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ARTICLE



# A new late Paleocene phenacodontid 'condylarth' *Lophocion* from the Clark's Fork Basin of Wyoming

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## ABSTRACT

Phenacodontidae are a group of archaic ungulates in the early Paleogene and are considered to play an important role in the origin of some other ungulates, including perissodactyls. The early Eocene *Lophocion asiaticus*, the only unequivocal phenacodontid from Asia, is most closely related to North American *Ectocion* and probably closer to perissodactyls than is the latter, as evidenced by its more lophodont teeth. Here we named a new species of *Lophocion*, *L. grangeri* sp. nov., from the latest Paleocene (Clarkforkian 3) deposit in the Clark's Fork Basin of Wyoming. Although the holotype of the new species is only known by a right maxilla with P4-M2, its degree of lophodonty is similar to that of *Lophocion* but diverges from *Ectocion* in having the incipient protoloph and metaloph on upper molars. In dental morphology, *Lophocion grangeri* is somewhat intermediate between *Ectocion* and *L. asiaticus*, and probably gave rise to the latter during the Paleocene-Eocene transition. Both *Lophocion* and *Ectocion* are included in Phenacodontinae rather than Meniscotheriinae, but their phylogenetic relationship with other ungulates still remains obscure.

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## Introduction

The paraphyletic 'condylarths' are a group of archaic ungulates, and consist of seven families (Rose 2006; Halliday et al. 2017). Phenacodontid 'condylarths' are distributed mainly in North America, temporally ranging from the late early Paleocene to early middle Eocene (Lofgren et al. 2004). Phenacodontids have been considered as to be ancestral to perissodactyls (Radinsky 1966), or closely related to the clade Altungulata that includes tethytheres, hyracoids, and perissodactyls (Prothero et al. 1988; Thewissen and Domning 1992; Gheerbrant et al. 2005; Kondrashov and Lucas 2012). However, phylogenetic analyses based on molecular and/or morphologic data suggest a deep split of Afrotheria and Laurasiatheria, with phenacodontids being allied with either of them (Asher 2007; Murphy et al. 2001; O'Leary et al. 2013; Gheerbrant et al. 2016; Halliday et al. 2017). Perissodactyls were further considered closely related to either cambaytheres from Indian subcontinent (Cooper et al. 2014; Rose et al. 2014) or to South American ungulates (Welker et al. 2015; Westbury et al. 2017).

The family Phenacodontidae is traditionally composed of *Tetraclaenodon*, *Phenacodus*, *Ectocion*, and *Copecion*, and species of the family are common in the Paleocene and lower Eocene deposits of North America (West 1976; Thewissen 1990). *Meniscotherium* with selenodont-lophodont teeth is either placed in Meniscotheriidae or Phenacodontidae, implying its close relationship either with European *Orthaspidotherium* and *Pleuraspidotherium* or with North American *Ectocion*, respectively (Simpson 1945; Gazin

1965; Williamson and Lucas 1992). In recent cladistic analyses, the monophyly of Phenacodontidae was not recovered (Kondrashov and Lucas 2012; Halliday et al. 2017).

In contrast to abundant phenacodontids from North America, those from Asia are much rare and taxonomically controversial due to their fragmentary material (Wang and Tong 1997; Kondrashov and Lucas 2004). Wang and Tong (1997) reported a phenacodont *Lophocion asiaticus* from the early Eocene Wutu Formation of Shandong Province, China. *Lophocion* is most similar to *Ectocion* from North America, but is more lophodont with relatively more complete protoloph and metaloph on upper molars (Wang and Tong 1997). Hooker and Dashzeveg (2003) and Hooker (2005) suggested that *Lophocion* is closer to perissodactyls than is *Ectocion*, which supports the Asian origin and initial radiation of perissodactyls (Beard 1998). Here we named a new species to *Lophocion* based on a maxilla with P4-M2 from the upper Paleocene deposit of North America, and conclude that the new taxon is morphologically intermediate between *Ectocion* and *L. asiaticus*, and probably gave rise to the latter during the Paleocene-Eocene transition.

