第45卷 第4期
2007年10月

古脊椎动物学报
VERTEBRATA PALASIATICA

pp.278－286
figs.1－2

江西池江盆地上古新统一种类似偶蹄类的古有蹄类[1)]

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摘要：奇蹄类和偶蹄类是现代的主要有蹄动物，它们的起源一直是古哺乳动物学界关心的课题。近年来的发现表明，在早始新世奇蹄类出现之前，亚洲已有牙齿形态与奇蹄类相近的有蹄类存在。偶蹄类的情况可能也是如此，这里记述的古新世新村里赣蹄兽就是一个明证。

新村里赣蹄兽（*Ganungulatum xincunliense* gen. et sp. nov.）化石产于江西大余青龙镇新村里附近的晚古新世池江组滥泥坑段，化石地点编号为72035（76）。在同一地点还发现南方古对锥兽 *Archaeoryctes notialis* Zheng, 1979 和滥泥坑赣脊兽 *Ganolophus lanikenensis* Zhang, 1979。赣蹄兽材料为一对不完整的下颌骨，右下颌骨保存 i2－3，c 和 p4－m3，左下颌骨存有 p3－m3（IVPP V 14154）。其特征是下齿式为 3?·1·4·3；i3 与颊齿列平行，i2 稍有些斜；犬齿小；p3 有初始的跟座，p4 三角座明显，跟座小；下臼齿为丘形齿，牙齿由 m1 向 m3 增大，三角座前后收缩，下前尖位于舌侧，并靠近下后尖，下后尖较下原尖靠后，m3 有一增大的跟座，跟盆向舌侧开放。

新村里赣蹄兽下颊齿低冠，呈丘形齿，下臼齿三角座前后收缩和 m3 下次小尖增大等特征，说明了赣蹄兽与亚洲古新世地层中常见的真兽类，例如狪兽类、裂齿类、中兽类和全齿类不同，而与 Prothero et al.（1988）提出的有蹄类（Ungulata）牙齿相似，表现出与某些有蹄类密切相关。

与已知的晚白垩世和古新世有蹄类比较，赣蹄兽与“踝节类”（“condylarths”）中的豕齿类（hyopsodontids）和睐兽类（mioclaenids）比较相近。但从其下犬齿小，p4 相对较大，臼齿化程度高，以及下臼齿下前尖在舌面位置和与下后尖接近等特征来看，赣蹄兽更接近 mioclaenids。修仁古亚兽（*Palasiodon siurensis*）是亚洲仅有的 mioclaenid，产于广东南雄盆地下古新统上湖组，但在牙齿形态上容易与这里记述的赣蹄兽区别，古亚兽下颊齿短宽，m3 很退化。与其他已

1）全国地层委员会“中国主要断代地层建阶研究项目”资助。
收稿日期：2006－09－13

知的 mioclaenids 比较,赣蹄兽在大小上和牙齿形态上与北美 Torrejonian 的 *Litaletes disjunctus* 最接近,两者都有小的匙状的下犬齿,相对臼齿化的 p4,下臼齿下前尖向舌侧位移,前、后齿带无或很弱,m3 增大。但赣蹄兽明显不同于 *L. disjunctus*, 前者 p3 更小,更简单,p4 下前尖更小,跟座不成盆状,下臼齿下前尖较大,更加舌位,并与下后尖靠近,下后尖在下原尖的后侧,m3 下内尖不明显。由此可见,赣蹄兽下颊齿和已知的"踝节类"是可以区别的,但更重要的区别点是在下颌骨的前面部分。在与 arctocyonids、hyopsodontids 和 phenacodontids 等"踝节类"对比时,我们发现赣蹄兽和"踝节类"之间的重大差异在于下门齿的排列上。这些"踝节类"的三个下门齿密集地排列在下颌骨的前端,呈圆弧状,与颊齿列斜交,而赣蹄兽的 i3 与颊齿列平行,i2 稍斜。赣蹄兽下门齿的排列形式与早期偶蹄类 *Diacodexis pakistanensis* 相似,在亚洲始新世的 *Gobiohyus robustus* 和 *Lophiomeryx angarae* 也有类似的情况。赣蹄兽与 *Diacodexis*、*Gobiohyus* 和 *Wutuhyus* 等早期的偶蹄类的相似之处还在于下颌骨形态,较细长,较浅,下颌骨深度向前变浅,下臼齿向后增大,下前尖在舌面位置,下后尖在下原尖的后面,m1 - 2 下次小尖在后缘上,m3 下次小尖增大,并形成第三叶。但在 p3 - 4 形态上,赣蹄兽与这些早期偶蹄类不同,赣蹄兽明显比早期偶蹄类复杂,即臼齿化程度较高。

