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Reconsideration of the systematics of the Early Pleistocene *Cervavitus* (Cervidae, Artiodactyla, Mammalia)

Reconsideración de la sistemática de Cervavitus *(Cervidae, Artiodactyla, Mammalia) del Pleistoceno Inferior*

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ABSTRACT

Cervavitus were usually found from the Late Miocene and Pliocene deposits in East Europe, Middle Asia and North China, but they were found recently in many Early Pleistocene localities in southern China. The latter resulted in the discussion of their systematic status between *Cervavitus* and *Cervus*. Here we show the Early Pleistocene forms from southern China are morphometrically more similar to northern China *Cervavitus* species, and the cladistic analysis shows that the southern China forms are closer to classic *Cervavitus* species than *Cervus* and that also proves their systematic status in *Cervavitus* rather than in *Cervus*. *Cervavitus* originated in Moldovan forests of East Europe in the late Vallesian (MN10) from a brachyodont and holometacarpal ancestor with two/three-tined antlers and *Palaeomeryx* fold and evolved into *C. novorossiae*. It dispersed into West Europe forests in the earliest Turolian and further west to France in the Ruscinian. It dispersed into northern China forests in the early Turolian and represented by *C. shanxius.* The great quantity of *C. shanxius* specimens with brachyodont teeth and complete lateral metacarpals implies the arid Loess Plateau of today was a humid forested region in the Late Miocene. *C. shanxius* migrated southwards in the Plio-Pleistocene probably due to the drying environment in northern China with uplifting of Himalayas and evolved into *C. ultimus* and *C. fenqii*, which survived in southern China until the Early Pleistocene (MNQ18).

Keywords: *Cervavitus*, Cervidae, Artiodactyla, systematics, Neogene, Early Pleistocene, paleoenvironment.

RESUMEN

La revisión sistemática de *Cervivatus* sugiere que deriva del principal clado de los cérvidos posteriores a los muntiacinos, e implica que Procervulinae, Dicrocerinae y la primeras formas de Munticiacinae serían holometacarpales, como también lo es *Cervivatus*, originario en los bosques de Moldavia (Europa del Este) durante el Vallesiense final (MN 10), a partir de un antecesor braquiodonto y holometacarpal, con astas con dos o tres candiles y pliegue paleomerícido, y que da lugar a *C. novorossiae*. Este se dispersó a Europa occidental durante el comienzo del Turoliense, y más al oeste a Francia durante el Rusciniense. Su dispersión en los bosques del norte de China se produjo también a comienzos del Turoliense, estando representado por *C. shanxius*. Existe una gran cantidad de ejemplares de *C. shanxius* con metápodos laterales completos, que debían ser útiles para equilibrar el cuerpo en las ramas de los árboles. Las áridas mesetas loésicas actuales fueron bosques húmedos durante el Mioceno final. *C. shanxius* emigró hacia el sur durante el Plio-Pleistoceno probablemente debido al ambiente más seco del norte de China, como consecuencia de la elevación de los Himalayas, dando lugar a *C. ultimus* y *C. fenqii,* que sobrevivieron en el sur de China hasta el Pleistoceno inicial (MNQ18).

Palabras clave: *Cervivatus*, Cervidae, Artiodactyla, Sistematica, Neógeno

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Introduction

The first time I met Professor Léonard Ginsburg was in 1986 when I went to France for my doctoral degree in vertebrate palaeontology at the Université de Poitiers. My Chinese colleagues asked me to pass their greetings to French colleagues and I began to know some French colleagues in person further than in literature. When my dissertation materials were focused on cervids, which also fit into Professor Ginsburg's interests (e.g. Ginsburg, 1985, 1999; Ginsburg & Azanza, 1991; Ginsburg & Bulot, 1987; Ginsburg & Crouzel, 1976; Ginsburg & Ukkakimapan, 1983; etc.), I had some discussion with him and I also learned a lot from him by personal communication or by his publications. My first research publication in France (Dong, 1996) was also with his kind help when he was the editor-in-chief of the *Bulletin du Muséum national d'Histoire naturelle*, which has been renamed as *Geodiversitas* since 1997. Although his Asian field work focused mainly on Thailand (e.g. Ginsburg & Mein, 1987; Ginsburg & Tassy, 1985; Ginsburg & Ukkakimapan, 1983; Ginsburg et *al*., 1983; etc.), he visited China and had some academic exchanges with Chinese colleagues (e.g. Qiu *et al*., 1985). I am recently working on the Early Pleistocene *Gigantopithecus* fauna in southern China (Jin *et al*., 2009; Dong *et al*., 2010; Dong *et al*., 2011) where the environments are similar to those in Thailand. I found one of cervid taxa in the fauna, *Cervavitus*, very problematic which I would discuss with late Professor Ginsburg and I'd like to take this opportunity to communicate with international colleagues who are interested in it.