## Materials and methods

The new species is represented by a single right maxilla with P4-M2 and the alveolus of M3 (AMNH FM 16060), which is deposited at the Division of Paleontology, American Museum of Natural History, New York. Specimens of *Lophocion asiaticus* (IVPP V 10707) and *Ectocion osbornianus* (AMNH FM 16099) were used for comparisons.

Micro-CT was utilized in order to enhance observation of the morphology. Scanning was carried out using 225 kV micro-computerized tomography (developed by the Institute of High Energy Physics, Chinese Academy of Sciences (CAS)) at the Key Laboratory of Vertebrate Evolution and Human Origins, CAS. The beam energy and the flux are 120 kV and 120  $\mu$ A, respectively. The resolution per pixel for AMNH FM 16060, 16099, and IVPP V 10707 are 18.04  $\mu$ m, 21.96  $\mu$ m, and 25.09  $\mu$ m, respectively. A 360° rotation with a step size of 0.5° and an unfiltered aluminium reflection target were used. A total of 720 transmission images were reconstructed in a 2048  $\times$  2048 matrix of 1536 slices using a two-dimensional reconstruction software developed by the Institute of High Energy Physics and Institute of Automation, CAS. The three-dimensional reconstructions were performed using software VG Studio 3.2.

The terminology and measurements of teeth follows Hooker (1989) and Thewissen (1990, Figure 1), respectively. Log-ratio diagrams were plotted for comparisons of tooth dimensions using the method described in Simpson (1941).

**Institutional abbreviations.**—AMNH FM, American Museum of Natural History, Fossil Mammals, New York, USA; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China.

### Systematic paleontology

Order 'Condylarthra' Cope, 1881  
 Superfamily Phenacodontoidea McKenna, 1995  
 Family Phenacodontidae Cope, 1881  
 Subfamily Phenacodontinae Cope, 1881

*Lophocion* Wang et Tong, 1997

### Type species

*Lophocion asiaticus* Wang et Tong, 1997

### Included species

*L. grangeri* sp. nov.

**Emended diagnosis:** (modified from Wang and Tong 1997) The most lophodont phenacodonts, and similar to *Ectocion* in morphology. Parastyle and mesostyle relatively large on P4-M3. Hypocone relatively small on M1-2 and absent on M3. On upper molars, prepraconule crista short or well-developed, the prehypocrista consistently present and relatively strong, and the postprotocrista absent or weak. A cingulum present between the base of the protocone and the hypocone.

**Distribution:** early Eocene of Asia and late Paleocene of North America.

*Lophocion grangeri* sp. nov.

### Holotype

AMNH FM 16060, a right maxilla with P4-M2.

### Etymology

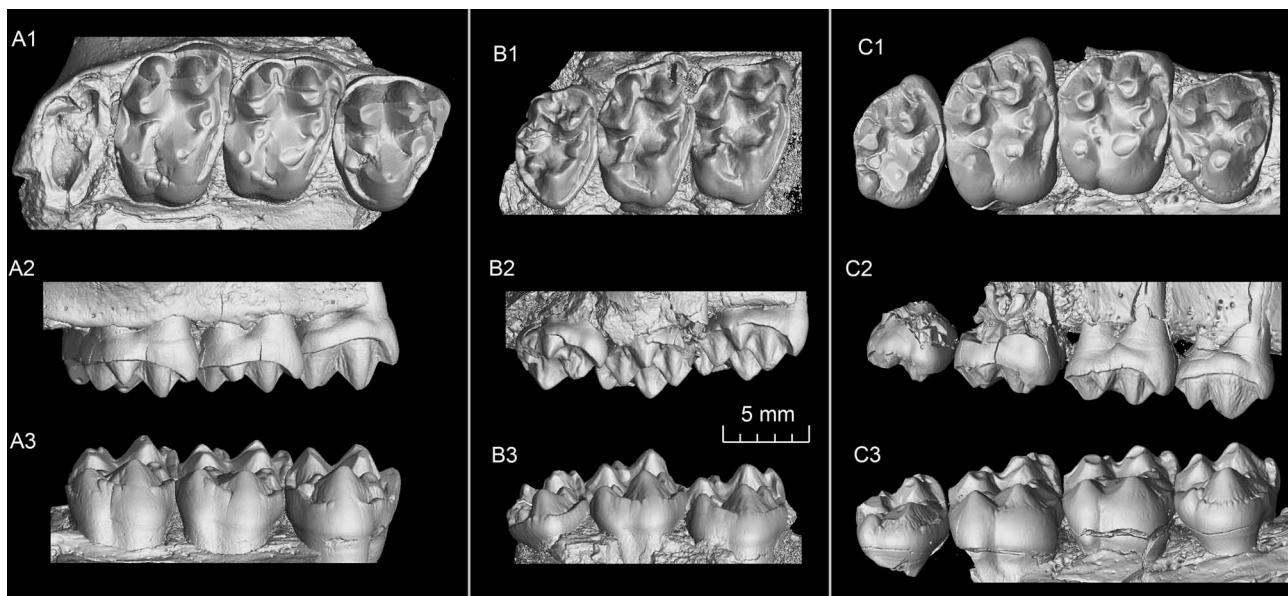
The specific name dedicated to Walter Granger (1872–1941), who collected the holotype (with assistance of W. Stein) in 1912, and probably first noticed its unusual characters.

