5, c5, d5) and *Hydropotes inermis* (Chinese water deer) (a6, b6, c6, d6); bar scale = 2 cm; arrow and number show that morphological characters (see table 1; characters no.11,12,13,14,15,16,17)

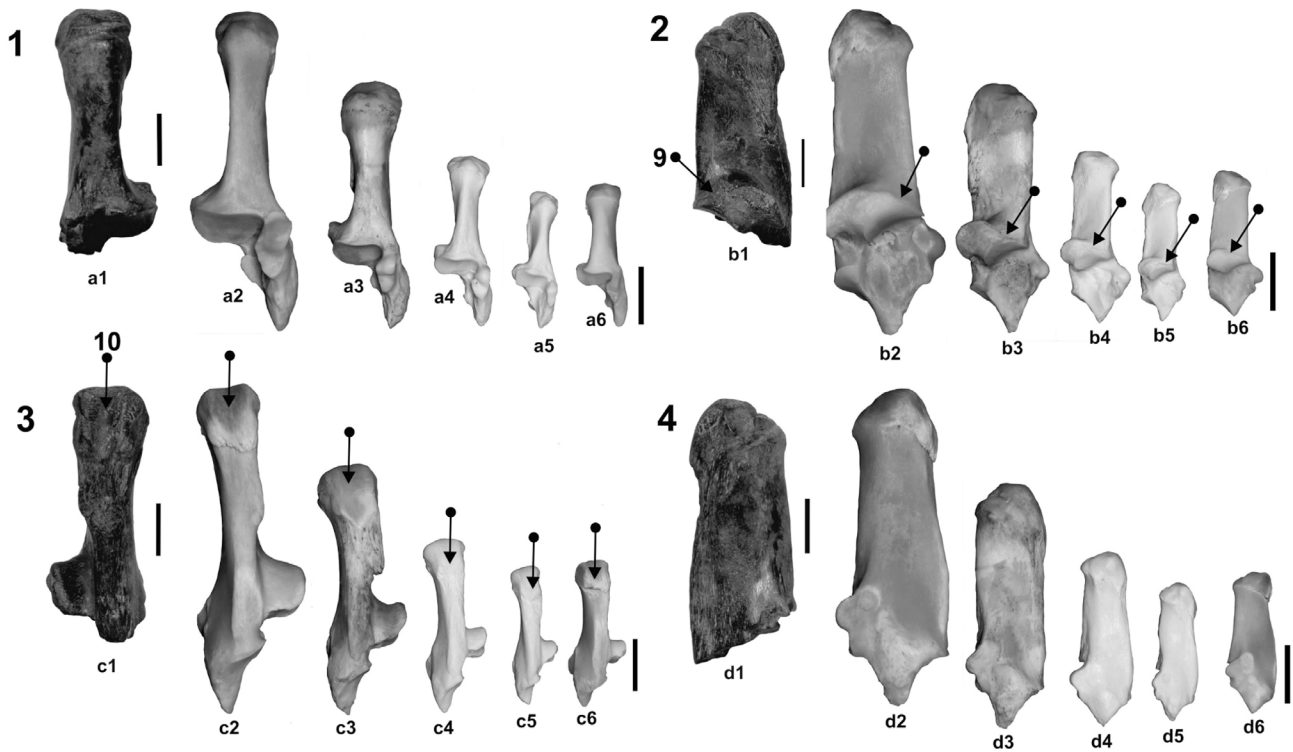


Fig. 6. Calcaneus (1) Anterior view; (2) Medial view; (3) Posterior view; (4) Lateral view; right calcaneus of *Cervus* sp. (a1, b1, c1, d1); left calcaneus of *Cervus elaphus* (Red deer) (a2, b2, c2, d2); *Dama dama* (Fallow deer) (a3, b3, c3, d3); *Capreolus capreolus* (Roe deer) (a4, b4, c4, d4); *Muntiacus reevesi* (Reeve's muntjak) (a5, b5, c5, d5) and *Hydropotes inermis* (Chinese water deer) (a6, b6, c6, d6); bar scale= 2 cm; arrow and number show that morphological characters (see table 1; characters no. 9, 10)

is on the mediolateral side, which is nearly a semicircular depression.

In the posterior view (Fig. 5 b1), most of the astragalus portion is covered by a sustentacular surface, which is convex and smooth. The proximal side of the sustentacular surface has two medial and lateral trochlear edges separated by a wide U shape intracochlear groove or notch, which is more steeply inclined (Fig. 5 b1). It is similar in *C. elaphus* and *O. virginianus* but less inclined in *D. dama* (Lister, 1996, Fig. 2.8). A proximal triangular fossa is distinct on the ventroproximal side of the lateral trochlea edge, restricted to the maximum flexion of the calcaneus on the astragalus. The proximal triangular fossa is larger than *O. virginianus* (Smart, 2009, Fig. 39). The sustentacular surface is separated from the lateral and medial edges by an interarticular groove. A thin, sharp ridge starts from the medial trochlea edge and connecting with the medial scala, while a ridge started from the lateral trochlea edge and joined the distal intracarpal fossa, which controls the maximum movement of cubonavicular processes. There are two depressions in the lateral view (Fig 5 c1), the proximal, a long, curved groove called lateral malleolar articular fossa, where the fibula is articulated. In contrast, the median depression is broad, nearly rounded, and is distally subelliptical calcaneus articular facet called paracuboid facet, where the articular facet of the calcaneus is connected.

Calcaneus: The calcaneus bone is stout and well preserved (Fig.6 a1-d 1). However, the distal part is missing with elongated calcaneal tuber and mesolaterally

compressed, and the lower limb extensor muscle is the primary attachment point. The anteroproximal side (Fig. 6 a1) is domed shaped with a thick broad anterior ridge (plantar fascia). Broad posterior and anterior ridges connect the processes, and a narrow furrow separates these ridges. The anterior ridge is semicircular and nearly equal in thickness, while the posterior one is forming a centrally rounded ridge. These ridges are similar to *Odocoileus virginianus* (Smart, 2009, Fig. 45; Adams and Crabtree, 2008, Fig. 5.19). on the posteroproximal side, two vertical ridges of which the medial one is longer than lateral and extending mid-distally of calcaneal tuber and both separated by moderately deep sulcus (tuber sulcus; Fig. 6 c1). The astragalus platform is missing and nonarticular area, between the calcaneal tuber and distal articular facet of the astragalus, distally elongated and placed slightly distal to the sustentacular facet. This portion is slightly preserved. The sustentacular facet and the ectal facet are connected with the calcaneal canal. Furthermore, it extends over the sustentacular facet, is placed to the proximal side of the sustentacular facet and forms a shallow groove where the interosseous ligament of the talus is attached. A nearly straight ridge is in between the sustentacular tali and the sustentacular facet at the calcaneal shaft, which is nearly similar to *C. elaphus*, *D. dama*, *C. capreolus* and *M. reevesi* but stepwise in *A. ardei* and *H. inermis* (Pfeiffer, 2019, Fig.13 a, b and Fig. 6B). The ectal facet (Fig. 6 b1) is slightly convex, and its proximal end extends over the middle side of the calcaneal tuber, which is flattened and has a groove for the tendon muscle flexor fibularis. The sustentacular facet

(Fig. 6 a1) is concave, nearly rounded. The maximum medial projection of the sustentacular facet is less than the ectal facet.