赣蹄兽保留了像某些"踝节类"(如 *Litaletes*)的 p3 - 4,而它的下门齿排列却与早期偶蹄类相似。赣蹄兽下臼齿形态与早期偶蹄类具有相似性,因而不能归入"踝节目"已知科,很有可能代表与偶蹄类相关的一支古有蹄类。赣蹄兽的发现也为偶蹄类起源打开了新思路。

关键词:中国江西,古新世,类似偶蹄类的有蹄类

中图法分类号:Q915.873　**文献标识码**:A　**文章编号**:1000 - 3118(2007)04 - 0278 - 09

GANUNGULATUM XINCUNLIENSE, AN ARTIODACTYL-LIKE MAMMAL (UNGULATA, MAMMALIA) FROM THE PALEOCENE, CHIJIANG BASIN, JIANGXI, CHINA

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Abstract　This paper reports a new artiodactyl-like mammal, *Ganungulatum xincunliense* from the Late Paleocene Nongshanian beds of the Chijiang Basin, Jiangxi Province, China. The new species shares some derived features in the anterior region of the mandible with that of early artiodactyls, such as *Diacodexis pakistanensis*, and possesses molar morphology very similar to that of *Wutuhyus primiveris*. It retains primitive features in the third and fourth lower premolars similar to mioclaenid condylarths, such as *Litaletes disjunctus*. *G. xincunliense* may represent a taxon closely related to a group basal to artiodactyls and sheds new light on the origin of artiodactyls.

Key words　Jiangxi, China; Paleocene; artiodactyl-like mammal

1　Introduction

A new Paleocene artiodactyl-like mammal from China, here named *Ganungulatum xincunliense*, may represent a taxon closely related to a group basal to artiodactyls. "Condylarthra" is a group of archaic ungulates from which many modern ungulates, including artiodactyls, were

probably derived. Species of the group are very common in the Paleocene deposits of North America, Europe, and South America; however, they are rare in Asian Paleocene deposits. The earliest known artiodactyl, *Diacodexis*, is found in the Early Eocene deposits of North America, Europe, and Asia, represented by well-preserved materials, including dentition, diagnostic double-pulley astragalus, and other skeletal elements; it therefore bears importantly on artiodactyl origin. It has been postulated that the artiodactyls might have originated from *Chriacus*, a North American arctocyonid "condylarth" (Van Valen, 1978; Rose, 1987, 1996) based on the similarities of dental morphology between *Chriacus* and *Diacodexis*. Other hypotheses on artiodactyls also exist, such as an African (Gingerich, 1989) and Asian (Beard, 1998) origin of the group. The primary argument for the Asian origin of artiodactyls is the discovery of a new suiform artiodactyl, *Wutuhyus primiveris*, from the Early Eocene of China (Tong and Wang, 1998, 2006) as well as *Diacodexis pakistanensis*, from the Early Eocene, Pakistan (Thewissen et al., 1983).

The new species reported here is based on a pair of lower jaws collected from the Late Paleocene Nongshanian beds of the Chijiang Basin, Jiangxi Province, China. The species displays a mosaic pattern of derived and primitive features. It shares with early artiodactyls, such as *Diacodexis*, derived features in the anterior region of the mandible, and possesses molar morphology very similar to that of *Wutuhyus primiveris*; however, it retains primitive features in the third and fourth lower premolars similar to mioclaenid "condylarths", such as *Litaletes disjunctus*. This species sheds new light on the origin of artiodactyls.

2 Systematic paleontology

Grandorder Ungulata Linnaeus, 1766

Ganungulatum xincunliense gen. et sp. nov.

(Figs. 1–2)

Holotype IVPP V 14154, a pair of incomplete right and left lower jaws, with right i2 – 3, c, p4 – m3, and left p3 – m3. (IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing)

Locality and horizon Holotype from IVPP locality number 72035 (76). Lannikeng Member of Chijiang Formation, Qinglong, Dayu County, Jiangxi, China. The locality also yields *Archaeoryctes notialis* and *Ganolophus lanikenensis*.

Age Late Paleocene (Nongshanian Asian Land Mammal Age).

Etymology The genus name, Gan, an abbreviated name of Jiangxi Province, in combination with ungulate. The species named after Xincunli, a village near the fossil site.

Diagnosis Lower dental formula: 3? · 1 · 4 · 3. Canine small. The i2 orientated obliquely in the jaw and i3 orientated parallel to the tooth row. The p3 having an incipient talonid and p4 bearing distinct trigonid and a small talonid. Lower molars, bunodont, increasing in size from m1 to m3, trigonid antero-posteriorly compressed, paraconid lingually located and close to metaconid, metaconid slightly posterior to protoconid, m3 bearing enlarged talonid with talonid basin wide open lingually.

3 Description

The terminology follows Muizon and Cifelli (2000). Two lower jaws were collected in the same pit (Tong et al., 1976, 1979). Identity in dental morphology, size, and the level of tooth wear indicate they belong to the same individual (Figs. 1, 2; Table 1). The mandible is slender, with the horizontal ramus being shallow and gradually decreasing in depth anteriorly. It measures 4.2 mm thick and 7.6 mm deep at m3, 6 mm deep at m1, and 3 mm deep at the ca-

nine. The masseteric fossa is shallow and ends anteriorly at the level under the m3 talonid. There are two mental foramina, one under the level of the anterior root of p2 and the other under the level of the anterior root of p4. A partial ascending ramus is preserved, indicating that the anterior border of the coronoid process and the alveolar border form a wide angle. The i1 is not preserved. The i2 and i3 are leaf-like in lateral view, convex labially and concave lingually. The i2 is slightly larger than i3. The anterior edge of the i2 is orientated slightly obliquely in the jaw. The i3 is orientated parallel to the tooth row. The posterior edge of i2 bears a wear facet. Wear striations on the facet indicates transverse movement of the lower jaw during mastication. The canine is relatively small and spatulate. A very short diastema separates the p1 from the canine. The p1 and p2 crowns are not preserved, but their alveoli show a single-rooted p1 and double-rooted p2. The p3 bears a distinct protoconid and an incipient talonid with a distinct cusp. The p4 is robust, larger, and bears a better developed trigonid and talonid basin. The protoconid, metaconid, and paraconid are distinct and situated in a subtriangular arrangement. The molars are low crowned and bunodont. The m1 is the smallest molar, rectangular, and deeply worn. Its trigonid is compressed antero-posteriorly and slightly higher than and about the same width as the talonid. The paraconid is lingually situated and conjoined with the metaconid. The metaconid is posterior to the protoconid. The precingulid is vestigial on the labial side. The hypoconid is larger than the entoconid. The hypoconulid is much smaller than the hypoconid and entoconid. There is no clear postcingulid. The m2 is similar to m1 in morphology, but larger. The paracristid is distinct. There is no pre-and postcingulid. The hypoconulid is smaller than that on m1. The m3 is the longest molar, with the trigonid similar to those in m1 – 2. The talonid is much longer, but slightly narrower than those of m1 – 2. The hypoconid is distinct. The entoconid is indistinct, so that the lingual side of the talonid basin is widely open. A well-developed hypoconulid, with an accessory conulid situated on each side of it, forms the third lobe of the m3.

Table 1　Measurements of teeth of *Ganungulatum xincunliense* gen. et sp. nov.　(mm)

Tooth	Rigth		Left	
	Length	Width	Length	Width
i2	1.2			
i3	1.3			
c	2			
p1	1(root)			
p2	2.3(root)			
p3	2.5(root)		3	
p4	3.2	2(trd)2.1(tad)	3.2	2(trd)2(tad)
m1	3.5	2.8(trd)2.7(tad)	3.5	2.7(trd)2.5(tad)
m2	3.9	3(trd)2.3(tad)	3.9	3(trd)3.4(tad)
m3	5.6	3(trd)2.3(tad)	5.4	3.2(trd)2.1(tad)

Abbreviations: trd. trigonid; tad. talonid.

4　Discussion

In a study of the phylogeny of ungulates, Prothero et al. (1988) proposed several synapomorphic dental features for Ungulata, including teeth relatively bunodont with low cusp relief, lower molar trigonids shortened anteroposteriorly, and m3 with large hypoconulids projecting posteriorly. These features distinguish the ungulates from some other early eutherians, such as anagalids, tillodonts, mesonychids, and pantodonts, which were the major components of Asian Paleocene faunas. The dental features of *Ganungulatum xincunliense*, such as low crowns, buno-

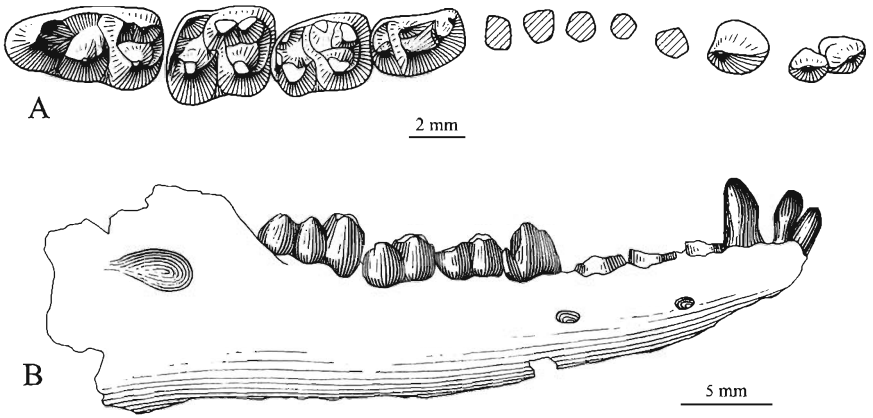

Fig. 1 Right mandible with i2 – 3, c, p4 – m3, of *Ganungulatum xincunliense* gen. et sp. nov. (IVPP V 14154)
A. occlusal view of i2 – m3; B. labial view of the mandible

