Quaternary International 212 (2010) 80–85

Contents lists available at ScienceDirect

Quaternary International

journal homepage: www.elsevier.com/locate/quaint

Dispersion of the genus *Procapreolus* and the relationships between *Procapreolus cusanus* and the roe deer (*Capreolus*)

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ARTICLE INFO

Article history:
Available online 24 November 2008

ABSTRACT

Procapreolus is a Eurasian genus included 10 species spanning to Late Miocene to the Early Pleistocene. The immigration of this and other taxa from the East to Central Europe marks a new step in evolution in European deer. *Procapreolus* will be replaced by *Capreolus*, the roe deer, considered a descendant of the former. *Procapreolus cusanus*, the younger European taxon (lacking the plesiomorph features of the genus), is shown to own a character in the skull typical of telemetacarpal deer, as modern roe deer and all its relatives do. This result strengthens the relationships between the two taxa and points out the necessity of a better definition of the genus *Procapreolus*.

1. Introduction

The genus *Procapreolus* has been created by Schlosser in 1924 with the type-species *Procapreolus latifrons*. This taxon is characterised by short metapodials, the presence of large upper canines and, in some individuals, a *Palaeomeryx* fold (Schlosser, 1924a; Heintz, 1970). The genus includes ten Eurasian species and it ranged from the Late Miocene to Early Pleistocene (McKenna and Bell, 1997).

1.1. *Spreading of* Procapreolus *in Eurasia*

In Europe, at present, six taxa are ascribed to this genus: *Procapreolus cusanus* (Croizet and Jobert, 1828) from the early Villafranchian (Late Pliocene) of France and Italy (Heintz, 1970; Abbazzi et al., 1995; Abbazzi and Croitor, 2003), *Procapreolus wenzensis* (Czyzewska, 1960) from the Early Pliocene of Poland, Germany and Russia (Czyzewska, 1960; Kahlke, 2001; Petronio et al., 2007), *Procapreolus moldavicus* (Janovskaya, 1954), from the Early Pliocene of Moldava (Croitor, 1997, 1999; Kahlke, 2001) and three Late Miocene taxa, *Procapreolus ucrainicus* Korotkevitsch, 1965 and *Procapreolus florovi* Korotkevitsch, 1974 from Ukraine, *Procapreolus loczyi* (Pohling, 1911) from Hungary and Austria (Vislobokova, 2007).

In Croitor's (2007) opinion, *Pliocervus kutchurganicus* Korotkevitsch, 1965, from Early Pliocene of Ukraine would be a junior synonymous of *P. moldavicus*. *Pliocervus graecus*, erected by Azanza in 1995 from antlers and dental material found in Maramena Late Miocene Greek fossiliferous deposit, has recently been transferred to the genus *Procapreolus* (see Kostopoulos, 2006; Croitor, 2007). Nevertheless, based on the actual level of knowledge on the genus, before including this taxon in the present survey, is better to wait for more complete remains. Nevertheless, it is worth to remark that ?*Procapreolus* sp. is signalled in Greece during the Turolian at Dytiko (Bouvrain and de Bonis, 2007) and the genus could also be present at Chomateri (Azanza, 1995).

"*Procapreolus*" *concudensis* (Hernàndez-Pacheco, 1930) of the Turolian (MN12) of Spain (Azanza and Menéndez, 1988–1990) was considered to belong to this genus because of the similarities in size and morphology of its pedicle with *P. latifrons* (Azanza et al., 1989). More recently, anyway, Azanza Asensio (2000) created for this taxon the new genus *Turiacemas*. *P. cusanus* has been signalled at Villaroya (Aguirre and Morales, 1990 quoted in Kahlke, 2001). Anyway, more recent studies point out that the genus *Procapreolus* would not be present in this site: the smallest cervid species found in that locality is *Croizetoceros ramosus* (Croizet and Jobert, 1828) (Azanza et al., 1997; Azanza pers. comm., 2008).

In Europe, *Procapreolus* is known between the Late Miocene (MN10) to the Pliocene (MN16; Lister et al., 1998; Gentry et al., 1999; Vislobokova, 2005). The first occurrence of the genus refers in MN10 of Ukraine (Berislav) and Azerbaijan (Eldar) with *P. ucrainicus* (Korotkevitsch, 1988 quoted in Vislobokova, 2005). The appearance of *Procapreolus*, together with *Cervavitus* Khomenko, 1913 and *Gazella* Blainville, 1816 among Ruminants, characterises the Upper Sarmartian, beginning at 10.5 My, in the region (Vislobokova, 2005). In Central Europe, *P. loczyi* is found in the Austrian localities of Nikitisch and Himberg (Thenius, 1956), during the Late Vallesian (MN10), at about 9.7 My. It is considered an immigrant from the

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doi:10.1016/j.quaint.2008.11.002

East Europe during the environmental changes occurred at the beginning of the Late Miocene in Austria and the Pannonian Basin (Vislobokova, 2006).