### Type locality

The Clark's Fork Basin of Wyoming, USA.

### Comments

According to the label in association with the holotype, the specimen (AMNH FM 16060) was collected from the head of the Big Sand Coulee in the Clark's Fork Basin during the expedition of the American Museum of Natural History in 1912 (Granger and Sinclair 1914). As pointed out by Rose (1981, p. 18), Granger's locality in the head of the Big Sand



**Figure 1.** Upper dentition of *Lophocion* and *Ectocion* from North America and Asia. (a) Right maxilla with P4-M1 of *Lophocion grangeri* sp. nov. (AMNH FM 16060) from the late Clarkforkian of Wyoming, USA, in occlusal (a1), buccal (a2), and lingual (a3) views. (b) Left maxilla with M1-3 (reversed) of *L. asiaticus* Wang et Tong, 1997 (IVPP V 10707) from the early Eocene Wutu Formation of Shandong Province, China, in occlusal (b1), buccal (b2), and lingual (b3) views. (c) Right maxilla with P4-M3 of *Ectocion osbornianus* (AMNH FM 16099) in occlusal (c1), buccal (c2), and lingual (c3) views.

Coulee (1911 and 1912 field catalogues) is probably equivalent to the *Phenacodus-Ectocion* Zone, the latest Clarkforkian (Cf3) (Lofgren et al. 2004).

**Type horizon.** The lower part of Willwood Formation, late Paleocene (Clarkforkian).

**Stratigraphic and geographic range.** Type locality and horizon only.

**Differential diagnosis.** Differs from *Lophocion asiaticus* in being less lophodont with more bunodont cusps, Upper molars with more convex buccal surface of the paracone and metacone, shorter and weaker preparaconule cristae, and the postprotocrista consistently absent.

### Description

The P4 is triangular in outline and relatively large (Figures 1(a), 2(a); Table 1). The paracone and metacone are conical, approximate in size, and well separated by a deep notch. The metacone is slightly more lingual to the paracone. The parastyle is relatively large and protruding, widely separated from the paracone. The protocone is the largest cusp and situates at the level of the midway between the paracone and metacone. The preprotocrista descends mesiobuccally from the protocone to the paraconule, which is considerably larger than the metaconule and slightly more mesially placed to the paracone. The preparacrista is indiscernible. Distal to the protocone there are two cristae distobuccally extended: The first one is distinct and descends to a small cusp on the distal cingulum. This crista is probably homologous with endoprotocrista in perissodactyls (Holbrook 2015). The second crista is weak, probably homologous with the postprotocrista in perissodactyls (Holbrook 2015); it extends to the small metaconule that is situated at the level of the metacone. The cingulum is strong and nearly complete except for an interruption at the lingual side of the protocone.