Cubonavicular: The cubonavicular is subrectangular in shape, having various features of articular facet and processes on dorsal and ventral views, which is 39.7 mm long and 50.9 mm wide (Fig. 7 a1-e1). There are two depressions in the dorsal view, such as the internal astragalar articular facet (iaaf) and external astragalar articular facet (eaaf), which are subelliptical to whom the astragalus head is attached. The iaaf is elongated, shallow and slightly raised than the eaaf, while the eaaf is broad, slightly deeper and having a small elliptical foramen near the contact of both the articulating facets. It is extended in the distal side where this is more elongated and similar to recent mule deer *O. hemionus* (Smart, 2009, Fig. 49), while absent in Giraffe (*Decennatherium pachecoi*), known from Miocene of Iberian Peninsula, Spain (Rios *et al.*, 2016, Fig. 12 K) and sheep (*Sinocapra willdownsi*) known from lower Pliocene of Panca Formation, Nevada, USA (Mead and Taylor, 2005, Fig. 11 A). on the antero-proximal side, the medial process (mp) and internal process (ip) are pronounced and parallel, while the ip is higher, robust than mp, and a broad U shaped valley separates both processes. These processes are similar to *O. hemionus* and *M. giganteus* while in *Cervalces* sp., *S. willdownsi* and *D. pachecoi*, the mp is placed slightly anterior (Breda, 2005 Fig. 28; Smart, 2009, Fig. 49; Mead and Taylor, 2005, Fig. 11 A; Rios *et al.*, 2016, Fig. 12 K).

In lateral view (Fig. 7 b1), a shallow, curved elongated depression known as calcaneus articulation facet (caf) adjacent and situated close to the astragalus articular surface and calcaneus. The caf is connected with eaaf without any gap, similar to *C. elaphus* but with a slight gap or depression in between caf and eaaf in *D. dama* (Lister, 1996, Fig. 2.9). The caf is extended from the anterior to the posterior side (Fig. 7 b1), which is similar in the *O. hemionus*, but *C. elaphus*, *D. dama* and *S. willdownsi* (sheep), it terminates slightly before the posterior side and the halfway in *Cervalces* sp. and *M. giganteus* (Smart, 2009, Fig. 49; Mead and Taylor, 2005, Fig. 11; Breda, 2005 Fig. 28; Lister, 1996, Fig. 2.9). In the ventral view (Fig. 7 e3), the medial side entocuneiform facet (ecf) and lateral side is anteroexternal metatarsal facet (amf) are well distinct. The ecf is slightly convex and suboval while the amf sub-elliptical and slightly raised. In the posterior view, there is a shallow sub-elliptical depression, the posterior metatarsal facet (pmf), and both facets (amf and pmf) are separated by a narrow elongated, moderately deep groove, called tendon muscle peroneus longus (tmpl) for the attachment of muscles (Fig.7 e3) which is similar to *O. hemionus* (Smart 2009, Fig.49), but broader in *S. willdownsi* (sheep) and narrow in *D. pachecoi*.

The tmpl is also prominent at the lateral side (Fig. 7 b1); the same feature is also seen in *M. giganteus* while it is not distinct on *Cervalces* sp. (Breda, 2005 Figs. 27, 28). The entocuneiform facet (ecf) suboval in shape, and the posterior cuneiform facet (pcf) subtriangular, slightly raised, and well separated from the entocuneiform facet, which is similar to *O. hemionus* and *Cervalces* sp., while fused in *M. giganteus*, *D. pachecoi*, and *S. willdownsi* (Smart, 2009, Fig. 49; Mead and Taylor, 2005, Fig. 11; Breda, 2005 Fig. 27; Rios *et al.*,

2016, Fig. 12 L). The ectomesocuneiform and entocuneiform are not attached to the navicular cuboid.

Ectomesocuneiform: The ectomesocuneiform (Fig. 7 f1) is small, complete, 29.00 mm long and maximum width 15 mm, nearly subelliptical in shape with both sides concave, and having an irregular boundary. The proximal facet of ectomesocuneiform is connected with cubonavicular/ectocuneiform, while the distal facet is connected with metatarsal.

Metatarsal: The metatarsal is well-preserved (Fig. 8 a1-e1) in the proximal part, but distal articulation is missing. The shaft is 254.10 mm long with proximal width is 42.93 mm, and a distal width is 34.67 mm. The proximal submit is smooth, rogues, and having an undulating boundary. The metatarsal shaft is flattened on the proximal side and nearly rounded on the distal side. The anterior and posterior sides of the shaft having two longitudinal grooves, which are also present in fossils and recent species of *O. virginianus*, *C. elaphus*, *D. dama*, *C. capreolus*, *M. reevesi* and *H. inermis*. In the anterior view (Fig. 8 a1), there is a small step between medial and lateral facets, which are placed at a different level, and in between these two facets, the metatarsal longitudinal groove is started and extended to the distal end. The groove opens on the proximal side, where it is shallow and increasing in depth towards the distal side and probably closed slightly before the distal side, where this portion is missing. On the distal side of the metatarsal, a moderate deep longitudinal groove is pronounced. In the posterior view (Fig. 8 b1), two small lateral and medial condyles are pronounced on the proximal side, separated by pygmaious (middle condyle), and a sharp zig-zag crest connects all these condyles. The lateral condyle is broad, robust, and lower in height, whereas the middle and medial condyles are smaller and thinner, but the middle one is the highest and massive. These condyles are separated on the posteroproximal side by groove, which is narrow, shallow between the lateral and middle condyles, and merged in a posterior longitudinal groove. An oval-shaped posteroproximal foramen is distinct and placed below the middle condyle, which continues to the proximal epiphysis. The posterior longitudinal groove is proximally deep and broad while very shallow on the distal side.

The proximal epiphysis (Fig. 8 e1) morphology is similar to the distal part of cubonavicular and ectomesocuneiform but having a deep, nearly rounded proximal epiphysis foramen and is connected with the posteroproximal foramen. The foramen is broad, elliptical as in *C. elaphus*, moderately large, elliptical surround by numerous small pores in *O. hemionus*, smaller and rounded central foramen enclosed by various tiny pores in the *Cervalces* sp., *O. virginianus*, and *D. dama*, while broad and elongated in *M. giganteus* (Jacobson, 2003, Fig. 6.1; Breda, 2005 Fig. 29; Lister, 1996, Fig. 2.10). In the anteroproximal view, the metatarsal is separated by a narrow groove, which is morphologically analogous to *M. giganteus* and *O. virginianus*, but separated by a wide groove in *O. hemionus*, and fused in *D. dama* and *Cervalces* sp. (Jacobson, 2003, Fig. 6.1; Breda, 2005 Fig. 29; Lister, 1996, Fig. 2.10). A long and elliptical posterior metatarsal facet (pmf) placed on the posteromediolateral side, is identical to *C. elaphus* and *Cervalces* sp. but small sub elliptical and centrally placed in *M. giganteus* and *D. dama*.

