# Postcranial morphology of Middle Eocene deperetellid *Teleolophus* (Perissodactyla, Tapiroidea) from the Shara Murun region of the Erlian Basin, Nei Mongol, China

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**Abstract**　Deperetellidae are a group of common, endemic Asian Middle Eocene tapiroids. Although five genera within the family have been named, most of them were represented by fragmentary maxillae and mandibles except for some skeletal material of *Deperetella*. Based exclusively on dental characters, different authors have proposed affinities of deperetellids with, for instance, helaletid *Colodon*, lophialetids, or rhodopagids. Here we described the partial postcranial skeleton of *Teleolophus medius*? recently discovered at Wulanhuxiu (=Ulan Shireh) of the Erlian Basin, China, and compared the postcranial skeletons of *Teleolophus* with those of *Lophialetes*, *Deperetella*, *Heptodon*, *Helaletes*, and *Colodon*. The postcranial skeleton of *Teleolophus* shares many similarities with that of *Deperetella* especially in having elongated and slender limbs, a relatively long, narrow lunar with a slightly concave medial border of the radial facet, a magnum with an anteriorly situated hump and a deeply excavated Mc IV facet, a slightly asymmetric trochlea of the femur, a fibula highly reduced or even fused with a tibia, Mt III contacting the cuboid, Mt II in contact with ectocuneiform only on the posterior end, and the pes with functional tridactyls. These similarities support the close relationship between *Teleolophus* and *Deperetella*. We interpreted some similarities of postcrania between *Teleolophus* and *Lophialetes* as a result of parallel evolution, due to their cursorial adaptations. *Colodon* is more similar to *Heptodon* than to *Teleolophus* in the postcranial features, suggesting a close relationship between *Colodon* and *Heptodon*. Whether or not Helaletidae and Deperetellidae are closely related await further investigation. Both morphological characters and ternary diagram indicate that *Teleolophus* adapted to fast running, as its contemporary *Lophialetes*.

**Key words**　Erlian Basin, Nei Mongol; Middle Eocene; Tapiroidea, *Teleolophus*; postcranial skeleton; CAE

## 1    Introduction

Deperetellidae are a group of endemic, peculiar tapiroids distributed in Middle Eocene deposits of Asia. The family includes five genera: *Teleolophus*, *Deperetella*, *Diplolophodon*, *Pachylophus*, and *Bahinolophus*, that have been reported from China, Mongolia, Kyrgyzstan, and Myanmar (Matthew and Granger, 1925a, b; Radinsky, 1965a; Tong and Lei, 1984; Tsubamoto et al., 2005; Zdansky, 1930). The generic taxonomy of Deperetellidae has been controversial. Radinsky (1965a) and Dashzeveg and Hooker (1997) suggested that *Diplolophodon* and *Pachylophus* are synonymies of *Deperetella* and *Teleolophus*, respectively. Although specimens of deperetellids are relatively abundant, most of them are fragmentary maxillae or mandibles; cranial and associated postcranial elements are rare. The only known postcrania of deperetellids, a partial skeleton of *Deperetella cristata*, were collected from the Shara Murun Formation at Ula Usu of the Erlian Basin, Nei Mongol (Inner Mongolia), China (Radinsky, 1965a).

Among tapiroids, deperetellid is characterized by an inverted U on upper molar crown formed by the protoloph, paracone, and metaloph, presence of the cement on cheek teeth, the Hunter-Schreger Band with compound configuration, and cursorial adaptations of postcrania (Radinsky, 1965a; von Koenigswald et al., 2011). Probably due to these peculiar characters, the phylogenetic relationship of deperetellids within Tapiroidea remains obscure. Matthew and Granger (1925a, b) suggested that *Teleolophus* and *Deperetella* were related to helaletid *Colodon* from North America in approaching the bilophodont molars, and this hypothesis is partially supported by the cladistic analysis of Colbert (2005). However, regarding the similarity between the *Teleolophus-Deperetella* clade and Helaletidae as convergency, Radinsky (1965a) erected a separate family Deperetellidae, and suggested it shares a common ancestry with contemporary lophialetids. Hooker (1989) considered Rhodopagidae to be a sister group of Deperetellidae. Dashzeveg and Hooker (1997) named a new genus, *Irdinolophus* for "*Helaletes*" *mongoliensis* from the Erlian Basin, and regarded it as a primitive member of Deperetellidae. However, Bai et al. (2017b) doubted *Irdinolophus* as a primitive deperetellid, and reassigned "*Helaletes*" *mongoliensis* to *Desmatotherium* as initially named by Matthew and Granger (1925b).

## 2    Locality background

The fragmentary maxilla with complete upper cheek teeth of *Teleolophus medius*? (AMNH FM 26286) was collected by the Central Asiatic Expedition (CAE) of the American Museum of Natural History from the Ulan Shireh Formation of the Wulanhuxiu (=Chimney Butte, Ulan Shireh) (Fig. 1). The locality of Wulanhuxiu was first investigated by the CAE in 1925, and was referred to as "8 miles north of Tukhum Lamasery" at "North Mesa" (Radinsky, 1964; Wang et al., 2012). In 1928, the CAE returned to the locality and named it as "Chimney Butte" (Radinsky, 1964; Wang et al., 2012). The Wulanhuxiu section is about 45 m (150

feet) in thickness; the mammalian fauna from the strata was considered to be homogenous and equivalent to or slightly older than Irdinmanhan (Radinsky, 1965a; Ye, 1983). Recently, Li et al. (2016) proposed a possible Irdinmanhan and Sharamurunian boundary in the upper horizon of the Wulanhuxiu section. Further, based on our fieldwork and preliminary analyses of mammalian fossils, the base deposits of Wulanhuxiu section may extend down to the Arshantan age.
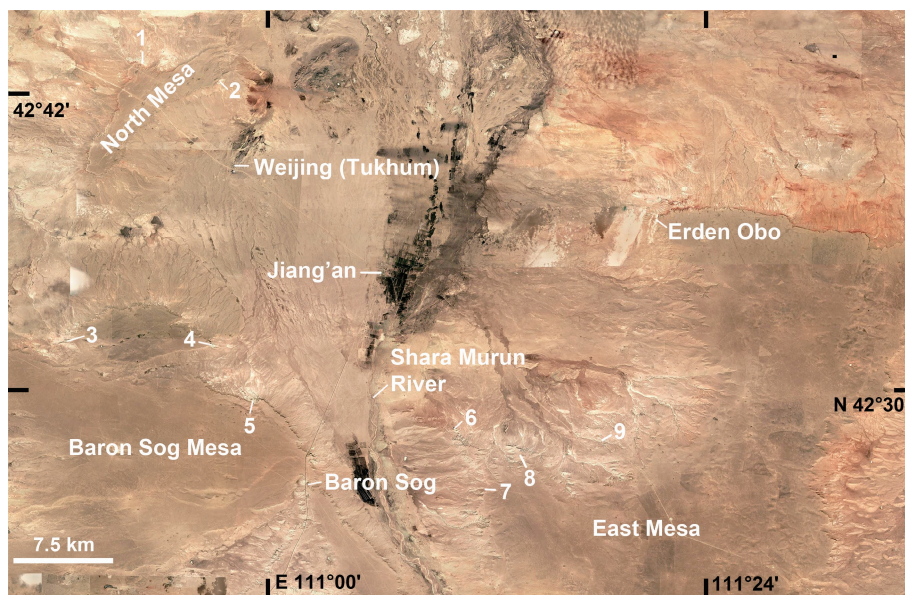


Fig. 1   Location of the Paleogene localities in the Shara Murun region of the Erlian Basin, Nei Mongol, China
1. Wulanhuxiu (=Ulan Shireh, Chimney Butte, 8 miles north of the Tukhum Lamasery);
2. Wulantaolegai (=4 miles north of the Tukhum Lamasery); 3. Ula Usu; 4. Ulan Gochu; 5. Xilin Nor North;
6. Bayan Obo (=Twin Oboes); 7. Jhama Obo; 8. Heretu (=Spring Camp); 9. Dalaiyin Bulage

Radinsky (1965a) tentatively assigned *Teleolophus* material from Wulanhuxiu to *T. medius*? because it is smaller than the holotype of *T. medius* and its M3 is slightly more square. Further, the holotype of *T. medius* was a mandible (AMNH FM 20166) from the Irdin Manha Formation at Irdin Manha, where few upper teeth were discovered. In contrast, the material of *Teleolophus* from Wulanhuxiu was composed of complete upper cheek dentition but few lower teeth, which hampered further comparisons with those from the Irdin Manha (Radinsky, 1965a).

In recent years, we have made extensive field investigation at Wulanhuxiu and other CAE localities in the Shara Murun region (Fig. 1). Many new specimens of *Teleolophus medius*?, including postcranial and dental materials, were discovered from the Ulan Shireh Formation at Wulanhuxiu. Pending a detailed comparison of *Teleolophus* between Wulanhuxiu and Irdin Manha material, we tentatively assigned the postcranial material from Wulanhuxiu to *Teleolophus medius*? as initially suggested by Radinsky (1965a). Here we focus on the postcranial morphology of *Teleolophus*, and briefly discuss its phylogenetic implications and functional morphology.