The M1 is roughly rectangular in outline, and wider than long (Figures 1(a), 2(b); Table 1). The paracone and the metacone are conical with prominent, convex ribs on the buccal sides. The metacone is more lingually placed and depressed than the paracone. The mesostyle is well developed, conjuncting a nearly mesiodistally oriented postparacrista and an oblique premetacrista. The parastyle is larger and more protruded than that of P4, and situates mesiobuccally close to the paracone. The protocone is the largest cusp of M1, and positioned at the level of the point slightly distal to the paracone. A distinct preprotocrista extends mesiobuccally to the paraconule, which is relatively smaller than that of P4. A very short preparaconule

crista is present, ending to the mesiolingual base of the paracone. The postprotocrista is completely absent. The hypocone is much smaller and slightly more lingually placed than the protocone. The prehypocrista, connecting the hypocone and the metaconule, is relatively distinct, straight, and less oblique than the preprotocrista. The metaconule is smaller than the paraconule with a faint premetaconule crista. A posthypocrista descends to the distal cingulum, although is partially obliterated by the worn. The cingulum is complete and continuous on the mesial, buccal, and distal borders. On the lingual side between the protocone and the hypocone, there is a cingulum that is made up of some small nodules and ascends towards the hypocone (Figure 1(a3)).

M2 is larger than but otherwise quite similar to M1 in morphology (Figure 2(e)); it is relatively wider owing to a more distinct metaloph (Figures 1(a), 2(c); Table 1). M3 is not preserved, but the alveolus shows a much smaller tooth than the preceding molars. It is roughly transversely elongated and oval in outline, indicating that the hypocone of M3 is probably absent or very weak.

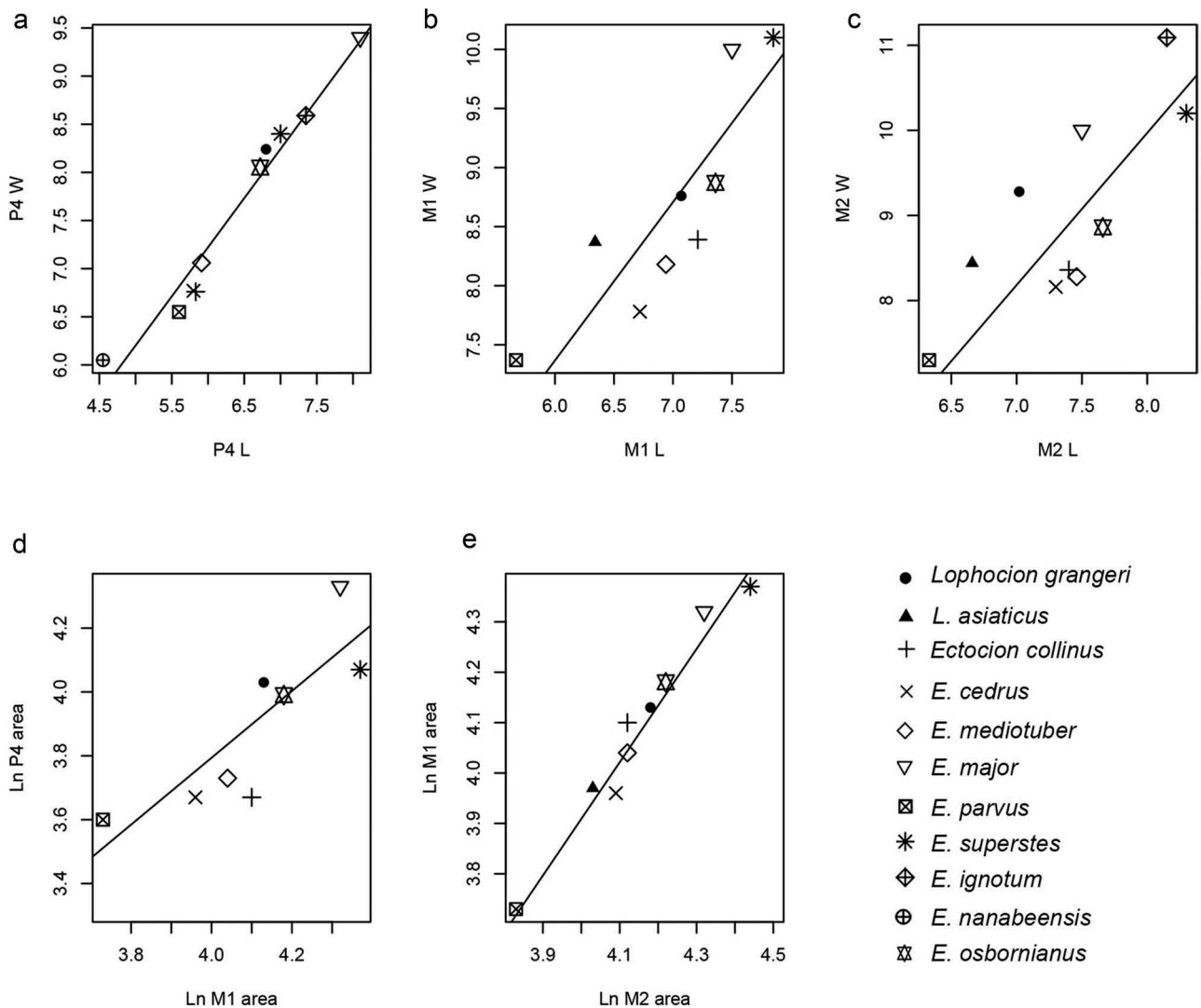
### Comparison and discussion

*Ectocion* is the most lophodont phenacodontid (except for *Meniscotherium*) in North America and differs from other phenacodontids by possessing large parastyle and mesostyle on upper molars (Rose 1981; Thewissen 1990). Because of its high lophodony, *Ectocion* was considered as a sister group to *Meniscotherium* and included in Meniscotheriinae by some authors (Williamson and Lucas 1992; McKenna and Bell 1997; Archibald 1998). However, *Meniscotherium* has more selenodont teeth with rib-like mesostyles on the upper molars, and its sister-group relationship with *Ectocion* was not supported by recent phylogenetic analyses (Kondrashov and Lucas 2012; Holbrook 2014). Nine species of *Ectocion* have been reported from North America, ranging from the Tiffanian through the early Bridgerian (West 1976; Thewissen 1990; Novacek et al. 1991; Archibald 1998; Beard and Dawson 2009). In general, AMNH FM 16060 has more lophodont teeth than all known species of *Ectocion*, especially in having a nearly complete metaloph (or prehypocrista) and in lacking a postprotocrista on M1-2 (Figure 1(a,c)). AMNH FM 16060 is similar to *Ectocion osbornianus* in size, on average, but larger than *E. parvus*, *E. cedrus*, and *E. nanabeensis*, and smaller than *E. major*, *E. superstes*, and *E. ignotum* (Figures 2, 3) (Patterson and West 1973; Thewissen 1990; Novacek et al. 1991; Beard and Dawson 2009). However, the size range of *Ectocion osbornianus* is wide and almost overlap mean values of other *Ectocion* species except for *E. parvus* (Figure 3). AMNH FM 16060 is further similar to *E. osbornianus* in having a relatively larger P4 in relation to M1, and has the approximately equal-sized, well-separated paracone and metacone on P4 (Figures 1, 2(d)). The well-separated paracone and metacone on P4 are also present in other species of *Ectocion* except for the primitive *E. collinus* from the Tiffanian (Thewissen 1990). In addition to the more lophodont dentition, AMNH FM 16060 further differs from *E. osbornianus* in having a relatively wider M2 as in *E. major* and *Lophocion* (Figure 2(c)), and a lingual cingulum between

**Table 1.** Measurements of *Ectocion* and *Lophocion* from the late Paleocene and early Eocene of North America and Asia. (mm).