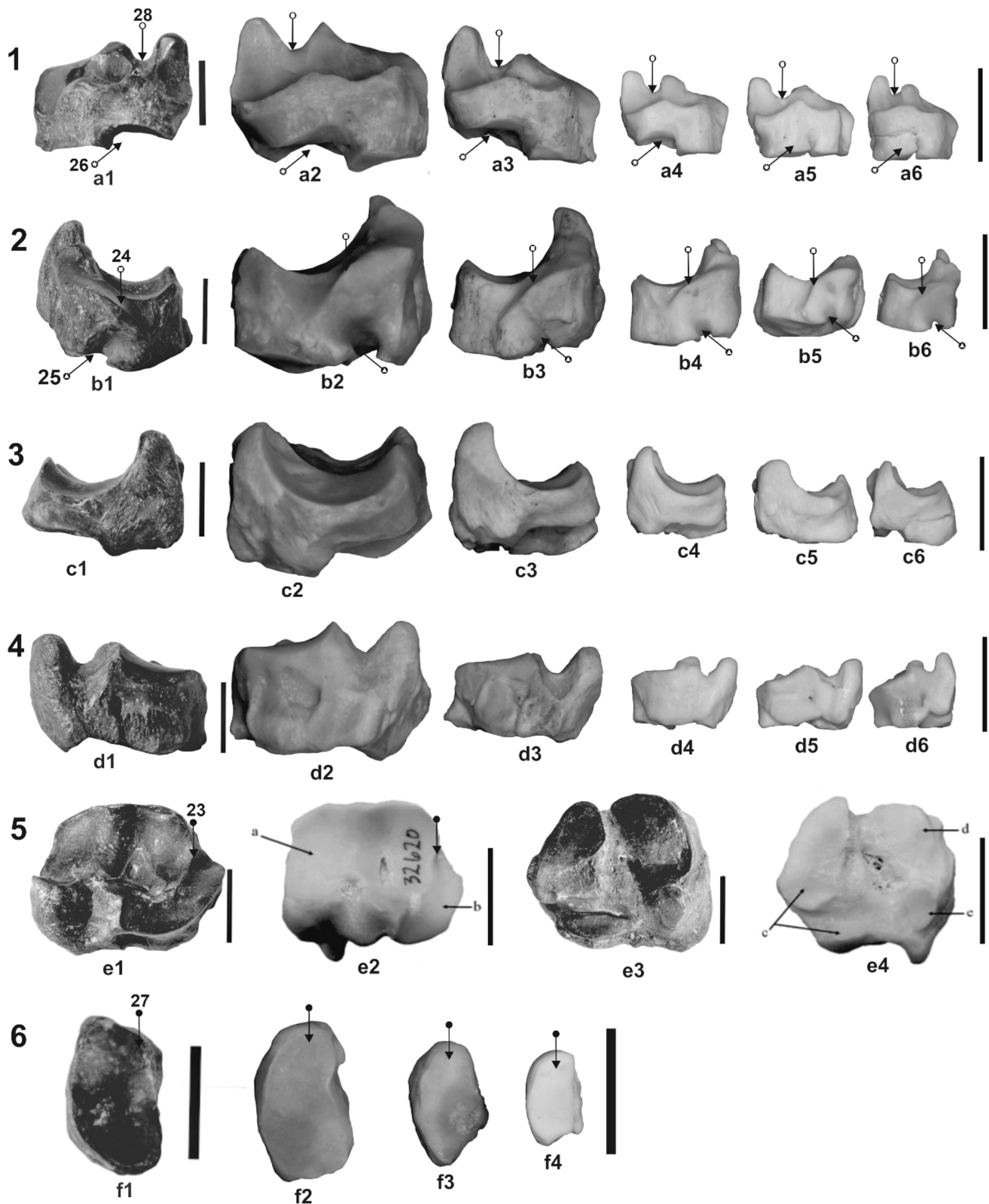


Fig. 7. Cubonavicular (1) Anterior view; (2) Lateral view; (3) Medial view; (4) Posterior view; right navicular cuboid of *Cervus* sp. (a1, b1, c1, d1; e1, e3, f1); left navicular cuboid of *Cervus elaphus* (Red deer) (a2, b2, c2, d2, f2); *Dama dama* (Fallow deer) (a3, b3, c3, d3, f3); *Capreolus capreolus* (Roe deer) (a4, b4, c4, d4, f4); *Muntiacus reevesi* (Reeve's muntjak) (a5, b5, c5, d5) and *Hydropotes inermis* (Chinese water deer) (a6, b6, c6, d6); *Odocoileus hemionus* (e2, e4) (5) Dorsal view (e1, e2) & ventral view (e3, e4); (6) Ectomesocuneiform; bar scale= 2 cm; arrow and number show that morphological characters (see table 1; characters no. 23, 24, 25, 26, 27,28)

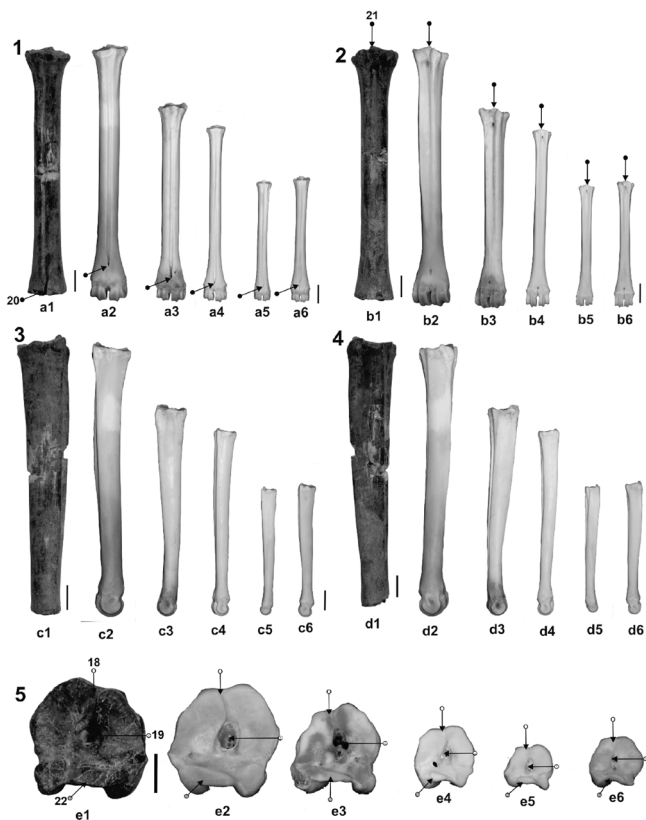


Fig. 8. Metatarsal (1) Anterior view; (2) Posterior view; (3) Medial view; (4) Lateral view; right (5) proximal epiphysis; metatarsal of *Cervus* sp. (a1, b1, c1, d1, e1); left metatarsal of *Cervus elaphus* (Red deer) (a2, b2, c2, d2, e2); *Dama dama* (Fallow deer) (a3, b3, c3, d3, e3); *Capreolus capreolus* (Roe deer) (a4, b4, c4, d4, e4); *Muntiacus reevesi* (Reeve’s muntjak) (a5, b5, c5, d5, e5) and *Hydropotes inermis* (Chinese water deer) (a6, b6, c6, d6, e6); bar scale= 2 cm; arrow and number show that morphological characters (see table 1; characters no. 18, 19, 20, 21, 22).

FUNCTIONAL MORPHOLOGY OF LIMB ELEMENTS

The present *Cervus* sp. limb elements form a hock joint and work as a dynamic system of three major joints: the upper ankle joint, transversal tarsal joint and lower ankle joints (Fig.9; Barr, 2014). The upper ankle joint is between the tibia and the astragalus, the lower ankle joint between the astragalus and calcaneus, and the transverse tarsal joint are between the astragalus and the cubonavicular (Fig. 9). The cervids astragalus is a double pully configuration and worked as a cam (a mechanism that transforms rotational movement to linear motion, Schaeffer, 1947). Structurally, the cervids are generally occupying heterogeneous (grassland, forest and swampy) habitats, which have cursorial adaptations and face numerous physical obstacles to survive from the carnivore predators. Thus, the cervids adapted to increase rotational limb mobility or jumping into the air (pronking), this is useful for negotiating a complex locomotor on the substrate and uneven path to save from the predator. The functional morphology analysis correlated cursorial habitat with the joints mobility of cervids limb elements.

The cervid astragalus works as a double hinge joint between the tarsus and the tibia (Schaeffer, 1947). The astragalus articular facet of the tibia is connected with the medial and lateral trochlea of the astragalus and simultaneously connect with the sagittal reorientation of the astragalus-calcaneum facet. Simultaneously, this mechanism controls the inversion and eversion processes, which is monitoring the ankle motion towards the anteroposterior direction. This rotation process is restricted the tibial malleolus facet and dorsal-distal part of cubonavicular movement until it will reach the maximum point at the collum tali (Fig.9). At the same time, the sustentacular facet is moved along the ventral articular surface of the astragalus. The hind limb functioned during plantarflexion and dorsiflexion processes with the distal tibia, which worked as a combination of the motion across two main joints (the upper ankle and transversal tarsal joints). The movement also takes place at the lower ankle joint between the astragalus and the calcaneus. The upper ankle and transverse tarsal joints rotation are parallel, and the hock joint movement is restricted to an anterior-posterior movement. The composite action of the hock joint at the sagittal plane maybe work as a lever arm system. The calcaneum is operated as a lever arm for the plantarflexion. While the length of remaining tarsals, such as the metatarsal and phalange, bearing the load arms and the astragalus, which work as the center of rotation (Fig.9.3, Schaeffer, 1947).