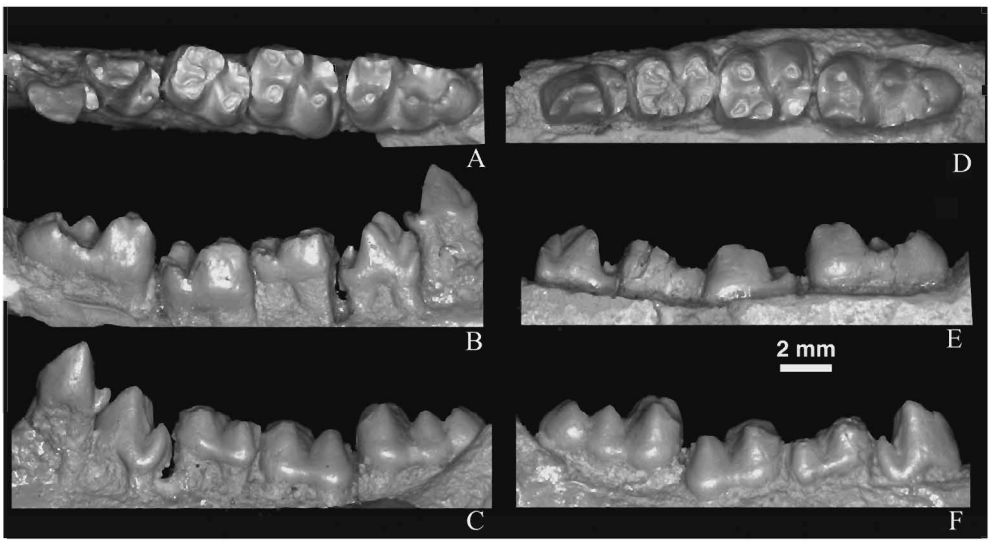

Fig. 2 Dentition of *Ganungulatum xincunliense* gen. et sp. nov. (IVPP V 14154)
A. occlusal view of left p3 – m3; B. lingual view of left p3 – m3; C. labial view of left p3 – m3; D. occlusal view of right p4 – m3; E. lingual view of right p4 – m3; F. labial view of right p4 – m3

donty, anteroposteriorly compressed lower molar trigonids, and enlarged m3 hypoconulids, clearly show its affinity to some ungulates.

Archibald (1996) proposed Ungulatomorpha to include Ungulata and the Asian Cretaceous "zhelestids" as a clade. *Ganungulatum* differs from "zhelestids" (Nessov et al., 1998) in having four lower premolars and bunodont teeth. It is not comparable to *Wania chowi* (Wang, 1995; Nessov et al., 1998) in either size or dental morphology. It also differs from the North American Cretaceous *Protungulatum* (Sloan and Van Valen, 1965; Kielan-Jaworowska et al., 1979) in having relatively molarized p3 – 4 and larger and more lingually located molar paraconids.

Within "condylarths", the arctocyonids are generally considered to be basal "condylarth" ungulates. The arctocyonids, such as *Desmatoclaenus*, *Claenodon*, and *Colpoclaenus*, differ from *Ganungulatum* in having primitive tritubercular teeth, relatively large canines, simple,