According to Vislobokova (2007), *P. ucrainicus* was a common species in the Early and Middle Turolian (MN11–MN12) of Ukraine. *P. loczyi* and *P. ucrainicus* would share a number of pleisiomorph characters and they may belong to two distinct phyletic lineage: *P. loczyi–P. cusanus* and *P. ucrainicus–P. wenzensis* (Vislobokova and Kalmykov, 1994 quoted in Vislobokova, 2007).

The last occurrence of the genus in Europe is probably that of *P. cusanus* from France (Perrier-Etouaires) at about 2.5 My (MN16; Poidevin et al., 1984; Guérin, 2007). This taxon could be present at Montopoli (Italy), at the same age (Abbazzi and Croitor, 2003). In any case, in Italy, *Procapreolus* sp. is signalled at Baccinnello (Formation V-3) during the Late Miocene, MN13–MN14 (Abbazzi, 2001) and the presence of the species *cusanus* seems well established at Triversa (Abbazzi et al., 1995), a fossil locality considered about 3.1/3.2 My in age (Gliozzi et al., 1997; Palombo, 2004 and references therein). According to Heintz (1970), at the same time, *P. cusanus* is probably present in France (Vialette) and, perhaps, in England (Red Crags) and in Germany (Wölfersheim-Watterau). Anyway, these last two specimens would need supplementary analysis. Some remains from South Ukraine sometimes ascribed to *P. cusanus* are considered too large for this taxon (Croitor, 1997 quoted in Kahlke, 2001). Fig. 1 shows the main findings of the European *Procapreolus*.

In China, four species have been described: *Procapreolus ruetimeyeri* (Schlosser, 1903), *Procapreolus stenos* (Lin and Pan, 1978), *Procapreolus jinensis* Dong and Ye (1996) and *P. latifrons*. The validity of the first species has been questioned by certain authors (e.g. Korotkevitsch, 1963, 1965 quoted in Czyzewska, 1968); nevertheless it is recognised as an authentic taxon by others (e.g. Kahlke, 2001). *P. latifrons* is probably the species with the longest life-span in the genus; it is known during the Late Miocene, in the *Hipparion* fauna from Baode, Shanxi Basin (MN12; Zdansky, 1925; Teilhard de Chardin and Young, 1931; Deng, 2006) and Ertemte, North China (where it is found together with *P. ruetimeyeri*; Qiu and Qiu, 1995), the Pliocene (Zdansky, 1927), until the Early Pleistocene (Zong et al., 1982). During the Early Pleistocene, also *P. stenos* was present in China. Its bones have been recognised in faunas from Yunnan Province (Yuanmou Formation), associated with *Homo erectus*

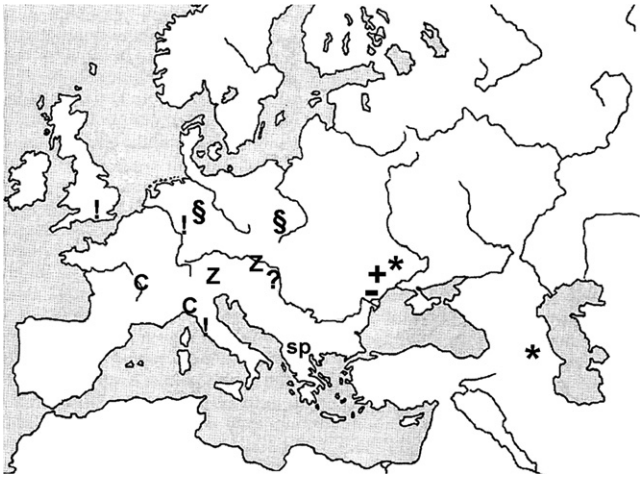

Fig. 1. European dispersion of *Procapreolus* species: "*" *P. ucrainicus*; "+" *P. florovi*; "Z" *P. loczyi*; "-" *P. moldavicus*; "§" *P. wenzensis*; "C" *P. cusanus*; "sp" Greek? *Procapreolus* sp.; "!" presumed *P. cusanus* (but it has to be confirmed); "?"presumed *P. latifrons* (but remains too scanty for a specific attribution). For more details about the fossiliferous deposits yielding *Procapreolus* remains see Fig. 2, page 468–469, in Kahlke (2001) and references therein.