Based on mechanical lever system principles, the relative proportion of lever and load arms will control the relative speed and power (Alexander and Bennett, 1987). The relative shortening of the calcaneum and relative elongation of the distal limb elements (metatarsal) will influence the lever system and do the rapid movement with less power (Scott, 1985). This condition (short calcaneum and long metatarsal) is found in the present *Cervus* sp. limb elements, and it also suggests that the *Cervus* represent the forest, woodland and grassland habitat. In the hock joint process of cervids, the astragalus is worked to rotated and takes the place of the hock joint, which developing a cavity due to the combination of the calcaneum, distal tibia and cubonavicular (Fig. 9.1). Thus, the joint rotation takes place when the distal trochlea brings the calcaneum to a more favorable place for the movement of the hock plantarflexion, and when it reaches an extreme position called dorsiflexion which assists the further movement of power when the foot is in contact with the ground.

During the movements of the hock joint to walk with a long step is an act in the different stages. At the beginning of the hind limb movement (stride cycle), when the ankle joint is maximum dorsiflexed, the distal limb element begins to rotate near the axis of the transverse tarsal joint (Fig. 9). The rotation takes place until the tibia and calcaneum reached maximum dorsiflexion. At that point, the astragalus, calcaneum, and cubonavicular reach a close-packed position, and no further rotation takes place at the transverse tarsal joint (Fig. 9.1). In the process of hock rotation, about the transverse tarsal joint during the plantarflexion, the calcaneum moves at the astragalus, and the displacement of calcaneum with respect to the transverse joint axis and indicate two stages of flexion such as a vertical line, representing an approximate position of the center of rotation at the transverse tarsal joint. Simultaneously, the distal trochlea head of the astragalus fills the position of extreme dorsiflexion, and the cavity between the cubonavicular and calcaneum is filled up (Fig. 9.1). During

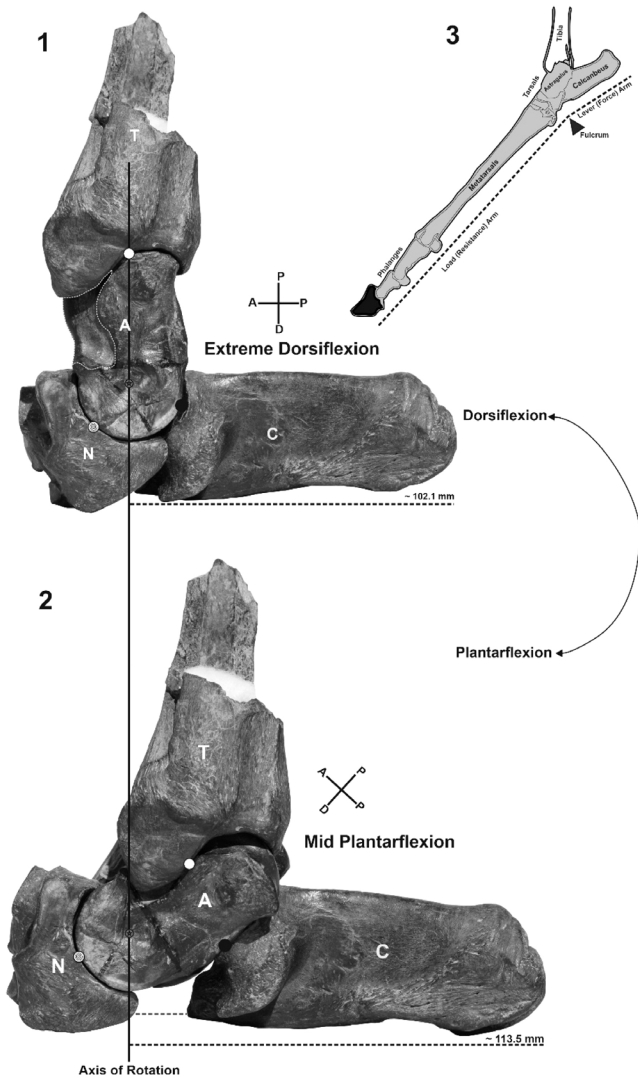


Fig. 9. (1) dorsiflexion position; (2) Plantarflexion position; (3) simple first class lever system during plantarflexion; The medial views of astragalus, calcaneus and cubonavicular of *Cervus* sp. in position attained during extreme dorsiflexion and Plantarflexion; star dot: center of rotation of astragalus; black line show the position of the axis of rotation; dotted line show of length of calcaneus; fill dot: Transverse Tarsal Joint; white dot: Upper ankle joint; black dot: Lower ankle joint; dotted line showing movement area of Tibia on astragalus and displacement between cubonavicular and calcaneus; A: Astragalus; C: Calcaneus; N: Cubonavicular; T: Tibia.

the plantarflexion, a cavity formed between the astragalus, calcaneum, and cubonavicular must accommodate astragalus rotation (Fig. 9.2). The astragalus rotation represents the cavity expansion due to the calcaneus displacement towards posteriorly, and the calcaneus moves across the astragalo-calcaneal facet (sustentacular facet, Fig. 9.2). In the present position, the displacement is about 12.9%. It shows that the available length of the astragalus is related to the size of the calcaneus. Thus the displacement of the calcaneus was observed during the extreme stage of plantarflexion and till the calcaneus, astragalus and cubonavicular reached the closed packed position (dorsiflexion), and the joint rotation happens at the upper ankle joint.

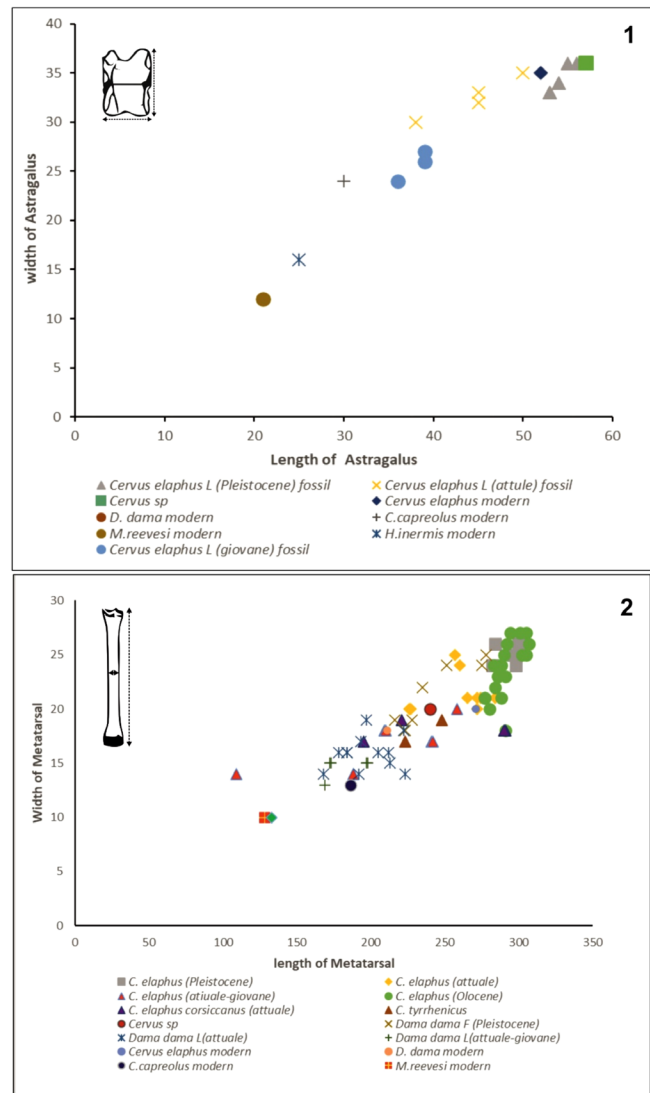


Fig. 10. The astragalus and metatarsal length and width and their comparison with fossils and modern cervids (1) Astragalus; (2) Metatarsal; measurement unit in mm

COMPARISON

The morphological characters of the limb elements of *Cervus* sp. are compared with the fossil and recent species of Cervidae and three outgroups such as Giraffidae, Camelidae and Bovidae (Table 1). Although, some characters of present limb bones are similar and some are different from these groups. The character numbers are shown in the figure and also indicated by the arrow.