large, and acute premolars, and molar paraconids smaller than metaconids. *Quettacyon parachai*, an arctocyonid from the later Paleocene to Early Eocene of Pakistan (Gingerich et al., 1997), differs from *G. xincunliense* in having a very simple p4, lacking paraconids on m1 – 2, and having m3 not enlarged. However, the p4 of *Q. parachai* is more like that of mioclaenids than arctocyonids, although it is much larger than the latter. The phenacodontids, Cope's original central concept of condylarths, differ from *Ganungulatum* in having p4 large and molarized and lower molar paraconids small or absent, based on comparison with *Phenacodus*, *Tetraclaenodon*, and *Ectocion*. The Hyopsodontidae, usually including Hyopsodontinae and Mioclaeninae (Matthew, 1937; Matthew and Granger, 1915; Simpson, 1937, 1945), has long been considered a "wastebasket" including small primitive ungulates (Cifelli, 1983). Van Valen (1978) raised the mioclaenids to familial status, because he considered that they seem to have arisen independently, the mioclaenids from *Protungulatum* and the hyopsodontids from *Oxyprimus*. Comparing *Ganungulatum xincunliense* with some hyopsodontids, such as *Litomylus*, *Haplatetes*, and *Hyopsodus*, we recognized that its dental characters, small canine, relatively large and molarized p4, molar paraconid lingually situated and conjoined with metaconid, and molar talonid basin open lingually, are similar to those of mioclaenids rather than hyopsodontids. *Ganungulatum* differs from *Ellipsodon*, *Tiznazinia*, and *Mioclaenus* among the mioclaenids in having p4 not really inflated, but relatively molarized, and in having an enlarged m3 (Van Valen, 1978; Matthew, 1937), differs from *Choeroclaenus* in p4 being not inflated, differs from *Promioclaenus* in p4 having a distinct paraconid and metaconid, molar paraconid more lingually located and conjoined with metaconid, and an enlarged m3, and differs from *Protoselene* in p4 being bunodont instead of trenchant and having a distinct molar metaconid and paraconid, the paraconid more lingually located and conjoined with the metaconid (Matthew, 1937; Simpson, 1937). Among North American mioclaenids, the size and overall dental morphology of *G. xincunliense* are closer to those of *Litaletes disjunctus*, a Torrejonian mioclaenid, than any other taxa. Both of them have small and spatulate canine, relatively molarized p4, lingually located paraconid, enlarged m3, and very weak or no precingulid and postcingulid on molars. However, *G. xincunliense* differs from *L. disjunctus* in having smaller and simpler p3, smaller p4 paraconid, p4 talonid not basined, larger and lingually located molar paraconids conjoined with the metaconids, the metaconid posterior to the protoconids, and the entoconid of m3 indistinct. The molar paraconid of *G. xincunliense* is larger, higher, and more lingually located and conjoined with the metaconids, the metaconid is posterior to the protoconids, the entoconid of m3 is much reduced and shifted to the end of talonid, and the hypoconulid is smaller than those of *L. disjunctus*. *G. xincunliense* is also similar to the South American Tiupampa kollpaniin "condylarths", *Molinodus suarezi* and *Simoclaenus sylvaticus* (Muizon and Cifelli, 2000), in having m3 unreduced, molar metaconid posterior to protoconid and inflated, short transverse paracristid, larger hypoconid, and entocristid absent. It is similar to *S. sylvaticus* in size and in having antero-posteriorly compressed molar trigonids, but differs from the latter in having larger paraconid on p4, larger and more lingually located molar paraconids, postcingulids weak or absent, and a smaller entoconid on m3. It differs from *M. suarezi* in being slightly larger, p4 having larger paraconid and slightly larger talonid basin, very weak or no pre-and postcingulids, and molar paraconids lingually closer to and conjoined with metaconids. *G. xincunliense* is smaller than *Abdounodus hamdii* from the Ypresian of Africa (Gheerbrant et al., 2001), and differs from the latter in having a distinct paraconid, better developed p4 talonid, and the molar paraconid more lingually located and conjoined with the metaconid. The absence of the anterior region of the mandible of *Litaletes disjunctus* and the South American species restricts further determination of their relationships with *G. xincunliense*.

Previously reported Chinese "condylarth" *Yuodon protoselenoides* (Zhou et al., 1977) was later moved to Anagalida (McKenna and Bell, 1997). The dental morphology of *Y. protosele-*

noides, especially the low-crowned teeth, less difference of height between trigonids and talonids, and molar paraconids medially located, differs from those of anagalids, and is more similar to "condylarths" as pointed out by the original authors (Zhou et al., 1977). *Ganungulatum xincunliense* is slightly smaller than *Y. protoselenoides*, but differs from the latter in having less molarized p3 – 4, more antero-posteriorly compressed molar trigonids, and molar paraconids lingually located and conjoined with the metaconids. McKenna and Bell (1997) also moved *Palasiodon siurenensis* to Anagalida. This species is defined based on poorly preserved material. However, its low crowned teeth with bunodont cusps and less difference in height between the trigonids and talonids indicate that it is more similar to "condylarths" (Zhou et al., 1977).

In comparing the anterior region of the mandible of *Ganungulatum xincunliense* with that of arctocyonids, hyopsodontids, and phenacodontids, we discovered that the most significant differences between *Ganungulatum* and "condylarths" is the arrangement of incisors. In those "condylarths", the three lower incisors are closely-packed and situated at the anterior margin of the mandible. However, in description of *Diacodexis pakistanensis*, Thewissen et al. (1983:157) mentioned "I/2... The tooth is orientated obliquely in the jaw." and "I/3... The root and crown of this tooth are orientated parallel to the tooth row... ." The i2 of *G. xincunliense* is obliquely to the jaw, and i3 is parallel to the tooth row, which is similar to the condition in *Diacodexis pakistanensis*. We consider this a derived feature for artiodactyls. The arrangement of the lower incisors is also clear in other Asian artiodactyls, such as the Middle Eocene *Gobiohyus robustus* (Matthew and Granger, 1925a) and *Lophiomeryx angarae* (Matthew and Granger, 1925b). *Ganungulatum* further shares the following features with *Diacodexis* and *Gobiohyus*: mandible slender, shallow, and gradually reduced in depth anteriorly, molars increasing in size from m1 to m3, lower molar paraconid lingually situated, metaconid slightly or strongly posterior to protoconid, hypoconulid positioned on posterior talonid rim on m1 – 2, and enlarged as a third lobe or basin on m3 (Stucky, 1998). *G. xincunliense* is about the same size as *D. pakistanensis* and similar to the latter in basic molar morphology and enlarged hypoconulid on m3, but differs from the latter in having more complicated p3 – 4, unreduced paraconid and conjoined with metaconid, hypoconulid splitting into two cusps, and relatively narrower talonid on m1 – 2. It is much smaller than *Gobiohyus robustus* (Matthew and Granger, 1925a), but similar to the latter in having a short space between c/p1 and p1/p2, but differs from the latter in having the canine small and incisor-like, more complicated p3 – 4, larger paraconid, metaconid more posteriorly positioned, relatively narrower talonids on m1 – 2, and a basin-like hypoconulid on m3. *G. xincunliense* is very similar to *Gobiohyus reshetovi* (Vislobokova, 2004) in mandibular shape. *G. xincunliense* is slightly smaller than *Wutuhyus primiveris* and is very similar to the latter in having a slender mandible with depth gradually reduced anteriorly, size increasing from m1 to m3, lower molar paraconids relatively large, lingually situated, and conjoined with the metaconids, metaconids posterior to protoconids, talonids short, hypoconulid enlarged with accessory conules on m3, and no cingulum. It differs from the latter in having less robust, semimolarized p3 – 4, and more slender molar cusps. A newly reported species, *Tsaganohyus pecus*, from the Bumban Member of the Naran Bulak Formation, Mongolia, is based on a fragmentary lower jaw with dp4 and m1 (Kondrashov et al., 2004). The size and morphology of m1 of *T. pecus* are very similar to *Wutuhyus primiveris*, but differ from the latter in having a slightly posteriorly located entoconulid. The m1 of *G. xincunliense* is about the same size as *T. pecus* and also similar in morphology to the latter, but differs from the latter in having the metaconid located slightly posterior to the protoconid.

Ganungulatum xincunliense retains the primitive p3 – 4 seen in some "condylarths", such as *Litaletes disjunctus*; however, its arrangement of lower incisors shared with some early artiodactyls. The similarities of the molar morphology with *Wutuhyus primiveris* exclude *G. xincunliense* from the "condylarths". Based on the shared derived features in the anterior region of the

mandible between *G. xincunliense* and some early artiodactyls, we suggest that *G. xincunliense* may represent a taxon closely related to a group basal to artiodactyls.

Acknowledgements This research is supported by National Geographic Society Grant #7329 – 02. We thank colleagues Chris Beard, Phillip Gingerich, Jeremy Hooker, Peter Kondra-shov, Spencer Lucas, Malcolm McKenna, Gregoire Metais, Ken Rose, Thierry Smith, and Shawn Zack for their suggestions and discussions. Alejandra Lora and Judith Galkin of the Americn Museum of Natural History are thanked for access to their collections during Ting's visit. Ting's trip to AMNH was supported by the National Science Foundation Grant #EAR – 0120727 to Meng and colleagues. We thank Mr. Xu Yong for making drawings.

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