The first *Cervavitus* and its follow-up members

During the study of the cervid materials from Tarakliya in Moldova, Khomenko established "*Cervavitus tarakliensis*" (Khomenko, 1913) for a cervid with two tined antlers, its first or basal tine set high above the burr. Two other cervid species were together named, i.e. "*Cervocerus Novorossiae*" and "*Damacerus Bessarabiae*". The former was a cervid with larger antlers than those of "*Cervavitus tarakliensis*", the three tines of the antlers well developed; while the latter a cervid which had antlers with flattened and somewhat palmate main beam. The three species were included in a new subfamily "Pliocervinae" (Khomenko, 1913). *Damacerus* was considered as a synonym of *Cervocerus* by Zdansky (1925), and the view was shared by Simpson (1945). But it was accepted as valid taxon by Teilhard de Chardin and Trassaert (1937). And *Cervocerus* was later regarded as a junior synonym of *Cervavitus* (Vislobokova, 1990) because the *Cervavitus* of Khomenko appears as a juvenile form of *Cervocerus* of Khomenko. Considering the age and environmental variation of antlers (Heintz, 1970), it is acceptable that both *Cervocerus* and *Damacerus* of Khomenko are synonymous of *Cervavitus*. The dentitions of *Cervavitus* from Tarakliya are characterized by the evident presence of *Palaeomeryx* fold on lower molars (Khomenko, 1913). Simpson (1945) included "Pliocervinae" into Cervinae based on close relationship between them and it was followed by many others such as Wang and Wu (1979), Vislobokova (1990), etc. Czyzewska (1968) proposed a new tribe Pliocervini under Cervinae to include primitive *Cervavitus* and *Pliocevus*. In addition, Khomenko's "Pliocervinae" is not a valid sub-family name according to arts. 35.3 & 36.1 of International Code of Zoological Nomenclature (http://iczn.org/code). Pliocervini proposed by Czyzewska (1968) was consequently widely accepted (e.g. Vislobokova, 1990; McKenna & Bell, 1997; Petronio et al., 2007).

Zdansky (1925) included some cervid materials from Henan Province (previously spelled as Honan) of northern China to "*Cervocerus Novorossiae*" of Khomenko. Teilhard de Chardin and Trassaert (1937) also included some similar cervid materials from Shanxi Province (previously spelled as Shansi) to this species, but they modified the diagnosis and added three diagnostic characters for Chinese materials: "pedicles prolonged by a ridge on the frontals, *Palaeomeryx* fold generally missing in the Chinese form, vestigial lateral metacarpals preserved along the whole length of the anterior canon bone" (Teilhard de Chardin & Trassaert, 1937). They also established a new species *Cervavitus demissus* for some antlers with long pedicle and low brow tine from Baode, Shanxi Province. The present author regards it as a junior synonym of *Cervavitus shanxius*, because the species was represented by a few specimens that fall well into the age and environmental variations of *C. shanxius*, and it is furthermore no longer discovered elsewhere since Teilhard de Chardin and Trassaert. The presence of *Cervavitus* in Shanxi Province was confirmed during the 1950's and 1980's field work in the Yushe

Basin (Dong & Hu, 1994; Dong & Ye, 1996), some dozens of skulls and some of which with partial frontal appendages, several hundreds of antlers and dentitions were identified and a sub-specific name, "*Cervavitus novorossiae shanxius*", was given to Chinese form to distinguish it from its Moldova counterpart (Dong & Hu, 1994). Petronio *et al*. (2007) proposed further to upgrade the subspecies to *Cervavitus shanxius* for distinction between eastern European and Chinese *Cervavitus*. The author shares the same view. *Cervavitus shanxius* was reported found in Yangjiashan fauna and Shilidun fauna in Linxia Basin, north-western China (Deng, 2009). A new pliocervine, *Cervavitus huadeensis* Qiu, 1979, was found from Huade in Nei Mongol (Inner Mongolia). It is represented by two fragmental skulls and some antlers, the latter differ from those of *C. shanxius* by larger and "dagger-like" appearance, slightly lyrated beam and four-tines (Qiu, 1979). The ridge on the frontal formed by prolonged pedicle is less strong in Huade specimens than in Shanxi specimens, and the antlers are similar to those of "*Damacerus Bessarabiae*" of Khomenko.

Chinese *Cervavitus* were usually found in northern China (Zdansky, 1925; Teilhard de Chardin & Trassaert, 1937; Qiu, 1979; Dong and Hu, 1994; Deng, 2009) and dated as the Late Miocene (formerly considered as "Pontian"). The first *Cervavitus* in southern China, *C. ultimus* (Lin *et al*. 1978), was reported from the Early Pleistocene Yuanmou Formation at Yuanmou Man Site. Yuanmou specimens are generally similar to those of Shanxi, e.g. pedicles prolonged by a ridge on the frontals, antlers three-tined, *Palaeomeryx* fold generally missing, but the second and third tines are shorter and the main beam longer in Yuanmou specimens than in Shanxi counterparts. The species is also found at Longgupo Site at Wushan in central China (Huang & Fang, 1991). The second *Cervavitus* in southern China, *Cervavitus fenqii* Han, 1987, was reported from the Early Pleistocene cave deposits at the *Gigantopithecus* Cave in Liucheng, Guangxi (Han, 1987). It is also characterised by pedicles prolonged by a ridge on the frontals, antlers three-tined, *Palaeomeryx* fold generally missing, and it differs from *C. ultimus* by its smaller antlers, shorter brow tine and main beam, and it differs from *C. shanxius* by its smaller antlers and shorter brow tine (Han, 1987). *C. fenqii* was also reported found at Mohui Cave in Bubing Basin, Guangxi (Wang *et al*., 2007), at Longgudong Cave of Jianshi, Hubei (Chen, 2004), at Renzidong Site of Fanchang, Anhui (Dong *et al*., 2009). And recently, some *Cervavitus*-like teeth were found from the Early Pleistocene deposits in Sanhe Cavern at Chongzuo, Guangxi (Dong *et al*., 2011).

Cervavitus was also reported found in the Early Pliocene (MN14) of Montpellier (France) as *C. cauvieri* (Dong, 1996). It was found from Poksheshty of Moldova in the Late Miocene (MN10), *C. variabilis* from the Late Miocene to the Early Pliocene (MN12-MN14) and *C. flerovi* from Esekartkan of Kazakhstan in the Early Pliocene (MN15) (Vislobokova, 1990; 2007). Meanwhile, some "*Cervavitus*" were included into other cervids, e.g. *Cervavitus bessarabiensis* to *Euprox* aff. *furcatus*, *Cervavitus sarmaticus* to *Euprox sarmaticus* (Vislobokova, 2007). For detailed research history on *Cervavitus*, please refer Petronio *et al*. (2007) who gave a very good and comprehensive review on the *Cervavitus* from Europe and some of the *Cervavitus* in China.

The Early Pleistocene *Cervavitus* or *Cervus*?

The *Cervavitus* materials found in the Late Miocene of northern China have no controversy for their generic attribution. But those found in the Early Pleistocene in southern and central China have two generic attributions: *Cervavitus* and *Cervus*.

The three tined antler materials and associated dentitions from Longgudong of Jianshi similar to those of *Cervavitus fenqii* from *Gigantopithecus* Cave in Liucheng were considered as a species of *Cervus* (Chen, 2004), and consequently the *Cervavitus ultimus* from Yuanmou Man Site and Longgupo, as well as the *Cervavitus fenqii* from *Gigantopithecus* Cave were also considered attributable to *Cervus* (Chen, 2004).

It is a common practice to evaluate first the morphology of antlers in the identification of cervid materials, and for three-tined antlers there are three choices for generic attribution: *Cervavitus*, *Axis* and *Cervus (Rusa)*. The *Axis* have curved and somewhat twisted main beam that is evidently different from that of *C. ultimus* and *C. fenqii*. The Early Pleistocene *Cervus (Rusa) elegans* from Nihewan (formerly spelled as Nihowan) Basin (Teilhard de Chardin & Piveteau, 1930) has three-tined antlers and comparable to *C. ultimus* and *C. fenqii*. The materials of *Cervavitus shanxius* are abundant in