The astragalus and metatarsal length and width and their comparison with fossils and modern cervids are given in Fig. 10 and some of the measurements data taken from Leonardi and pteronio, 1974.

In the present distal part of the tibia, the lateral margin of the cochlea tibia is missing but shows a nearly straight outline (without bulge) as found in *C. elaphus*, *C. capreolus*, *M. reevesi* and *H. inermis* while bulge is found in *A. ardei* and *M. giganteus*. The medial malleolus ligament of the

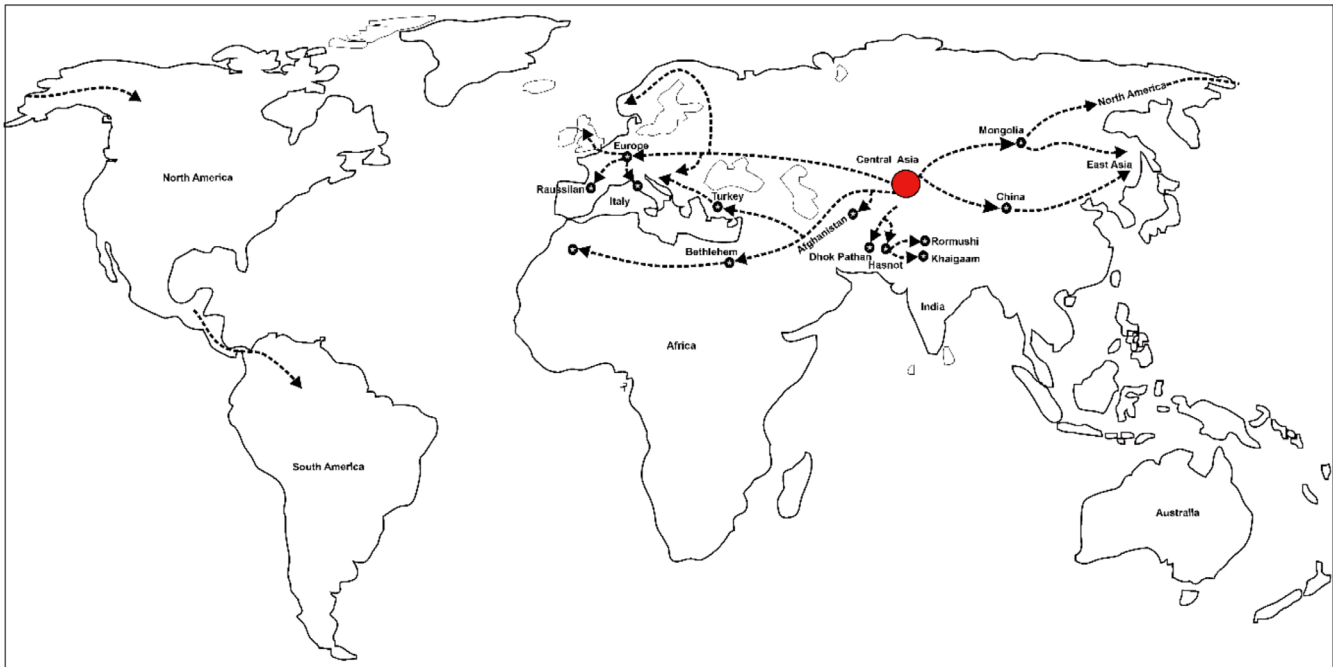


Fig. 11. The migration routes of Cervidae where dotted line arrows show definite routes (modified after Ludt *et al.*, 2004).

present tibia is represented by a nearly straight line similar *C. elaphus*, *M. reevesi* and *M. giganteus* while curved upwards is in *D. dama*, *C. capreolus*, *A. ardei* and *Cervalces/Alces*. The lateroanterior and lateroposterior malleolus of *Cervus* sp. are divided by a shallow and broad valley as in *C. elaphus*, *C. capreolus*, *M. reevesi* and *M. giganteus* but deep and narrow valley (nearly U shape) in *D. dama*, *H. inermis*, *A. ardei* and *Cervalces/Alces*. The edge of the malleolus facet of the present tibia is roughly L shape as on *C. elaphus*, *D. pachecoi* while U shape in *D. dama*, *H. inermis*, *C. capreolus*, *M. reevesi*, *Cervalces/Alces* and *M. giganteus*. The distal epiphysis of the present *Cervus* sp. is laterally more wider with respect to diaphysis and postero-medial surface covered by a longitudinal ridge similar is in *C. elaphus*, *M. reevesi*, and *M. giganteus* but absent in *D. dama*, *C. capreolus*, *H. inermis* and *Cervalces/Alces*. A bulge is present at the anteromedial side of distal part of the present tibia similar bulge is found in *C. elaphus*, *A. ardei* and *M. giganteus* while the absence of this bulge in *C. capreolus*, *D. dama*, *M. reevesi* and *H. inermis*.

The anterior view of *Cervus* sp. astragalus is a broad, deep triangular central fossa, nearly oval in *C. elaphus*, *A. ardei*, *D. dama*, *Cervalces* sp., *M. giganteus*, rounded in *C. capreolus*, *M. reevesi*, *H. inermis*, *O. hemionus*, and elliptical is in *O. virginianus*. The collum tali ridge is nearly straight, thick in *Cervus* sp. while in *C. elaphus* is thin, undulating upward and downward in lateral sides but weaker in *D. dama*, *O. virginianus* and *O. hemionus*, *C. capreolus*, *M. reevesi* and *H. inermis*. The medial bulge at collum tali in *Cervus* sp. more prominent, which is similar in *C. elaphus*, *C. capreolus*, *M. reevesi*, while less noticeable in *D. dama*, *H. inermis*, *Cervalces* sp. and *M. giganteus*. The lateral extension of medial trochlea in *Cervus* sp. is wider on the proximal side and narrow on the distal side, which is identical in *C. elaphus*, *C. capreolus*, *Cervalces* sp., and *O. virginianus* whereas

nearly equally broad on *O. hemionus*, *M. reevesi*, *H. inermis*, *A. ardei*, and *M. giganteus*, but in *D. dama* lateral extension of the medial trochlea is narrow in the proximal side and broad in the distal side. In posterior view, intratrochlear notch is more steeply inclined in *Cervus* sp. similar in *C. elaphus*, *C. capreolus* and *H. inermis* while less inclined in *D. dama*, *M. reevesi*, *Cervalces* sp., *M. giganteus*, *O. virginianus* and *O. hemionus*.

In *Cervus* sp. antero-proximal side of the calcaneum is a domed shape with a broad undulated anterior ridge, like in *C. elaphus*, *D. Dama*, *H. inermis* and *M. giganteus* while more convex in *Cervalces* sp., *C. capreolus* and *M. reevesi*. The posteroproximal side has two vertical ridges in the present calcaneum known as medial and lateral ridges; the lateral ridge is shorter than the medial ridge, where the medial ridge and calcaneal tuber are meeting together to form a step-like structure. This structure similar in *C. elaphus* and *D. dama* while without a step in *C. capreolus*, *M. reevesi* and *H. inermis*. The medial and lateral ridges are separated by a deep narrow tuber (sulcus) in present *Cervus* sp., the identical sulcus is found in *C. elaphus* and *D. dama*, while shallow and broad tuber is in *C. capreolus*, *M. reevesi* and *H. inermis*. In medial view, the ectal facet is concave and centrally projected towards the calcaneal tuber in *Cervus* sp. which is similar in *C. elaphus*. In contrast, the ectal facet has more projection toward the lateral side on *D. dama*, *C. capreolus*, *M. reevesi* and *H. inermis*.