## 3    Materials and methods

Material described here is housed at the Institute of Vertebrate Paleontology and Paleo-anthropology (IVPP), Chinese Academy of Sciences. The postcranial specimens identified as *Teleolophus medius*? consist of fragmental carpals and metacarpals, hind limb, and pes. These postcranial materials were found from several sites, but the same horizon of a white sandstone in the middle of layer 2 at the Wulanhuxiu section (Li et al., 2016). A quarry (field number: 100705WP02) preserved a number of postcranial elements and a lower jaw with m1–3 of *Teleolophus*, representing multiple individuals. They include: an associated left hind limb and pes (IVPP V 23887); a left patella (V 23888.1); a fragmental trochlea of a left femur (V 23888.2); a left tibia and fibula without the proximal ends (V 23888.3); an incomplete left calcaneus (V 23888.4); a left navicular (V 23888.5); a left mesocuneiform (V 23888.6). Additional specimens unearthed from the site 090703LP01 include: a fragmental right magnum (V 23890.1); a proximal end of a left Mc III (V 23890.2); a proximal end of a right Mc IV (V 23890.3); two left astragali (V 23890.4–5); a left entocuneiform (V 23890.6); a left ectocuneiform (V 23890.7); a distal end of Mc III (V 23890.8). Finally, from the site 090703BB01, a fragmental right lunar (V 23891.1) and a left ectocuneiform (V 23891.2) were collected. Besides the material from the site 100705WP02 in association with a mandible of *Teleolophus*, we assigned other specimens to *Teleolophus* rather than the contemporary *Lophialetes* or *Triplopus*? *proficiens* mainly based either on the larger size of *Teleolophus* or their some unique features shared with *Deperetella* as discussed below.

We describe the postcranial elements of *Teleolophus medius*? along with comparison with those of its close relatives (or presumably close relatives), including *Deperetella*, *Lophialetes*, and three helaletids (*Heptodon*, *Helaletes*, and *Colodon*) (Holbrook, 2001; Osborn and Wortman, 1892; Peterson, 1919; Radinsky, 1965a, b; Schoch, 1984; Scott, 1941). The terminology of postcrania follows Bai et al. (2017a) and Qiu and Wang (2007).

The ternary diagram was used to visualize the hind limb proportions of *Teleolophus* in ternary morphospace relative to different locomotion of ungulates (Gatesy and Middleton, 1997). The ternary diagram was plotted in R 3.4.1 using the package "ggtern" (Hamilton, 2017).

## 4    Comparative description

### 4.1   Manus

Several fragmental carpals and metacarpals are preserved (Fig. 2), including a right lunar without the posterior process (IVPP V 23891.1), a right magnum without the anterior part (V 23890.1), a proximal end of a left Mc III (V 23890.2), a distal end of Mc III (V 23890.8), and a proximal end of a right Mc IV (V 23890.3).

#### 4.1.1  Carpals

**Lunar**    A right lunar is preserved without the posterior process (V 23891.1) (Fig. 2A–E). The lunar is relatively long and narrow in proximal view, and relatively lower and wider
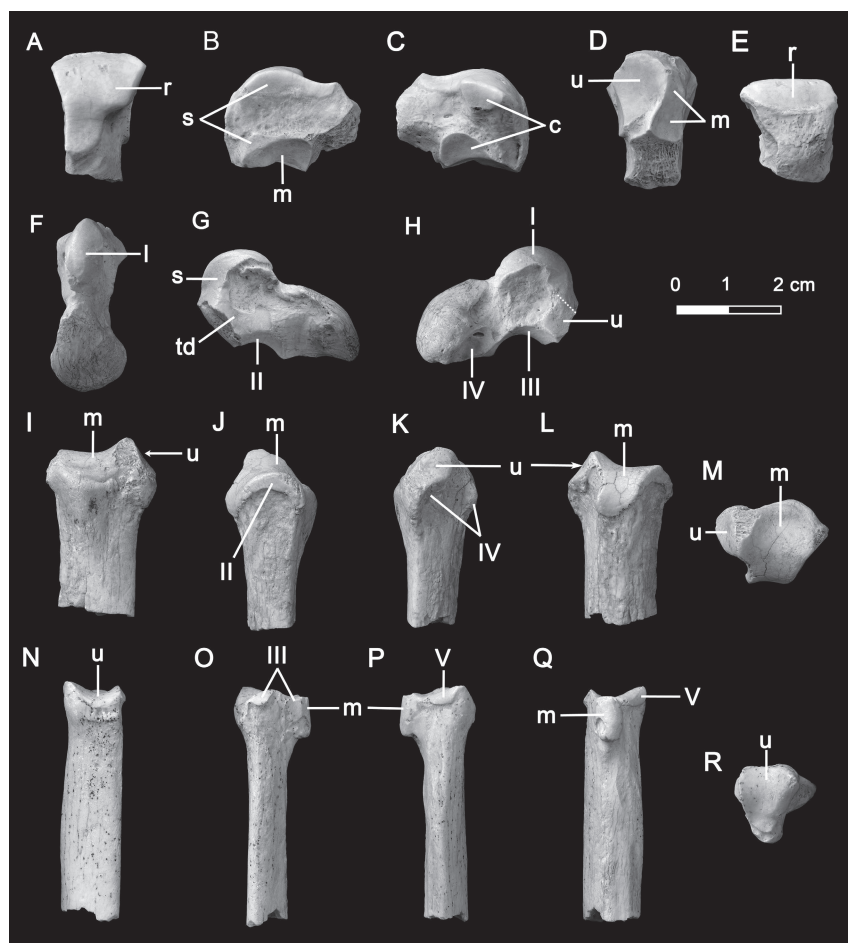
Fig. 2   Partial carpals and metacarpals of *Teleolophus medius*?
A–E. right lunar (IVPP V 23891.1) in proximal (A), medial (B), lateral (C), distal (D), and anterior (E) views;
F–H. right magnum (V 23890.1) in proximal (F), medial (G), and lateral (H) views; I–M. partial left Mc III (V 23890.2) in anterior (I), medial (J), lateral (K), posterior (L), and proximal (M) views; N–R. partial right Mc IV (V 23890.3) in anterior (N), medial (O), lateral (P), posterior (Q), and proximal (R) views
Abbreviations: c. cuneiform; l. lunar; m. magnum; r. radius; s. scaphoid; td. trapezoid; u. unciform;
II, III, IV, V. the second, third, fourth, and fifth metacarpals

in anterior view than those of *Deperetella*, *Heptodon*, and *Colodon*. The anterior part of the radial facet is convex anteroposteriorly and considerably extends onto the anterior surface (Fig. 2A, E), while the posterior part is slightly concave, narrow, and situates in the medial half of the posterior part, as in *Deperetella*. The medial border of the radial facet is slightly concave. By contrast, the posterior part of the radial facet in *Lophialetes* and *Heptodon* is situated in the middle with a more concave medial border. The medial border of the radial facet is also weakly concave in *Colodon*, but the posterior part of the radial facet is rather narrow and nearly indiscernible. On the medial side there are two scaphoid facets (Fig. 2B). The proximal one is band-like, slightly concave anteroposteriorly, whereas the distal one is narrow, strip-like with the anterior part being wider than the posterior part. On the lateral side there are two flat facets for

the cuneiform (Fig. 2C). The proximal one is short and roughly trapezoid in outline, whereas the distal one is lunate, slightly longer, and more posteriorly situated. On the distal side (Fig. 2D), the unciform facet occupies the anterolateral part, concave, and slightly laterally directed, in contrast with more laterally facing in *Deperetella* and *Colodon*. The anterior part of the magnum facet is small, flat, more medially directed than distally, and separated from the distal scaphoid facet by a weak ridge, whereas the anterior magnum facets are absent in *Lophialetes* and *Deperetella* and relatively large and vertically placed in *Heptodon* and *Colodon*. The posterior part of the magnum facet is spherically concave, but the posterior end was broken off. The posterior magnum facet of lunar in *Lophialetes* is more vertically placed, whereas that of *Colodon* is nearly distally directed.

**Magnum**   A fragmental right magnum is preserved without the anterior part (V 23890.1) (Fig. 2F–H). The proximal hump is relatively high, anteriorly situated with a steep anterior border, and bears a nearly vertical facet for the posterior scaphoid facet, as in *Lophialetes* and *Deperetella* (Fig. 2F–H), whereas those of *Heptodon*, *Helaletes*, and *Colodon* are more posteriorly placed with gradual anterior borders. On the medial side, the trapezoid facet is a confluent single facet as in *Heptodon* and *Helaletes* (Fig. 2G). The distal portion of the trapezoid facet is more posteriorly extended than the proximal one. Distal to the trapezoid facet there is a narrow, strip-like, and distomedially directed facet for Mc II (Fig. 2G), whereas the Mc II facets in *Heptodon*, *Helaletes*, and *Colodon* are relatively wider and more vertical. On the lateral side, the unciform facet is flat (Fig. 2H). The anterior lunar facet is narrow and confluent with the unciform facet, whereas the posterior lunar facet is restricted to the lateral surface of the proximal hump and roughly spherically convex (Fig. 2H). On the distal side, Mc III facet is deeply concave anteroposteriorly and slightly convex laterally as in *Lophialetes* and *Deperetella*, whereas those of other compared taxa are less concave anteroposteriorly. The posterior process is separated from the proximal hump by a relatively deep notch, nearly horizontally extended, and gradually expanded transversely towards the posterior end as in *Deperetella* (Fig. 2F–H), but in *Lophialetes*, *Heptodon*, and *Colodon*, the posterior processes are more distally extended and even medially projected in the latter two genera. In proximal view, the posterior process is roughly pear-shaped in outline as in *Deperetella* and *Lophialetes* (Fig. 2F), but those of *Heptodon* and *Colodon* taper posteriorly. On the lateral side of the posterior process, there is a deeply excavated facet for Mc IV (Fig. 2H), contacting Mc III facets anterodistally. Mc IV facets of the magnum are absent in *Heptodon* and *Colodon*, but is present as a concave facet in *Lophialetes* (Radinsky, 1965a). Radinsky (1965a) also noted the absence of Mc IV facet of the magnum in *Deperetella*; however, the Mc IV facet is indeed present on an uncatalogued magnum recently discovered from Ula Usu.

4.1.2   Metacarpals

Scott (1941) interpreted that there were four metacarpals in *Colodon*, but Radinsky (1965a) considered *Colodon* had a tridactyl manus. The metacarpals of *Teleolophus* are presumably long and slender.

**Mc III**    Proximally, the magnum facet is strongly convex anteroposteriorly and slightly concave mediolaterally with the posterior border more distally extended than the anterior one (Fig. 2I–M). Below the magnum facet on the anterior surface, there is a relatively large tubercle (Fig. 2I). Lateral to the magnum facet, the unciform facet is relatively large, laterodistally inclined, triangular in outline, and slightly convex anteroposteriorly (Fig. 2I, K–M). The relatively large unciform facet of Mc III in *Teleolophus* is similar to those of *Deperetella*, *Heptodon*, and *Colodon* (Radinsky, 1965b:fig. 13), whereas *Lophialetes* has a relatively small unciform facet. The unciform facet is confined to the anterior half of proximal end, and demarcated posteriorly by a wide notch (Fig. 2M). On the medial side, the Mc II facet is nearly vertical, strip-like, and proximally bowed (Fig. 2J) as in *Deperetella*. In contrast, the Mc II facets of Mc III are usually small and less prominent in other compared groups. On the lateral side, the Mc IV facet is composed of two facets separated by a large rugose area (Fig. 2K): the anterior one is relatively large and overhung by the unciform facet, whereas the posterior one is rather small. The distal end is longer than wide (IVPP V 23890.8). The median keel, although broken off, extends anteriorly beyond the transverse midline of the distal articular facet. There is a distinct, projected tubercle on either lateral side of the distal end.

**Mc IV**    On the proximal end, the unciform facet is triangular in outline, strongly concave laterally, and nearly flat anteroposteriorly (Fig. 2R). The lateral border of the unciform facet is slightly higher than the medial border in anterior view (Fig. 2N), which is similar to those of *Lophialetes*, *Colodon* and more exaggerated in *Deperetella*, whereas the unciform facets of Mc IV in *Heptodon* and *Helaletes* have the lateral borders lower than the medial ones. On the medial side, there are two flat Mc III facets separated by a rough area (Fig. 2O): the anterior one is oval, medially inclined, whereas the posterior one is quadrilateral, vertically placed, and nearly confluent with the magnum facet. On the lateral side, the Mc V facet is narrow, slightly convex, and continuous with the unciform facet (Fig. 2P). The posterior process bears a semicylindrically convex, proximodistally elongated facet for the magnum as discussed above (Fig. 2O–Q).

## 4.2   Hind limbs

**Femur**    The femur is only known from the distal two thirds of the shaft and the distal epiphysis (Figs. 3, 4A). The femur is slender, and the preserved shaft is slightly anteriorly bowed, which is partially attributed to a distortion in preservation. Although both lesser trochanter and third trochanter are broken, the former is relatively more proximally situated than the latter judging from the preserved bases as those of *Lophialetes* (Reshetov, 1979) (Fig. 3A). In contrast, the lesser trochanter is only slightly higher than the third trochanter in *Heptodon* and *Helaletes*. The anteroposterior length of the distal shaft is greater than its width. A supracondyloid fossa is shallow, and situated in a relatively low position above the lateral condyle.

The trochlea is partially damaged in V 23887 (Fig. 3A), whereas it is more complete in V 23888.2. The width of the distal end is 47.24 mm, and the anteroposterior distance is about 60 mm in V 23887. The trochlea is slightly constricted distally and asymmetrical with the medial
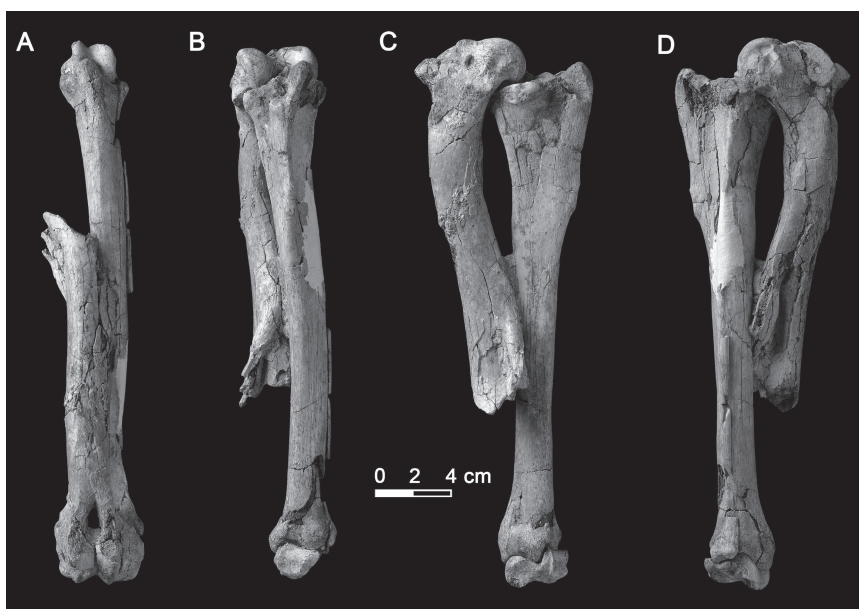
Fig. 3　Left femur, tibia, fibula, and astragalus of *Teleolophus medius*? (IVPP V 23887) in articulation
A. anterior view of femur and posteromedial view of tibia; B. anterior view of tibia and fibula, and partial
posterior view of femur; C–D. medial (C) and lateral (D) views of hind limbs and astragalus

trochlear ridge more anteriorly expanded and straight than the lateral one, and the medial surface of trochlea wider than the lateral one (Figs. 3A, 4A). The lengths of the medial and lateral trochlear ridges are 40.64 and 38.72 mm, respectively, in V 23888.2. The median groove of the trochlea is slightly oblique to the long axis of the shaft. The trochlea of *Lophialetes* is also asymmetrical, whereas those of *Heptodon*, *Helaletes*, and *Deperetella* are relatively narrow and symmetrical. However, it is necessary to mention that the distal end of the femur of *Deperetella* (AMNH FM 81830) was glued from the two laterally separated parts roughly along the groove of the trochlea, thus, the symmetrical trochlea is more likely attributed to an artificial modification. As a result, we suggest that the trochlea of the femur in *Deperetella* is also somewhat asymmetrical as in *Teleolophus*, pending the discovery of more complete specimens. The supratrochlear fossa is deep and high, although it is partially damaged (Fig. 3A). The medial condyle is wider with a more gradual articular facet than the lateral condyle (Fig. 4A). However, in *Lophialetes* and *Heptodon*, the lateral condyles are larger and wider than the medial ones, and the femur of *Deperetella* has a lateral condyle roughly as large as a medial condyle. The intercondyloid fossa is relatively wide and deep. A triangular, deep extensor fossa interrupts the trochlea and the lateral condyle as in *Lophialetes* and *Deperetella* (Fig. 4A). The medial epicondyle is more prominent and proximally situated than the lateral epicondyle, which bears a large, shallow depression in the middle (Fig. 3C, D). Distal to the depression there is a small, deep fossa for the insertion of the popliteus muscle.

**Patella**　　A left patella is preserved, with the base being partially broken (Fig. 4C–H; Table 1). The patella is roughly shield-shaped, considerably longer than wide, and somewhat

anteroposteriorly compressed, as in *Lophialetes*. The base of patella in *Deperetella* thickened anteroposteriorly. The medial and lateral borders are straight and parallel to each other, whereas the distal border is composed of two lines convergent distally (Fig. 4C). The articular surface occupies the whole posterior side, and is divided by a blunt ridge into two parts (Fig. 4D–F): the medial one is wide, flat or slightly concave transversely, and convex proximodistally at the distal end, whereas

**Table 1  Measurements of patella of *Teleolophus medius*? (IVPP V 23888.1) (mm)**

| | |
|---|---|
| 1. Height | 46.87[a] |
| 2. Width | 26.74 |
| 3. Articular facet, width of lateral half | 13.47 |
| 4. Articular facet, width of medial half | 16.13 |
| 5. Maximum APD of PE | 16.06 |
| 6. Max APD of patella | 18.80 |
| Ratio (%) | |
| 2:1 | 57.05 |
| 3:4 | 83.51 |
| 6:1 | 40.11 |

a) Approximate measurement. APD=anteroposterior distance; PE=proximal end.

the lateral one is narrow, more concave transversely, and flat proximodistally at the distal end. The angle between the two surface is about 90° in proximal view and less than 90° in distal view (Fig. 4G, H). The base is raised above the articular surface and extended anteromedially (Fig. 4D, G). The anterior surface is rugose and generally flat with a slightly swollen tubercle just above the apex (Fig. 4C). Along the distal half of the medial border there is a depressed area for the patellar ligament (Fig. 4E), whereas the medial surface of the patella becomes wider and bears a more distinct depressed area in *Deperetella*.

**Tibia**  The tibia is nearly complete, however, the medial part of the tibial tuberosity and lateral condyle are damaged, and the distal end of the shaft is cracked (Figs. 3, 4A–B; Table 2). Further, of specimen V 23887, the posterior part of the proximal end of the tibia articulates with the femur and the distal end articulates with the astragalus in position.

The tibia is long and slender (Fig. 3B; Table 2). The proximal end is anteroposteriorly deeper than its transverse width (Fig. 4A). The lateral intercondyloid eminence is higher than the medial one as in *Lophialetes*, *Deperetella*, and *Heptodon*, although the intercondyloid eminences are partially damaged on V 23887. The tibial tuberosity is excavated by a very deep and narrow groove (sulcus tuberosititas tibiae) as in *Lophialetes* and *Deperetella* (Figs. 3B, C, 4A), whereas that of *Heptodon* is relatively wider and shallower. The lateral part of the tibial tuberosity, forming the lateral border of the groove, is mediolaterally compressed and more ridge-like rather

**Table 2  Measurements of tibiae of *Teleolophus medius*?**     (mm)

| Measures | IVPP V 23887 | IVPP V 23888.3 |
|---|---|---|
| 1. Total length | 270.00 | ? |
| 2. Proximal end, width | 47.28 | ? |
| 3. Proximal end, APD | 51.00[a] | ? |
| 4. Distal end, width | 33.76 | 32.86 |
| 5. Distal end, APD | 31.03 | 28.91 |
| 6. Width at middle of shaft | 22.26 | ? |
| 7. Trochlea, width | 27.28[a] | 24.88 |
| 8. Trochlea, APD | ? | 26.87 |
| Ratio (%) | | |
| 2:1 | 17.51 | ? |
| 4:1 | 12.50 | ? |
| 8:7 | ? | 108.00 |

a) Approximate measurements. APD=anteroposterior distance.
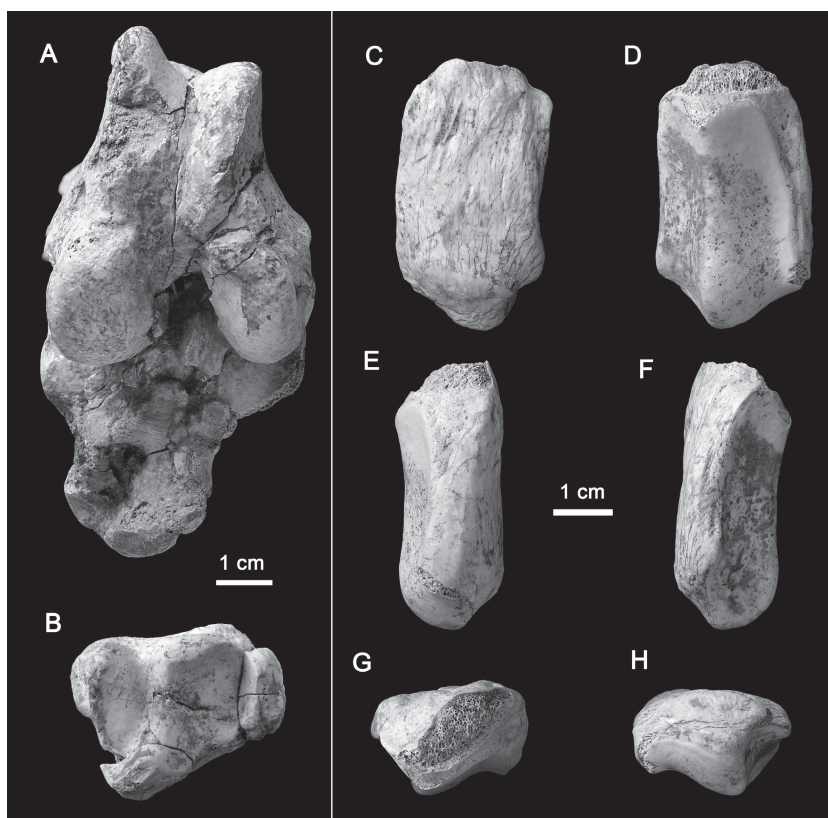
Fig. 4   Extremities of left hind limbs and left patella of *Teleolophus medius*?
A. distal view of femur and partially proximal view of the tibia (IVPP V 23887);
B. distal view of tibia and fibula (V 23888.3); C–H. left patella (V 23888.1) in anterior (C), posterior (D),
medial (E), lateral (F), proximal (G), and distal (H) views

than a tuberosity (Fig. 3B). The medial part of the tibial tuberosity was broken off. The extensor sulcus is probably wide and open, although the lateral border of the lateral condyle was broken off. On the posterolateral corner just below the lateral condyle there is a concave facet slightly overhanging the shaft for the articulation with the head of the fibula (Fig. 3D). The tibial crest extends from the tibial tuberosity distally to a rough nodule at about proximal one-fourth of the shaft length (Fig. 3B).

The left tibia shaft is slightly S-shaped in anterior view (Fig. 3B). The proximal end of the shaft is concave on the lateral and posterior surface, but is flat on the medial surface (Fig. 3C, D). The shaft is a roughly triangular prism with a posterior, anteromedial, and anterolateral sides. The anterior border of the shaft is prominent and long, extending from the tibial crest to the distal epiphysis. The cross section of the shaft is generally triangular with a posterior edge shorter than the either lateral edge proximally, and with equal lengths of the edges in the middle and distal parts. The lateral side of the shaft gradually curves anteriorly near the distal end of the shaft (Fig. 3B, C), whereas that of *Heptodon* completely curves anteriorly from the proximal one-thirds of the shaft with a quadrilateral instead of a triangular outline of the cross section distally.

The distal end of the tibia is roughly trapezoid in outline with a pointed posterior end (Fig. 4B), similar to those of *Lophialetes* and *Deperetella*. However, the distal ends of *Heptodon* and *Colodon* are more rectangular in outline. The two articular grooves for the astragalus extend anterolaterally and are roughly equal in width as in *Deperetella* and *Colodon*. In contrast, the medial groove is slightly wider than the lateral one in *Lophialetes*, and the medial one is narrower in *Heptodon*. The grooves are separated by a blunt, anteroposteriorly concave ridge. On the distal end there is a moderately developed medial malleolus, to which a shallow malleolus sulcus for the long digital flexor is situated posteriorly. From the posterior view, the posteromedial process is considerably more distally extended than the lateral part (Fig. 3A), whereas the former is slightly more distally extended than the medial malleolus (Fig. 3C).

**Fibula**    There preserves a distal shaft and distal end of fibula, which articulates with the tibia in position on IVPP V 23887 (Fig. 3).

The fibula is extremely reduced and even fused with the tibia in V 23888.3 at least at the distal one-third of the thin shaft as in that of *Deperetella*. The fibula of *Heptodon* is less reduced and relatively thick, and that of *Lophialetes* shows no sign of fusion. In *Teleolophus*, the distal end of the fibula is deeper than wide, bearing a narrow, indistinct groove on the posterior side as in *Deperetella* (Figs. 3D, 4B), whereas in *Lophialetes* and *Heptodon* the groove is posterolaterally placed. The facet for the astragalus is flat, bean-shaped, and facing distomedially (Fig. 4B). There is no facet for the calcaneus, in contrast to the presence in *Lophialetes*, *Heptodon*, and *Helaletes*. However, a small calcaneus facet of fibula should be present in *Deperetella* as deduced from the corresponding pit proximal to the ectal facet of the calcaneus (Radinsky, 1965a).

### 4.3   Pes

Some isolated astragalus, calcaneus, navicular, entocuneiform, and ectocuneiform are preserved (Figs. 5, 6). One articulated pes of *Teleolophus* (IVPP V 23887) is preserved but lacking distal phalanges and the fourth digit (Fig. 7). The shafts of the metatarsals in V 23887 are also damaged.

#### 4.3.1   Tarsals

**Astragalus**    Three right astragali are preserved. One left astragalus is articulated with the tibia in position (IVPP V 23887) (Fig. 3), and two isolated left astragali are also preserved (IVPP V 23890.4–5) (Fig. 5A–E; Table 3). The height of the trochlea is about equal to its width (Fig. 5A). The median groove is relatively wide and moderately deep. The trochlea is asymmetrical with a lateral part wider and more gradual than a medial one. The ridges of the trochlea are blunt, and the medial ridge is separated from the navicular facet by a short distance as in *Heptodon* and *Helaletes*. However, the medial ridge of the trochlea either contacts the navicular facet or is separated from the latter by a short distance in *Deperetella* (AMNH FM 81817). The ridges of trochlea are sharper with the medial ridge contacting the navicular facet in *Lophialetes*. The astragalus of *Helaletes* is high and narrow, having relatively sharper ridges of the trochlea and a longer neck than that of the *Teleolophus* (Peterson, 1919:pl. 42, fig. 8).
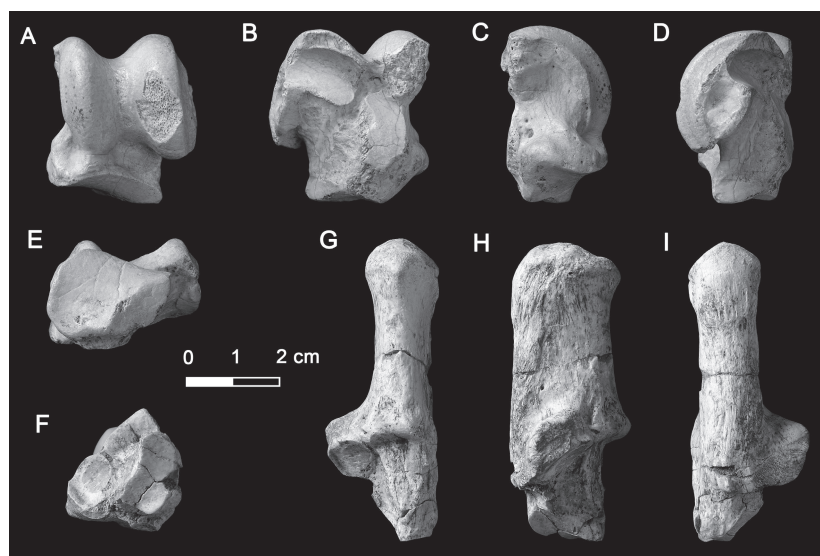
Fig. 5   Left astagalus and calcaneus of *Teleolophus medius*?
A–E. left astagalus (IVPP V 23890.4) in anterior (A), posterior (B), medial (C), lateral (D), and distal (E)
views; F–I. left calcaneus (V 23887) in distal (F), anterior (G), medial (H), and posterior (I) views

The astragalus of *Colodon* has a relatively lower and wider trochlea than that of *Teleolophus* with a medial ridge joining the navicular facet (Scott, 1941). The lateral surface of the trochlea for the fibula is slightly concave and lacks a laterally projected process on the distal end as in *Deperetella* (Fig. 5A, D), whereas the laterally projected process is present in other compared taxa. The medial surface of the trochlea for the medial malleolus is slightly convex without a proximal, medially projected process as that of *Deperetella* (Fig. 5A, C), whereas the proximal process is present in *Lophialetes*. Distomedial to the medial ridge of the trochlea there is a moderately deep fossa. The neck is relatively short.

Table 3   Measurements of astragali of *Teleolophus medius*?                 (mm)

| Measures | IVPP V 23890.4 | IVPP V 23890.5 |
|---|---|---|
| 1. Maxium height | 36.74 | 32.77 [a] |
| 2. Maxium width | 31.64 | 27.86 |
| 3. Trochlea, medial length | 28.63 | 25.38 |
| 4. Trochlea, lateral length | 28.18 | ? |
| 5. Trochlea, maximum width | 28.22 | 24.97 |
| 6. Distal end, width | 23.37 | 20.15 |
| 7. Navicular facet, width×length | 22.07×19.06 | 18.42×17.2 |
| 8. Cuboid facet, width×length | 7.44×17.48 | 4.88 [a]×14.58 [a] |
| 9. Ectal facet, height×width | 11.13×15.77 | 9.68×2.91 |
| 10. Sustentacular facet, height×width | 17.18×10.18 | 15.13×10.00 |
| 11. Inclination angle, α | 120° | 110° |
| 12. Torsion angle, β | 20° | 25° |
| Ratio (%) | | |
| 2:1 | 86.12 | 85.02 |
| 6:2 | 73.86 | 72.33 |
| 3:4 | 101.6 | ? |

a) Approximate measurements.

On the posterior side, the ectal facet is wider than long and deeply concave (Fig. 5B). A long facet (lappet), extending from the distolateral corner of the ectal facet distally almost to the lateral surface of the trochlea, is slightly convex, strip-like, and forms a nearly right angle with the ectal facet. In contrast, the lappet is relatively short in other compared taxa. The sustentacular facet is slightly convex or flat and approximately quadrilateral in outline with rounded corners, bearing a small sustentacular hinge proximally. The astragalar sulcus is relatively narrow and shallow. The sustentacular facet is separated from the navicular and cuboid facets by a rugose area. The distal calcaneal facet is flat, confined to the anterolateral corner of the posterior side, and separated from the sustentacular facet. The sustentacular facet of the calcaneus in *Lophialetes* is slightly concave mediolaterally and contacts the distal calcaneal facet as in *Deperetella*. The contact between the sustentacular facet and the distal calcaneal facet is present in *Heptodon calciculus* and *Colodon*, but is absent in *H. posticus* (Radinsky, 1965b).

On the distal end, the navicular facet is roughly trapezoid in outline and saddle-shaped as in *Lophialetes*, *Deperetella*, and *Colodon* (sub-quadrate) (Fig. 5E). The navicular facet of the astragalus is more rounded and slightly wider than long in *Heptodon*. The cuboid facet, which is narrow, strip-like, and pointed anteriorly, has a slightly convex anterior surface and a concave posterior facet.

**Calcaneus**   Two left calcanei (V 23887, 23888.4) are preserved and V 23887 is associated with other tarsals.

The calcaneus is relatively deep (anteroposteriorly) and long (Fig. 5F–I; Table 4). The calcaneal tuber has a rugose free end, which is roughly anteroposteriorly elongated and oval in outline. The ectal facet is placed at the distal 37%–40% of the length of the calcaneus (Fig. 5G) and is composed of two facets: the distal one is slightly concave and faces distally, and the proximal one is slightly convex, facing anteromedially and perpendicular to the distal facet. A long, strip-like facet extends from the ectal facet distally along the lateral border of the calcaneus. Proxiolateral to the ectal fact there is a prominent fossa for the fibula in *Lophialetes*, *Heptodon* and *Colodon*, whereas the fossa is absent in *Teleolophus* and shallow in *Deperetella*. The sustentaculum is relatively thick, bearing a large, concave, irregular oval facet for the astragalus distally, and a small, distinct facet for the sustentacular hinge of the astragalus proximally (Fig. 5F–H). The astragalar facet on the sustentaculum is nearly confluent with the distal portion of the ectal facet, whereas in *Lophialetes* and *Heptodon* they are more separated. The distal astragalar facet is fusiform, concave, relatively short, and separated from the astragalar facet of the sustentaculum, whereas

**Table 4   Measurements of calcaneus of *Teleolophus medius*? (IVPP V 23887)   (mm)**

|  |  |
|---|---|
| 1. Total length | 66.31 |
| 2. PE-middle of ectal facet | 42.09 |
| 3. DE-middle of ectal facet | 22.22 |
| 4. Maximum, width | 25.57 |
| 5. Width, tuber | 16.20 |
| 6. APD, tuber | 24.87 |
| Ratio (%) |  |
| 4:1 | 38.56 |
| 3:2 | 52.79 |
| 5:6 | 65.14 |

PE=proximal end; DE=distal end; APD=anteroposterior distance.

the distal astragalar facet is relatively long in *Deperetella*. On the distal end, the cuboid facet is anteroposteriorly long with a roughly rectangular outline (Fig. 5F). The cuboid facet is slightly convex anteriorly and concave posteriorly as in *Lophialetes* and *Deperetella*, whereas the cuboid facet is saddle-shaped in *Heptodon* and generally flat in *Colodon*.

**Navicular**    Two left naviculars (IVPP V 23887, 23888.5) are preserved, of which the V 23887 is associated with other tarsals (Table 5). The proximal astragalar surface is roughly rectangular in outline with a nearly straight medial border and a small triangular apex at the anterolateral side (Fig. 6A). The surface is concave anteroposteriorly and flat transversely. On the lateral side, the cuboid facet is composed of the two part (Fig. 6B): the posterior one is large, nearly flat, and contacts the proximal and distal surface, whereas the anterior one is strip-like, narrow, and extends along the proximal border. The posterior cuboid facet is more or less bilobed in *Deperetella* (AMNH FM 81820), and an additional small cuboid facet is present at the anterodistal corner in *Colodon*. On the distal surface, the ecto-, meso-, and entocuneiform facets are nearly confluent (Fig. 6C), and the latter two facets are almost in the same plane as in *Deperetella*. The ectocuneiform facet is nearly triangular in outline, and its anterolateral part rises pronouncedly in relation with the posterior part as in *Deperetella*. As a result, in the lateral view, the distal border has an angled profile, and the anterior part is proximodistally lower than
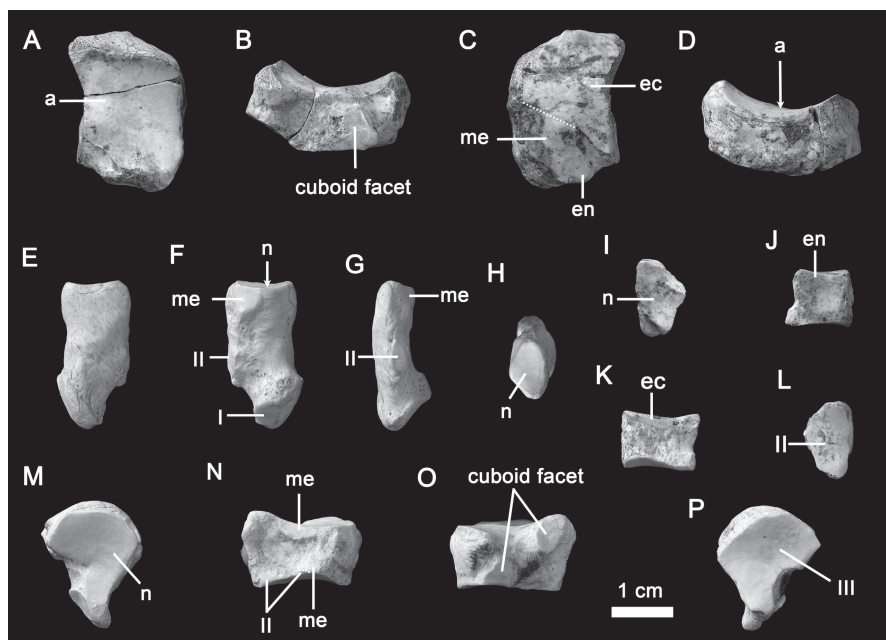


Fig. 6   Partial tarsals of *Teleolophus medius*?
A–D. left navicular (IVPP V 23888.5) in proximal (A), lateral (B), distal (C), and meidal (D) views;
E–H. left entocuneiform (V 23890.6) in posterior (E), anterior (F), medial (G), and proximal (H) views;
I–L. left mesocuneiform (V 23888.6) in proximal (I), medial (J), lateral (K), and distal (L) views;
M–P. left ectocuneiform (V 23890.7) in proximal (M), medial (N), lateral (O), and distal (P) views
Abbreviations: a. astragalus; ec. ectocuneiform; en. entocuneiform; me. mesocuneiform; n. navicular;
I, II, III. the first, second, and third metatarsals

**Table 5　Measurements of navicular and cuboid of *Teleolophus medius*?**　　　(mm)

| Navicular (IVPP V 23888.5) | | Cuboid (IVPP V 23887) | |
|---|---|---|---|
| 1. Anterior height at mid | 10.40 | 1. Anterior height | 22.11 |
| 2. Max width | 20.10 | 2. Anterior width | 9.70 [a] |
| 3. Max APD | 25.05 | 3. APD | 26.35 |
| 4. Ectocun. facet, width×APD | 19.08×21.6 | 4. Calcan. facet, width | 11.33 |
| 5. Mesocun. and entocun. facet, width×APD | 17.3×9.27 | 5. Calcan. facet, APD | 15.77 [a] |
| Ratio (%) | | 6. Astrag. facet, width | 4.93 |
| 　　1:2 | 51.74 | 7. Distal facet, width | 13.01 |
| 　　2:3 | 80.24 | Ratio (%) | |
| | | 　　1:2 | 227.94 |
| | | 　　1:3 | 83.91 |
| | | 　　2:3 | 36.81 |
| | | 　　6:4 | 43.51 |

a) Approximate measurements. APD=anteroposterior distance.

the posterior part (Fig. 6B). By contrast, the ectocuneiform facets of *Lophialetes*, *Heptodon*, and *Colodon* are less raised anteriorly. The anterior, medial, and posterior sides are rugose (Fig. 6D).

**Cuboid**　The cuboid (IVPP V 23887) is associated with other tarsals in nearly anatomical position (Fig. 7; Table 5). The cuboid is relatively high and narrow in anterior view. The proximal surface is roughly rounded, and slightly anterior concave and posterior convex. The calcaneal and astragalar facets are confluent without a distinct boundary, however, a small process at the anteromedial corner discriminates their boundary. In contrast, the proximal surface of the cuboid in *Deperetella* is roughly anteroposteriorly elongated oval in outline. On the distal half of the medial side there should be two facets for the ectocuneiform as deduced from the corresponding facets on the ectocuneiform: posteroproximally and anterodistally placed, respectively. But the anterior facet for the ectocuneiform of the cuboid in *Colodon* is high, joining the anterodistal navicular facet. On the distomedial side of the cuboid there is a small facet for the Mt III as in *Lophialetes* and *Deperetella* (Fig. 7E), whereas in *Heptodon*, *Helaletes*, and *Colodon* the cuboids do not contact the third metatarsals. The posterior process is relatively large, constricted proximally and expanded distally (Fig. 7D). The posterior process is relatively more proximally situated than that of *Lophialetes*, and extends distally not beyond the distal facet.

**Entocuneiform**　Two left entocuneiforms are preserved. One specimen (IVPP V 23887) in the articulation is completely fused with the Mt I (Fig. 7) as in *Colodon* (Radinsky, 1963), whereas V 23890.6 is isolated.

The entocuneiform is long (proximodistally), narrow, and flat as those of *Deperetella* and *Lophialetes* (Fig. 6E–H; Table 6), whereas those of *Heptodon* and *Colodon* are circular and diamond-shaped, respectively, in posterior view (Radinsky, 1963). The medial and lateral borders of the entocuneiform are straight (Fig. 6E, F). Proximally, the navicular facet is triangular in outline, and slightly concave (Fig. 6H). On the anterior side there is a flat, tongue-shaped facet for the mesocuneiform adjacent to the navicular facet as in *Deperetella* (Fig. 6F, G). In contrast, the mesocuneiform facet is anteromedially placed to the navicular facet in *Heptodon*.
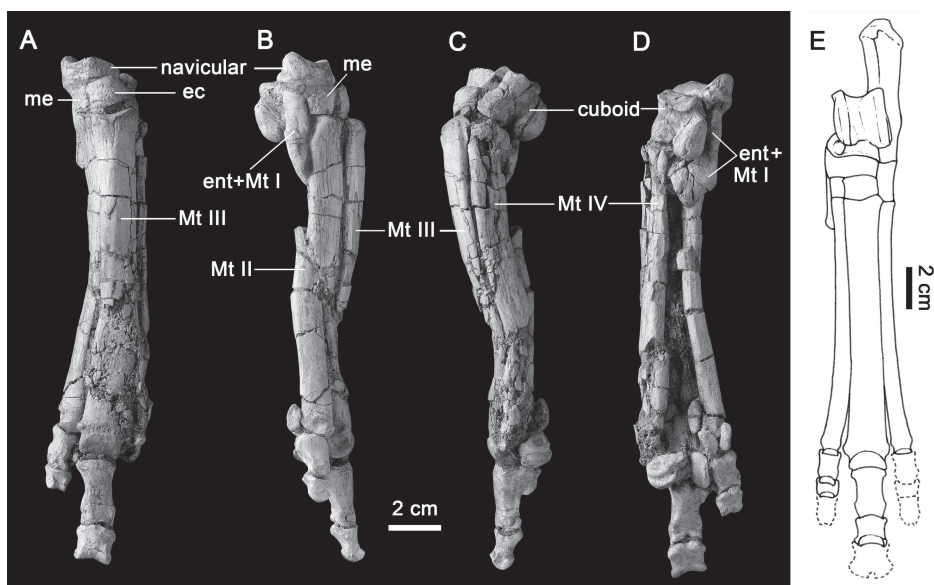
Fig. 7   Left pes of *Teleolophus medius*? (IVPP V 23887) in articulation
A. anterior, B. medial, C. lateral, and D. posterior views, E. reconstruction of left pes
Abbreviations: ec. ectocuneiform; ent. entocuneiform; me. mesocuneiform;
Mt I, II, III, and IV. the first, second, third, and fourth metatarsals

Table 6   Measurements of ento-, meso-, and ectocuneiform of *Teleolophus medius*?   (mm)

| Measures | Entocuneiform (IVPP V 23890.6) | Mesocuneiform (V 23888.6) | Ectocuneiform (V 23890.7) |
|---|---|---|---|
| 1. Length | 24.22 | 12.94 | 20.72 |
| 2. Width | 12.21 | 8.14 | 16.78 |
| 3. Anteroposterior distance or height | 6.42 | 9.45 | 10.03 |
| Ratio (%) | | | |
| 2:1 | 50.41 | 62.91 | 80.98 |
| 3:2 | 52.58 | 116.09 | 59.77 |

On the medial border of the anterior surface there is a strip-like, long, and uneven facet for Mt II (Fig. 6F, G). The distal process is hook-like in posterior view (Fig. 6E). A short process extends anteriorly from the distal end of the entocuneiform, bearing an oval, slightly concave facet for the Mt I on the distal surface (Fig. 6F, G). The anterior process of the distal end is relatively longer and more prominent in *Deperetella* than in *Teleolophu*s, whereas the distal end of the entocuneiform is slightly thickened without a hook in *Lophialetes* and *Colodon*.

**Mesocuneiform**   Two mesocuneiforms are preserved (IVPP V 23888.6, V 23887) and V 23887 is articulated with other pes (Figs. 6I–L, 7A, B; Table 6). The anterior surface is rectangular in outline (Fig. 7B, E), wider than high as in *Heptodon* and *Colodon*, or square in outline. In contrast, the anterior surface of the mesocuneiform is rounded in *Lophialetes*. The height of mesocuneiform is nearly as high as that of ectocuneiform as in *Lophialetes* and *Deperetella* (Radinsky, 1965a:fig. 29) (Fig. 7E), whereas those of *Heptodon* and *Colodon* are distinctly lower than the ectocuneiforms in anterior view. The proximal surface for the

navicular is triangular in outline with a slightly convex lateral border, and slightly concave anteroposteriorly and flat transversely (Fig. 6I). On the medial side, the entocuneiform facet is semicircular, flat, and posteroproximally situated (Fig. 6J). On the lateral side the ectocuneiform facet is narrow, strip-like, and running along the anterior two-thirds length of the proximal border (Fig. 6K). The distal surface for the Mc II is anteroposteriorly elongated oval in outline, concave anteroposteriorly and slightly convex transversely (Fig. 6L).

**Ectocuneiform**   Three left ectocuneiforms are preserved (IVPP V 23887, V 23890.7, V 23891.2), and V 23887 is associated with other tarsals (Figs. 6M–P, 7; Table 6).

The ectocuneiform of *Teleolophus* is relatively wider (transversely) and lower (proximo-distally) than that of *Heptodon*, and slightly higher than the navicular (Fig. 7A, E). The navicular facet is slightly concave, roughly triangular with an indented lateral border, and its posterior half raised considerably compared to the anterior half in lateral view as in *Deperetella* (Fig. 6M, O), corresponding to the angled-profile ectocuneiform facet of the navicular. However, in *Lophialetes*, *Heptodon*, and *Colodon* the navicular facet is generally plane. The posterior process is short and reduced as in *Lophialetes*, *Deperetella*, and *Colodon*, whereas that of *Heptodon* is more distinct (Radinsky, 1965b:fig. 21). On the lateral side there are two cuboid facets (Fig. 6O): a posteroproximal one is oval in outline, nearly flat, adjacent to the navicular facet, and vertically placed or slightly directed proximally; an anterodistal one is triangular in outline, flat, adjacent to the Mt III facet, and vertically placed. The medial side bears a strip-like, flat facet for the mesocuneiform along the middle portion of the proximal border, and two small, anteroposteriorly separated distal facets (Fig. 6N). However, it is uncertain that whether the distal two facets of the medial side articulate with either the Mt II or the mesocuneiform. Regarding the height of mesocuneiform nearly as same as the ectocuneiform based on V 23887, we deduce that the anterior facet is mainly articulated with the mesocuneiform, whereas the posterior facet is for the articulation of Mt II. The Mt II facet is barely proximally extended beyond the line at the level of the distal border of anterior mesocuneiform facet. Further, a rather small, faint facet for the Mt II is posterodistally placed to the anterior mesocuneiform facet. The Mt II facets of the ectocuneiforms in *Lophialetes* and *Deperetella* probably have similar conditions as that of *Teleolophus*, but the features were not clearly figured out by Radinsky (1965a:fig. 31, 40). By contrast, the ectocuneiform of *Heptodon* and *Colodon* articulates with both Mt II and Mt IV on the medial and lateral sides, respectively (Radinsky, 1965b:fig. 21). The Mt III facet occupies the distal surface of the ectocuneiform (Fig. 6P). It is roughly triangular in outline with a convex anterior border and an indented lateral border, concave anteroposteriorly and nearly flat transversely.

## 4.3.2  Metatarsals

The metatarsals are articulated in position (Fig. 7A–E). The metatarsals are relatively long with lateral metatarsals closely appressed to the median one and flatter than the latter. The Mt I is fused with entocuneiform in V 23887, and rhombic in outline in posterior view (Fig. 7D). The proximal end of Mt III bears a laterally concave facet for the ectocuneiform, and a

small, lateroproximally directed facet for the cuboid on the lateral side as in *Deperetella* and *Lophialetes*. By contrast, the Mt III of *Heptodon* and *Colodon* does not contact the cuboid due to the articulation between the ectocuneiform and Mt IV. The distal end of Mt III bears two prominent tubercles on each side, whereas the tubercles are highly reduced on the lateral metatarsals.

The lengths of Mt II, III, and IV in V 23887 are about 125, 135, and 120 mm, respectively.

### 4.3.3 Phalanges

As pointed out by Radinsky (1965), the phalanges of pes are similar to those of manus except for being longer and relatively narrower (Fig. 7; Table 7), and the proximal lateral phalanges of pes lack the prominent tuberosities that can be seen on the axial side of those phalanges in the manus. Furthermore, the PhI of pes is somewhat depressed on the lateral sides.

Table 7   Measurements of pedal phalanges of *Teleolophus medius*? (IVPP V 23887)   (mm)

| Digit | PhI | | | PhII | | |
|---|---|---|---|---|---|---|
| | H | W | L | H | W | L |
| D-III | 25.42 | 15.40 | 15.52 | 17.15 | 15.36 | 10.67 |
| D-IV | 18.51 | 12.68 | 12.08 | 11.62 | 11.04 | 9.1 |

Abbreviations: H=height; W=width; L=proximally anteroposterior length.

## 5    Discussion

### 5.1   Phylogenetic implications

Based on the above-mentioned comparisons, it is clear that the postcranial skeleton of *Teleolophus* is strikingly similar to that of *Deperetell*a; these include: 1) the lunar is relatively deep and narrow with a slightly concave medial border of the radial facet; 2) the trapezium has a scaphoid facet; 3) the magnum has a posterior process nearly horizontally extended with a pear-shaped outline in the proximal view; 4) an unciform facet of Mc IV has the lateral border higher than the medial border; 5) the trochlea of the femur is asymmetrical with the medial ridge more anteriorly expanded; 6) the patella is roughly shield-shaped and somewhat flattened; 7) the tibial tuberosity is excavated by a very deep and narrow groove; 8) the fibula is highly reduced; 9) the astragalus has the medial ridge not in contact with the navicular facet; 10) the calcaneus lacks a prominent fossa proximolateral to the ectal facet for the fibular articulation; 11) the navicular has the anterior part of the ectocuneiform facet considerably arising compared with the posterior part; 12) the cuboid has a small facet for Mt III; 13) the entocuneiform is proximodistally long, narrow, and flat; 14) the mesocuneiform is about as high as the ectocuneiform; and 15) a navicular facet of the ectocuneiform raised considerably on the posterior half compared to the anterior half. Nevertheless, the postcranial skeleton of *Teleolophus* differs from that of *Deperetella* in being smaller, and in having the lunar with an anterior magnum facet, and the distal end of the entocuneiform with a shorter anterior process.

The sister group relationship between Deperetellidae and Lophialetidae has been proposed by some authors (Holbrook, 1999; Rose et al., 2014). The postcranial skeleton of *Teleolophus* also shows some similarities with that of *Lophialetes* in having above-mentioned characters 5–8, and 12–14. However, these features are potentially convergent or parallel because the two groups exhibit prominent differences in dental morphology (Radinsky, 1965a); this idea should be further tested within a phylogenetic framework.

*Colodon* was also considered to be closely related to Deperetellidae (Colbert, 2005; Matthew and Granger, 1925a). However, *Colodon* shares more postcranial features with *Heptodon* than *Teleolophus* that include the lunar with the posterior part of the radial facet situated in the middle, the proximal hump of the magnum posteriorly placed with gradual anterior borders, the posterior process of the magnum more distally extended and even medially projected, the unciform facet of the Mc IV with the lateral border lower than the medial border, the sustentacular facet of the astragalus contacting the distal calcaneal facet, the cuboid not in contact with Mt III, and the ectocuneiform articulating with both Mt II and Mt IV on the medial and lateral sides. The relationship between Helaletidae and Deperetellidae needs further investigation, pending the discovery of more primitive deperetellids.

## 5.2   Locomotor analysis

The postcranial morphology of *Teleolophus* clearly shows adaptation for the increased cursoriality relative to other related forms. The magnum has a deeply concave Mc III facet on the distal end, corresponding to the convex magnum facet of Mc III, which indicates the great degree of the anteroposterior motion. The fibula is highly reduced and even fused on some specimens. The metatarsals are elongated. The asymmetrical trochlea of the femur is probably correlated with the relatively large size of *Teleolophus* (Janis et al., 2012). Although ceratomorphs do not show any clear pattern of difference in asymmetry with the habitat types (Janis et al., 2012), the asymmetrical trochlea of the femur may indicates that *Teleolophus* preferred a relatively open-habitat and was consequently adapted to fast running, which is consistent with results as inferred from other postcranial morphologies.

The ternary diagram of the femur, tibia, and Mt III lengths separates out cursorial perissodactyls from other compared locomotor groups (Fig. 8; Appendix I). The diagram shows that the cursorial generally scores higher on the length of the Mt III and lower on length of femur than graviportal, ambulatory and medioportal (Osborn, 1929; Smith and Savage, 1956). However, their tibial lengths overlap to some extent. One subcursorial taxon, *Phenacodus primaevus*, is grouped with ambulatory and medioportal. Recently, Gould (2016) suggested cursorial specilizations are not key innovations of Eocene perissodactyls, which accounts for the decline of condylarths in the Early Eocene. *Equus* and most cursorial artiodactyls have relatively longer Mt III and shorter femurs than extinct cursorial perissodactyls. However, Eocene oromerycid *Eotylopus reedi* is grouped with latter group. *Teleolophus* (with estimated femur length 260 mm) is clearly grouped with extinct cursorial perissodactyls, scoring higher

Mt III length and lower femoral length within the group (Fig. 8). The result also suggests *Teleolophus* with an increased cursoriality as its contemporary *Lophialetes* among extinct cursorial perissodactyls, which is consistent with morphological analyses.
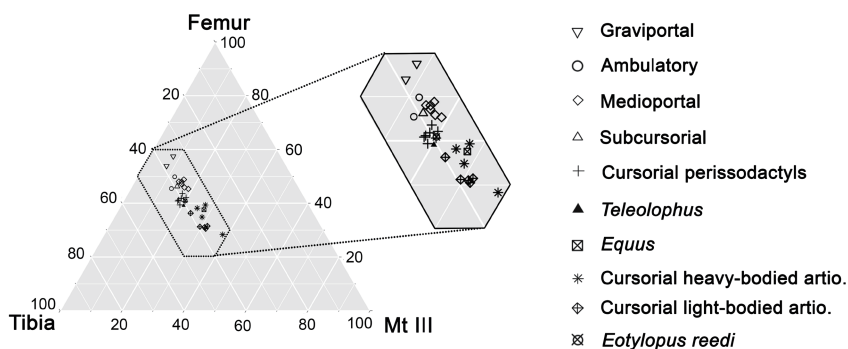


Fig. 8   Ternary diagram of relative lengths of the femur, tibia, and Mt III among different types of locomotion in perissodactyls and a few other ungulates (Appendix I)

The length of the third metatarsal, tibia, and femur are shown on their respective axes as a percentage of the combined length of three elements. The plot shows *Teleolophus* is grouped with extinct cursorial perissodactyls with an increased cursoriality

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摘要：戴氏貘科(Deperetellidae)是亚洲中始新世地层中常见且特有的貘类，目前包括了5个属。但已知的戴氏貘材料大部分都是破损的上、下颌骨，仅有*Deperetella*保存有部分头后骨骼。仅依据牙齿的特征，戴氏貘在貘超科中的系统发育位置有很大争议，比如沼貘科的*Colodon*, 脊齿貘(lophialetids)或红山貘(rhodopagids)都被认为可能和戴氏貘有较近的亲缘关系。最近几年，在内蒙古二连盆地不同地点和层位采集到数量丰富的戴氏貘化石，其中包括头骨和头后骨骼材料。本文即是对其中采自沙拉木伦地区乌兰胡秀地点全脊貘(*Teleolophus*)头后骨骼的研究报告，材料包括前足、后肢及后足。通过对全脊貘头后骨骼的形态描述，以及和相关类群(*Deperetella*, *Lophialetes*, *Heptodon*, *Helaletes*和*Colodon*)的比较，表明全脊貘属和戴氏貘属具有很多相似特征，支持了两者具有较近的亲缘关系。这些特征主要包括长而纤细的四肢，后足三趾；月骨较长而窄，其近端桡骨关节面内侧缘略凹；巨骨近端的头状隆起位置靠前，外侧具有和Mc IV的关节面；股骨滑车略微不对称；腓骨非常退化，甚至和胫骨愈合；Mt III与骰骨关节；Mt II主要在后方与外楔骨关节。虽然全脊貘头后骨骼也有一些和脊齿貘(*Lophialetes*)相似的特征，但考虑到两者臼齿上明显的区别，它们在骨骼上的相似特征可能归因于平行演化的结果。和全脊貘相比，*Colodon*的头后骨骼和*Heptodon*的更为接近，表明后两者具有更近的亲缘关系。但戴氏貘科在貘超科中的系统发育位置以及和沼貘科(Helaletidae)的亲缘关系，仍需进一步的研究工作。形态特征和后肢的"三元图"分析都表明，全脊貘已经具有较为快速的奔跑能力，这和同时期的脊齿貘相似。

关键词：内蒙古二连盆地，中始新世，貘超科，全脊貘，头后骨骼，中亚考察团

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**Appendix 1**  Measurements (in mm) of hind limbs among ungulates with different types of locomotion as defined by Osborn (1929)

| Taxa | Femur L | Tibia L | MtIII L | Locomotion |
|---|---|---|---|---|
| *Loxodonta africanus*[a] | 1050 | 755 | 144 | Graviportal |
| *Elephas indicus*[a] | 1020 | 618 | 138 | |
| †*Pantolambda bathmodon*[a] | 149 | 114 | 36 | Ambulatory |
| †*Meniscotherium terraerubrae*[a] | 100 | 91 | 29 | |
| *Tapirus terrestris*[a] | 262 | 208 | 108 | Medioportal |
| *Tapirus inducs*[a] | 320 | 258 | 120 | |
| †*Palaeosyops major*[a] | 433 | 332 | 137 | |
| †*Palaeosyops leidyi*[a] | 370 | 290 | 110 | |
| †*Mesatirhinus petersoni*[a] | 358 | 283 | 118 | |
| †*Limnohyops monoconus*[a] | 387 | 283 | 123 | |
| †*Phenacodus primaevus*[a] | 234 | 198 | 74 | Subcursorial |
| †*Tetraclaenodon*[a] | 105 | 107 | 45 | Cursorial condylarths and perissodactyls |
| †*Hyracotherium grangeri*[b] | 138.3 | 123 | 56 | |
| †*Eohippus*[a] | 167 | 162 | 82 | |
| †*Heptodon calciculus*[a] | 175 | 175 | 75 | |
| †*Hyrachyus modestus*[a] | 254 | 243 | 110 | |
| †*Hyrachyus modestus*[c] | 241.8 | 219.8 | 112.2 | |
| †*Teleolophus medius*? | 260 | 270 | 135 | |
| †*Lophialetes*[d] | 187 | 198 | 90 | |
| †*Juxia*[e] | 610 | 585 | 265 | |
| *Equus caballus*[a] | 392 | 363 | 288 | |
| *Camelus arabicus*[a] | 470 | 400 | 325 | Cursorial heavy-bodied artiodactyls |
| *Bison bison*[a] | 369 | 355 | 243 | |
| *Giraffa camelopardalis*[a] | 466 | 550 | 630 | |
| †*Cervus megaceros*[a] | 430 | 454 | 350 | |
| †*Eotylopus reedi*[a] | 148 | 142 | 72 | Cursorial light-bodied artiodactyls |
| *Tragulus napu*[a] | 94 | 103 | 62 | |
| *Odocoileus hemionus*[a] | 253 | 295 | 255 | |
| *Antilope cervicapra*[a] | 183 | 223 | 183 | |
| *Antilocapra americana*[a] | 210 | 260 | 218 | |
| *Gazella doreas*[a] | 140 | 176 | 132 | |

Based on a) Osborn, 1929; b) Wood et al., 2011; c) Bai et al., 2017a; d) Reshetov, 1979; e) Qiu and Wang, 2007.