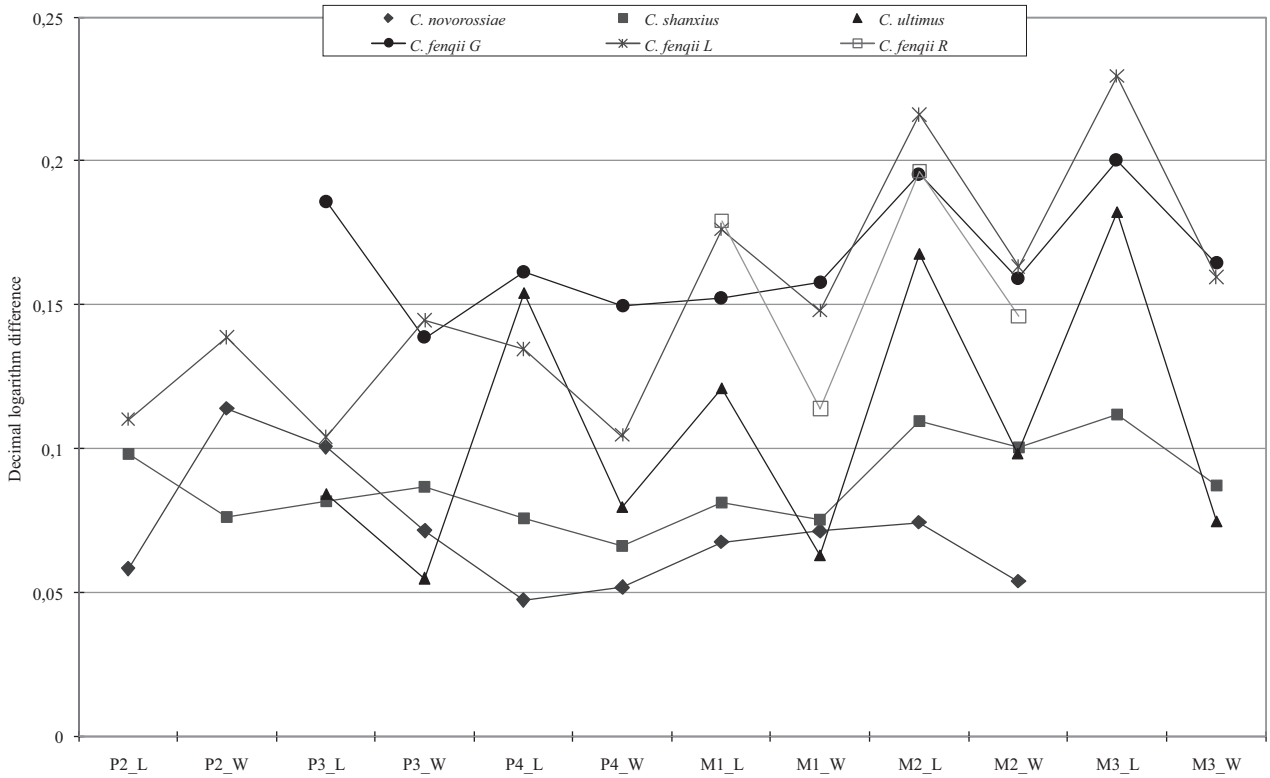

Fig. 1.—Simpson diagram of comparison of upper cheek teeth within *Cervavitus* (Reference species: *Metacervulus lepidus*). (*C. fenqii G*: from *Gigantopithecus* Cave; *C. fenqii L*: from Longgudong Site; R: *C. fenqii R*: from Renzidong Site; L: length; W: width).

the Late Miocene deposits (Zdansky, 1925; Teilhard de Chardin & Trassaert, 1937; Dong and Hu, 1994; Deng, 2009) and the *Cervavitus* in western Eurasia are found only in the Late Miocene and Early Pliocene (Vislobokova, 1990; Dong, 1996). That gives an impression that *Cervavitus* is a Late Tertiary genus and both *C. ultimus* and *C. fenqii* should be affined to the Early Pleistocene *Cervus (Rusa) elegans*, and they should be attributed to *Cervus* or *Cervus (Rusa)* as indicated by Chen (2004).

Teilhard de Chardin and Trassaert (1937) considered their "Pliocervinae" as a group of "Medium sized Cervidae, connecting in some way the *Cervulinae* and *Cervinae*. Pedicles of antlers prolonged by strong frontal ridges. Antlers three-tined in the most typical forms. Lateral metacarpals preserved on their whole length. *Palaeomeryx* fold sometimes present" (Teilhard de Chardin and Trassaert,1937, p.30). It is noticeable that the pedicles of both *C. ultimus* and *C. fenqii* are prolonged on frontal by a strong ridge (Lin *et al*., 1978; Han, 1987) as in the Late Tertiary Tarakliya forms (Khomenko, 1913) and northern China forms (Zdansky, 1925; Teilhard de Chardin & Trassaert, 1937; Dong & Hu, 1994). The ridge is also present on Longgudong materials (Chen, 2004, fig. 5.79). The ridge is a typical character of most muntiacines and Pliocervini, but it is very weak or absent in Cervini. This character supports the attribution of the Pleistocene *C. ultimus* and *C. fenqii* to *Cervavitus*. Simpson diagrams of cheek teeth also support the similarities of *C. ultimus* and *C. fenqii* with previous species of *Cervavitus* (Figs. 1-2).

In order to test further whether the Early Pleistocene species from southern China are attributable to *Cervavitus* or *Cervus*, a cladistic analysis was performed. 17 taxa, including three classical and two controversial *Cervavitus* species, were selected and 24 characters were chosen for construction of data matrix (Table 1). 17 characters of frontal appendages, one dental character, two cranial characters, two postcranial character, one soft tissue character and body size character were listed as follow:

1. Parallel pedicles: (0) no; (1). yes.
2. Position of pedicle: (0) above orbit; (1) behind orbit.
3. Pedicle crest on frontal: (0) weak; (1) medium; (2) strong.
4. Backward pedicle inclination: (0) weak; (1) medium; (2) strong.