	P4L	P4W	M1L	M1W	M2L	M2W	M3L	M3W
<i>L. grangeri</i>	6.80	8.24	7.07	8.76	7.02	9.28	?	?
<i>E. osbornianus</i> <sup>a</sup>	6.72	8.05	7.36	8.87	7.66	8.86	6.36	7.33
<i>E. parvus</i> <sup>a</sup>	5.60	6.55	5.67	7.37	6.33	7.30	5.20	6.06
<i>L. asiaticus</i>	?	?	6.34	8.37	6.66	8.44	5.54	6.72

<sup>a</sup> Measurements based on the mean values from Thewissen (1990, Table A-9, A-13)

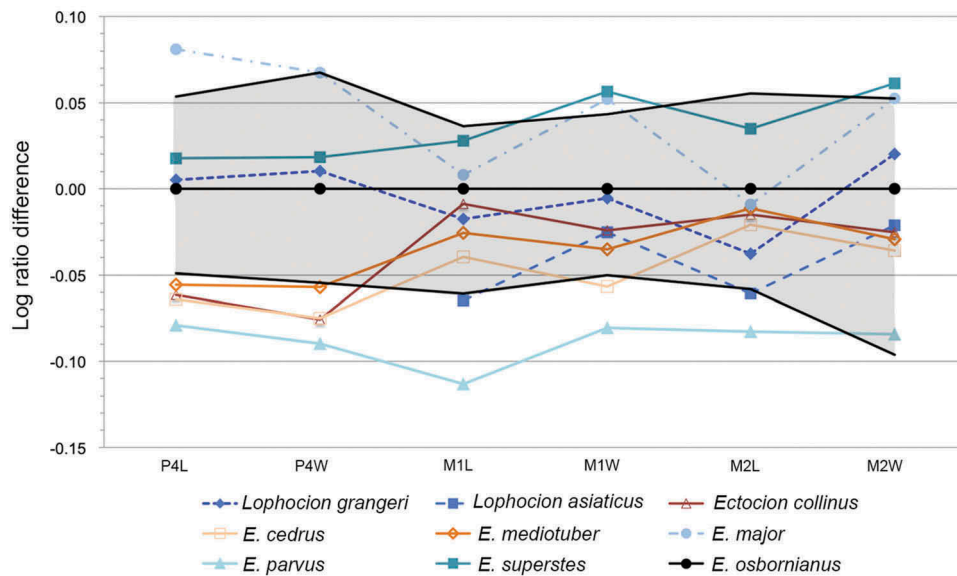


**Figure 2.** Scatter plot of P4-M2 width versus length and size proportions of *Lophocion* and *Ectocion*. (a-c) P4-M2 width versus length (in mm), and the regression lines for width as a function of length in *Ectocion*. (d-e) The size proportions of P4 versus M1 (d) and M1 versus M2 (e), and the regression lines for teeth size as a function of compared one in *Ectocion*. (Appendix Table 1).

the protocone and the hypocone on M1-2, as in *E. collinus*. In *E. parvus* and *E. superstes*, the lingual cingula are even better developed, extending along the lingual bases of the protocones (Thewissen 1990). Unfortunately, lack of the lower dentition, especially the premolars, of AMNH FM 16060 prevents further comparison with *Ectocion*, species of which are best distinguished by the premolars (Thewissen 1990).

Dental variations of *Ectocion* have been noticed by different authors. When discussing variation of upper molar metaconules in *Ectocion* among numerous specimens, Granger (1915, p. 349) noticed 'the metaconule sometimes isolated, often connected with the protocone, and in some cases connected with both the protocone and the hypocone'; he further mentioned that only one specimen with 'the metaconule found connected with the hypocone and separated from the protocone by a deep valley as in *Perissodactyla*', which he considered as 'an isolated example of deviation from the ordinary condition, rather than any distinct phylum'. It is uncertain whether or not AMNH FM 16060 is 'the only one specimen' mentioned by Granger (1915); given the tooth morphology of AMNH FM 16060, we think that

the possibility cannot be excluded. We also noted that a label in association with the specimen shows that it was initially assigned to *E. ralstonensis* ? and later transferred to *E. osbornianus*. Further, AMNH FM 116060 was found from the 'Head of the Big Sand Coulee' in the Clark's Fork Basin (Rose 1981), where *E. osbornianus* (= *E. ralstonensis*) and *E. parvus* have been reported by Granger (1915). The teeth of *E. osbornianus* from Clark's Fork Basin mainly varies in the morphology of p4, relative size of m3, relative breadths of the trigonids and talonids, and the proportions of the molars (Rose 1981). Rose et al. (2012) pointed out the upper molars of *E. parvus* varies in the development of lingual cingulum, twinned metaconule, and the position of the metaconule. However, the different degree of lophodonty was not mentioned, and both *E. osbornianus* and *E. parvus* likely consistently have relatively more bunodont rather than lophodont teeth. Thus, we interpret the lophodont upper molars in AMNH FM 16060 with a consistent connection between the hypocone and metaconule, and a separation between the metaconule and protocone as diagnostic characters rather than the intraspecific variation.



**Figure 3.** Log-ratio diagram for P4-M2 measurements of *Ectocion* and *Lophocion*. *E. osbornianus* is used as a standard for comparison (straight line at zero). The mean values of six species of *Ectocion* are from Thewissen (1990), and those of *E. osbornianus* are based on material from *Phenacodus-Ectocion* zone with a minimum-maximum range represented by the gray area (Thewissen 1990, table A-9). The measurements of P4 in *E. major* are from Patterson and West (1973), and those of M1-2 are from the figure of Thewissen (1990, fig. 23).

In addition to *Ectocion osbornianus* and *E. parvus*, three more phenacodontids are also known from the contemporary late Clarkforkian (*Phenacodus-Ectocion* Zone) as AMNH FM 16060: *Copecion brachypternus*, *Phenacodus vortmani*, and *P. intermedius* (Thewissen 1990). *Copecion brachypternus*, similar in size to *E. osbornianus*, differs from AMNH FM 16060 in having more bunodont teeth, a more elongated P4, weaker parastyle and mesostyle on M1-2, and a vertical furrow separating the protocone and the hypocone on M1-2 without the lingual cingulum (Gingerich 1989; Thewissen 1990; Rose et al. 2012). *Phenacodus vortmani* and *P. intermedius* are distinguished from AMNH FM 16060 by larger size, more bunodont and less lophodont molars, a squarer outline of P4-M2, weaker parastyle and mesostyle on M1-2 with a stronger hypocone, and the metaconule aligned in line between the metacone and the hypocone on upper molars (Thewissen 1990). *Phenacodus vortmani* is further different from AMNH FM 16060 in lacking the metaconule on P4 (Thewissen 1990).

AMNH FM 16060 also resembles Asian *Lophocion* in having more lophodont teeth with more complete protoloph and metaloph, and relatively wider upper molars (Figures 1(a,b), 2, 3). However, the degree of lophodonty of AMNH FM 16060 is less than that of *Lophocion asiaticus* in having more bunodont cusps, less sharp cristae, more convex buccal surface of the upper molar paracones and metacones, and a weaker, shorter prepraconule crista (Figure 1(a,b); Table 1). Moreover, the postprotocristae of upper molars are either present or weak in *Lophocion asiaticus*, contrasting to absence of those in AMNH FM 16060. Because of these dental structures, we consider that AMNH FM 16060 represents a taxon somewhat intermediate between *Ectocion* and *Lophocion asiaticus*.

It is ambiguous that whether AMNH FM 16060 should be assigned to *Ectocion* or to *Lophocion*. Considering its horizon and locality, as well as general dental morphology,

one may assign the specimen to *Ectocion*, which usually has a relatively high intraspecific variation (Granger 1915; Rose 1981). On the other hand, the difference between AMNH FM 16060 and the contemporary *Ectocion osbornianus* is probably at the generic level, as inferred from those between *E. osbornianus* and a similar size *Copecion brachypternus* from the same horizon. However, given its derived characters with an incipient protoloph and metaloph and without the postprotocrista, which indicate a more transverse shear than in *Ectocion* (Radinsky 1966), assigning the specimen to *Lophocion* appears more reasonable. Thus, instead of erecting a new genus, we prefer assigning the specimen to *Lophocion* rather than to *Ectocion*. The derived characters between *Lophocion grangeri* and *L. asiaticus* suggest that the latest Paleocene *L. grangeri* probably dispersed to Asia via the Bering Strait, as some other mammals did during the Paleocene-Eocene transition (McKenna 1983; Krause and Maas 1990; Tong and Wang 2006; Bai et al. 2018), and gave rise to the early Eocene *L. asiaticus*. However, the age of Wutu Fauna is controversial, and is considered to be either latest Paleocene (Beard and Dawson 1999) or early Eocene (Tong and Wang 2006). Similarly, North American *Phenacodus vortmani* likely migrated to Europe and gave rise to European *Phenacodus* during the Paleocene-Eocene transition (Thewissen 1990).

As discussed above, a close relationship between *Ectocion* and *Meniscotherium* is not supported (Kondrashov and Lucas 2012; Holbrook 2014), so we include both *Ectocion* and *Lophocion* in Phenacodontinae (within Phenacodontidae) rather than in Meniscotheriinae as suggested by Kondrashov and Lucas (2004) and McKenna and Bell (1997). Hooker and Dashzeveg (2003) proposed *Lophocion* as the sister group to perissodactyls, and considered *Lambdaotherium*-like perissodactyls probably from late Paleocene deposit of China as the basal

perissodactyl (Meng et al. 1998); however, current fossil records do not indicate an unequivocal choice for the ancestral morphotype of perissodactyls. Bai et al. (2018) recently proposed that different groups of perissodactyls may have diverged as early as in the earliest Eocene and dispersed among Holarctic regions during the Paleocene-Eocene transition, which further obscures the ancestral morphotype of perissodactyls. The phylogenetic position of *Lophocion* as well as other phenacodontids within ungulates obviously requires more investigation and the discoveries of more complete material of *Lophocion*.

## Conclusions

We described a new species *Lophocion grangeri* sp. nov. from the upper Paleocene Willwood Formation in the Clark's Fork Basin of Wyoming, USA. The new species is based on a right maxilla with P4-M2 that shows an intermediate morphology between contemporary *Ectocion osbornianus* and early Eocene *Lophocion asiaticus*. Compared with relevant genera of Phenacodontidae, we assign the new species to *Lophocion* rather than to *Ectocion* (or to erect a new genus); this is mainly based on its derived incipient lophodont protoloph and metaloph, which is shared with *L. asiaticus*. Future investigation on the variation of *Ectocion* and discovery of more specimens of *Lophocion* will provide more information on radiation and dispersal of phenacodontid condylarths.

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## Disclosure statement

No potential conflict of interest was reported by the authors.

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## Appendix

**Table 1.** Measurements of P4-M2 of *Lophocion* and *Ectocion*. The values of *Ectocion nanabeensis* and *E. ignotum* are from Beard and Dawson (2009) and Novacek et al. (1991), respectively. The mean values of other species of *Ectocion* are from Thewissen (1990) except for *E. major* (Patterson and West 1973).

Species	P4L	P4W	M1L	M1W	M2L	M2W	Ln P4 area	Ln M1 area	Ln M2 area
<i>Lophocion grangeri</i>	6.8	8.24	7.07	8.76	7.02	9.28	4.03	4.13	4.18
<i>L. asiaticus</i>	NA	NA	6.34	8.37	6.66	8.44	NA	3.97	4.03
<i>Ectocion collinus</i>	5.83	6.76	7.21	8.39	7.4	8.36	3.67	4.10	4.12
<i>E. cedrus</i>	5.8	6.77	6.72	7.78	7.3	8.16	3.67	3.96	4.09
<i>E. mediotuber</i>	5.91	7.06	6.94	8.18	7.46	8.28	3.73	4.04	4.12
<i>E. major</i>	8.1	9.4	<b>7.5</b>	<b>10</b>	<b>7.5</b>	<b>10</b>	4.33	4.32	4.32
<i>E. parvus</i>	5.6	6.55	5.67	7.37	6.33	7.3	3.60	3.73	3.83
<i>E. superstes</i>	7	8.4	7.85	10.1	8.3	10.2	4.07	4.37	4.44
<i>E. ignotum</i>	7.35	8.59	NA	NA	8.15	11.09	4.15	NA	4.50
<i>E. nanabeensis</i>	4.55	6.05	NA	NA	NA	NA	3.32	NA	NA
<i>E. osbornianus</i> (A9-mean)	6.72	8.05	7.36	8.87	7.66	8.86	3.99	4.18	4.22

Bold number: measured from the plates.

Italic number: approximate measurements.