remains (Dong et al., 2000). In Vislobokova's (1994) opinion, *P. latifrons* and *P. stenos* could form a phyletic lineage. *P. jinensis* seems limited to the Early Pliocene of Yushe basin (Shanxi Province, China; Dong and Ye, 1996). Remains of *P. ruetimeyeri* et *P. latifrons* have also been found by Schlosser (1924a,b) in Inner Mongolia (China), and the latter was eventually present in Hungary, but the specimens seem to be too scanty in order to ascribe them to a specific taxon (see Kahlke, 2001). According to our actual knowledge, the genus could have originated in Asia (perhaps China?) or in East Europe.

1.2. *Spreading of* Capreolus *in Eurasia*

The genus *Capreolus* Gray, 1821 includes small telemetacarpal deer species characterised by (generally) three pointed tuberculated antlers, inserted closed together at their base and developed vertically on the skull (Groves and Grubb, 1987; Delpech and Guérin, 1996; Sempere et al., 1996; Lister et al., 1998). Two modern species are inscribed within this genus (Von Lehmann, 1958; Sokolov and Gromov, 1990): *Capreolus capreolus* (Linnaeus, 1758) the European roe deer, and *Capreolus pygargus* (Pallas, 1711) the Asian form, slightly larger of the former.

Roe deer appears at the same time as the last *Procapreolus* roam in Europe. *Capreolus constantini*, Vislobokova et al., 1995 from the Late Pliocene (MN16) of Udunga (Western Trans-Baikal, Russia), is considered as the oldest species belonging to this genus. The postcranial bones look similar, by dimensions, to those of the Asian roe deer, *C. pygargus*, as the antlers do. On the teeth, the lower premolars are long in proportion to the molars (plesiomorphic features), and on some slightly worn teeth, the *Palaeomeryx* fold could be observed (Vislobokova et al., 1995). Another old roe deer (*Capreolus* sp.) has been found in Western Siberia, at about 2.2–1.8 (Vislobokova, 1996). In Slovakia (Hajnáčka I) the genus *Capreolus* is signalled during the early Villafranchian (MN16, about 3 My ago; Kahlke, 2001; Sabol et al., 2006). According to Heintz (1970), in Romania, at the same age, the genus is reported by Samson and Rădulescu (1963). The Late Pliocene seems to be a crucial period for the evolution of *Capreolus* and the replacing of *Procapreolus* by the former.

In Central Europe, according to Kahlke (2004), the oldest roe deer is *C. cusanoides* Kahlke, 2001 from Untermassfeld (Germany, about 1/1.1 My), which is morphologically and metrically intermediate between *P. cusanus* and the younger roe deer (Kahlke, 2001, 2007). The roe deer is also present at Solilhac (France; Fosse and Bonifay, 1989; Crégut, 2002; Palombo and Valli, 2003–2004), locality slightly younger (about 1 My; Thouveney and Bonifay, 1984) than Untermassfeld. At the beginning of the Middle Pleistocene, the roe deer is generally known by individuals larger than the modern European taxon, generally ascribed at the subspecies level (sometimes erected to true species; e.g. Pfeiffer, 1998) *C. capreolus suessenbornensis* Kahlke, 1956, defined at Süssenborn (Germany). An early Middle Pleistocene small form Mauer (Germany) is sometimes attributed to *Capreolus priscus* Soergel, 1914 (Kahlke, 2007). Since the Late Pleistocene, in Western Europe, roe deer is identical to the modern species and it is widespread (Delpech and Guérin, 1996; Lister et al., 1998).

In China, where the genus *Procapreolus* is present until the Early Pleistocene, the roe deer appears later than in Europe or Siberia. Some remains of *Capreolus* sp. have been recognised from Xicun fauna (Tunlius County, Shanxi Basin; Zong et al., 1982), considered Late Early Pleistocene (even if an early Middle Pleistocene age cannot be ruled out), from a fauna lacking *Procapreolus* or other similar sized deer. *Capreolus* sp. is also present in Yunnan Province where *P. stenos* has been signalled, but the two deer are not present in the same layers (Dong et al., 2000). Teilhard de Chardin and Leroy (1942) relate three new *Capreolus* species from China: