



A new species of *Euprox* (Cervidae, Artiodactyla) from the upper Miocene of the Linxia Basin, Gansu Province, China, with interpretation of its paleoenvironment

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Abstract

The Linxia Basin, Gansu Province, China, is known for its abundant and well preserved fossils. Here a new species, *Euprox grandis* sp. nov., is established based on a skull and antlers collected from the upper Miocene Liushu Formation of the Linxia Basin. The new species is distinguishable from other *Euprox* species by its large body size, notably long pedicle and weak burr. The main beam and the brow tine are slightly curved both medially and backwards, and the apex of the main beam turns, curving slightly laterally. The upper cheek teeth are brachydont, with a clear central fold on the premolars and internal postprotocrista and metaconule fold on M1-M2. The cingulum is almost absent, only occasionally weakly developed at the anterior and lingual surface of the teeth. Cladistic analysis was carried out using the TNT software, and two most parsimonious trees were retained. As the strict consensus tree shows *E. grandis* appears to be an advanced muntiacine form, which may have a close relationship with the genus *Muntiacus*. The presence of *E. grandis* in the Linxia Basin adds new evidence to support a warm and humid environment during the late Miocene in the basin.

Key words: Linxia Basin, upper Miocene Liushu Formation, Cervidae, Muntiacinae, *Euprox*

Introduction

The Linxia Basin, Gansu Province, China, known for its abundant and well preserved fossils, is located in the transitional zone between the Tibetan and Loess plateaus, and filled with 700–2000 m of Cenozoic deposits. The currently accepted lithostratigraphical subdivisions of the Linxia Cenozoic deposits (Deng *et al.* 2004a, 2004b, 2013; Deng 2005), in ascending order, are as follows. Oligocene: Tala and Jiaozigou formations; Miocene: Shangzhuang, Dongxiang, Hujialiang, and Liushu formations; Pliocene: Hewangjia and Jishi formations; early Pleistocene: Wucheng Formation.

Here, a new species of two-pronged antlered deer is described based on the specimens collected from the upper Miocene deposits of the Linxia Basin. The Miocene two-pronged antlered cervids with true burr and strongly inclined pedicle in side view, such as *Euprox* Stehlin 1928, *Muntiacus* Rafinesque 1815, *Paracervulus* Teilhard de Chardin & Trassaert 1937, *Eostylloceros* Zdansky 1925 and *Amphiprox* Haupt 1935, were proposed to be the predominant representatives of the subfamily Muntiacinae (Azanza, 1993; Azanza & Montoya 1995; Azanza *et al.* 2013; Wang & Zhang 2011). The new specimens from the Linxia Basin resemble the genus *Euprox* by the relatively large body size, long pedicle and short antler base, thus were placed in *Euprox*, and a new species, *Euprox grandis* sp. nov. was erected based on the notably large body size and long pedicle and relatively weak burr.

Previously, only *Euprox* cf. *furcatus* from Shanxi Province, *E. sp.* from Tunggur and the Qsaidam Basin, *E. robustus* from Yuanmou and *E. altus* from Nei Mongol were reported in China, and were usually rare or fragmentary, without associated skull and antlers (Zdansky 1925; Bohlin 1937; Colbert 1936, 1940; Dong *et al.*