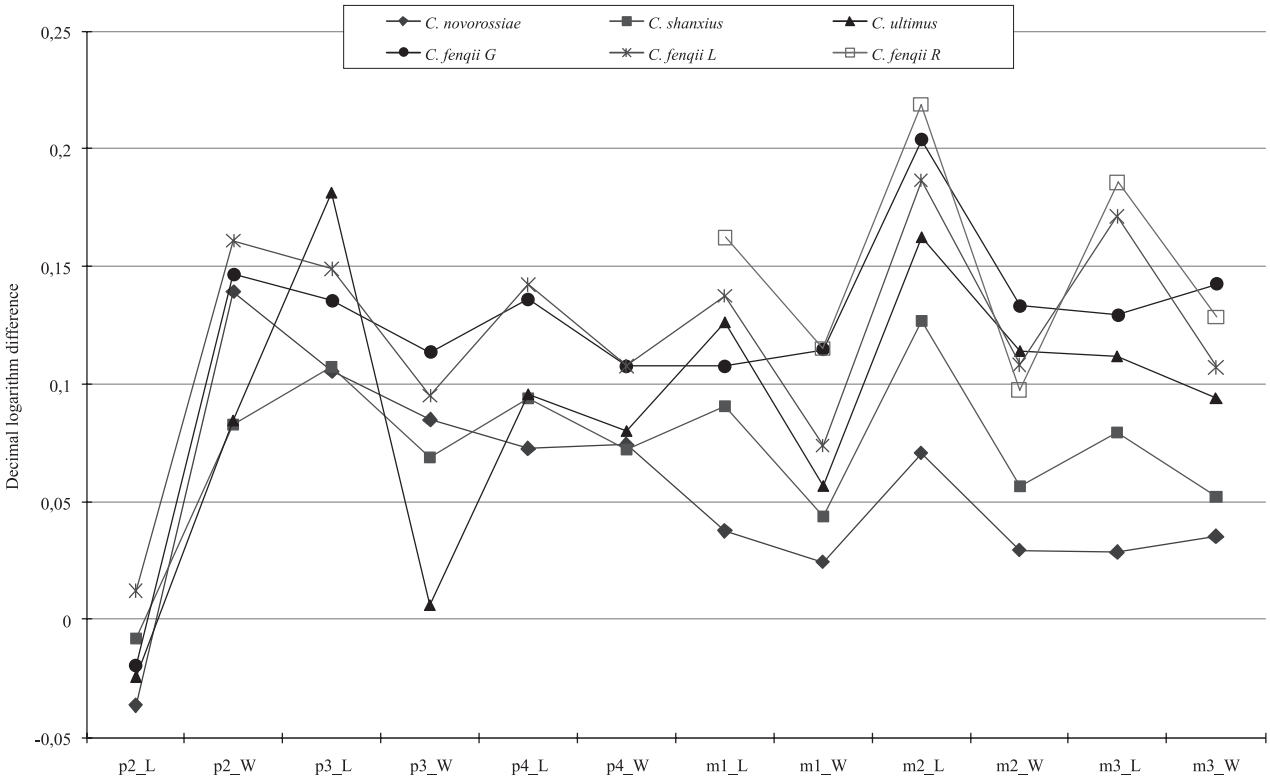

Fig. 2.—Simpson diagram of comparison of lower cheek teeth within *Cervavitus* (Reference species: *Metacervulus lepidus*). (*C. fenqii G*: from *Gigantopithecus* Cave; *C. fenqii L*: from Longgudong Site; R: *C. fenqii R*: from Renzidong Site; L: length; W: width).