In lateral view of the present cubonavicular, calcaneus articulation facet (caf) is less curved and extended from anterior to posterior sides in *Cervus* sp., which is similar to *O. hemionus* and *D. dama*, while steep like, more curve and terminates before the posterior side or halfway on *C. elaphus*, *C. capreolus*, *M. reevesi*, *H. inermis*, *Cervalces* sp., *M. giganteus* and *S. willdownsi* (sheep). The extension of tendon musculus peroneus longus (tmpl) in the lateral side is more

prominent in *Cervus* sp. and *C. elaphus* and *M. giganteus* while less prominent in *D. dama*, *C. capreolus*, *M. reevesi*, *H. inermis*. In the posteroproximal side, the medial process (mp) and internal process (ip) are separated by a broad U shaped valley, and the medial process ridge is less steep in *Cervus* sp., *C. elaphus*, *D. dama*, *C. capreolus* while nearly vertical in *M. reevesi* and *H. inermis*.

The ectomesocuneiform and entocuneiform are not fused to the navicular cuboid in *Cervus* sp., *C. elaphus*, *D. dama* and *C. capreolus* while it is fused in *M. reevesi* and *H. inermis*.

The view of proximal epiphysis metatarsal, the shape of the foramen is large, elliptical in *Cervus* sp. *C. elaphus* and *M. reevesi*, while it is large and elongated in the *M. giganteus*. At the same time, it consists of a smaller central pit, enclosed in a porous area, which can vary in shape, in the *Cervalces* sp., *O. virginianus*, *D. dama*, *C. capreolus* and *H. inermis*. The anteroproximal side of metatarsal III or IV is separated by a narrow groove in *Cervus* sp. which is similar to *C. elaphus*, *M. giganteus*, *O. virginianus* and *H. inermis* while fused in *D. dama*, *C. capreolus*, *M. reevesi* and *Cervalces* sp.

DISCUSSION AND CONCLUSIONS

Cervidae fossil records are mainly known based on antelary and dentitions, while many of them are poorly preserved and not well illustrated. Although the work on fossil cervids was carried out a century ago, due to a lack of uniform methodological criteria, multiple synonymies, and systematic taxonomy, it is complicated to compare with the modern genera and species (Croitor, 2014). We followed the uniform morphology criteria of the present paper limb elements and compared them with fossil and recent species bones.

The report of *Dermotherium*, *Bedenomeryx* from Eurasia and *Blastomeryx* from North America in late Oligocene and early Miocene, and considered to be an ancestor of Cervidae, but latter *Blastomeryx* assigned under the family Bovidae (Gentry, 1994), and postulate that Cervidae has quick diversifications into several genera and species (Ludt *et al.*, 2004; Lorenzini and Garofalo, 2015; Heckeberg, 2020). The divergence of major cervids lineages was a very short period since this group was originated (DeMiguel *et al.*, 2014). It is also considered that during the Oligocene to middle Pliocene (as well as during the Miocene climatic maximum, warm climate) changes in the global climate, geographical position and vegetation, which is suggested that there are several successive rapid radiations within the Cervidae (Hernandez *et al.*, 2005). The cold and arid climate was led to the replacement of forest habitats with open grasslands in Europe and Central Asia which were favoring the diversification, evolution, and dispersal of cervids (Meijaard and Groves, 2004; Gilbert *et al.*, 2006; Lorenzini and Garofalo, 2015; Heckeberg, 2020). The earliest true Cervidae has appeared in the middle Miocene in Central Asia/ Eastern Eurasia (Scott and Janis, 1987; Vislobokova, 1990; Wang *et al.*, 2009; Heckeberg, 2017), while fossils evidence indicate that the origin of cervid may be in the Europe (Heckeberg, 2017) which migrated from central

Asia/Eastern Eurasia to Europe in the middle Miocene, and the same time to North America probably through Bering Land Bridge because of no any other records of cervids from North America known before late Miocene (Ludt *et al.*, 2004; Webb, 2000). It can also be possible that same time cervids migrated to the Indian subcontinent (Fig. 11) after the origin of the Himalaya and regression of Tethys Sea due to which formation of lowland platform for the dispersal from Europe to the Indian subcontinent probably via Neotethys (Fig. 11). This hypothesis is also supported by the mitochondrial (DNA) studies of recent cervids and suggested that the Cervidae originated from Central Asia/Eastern Eurasia and migrated to the Indian subcontinent, Europe and Europe to North America (Ludt *et al.*, 2004), while the dispersal from North America to South America was through the Isthmus land bridge during the late Pliocene (Webb, 2000).

The extant cervids are habitat in the arctic, tropical to temperate, and cold places such as tundra to rainforests in the new and old worlds and generally live in lowlands, which suggested that the formation of a long mountain belt resulting from the closure of the Neotethys Ocean and their southward dispersal from Central Eurasia to Europe and Southeast Asia at the same time (Brunet *et al.*, 1984). The climate change cooler in winter and decreases in summer, including rainfall, followed by growing grasses, dense forest over a vast stretch of Europe and Asia during Miocene/Pliocene, which enabled large and fast-moving grazers such as cervids to radiate. In contrast, the medium-sized to large-sized cervids occurred in the late Pliocene and adapted to more temperate climatic conditions (Heintz, 1970). The fossil records of grazing and browsing forms, such as Equidae, Elephantidae, along with Cervidae from the lower Karewa Formation (Kotlia, 1985), indicate that a dominant mosaic grassland, wooded grassland with subordinate woodland and some bushland close to the ancient lake, which was more open and supported grassy vegetation with some tree and bush cover present during the deposition of Karewa. It is a favorable environmental condition for the survival of the cervids.

The functional morphology of the present limb elements represents short calcaneum with relation to long metatarsal indicate that rapid movement and less power during the locomotion to save from the carnivore predator, it also suggests that the *Cervus* has adapted ecotone habitat. It also postulates that collum tali of the astragalus is controlled the maximum movement of the tibia malleolus facet and dorsal-distal part of cubonavicular during the locomotion. The small size of the astragalus with relation larger size of the calcaneum and metatarsal is indicated that this condition is more favorable for the striding of the animal during the plantarflexion and dorsiflexion.

ACKNOWLEDGEMENTS

The authors are thankful to Prof. K.D. Rose, Johns Hopkins University School of Medicine, Baltimore, Maryland 21205, USA; and Dr. Thierry Smith and Annelies Foile, Royal Belgian Institute of Natural Sciences, B-1000 Brussels, Belgium, for their valuable suggestions during the preparation of this manuscript. The authors also thankful to the anonymous referees for critically reviewing the present paper.

REFERENCES

- Adams, B. J. and Crabtree, P. J. 2008. Comparative skeletal anatomy, A photographic atlas for medical examiners, Coroners Forensic Anthropologists and Archeologists. IBN 978-1-59745-132-1.
- Agrawal, D.P., Kusumgar, S. and Krishnamurthy R. V. 1985. Climate and Geology of Kashmir and Central Asia: The Last 4 Million Years. Today and Tomorrow's Publishers, New Delhi. 247.
- Agrawal, D.P., Dodia, R., Kotlia, B. S., Razdan, H., Sahni, A. 1989. The Plio- Pleistocene geologic and climatic record of Kashmir valley, India: A review and new data. Palaeogeography Palaeoclimatology Palaeoecology. 73: 267-286.
- Agarwal, K.K., Agarwal, G. K. 2005. A genetic model thrus- bound intermontane basin using scaled sandbox analogue models: an example from the Karewa Basin, Kashmir Himalaya, India. International Journal Earth Sciences. 94: 47-52.
- Alam, A., Ahmad, S., Bhat, M .S., Ahmad, B. 2015. Response to the commentary by Shah, AA and further evidence supporting the dextral strike-slip pull-apart evolution of the Kashmir basin along the central Kashmir fault (CKF). Geomorph. 253: 558-563.
- Akhtar, M.A., Ghaffar, M.A., Qureshi. 1999. On Cervus punjabiensis Brown from the Siwalik Hills of Pakistan and Azad Kashmir. Punjab University Journal of Zoology 14: 93-96.
- Alexander RM, Bennett MB. 1987. Some principles of ligament function, with examples from the tarsal joints of the sheep (*Ovis aries*). J Zool 211:487–504.
- Arif, M., Shah, S.M.I. 1991. New findings of Cervidae (Mammalia) from the Upper Siwaliks of Pakistan. Pakistan Geol. Survey. Mem. 17: 11.
- Azzaroli, A. 1954. Critical observations upon Siwalik deer. Proceedings of the Linnean Society London 165: 75-83.
- Badam, G.L. 1968. Note on the occurrence of fossil vertebrates in the Karewas of Kashmir. Research Bulletin Panjab University. 19(3-4): 453-55.
- Barr, W. Andrew 2014. Functional morphology of the bovid astragalus in relation to habitat: Controlling phylogenetic signal in ecomorphology. Journal of Morphology, 275(11), 1201–1216. doi:10.1002/jmor.20279
- Badam, G.L. 1972. Additional mammalian fossils in the Karewas of Kashmir. Current Science 41(4): 529–530.
- Bhargava, O.N. 2015. Evolution of the Tethyan and Karewa successions in Kashmir: a synthesis. Jour Palaeont Soc India. 60(1):51–72.
- Bhatia, S.B., Soulié-Marsche, I., Gemayel, P. 1998. Late Pliocene and Early Pleistocene Charophyteora of the Hirpur Formation, Karewa Group, Kashmir, India. N. Jb. Geol. Paläont. Abh. 210(2): 185-209.
- Bhatt, D.K. 1976. Stratigraphical status of Karewa Group of Kashmir India. Himal. Geol. 6: 197–208.
- Bhatt, D.K. 1989. Lithostratigraphy of the Karewa Group, Kashmir valley, India and a critical review of its fossil record. Mem. Geol. Surv. India. 122: 1–85
- Bhat, M.I. 1982. Thermal and tectonic evolution of Kashmir basin vis-à-vis petroleum prospects. Tectonophysics. 88: 117–132.
- Breda, M. 2005. The morphological distinction between the postcranial skeleton of Cervalces/Alces and Megaloceros giganteus and comparison between the two Alceini genera from the Upper Pliocene–Holocene of Western Europe. Geobios. 38(2): 151–170.
- Brunet, M., Heintz, E., Bataill, B. 1984. Molayan (Afghanistan) and the Khaur Siwaliks of Pakistan; an example of biogeographic isolation of late Miocene mammalian faunas. Geol Mijnbouw. 63: 31–38.
- Brown, B. 1926. A new deer from the Siwaliks. American Mus. Novitates. 242:6p.
- Burbank, D.W. 1983. The chronology of intermontane-basin development in the north- west Himalaya and the evolution of the Northwest Syntaxis. Earth Planet. Sci. Lett. 64: 77–92.
- Burbank, D.W. and Johnson, G.D. 1982. Intermontane-basin development in the past 4 Myr in the northwest Himalaya. Nature 298: 432–436.
- Burbank, D.W. and Johnson, G.D. 1983. The late chronologic and stratigraphic development of the Kashmir intermontane basin, northwestern India. Palaeogeogr. Palaeoclimatol. Palaeoecol. 43: 205–235.
- Colbert, E.H. 1935. Distributional and phylogenetic studied on Indian fossil mammals. The classification and the phylogeny of the Giraffidae. Am. Mus. Nov. 800: 1-15.
- Croitor, R. 2014. Deer from Late Miocene to Pleistocene of Western Palearctic: Matching fossil record and molecular phylogeny data. Zitteliana Reihe B: Abhandlungen Der Bayerischen Staatssammlung Fur Palaontologie Und Geologie. 32: 115–153.
- DeGusta, D., Vrba, E. 2003. A method for inferring paleohabitats from the functional morphology of bovid astragali. J Archaeol Sci 30:1009–1022.
- DeMiguel, D., Azanza, B., Morales, J. 2014. Key innovations in ruminant evolution: a paleontological perspective. Integrative Zoology 9(4): 412–433 DOI 10.1111/1749-4877.12080.
- De Terra, H., Paterson, T. T. 1939. Studies on Ice Age in India and Associated Human Cultures. Carnegie Institution, Washington. 493: 1-453.
- Farooqi, Z.A., Dssai, R.N. 1974. Stratigraphy of Karewas Kashmir, India. Jour. Geo l. Soc. India. 15(3): 299-305.
- Gentry, A.W. 1994. The Miocene differentiation of Old World Pecora (Mammalia). Hist. Biol. 7: 115–158.
- Ghaffar, A., Khan, M.A., Akhtar, M. 2006. The oldest Cervid from the Siwalik Hills of Pakistan. Journal of Applied Sciences. 6 (1):127-130.
- Ghaffar, A. 2005. Studies on equids, cervids and Carnivora from the Siwalik Hills of Pakistan, Ph.D. thesis, University of the Punjab, Lahore, 1-389.
- Ghaffar, A., Khan, M.A., Akhtar, M. 2010. Early Pliocene Cervids (Artiodactyla-Mammalia) from the Siwaliks of Pakistan. Yerbilimleri. 31(3): 217-231.
- Ghaffar, A., Akhtar, M., Khan, M.A., Nazir, M. 2004. Report on Cervus sivalensis from the Upper Siwaliks of Pakistan. Punjab Univ. J. Zool. 19: 83-88.
- Ghaffar, A., Akhtar, M., Nayyer, A. Q. 2011. Evidences of Early Pliocene fossil remains of tribe Cervini (Mammalia, Artiodactyla, Cervidae) from the Siwaliks of Pakistan. Journal of Animal and Plant Sciences. 21(4): 830–835.
- Gilbert, C., Ropiquet, A., Hassanin, A. 2006. Mitochondrial and nuclear phylogenies of Cervidae (Mammalia, Ruminantia): systematics, morphology, and biogeography. Molecular Phylogenetics and Evolution 40(1):101-11
- Godwin-Austen, H.H. 1859. On the lacustrine Karewa deposits of Kashmir. Quart. Jour. Geol. Soc. London. 15(1): 221-229.
- Heckenberg, N.S. 2017. Origination of antlerogenesis. Journal of Morphology 278(2):182–202.
- Heckenberg, N.S. 2020. The systematics of the Cervidae: a total evidence approach. Peer Jour. 8:e8114 DOI 10.7717.
- Heintz, E. 1970. Les cervides villafranchiens de France et d'Espagne. Memoires du Museum national d'histoire naturelle. 22(1-2): 5-303.
- Hernández Fernández, M., Vrba, E.S. 2005. A complete estimate of the phylogenetic relationships in Ruminantia: a dated species-level supertree of the extant ruminants. Biological Reviews 80(2): 269–302 DOI 10.1017/S1464793104006670.
- Hora, S.L. 1937. On fossil fish remains from the Karewas of Kashmir. Rec. Geol. Surv. India. 72(2): 178-181.
- Jacobson, J.A. 2003. Identification of Mule Deer (*Odocoileus hemionus*) and White-Tailed Deer (*Odocoileus virginianus*) Postcranial Remains as a Means of Determining Human Subsistence Strategies, Plains. Anthropol. 48:187-287.,DOI: 10.1080/2052546.2003.11949269.
- Kotlia, B.S. 1985. Quaternary rodent fauna of the Kashmir valley, NW India; Systematics, biochronology and paleoecology. Jour. Palaent. Soc. India. 30: 81-91.
- Kotlia, B. S. 1990. Large Mammals from the Plio-Pleistocene of Kashmir intermontane Basin, Indi, with Reference to thier Status in Magnetic Polarity time scae. Eiszeitalter u. Gegenwart. 40: 38-52.
- Kotlia, B.S. 1992. Pliocene murids (Rodentia, Mammalia) from Kashmir basin, northwestern India. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen. 184(3): 339-357.

- Kotlia, B.S. 1994. Evolution of Arvicolidae in South Asia, In: Y. Tomida, C.K. Li & T. Setoguchi (eds.), *Rodent and Lagomorph Families of Asian Origins and Diversification*. National Science Museum Monographs, 8: 157-171.
- Kotlia, B.S., Koenigswald, W.V. 1992. Plio-Pleistocene arvicolids (Rodentia, Mammalia) from Kashmir intermontane basin, northwestern India. *Paläontographica Abt. A*, 223: 103-135.
- Kotlia, B.S., Sahni, A., Agrarwal, D.P., Pant, R. K. 1982. New vertebrate evidence for the age of Karewa sediments, Kashmir. *Man & Environment*. 6: 13-15.
- Kusumgar, S., Agarwal, D.P., Krishnamuthy, R.V., Kotlia, B.S. 1985. Magnetic stratigraphy of the Karewas of the Kashmir valley, p. 13-17. In: *Current Trends in Geology VI (Climate of Kashmir and Central Asia)* (Eds. Agarwal, D.P. et al.), Today and Tomorrow's Printers and Publishers, New Delhi.
- Lister, A.M. 1996. The Morphological Distinction Between Bones and Teeth of Fallow Deer (*Dama dama*) and Red Deer (*Cervus elaphus*). *Internat. Jou. Osteoarch.* 6: 119-143.
- Lorenzini, R., and Garofalo, L. 2015. Insights into the evolutionary history of *Cervus* (Cervidae, tribe Cervini) based on Bayesian analysis of mitochondrial marker sequences, with first indications for a new species. *Journal of Zoological Systematics and Evolutionary Research* 53(4):340-349 DOI 10.1111/jzs.12104.
- Leonardi, G., Petronio, C., 1974. I cervi pleistocenici del bacino diomiticco di Riano (Roma). *Mem. Accad. Naz. Lincei* 223: 101-208.
- Ludt, C.J., Schroeder, W., Rottmann, O., Kuehn, R. 2004. Mitochondrial DNA phylogeography of red deer (*Cervus elaphus*). *Mole. Phylog. and Evol.* 31(3): 1064-1083.
- Lydekker, R. 1876. Notes on the fossil mammalian faunas of India & Burma. *Ree Geol. Surv. India*. 9: 86-106.
- Lydekker, R., 1884. Indian Tertiary and post-Tertiary Vertebrata. Part III. Rodents and new ruminants from the Siwaliks, and a synopsis of Mammalia. *Palaeont. Ind., Mem. Geol. Surv. Ind., Ser. 10*, 105-134.
- Mead, J.I., and Taylor, L.H. 2005. New Species of *Sinocapra* (Bovidae, Caprinae) from the Lower Pliocene Panaca Formation, Nevada, USA, *Palaeont. Electr.* 8(1): 1-20.
- Meijaard, E., and Groves, C.P. 2004. Morphometrical relationships between Southeast Asian deer (Cervidae, tribe Cervini): evolutionary and biogeographic implications. *Journal of Zoology* 263(2):179-196 DOI 10.1017/S0952836904005011.
- Nanda, A.C. 2002. Upper Siwalik Mammalian faunas of India and associated events. *Jour. Asian Earth Sci.* 21: 47-58.
- Nanda, A.C. 2008. Comments on the Pinjor Mammalian Fauna of the Siwalik Group in relation to the Post-Siwalik Faunas of Peninsular India and Indo-Gangetic Plain. *Quat. Internat.* 192: 6-13.
- Pant, R.K., Agarwal, D.P., Krishnamurthy, R.V. 1978. Scanning electron microscope and other studies on the Karewa beds of Kashmir, p. 275-282. In: *Scanning Electron microscopy in the study of sediments* (Ed. Whalley, W.B.). Norwich. Geology, Abstracts
- Pfeiffer, D.T. 2019. Distinction of *Arvenceros ardei* and *Cervus perrieri* (Cervidae, Mammalia) from the late Pliocene site of Perrier (France) based on the postcranial skeleton: taxonomic and phylogenetic conclusions. *PalZ.* doi:10.1007/s12542-019-00473-y.
- Pascoe, E.H. 1973. *A Manual of Geology of India and Burma*. Controller of Publications, Government of India, Delhi. 1-3.
- Ríos, M., Sánchez, I.M., Morales, J. 2016. Comparative anatomy, phylogeny, and systematics of the Miocene giraffid *Decennatherium pachecoi* Crusafont, 1952 (Mammalia, Ruminantia, Pecora): State of the art. *Jou. Verte. Paleont.* 36(5): e1187624.
- Sahni, A. 1982. Karewa vertebrates: biostratigraphy, palaeontology and palaeoecology. *Man and Environment*. 6: 16-20.
- Sahni, A., Kotlia, B.S. 1985. Karewa microvertebrate: biostratigraphical and paleoecological implications, p. 29-43. In: *Current Trends in Geology VI (Climate of Kashmir and Central Asia)* (Eds. Agarwal, D.P. et al.) Today and Tomorrow's Printers and Publishers, New Delhi.
- Schaeffer, B. 1947. Notes on the origin and function of the artiodactyl tarsus. *Am Mus Novi* 1356:1-24.
- Scott, K., and Janis, C. 1987. Phylogenetic relationships of the Cervidae, and the case for a superfamily 'Cervoidea'. In: Wemmer C, ed. *Biology and management of the Cervidae*. Washington, London: Smithsonian Institution, 3-20.
- Scott K. 1985. Allometric trends and locomotor adaptations in the Bovidae. *Bull Am Mus Nat Hist* 179:197-288.
- Singh, I.B. 1982. Sedimentation pattern in the Karewa basin, Kashmir valley India and its geological significance. *Jour. Palaeont. Soc. India* 27: 71-110.
- Smart, T.S. 2009. Carpals and tarsals of mule deer, black bear and human: an osteology guide for the archaeologist. WWU Graduate School Collection. 19. <https://cedar.wvu.edu/wwuet/19>.
- Thakur, V.C., Rawat, B.S., 1992. Geological map of the Western Himalaya. Published under the Authority of the Surveyor General of India. Printing Group of Survey of India, 101 (HLO).
- Tiwari, B.S., and Kachroo, P.K. 1977. On the occurrence of *Equus sivalensis* from Karewas of Shupiyar, Kashmir Valley. *Recent Res. Geol.*, 3: 468-477.
- Tripathi, C., and Chandra, P.R. 1972. Fossils from Karewa near Nichahom, Kashmir. *Misce. Pub. Geol. Surv. India*. 15: 261-264.
- Vislobokova, I.A. 1990. The fossil deer of Eurasia. *Transactions of the Palaeontological Institute* 240:1-206.
- Wang, X., Xie, G., Dong, W. 2009. A new species of crown-antlered deer *Stephanocemas* (Artiodactyla, Cervidae) from the middle Miocene of Qaidam Basin, northern Tibetan Plateau, China, and a preliminary evaluation of its phylogeny. *Zool. Jour. Linnean Society*, 156: 680-695.
- Wadia, D.N. 1941. Pleistocene Ice Age deposits of Kashmir. *Proceedings National Institute of Science, India*, 7(1): 49-59.
- Webb, S.D. 2000. Evolutionary history of New World Cervidae. Pp. 38-64 in *Antelopes, deer, and relatives: fossil record, behavioral ecology, systematics, and conservation* (E. S. Vrba and G. B. Schaller, eds.). Yale University Press, New Haven, Connecticut.