The climate of northern China has been interpreted as being influenced partly by the intensification of monsoon circulation that resulted from the uplift of the Tibetan Plateau. Located in the transitional zone between the Tibetan and Loess plateaus, the Linxia Basin is undoubtedly deeply influenced. A surprisingly humid climate during the late Miocene in northern China was suggested, while Europe was experiencing arid conditions, based on the hypsodonty of Neogene herbivores; and the “*Hipparion* Red Clay” of northern China was suggested to be apparently deposited under these humid conditions (Fortelius *et al.* 2002). The composition of the late Miocene mammalian faunas of northern China has been interpreted as indicating regional differentiation between a close and humid environment in the east and an open and arid one in the west, which was closely related to the intensification of the summer monsoon (Zhang 2006). The Linxia Basin strata dating to the middle-late late Miocene are thought to have been deposited in an open but humid environment, based on a cenogram analysis of their fossil mammal fauna (Deng 2009). Stable carbon isotope analysis of the tooth enamel of Chinese late Neogene mammals shows that, during the late Miocene before 7 Ma, northern China was covered in steppe dominated by C3 grasses instead of savanna dominated by C4 plants; then between 7 Ma and the early Pliocene, the Chinese Loess Plateau was characterized by a pattern of northward-increasing C4 vegetation, but there were still nearly pure C3-plant ecosystems in the southern Chinese Loess Plateau and the Linxia Basin which lies on the western margin of the Chinese Loess Plateau (Hou *et al.* 2006; Passey *et al.* 2009). The discovery of *Sinohippus*, *Tapirus* and *Chleuastochoerus* in the late Miocene of Linxia Basin also implies a relatively open and humid environment (Hou *et al.* 2007, 2014; Deng *et al.* 2008).

Conclusions

The new species, *Euprox grandis*, from the Linxia Basin bears large body size, notably long pedicle and a relatively weak true burr; the relatively brachydont upper cheek teeth of the new species bear clear internal postprotocrista and metaconule fold, and lack strong cingula. Phylogenetic analysis suggests the new species may represent an advanced form of *Euprox*. The Linxia Basin discoveries of the largest known *Euprox* that bears the longest pedicle and has relatively brachydont cheek teeth add new evidence to support a relatively warm and humid environment during the late Miocene in the Linxia Basin.

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References

- Azanza, B. (1993) Sur la nature des appendices frontaux des cervidés (Artiodactyla, Mammalia) du Miocène inférieur et moyen. Remarques sur leur systématique et leur phylogénie. *Comptes rendus de l'Académie des sciences*, 316, 1163–1169. [Série 2]
- Azanza, B. & Montoya, P. (1995) A new deer from the Lower Turolian of Spain. *Journal of Paleontology*, 69, 1163–1175.
- Azanza, B., Rössner, G.E. & Ortiz-Jaureguizar, E. (2013) The early Turolian (late Miocene) Cervidae (Artiodactyla, Mammalia) from the fossil site of Dorn-Dürkheim 1 (Germany) and implications on the origin of crown cervids. *Palaeobiodiversity & Palaeoenvironments*, 93, 217–258. <http://dx.doi.org/10.1007/s12549-013-0118-8>
- Bärmann, E.V. & Rössner, G.E. (2011) Dental nomenclature in Ruminantia: Towards a standard terminological framework. *Mammalian Biology*, 76, 762–768. <http://dx.doi.org/10.1016/j.mambio.2011.07.002>