Tabla 1.—**Data matrix of the characters**

Taxa	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
Hypothetic ancestor	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Procervulus ginsburgi	1	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	?	?	?	?	?	0
Heteroprox larteti	1	0	?	0	0	0	0	0	0	0	0	1	0	0	1	0	0	?	?	?	?	?	?	0
Dicrocerus elegans	1	0	0	0	1	1	0	0	2	0	1	2	0	1	1	1	0	0	?	?	?	?	?	1
Muntiacus bohlini	0	1	2	2	0	2	0	1	1	1	0	0	0	2	1	0	0	1	?	1	?	?	1	0
Muntiacus vuquangensis	0	1	2	2	0	2	0	1	1	2	1	1	0	2	1	1	0	?	0	2	1	2	1	1
Euprox robustus	?	1	1	?	0	2	0	1	0	0	1	1	0	2	1	1	0	1	?	?	?	?	?	2
Paracervulus australis	0	1	1	2	1	2	1	1	0	0	2	1	0	2	1	1	0	1	?	?	?	?	?	2
Metacervulus lepidus	0	1	2	2	0	2	1	1	1	2	1	1	1	2	1	1	1	?	?	?	?	?	?	2
Cervavitus novorossiae	0	1	2	2	1	2	1	1	1	1	1	1	0	2	1	1	1	0	?	?	?	?	?	2
Cervavitus shanxius	0	1	2	2	1	2	1	1	1	1	1	1	0	2	1	1	1	1	?	1	0	2	?	2
Cervavitus huadeensis	0	1	2	2	1	2	1	1	1	1	1	1	0	2	1	1	1	?	?	?	?	?	?	2
Cervavitus ultimus	0	1	2	2	1	2	1	1	1	1	1	1	0	2	1	1	1	1	?	?	?	?	?	2
Cervavitus fenqii	0	1	2	2	1	2	1	1	1	1	1	1	0	2	1	1	1	1	?	?	?	?	?	2
Cervus (Rusa) elegans	0	1	0	1	2	2	2	1	1	1	2	2	0	2	1	2	1	?	?	?	?	?	?	3
Cervus elaphus	0	1	0	1	2	2	1	1	1	1	2	1	1	2	1	2	2	1	0	1	1	2	0	3
Rangifer tarandus	0	1	0	0	2	2	1	1	1	2	2	2	1	2	1	2	2	1	0	1	2	2	0	3
Odocoileus virginianus	0	1	0	1	2	2	1	1	1	2	2	1	0	2	1	2	2	1	1	1	2	2	0	2

N. B. "?" in the matrix means missing character due to incomplete material.

5. Shortening of pedicle: (0) absent; (1) weak; (2) strong.
6. Burr development: (0) absent; (1) weak; (2) strong.
7. Antler basal segment: (0) short; (1) medium; (2) long.
8. Centripetal mineralization of antler: (0) absent; (1) present.
9. Cross section of main beam (or posterior branch) base: (0) nearly round; (1) oval; (2) elongated.
10. The growth style of the main beam (or posterior branch): (0) nearly straight; (1) simply curved; (2) multi-curved

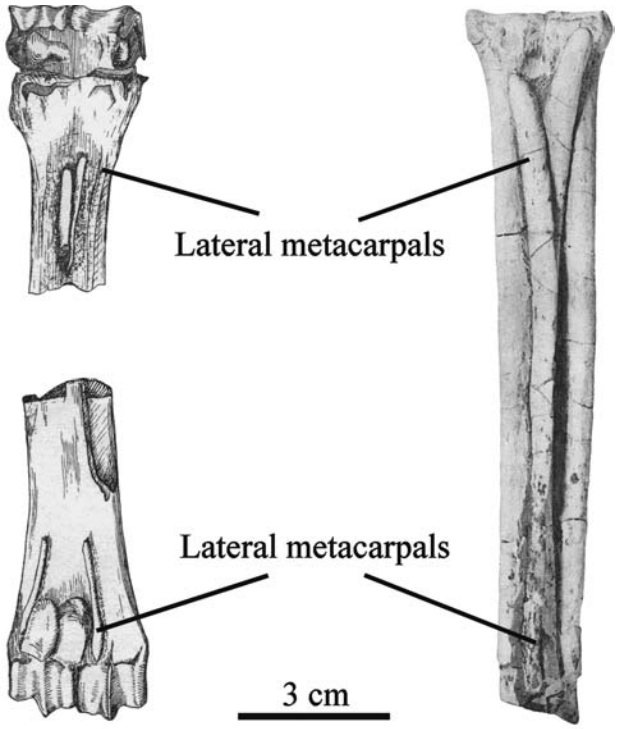

Fig. 3.—Presence of lateral metacarpals along the whole length of canon in *Cervavitus shanxius* (After Zdansky, 1925 and Teilhard de Chardin & Trassaert, 1937).

11. Main beam (or posterior branch) size: (0) small; (1) medium; (2) large.
12. Brow (or anterior) tine size: (0) small; (1) medium; (2) large.
13. Angle between main (or posterior) beam and brow (or anterior) tine: (0) small; (1) large.
14. Antler shedding: (0) uncertain; (1) irregular; (2) regular.
15. Antler ornamentation: (0) absent; (1) present.
16. Antler size: (0) small; (1) medium; (2) large.
17. Number of tines: (0) two; (1) three; (2) four or more.
18. *Palaeomeryx* fold on lower molars: (0) present; (1) absent.
19. Relation between nasal and premaxilla: (0)connected; (1) separate.
20. Lachrymal pit: (0) small; (1) medium; (2) large.
21. Lateral metacarpals: (0) holometacarpal; (1) plesiometacarpal; (2) telemetacarpal.
22. Metatarsal length: (0) short; (1) medium; (2) long.
23. Frontal gland: (0) absent; (1) present.
24. Body size: (0) small; (1) medium; (2) large; (3) very large

Characters 1-4, 6, 8, 14 are selected after Azanza (1993), characters 5, 7, 9, 13 are selected after Heintz (1970), characters 19-20 are selected after Ma *et al*. (1986), the rest are from Dong (2007).

The data matrix was edited by NEXUS Data Editor (Version 0.4.8 by Roderic D.M. Page), and then processed by PAUP* (Version 4.0b10 for 32-bit Microsoft Windows by David L. Swofford). 61 best trees were found among 21129 parsimony trees. In considering the importance of the characters as holometacarpal, the state of *Palaeomeryx* fold, the prolonged pedicle ridge on frontal, etc. the most acceptable tree was selected among these 61 best trees as shown in Fig. 4. The *Cervavitus* as a whole forms a monophyly that appears in many trees found by Paup*, and they appear at least closer to each other than to the other taxa. It supports the classification of five species into *Cervavitus* although *Palaeomeryx* fold is only present in *Cervavitus novorossiae* and probably in *Cervavitus huadeensis*. It supports also the inclusion of the Early Pleistocene *C. ultimus* and *C. fenqii* into *Cervavitus* rather than to *Cervus*. The systematic position of *Cervavitus* is between muntiacines and cervini.

Biochronological and paleoenvironmental considerations

Much work was done in the last decades for establishing Chinese Land Mammal Age or Terrestrial Biozanation. During the Symposium on Asian Neogene Biostratigraphy and Geochronology held in 2009 in Beijing, many colleagues expressed their impression that it was still premature to form a standard chronological chart based on the existing land mammal sequences. The problem is that no Neogene marine deposits exist in the mainland for large scaled stratigraphic correlation as in Paratethys region. Nevertheless, the European Neogene Biozonation based on mammals has been available for many years and can be used as a reference for chronological distribution of *Cervavitus*. In addition, the complete merging of European continent with Asian one since the Miocene has undermined the geographic barriers for fauna exchanges between two continents that make the biochronological correlation between two ends of Eurasian continents possible. All recognized species of *Cervavitus* appeared in publications corresponding to relevant European Neogene (including Quaternary) Mammal Zones are listed in Table 2.

The first *Cervavitus*, *C. novorossiae*, appeared in the Vallesian known from Poksheshty (MN10) in Moldova of eastern Europe (Vislobokova, 2007), its last appearance was found in the Turolian at MN12 (Vislobokova, 1990). The second earliest

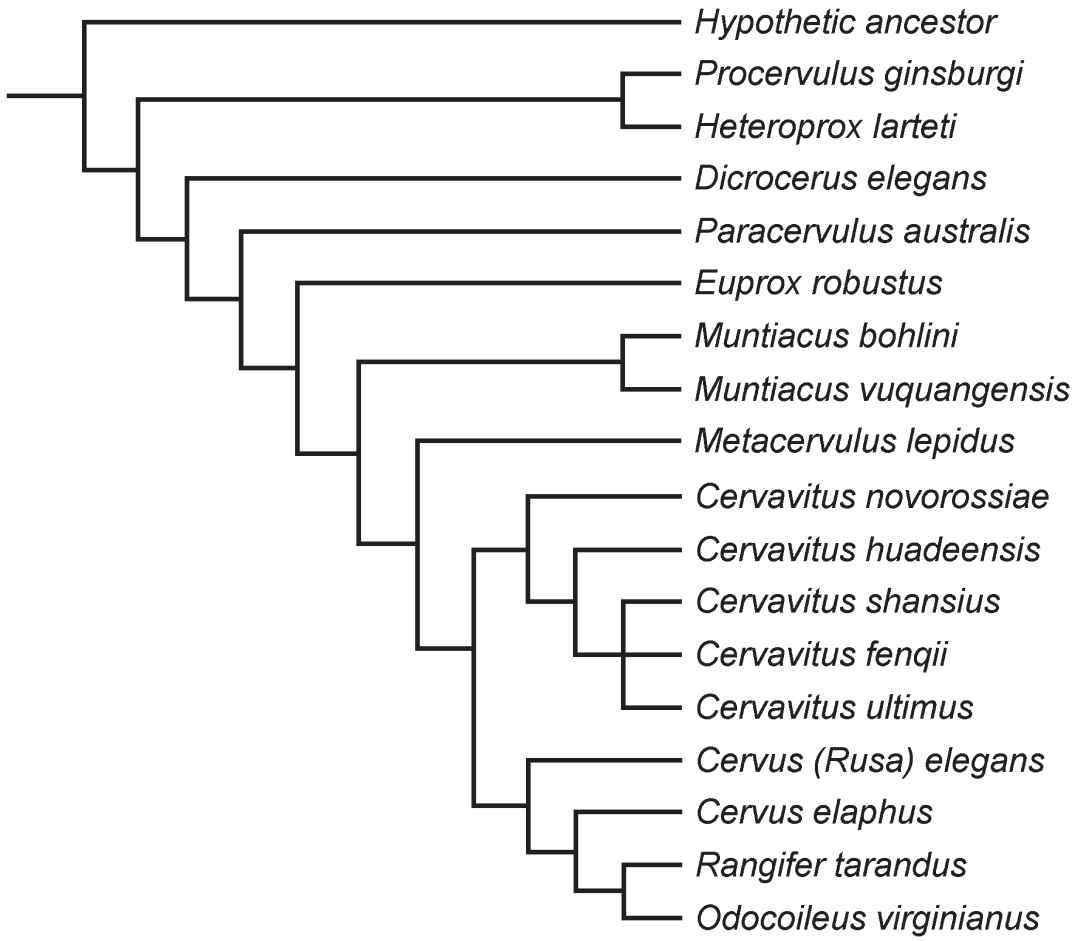

Fig. 4.—Selected cladogram for systematic position of *Cervavitus*.

Tabla 2.—**Biochronological distribution of *Cervavitus***

Geological Age	Late Miocene				Pliocene		Early Pleistocene		
European Mammal Age	Vallesian	Turolian			Ruscinian		Villafranchian		
MN(Q) Zone	MN10	MN11	MN12	MN13	MN14	MN15	MNQ16	MNQ17	MNQ18
Taxa									
Cervavitus novorossiae	+	+	+						
Cervavitus shanxius		+	+	+	+	?			
Cervavitus huadeensis			+	+					
Cervavitus variabilis			+	+	+				
Cervavitus cauvieri					+				
Cervavitus flerovi						+	+		
Cervavitus ultimus							+	+	?
Cervavitus fenqii							+	+	+

Cervavitus, C. shanxius, was found from Yanjiashan Formation in north-western China (Deng, 2009) equivalent to the early Turolian (MN11). Its last appearance was found from Mazegou Formation in northern China, equivalent to Ruscinian (MN14 and probably extended to MN15). The latest *Cervavitus* was supposed to be *C. flerovi*, its last appearance was found from Esekartkan (MNQ16) of Kazakhstan in Central Asia (Vislobokova, 2007). *C. ultimus* was thought to be the

ultimate *Cervavitus* and so named (Lin *et al*., 1978). Its earliest appearance was found from Longgupo Site dated earlier than 2Ma (Huang & Fang, 1991), and its last appearance was found from Yuanmou Formation biochronologically equivalent to MNQ17 and probably to MNQ18. The latest *Cervavitus* known so far is *C. fenqii*. Its first appearance was found at Renzidong Site in eastern China dated earlier than 2 MA or equivalent to MNQ16 (Dong *et al*, 2009), and its last appearance was found from the *Gigantopithecus* Cave in southern China (Han, 1987) dated equivalent to MNQ18 (Jin *et al*., 2009).

Based on the chronological distribution of *Cervavitus* data available, it can be concluded that the genus originated in Moldovan forests of East Europe in the Vallesian from an ancestor with two/three-tined antlers, *Palaeomeryx* fold, brachyodont cheek teeth and complete lateral metacarpals and evolved into *C. novorossiae*. It dispersed westwards into West Europe forests (e.g. Kohfidisch, Austria) in the earliest Turolian as *Cervavitus* sp. (Vislobokova, 2007). It dispersed further west to France (e.g. in Montpellier) and evolved into *C. cauvieri* in the Early Pliocene. The *C. novorossiae* in East Europe continued to evolve and *C. variabilis* was derived in the middle Turolian and survived until the early Ruscinian. On the other side, the *C. novorossiae* dispersed eastwards into Central Asian and evolved into *C. flerovi* in the Late Pliocene (Vislobokova, 2007). The *C. novorossiae* dispersed further eastwards into East Asian forests in the early Turolian and evolved into two forms, *C. shanxius* which was widespread in northern China in the Late Miocene, and *C. huadeensis*, which was larger and limited in Inner Mongolia. The extant holometacarpal tragulids (Shen, 1992) and suids are forest dwellers, the complete lateral metacarpals are of great help for balancing the body on irregular slopes. Judged by the presence of brachyodont cheek teeth and complete lateral metacarpals in *C. shanxius*, the species should be a forest dweller on irregular slopes. The specimens of *C. shanxius* from the Late Miocene sediments are of great quantity implying large populations of the species. Although the specimens are mostly found from the arid Loess Plateau of today, the areas were quite humid for forest vegetation to feed such large population of *C. shanxius* in the Late Miocene. *C. shanxius* disappeared from northern China and dispersed southwards in the Plio-Pleistocene probably due to the drying environment in northern China with uplifting of Himalayas and evolved into *C. ultimus* and *C. fenqii*, they survived until the middle stage of the Early Pleistocene (MNQ18) and evolved into or replaced by some other larger Cervini such as *Axis* and *Rusa*.

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