- Bohlin, B. (1937) Eine Tertiäre säugetier-Fauna aus Tsaidam. *Palaeontologia Sinica*, 14, 1–111. [Series C]
- Bubenik, A.B. (1990) Epigenetical, morphological, physiological, and behavioral aspects of evolution of horns, pronghorns, and antlers. In: Bubenik, G.A. & Bubenik, A.B. (Eds.), *Horns, pronghorns, and antlers*. Springer-Verlag, New York, pp. 1–113.
http://dx.doi.org/10.1007/978-1-4613-8966-8_1
- Bubenik, A.B. (1993) Evolution of cranial protuberances of Cervoids from velericorn stage into annually deciduous antlers. In: Ohtaishi, N. & Sheng, H.L. (Eds.), *Deer of China*. Elsevier Science Publishers, pp. 44–55.
- Colbert, E.H. (1936) Tertiary deer discovered by the American Museum Asiatic expeditions. *American Museum Novitates*, 854, 1–21.
- Colbert, E.H. (1940) Some cervid teeth from the Tung Gur Formation of Mongolia, and additional notes on the genera *Stephanocemas* and *Lagomeryx*. *American Museum Novitates*, 1062, 1–6.
- Czyżewska, T. & Stefaniak, K. (1994) *Euprox furcatus* [Hensel, 1859] [Cervidae, Mammalia] from Przeworno [Middle Miocene, Lower Silesia, Poland]. *Acta Zoologica Cracoviensia*, 37, 55–74.
- DeMiguel, D., Fortelius, M., Azanza, B. & Morales, J. (2008) Ancestral feeding state of ruminants reconsidered: earliest grazing adaptation claims a mixed condition for Cervidae. *BMC Evolutionary Biology*, 8, 1–13.
<http://dx.doi.org/10.1186/1471-2148-8-13>
- Deng, T. (2005) Character, age and ecology of the Hezheng Biota from northwestern China. *Acta Geologica Sinica*, 79, 739–750.
<http://dx.doi.org/10.1111/j.1755-6724.2005.tb00927.x>
- Deng, T. (2009) Late Cenozoic environmental changes in the Linxia Basin (Gansu, China) as indicated by cenograms of fossil mammals. *Vertebrata Palasiatica*, 47, 282–298.
- Deng, T., He, W. & Chen, S.Q. (2008) A new species of the Late Miocene *Tapirs* (Perrisodactyla, Tapiridae) from the Linxia Basin in Gansu, China. *Vertebrata Palasiatica*, 46, 190–209.
- Deng, T., Qiu, Z.X., Wang, B.Y., Wang, X.M. & Hou, S.K. (2013) Late Cenozoic biostratigraphy of the Linxia Basin, northwestern China. In: Wang, X.M., Flynn, L.J. & Fortelius, M. (Eds.), *Fossil Mammals of Asia: Neogene Biostratigraphy and Chronology*. Columbia University Press, New York, pp. 243–273.
- Deng, T., Wang, X.M., Ni, X.J. & Liu, L.P. (2004a) Sequence of the Cenozoic mammalian faunas of the Linxia Basin in Gansu, China. *Acta Geologica Sinica*, 78, 8–14.
- Deng, T., Wang, X.M., Ni, X.J., Liu, L.P. & Liang, Z. (2004b) Cenozoic stratigraphic sequence of the Linxia Basin in Gansu, China and its evidence from mammal fossils. *Vertebrata Palasiatica*, 42, 45–66.
- Dong, W. (2004) The morphological characteristics and evolution of teeth of fossil cervid. *Acta Anthropologica Sinica*, 23 (Supplement), 286–295.
- Dong, W. (2007) New material of Muntiacinae (Artiodactyla, Mammalia) from the Late Miocene of the northeastern Qinghai-Tibetan Plateau, China. *Comptes Rendus Palevol*, 6, 335–343.
<http://dx.doi.org/10.1016/j.crpv.2007.05.002>
- Dong, W. (2008) A review on morphology and evolution of antlers. In: Dong, W. (Ed.), *Proceedings of the Eleventh Annual Meeting of the Chinese Society of Vertebrate Paleontology*. Chinese Ocean Press, Beijing, pp. 127–144.
- Dong, W. & Hu, C.K. (1994) The Late Miocene Cervidae from Hounao, Yushe, Shanxi. *Vertebrata Palasiatica*, 32, 209–227.
- Dong, W., Ji, X.P., Jablonski, N.G., Su, D.F. & Li, W.Q. (2014) New materials of the Late Miocene *Muntiacus* from Zhaotong hominoid site in southern China. *Vertebrata Palasiatica*, 52, 316–327.
- Dong, W., Liu, J.H. & Pan, Y.R. (2003) A new *Euprox* from the late Miocene of Yuanmou, Yunnan Province, China, with interpretation of its paleoenvironment. *Chinese Science Bulletin*, 48, 485–491.
<http://dx.doi.org/10.1007/BF03183257>
- Fortelius, M., Eronen, J., Jernvall, J., Liu, L.P., Pushkina, D., Rinne, J., Tesakov, A., Vislobokova, I., Zhang, Z.Q. & Zhou, L.P. (2002) Fossil mammals resolve regional patterns of Eurasian climate change over 20 million years. *Evolutionary Ecology Research*, 4, 1005–1016.
- Gentry, A.W. & Heizmann, E.P.J. (1993) *Lagomeryx* Roger, 1904 (Mammalia, Artiodactyla): proposed designation of *L. ruetimeyeri* Thenius, 1948 as the type species. *Bulletin of Zoological Nomenclature*, 50, 133–136.
- Gentry, A. (1994) The Miocene differentiation of Old World Pecora (Mammalia). *Historical Biology*, 7, 115–158.
<http://dx.doi.org/10.1080/10292389409380449>
- Gentry, A.W., Rössner, G.E. & Heizmann, E.P.J. (1999) Suborder Ruminantia. In: Rössner, G.E., Heissig, K. & Alcover, A.J. (Eds.), *The Miocene Land Mammals of Europe*. Verlag Dr Friedrich Pfeil, München, pp. 225–258.
- Ginsburg, L. & Crouzel, F. (1976) Contribution à la connaissance d'*Heteroprox larteti* (Filhol) Cervidé du Miocène européen. *Bulletin du Muséum national d'histoire naturelle*, 399, 345–357. [sér. 3]
- Goloboff, P.A., Farris, J.S. & Nixon, K.C. (2008) TNT, a free program for phylogenetic analysis. *Cladistics*, 24, 774–786.
<http://dx.doi.org/10.1111/j.1096-0031.2008.00217.x>
- Heintz, E. (1970a) Les Cervidés villafranchiens de France et d'Espagne. Volume I: texte et planches. *Mémoires du Muséum National d'Histoire Naturelle, Nouvelle série*, 22, 1–303.
- Heintz, E. (1970b) Les Cervidés villafranchiens de France et d'Espagne. Volume II: Figures et tableaux. *Mémoires du Muséum National d'Histoire Naturelle, Nouvelle série*, 22, 1–206.
- Heizmann, E.P.J. & Kubiak, H. (1992) Felidae and Hyaenidae (Carnivora, Mammalia) from the Miocene of Przeworno (Lower

- Silesia, Poland), with general remarks on the fauna complex. *Acta Zoologica Cracoviensia*, 35, 241–263.
- Hou, S.K., Deng, T., He, W. & Chen, S.Q. (2007) New materials of *Sinohippus* from Gansu and Nei Mongol, China. *Vertebrata Palasiatica*, 45, 213–231.
- Hou, S.K., Deng, T., He, W. & Chen, S.Q. (2014) Foraging behavior of *Chleuastochoerus* (Suidae, Artiodactyla): A case study of skull and mandible morpho-functional analysis. *Science China: Earth Sciences*, 57, 988–998.
<http://dx.doi.org/10.1007/s11430-013-4733-z>
- Hou, S.K., Deng, T. & Wang, Y. (2006) Stable carbon isotopic evidence of tooth enamel for the Late Neogene habitats of the *Hipparion* fauna in China. In: Dong, W. (Ed.), *Proceedings of the Tenth Annual Meeting of the Chinese Society of Vertebrate Paleontology*. China Ocean Press, Beijing, pp. 85–94.
- Janis, C.M. & Scott, K.M. (1987) The interrelationships of higher ruminant families: with special emphasis on the members of the Cervoidea. *American Museum novitates*, 2893, 1–85.
- McKenna, M.C. & Bell, S.K. (1997) *Classification of Mammals Above the Species Level*. Columbia University Press, New York, 640 pp.
- Morales, J. & Soria, D. (1981) Los artiodáctilos de los Valles de Fuentidueña (Segovia). *Estudios geológicos*, 37, 477–501.
- Passey, B.H., Ayliffe, L.K., Kaakinen, A., Zhang, Z.Q., Eronen, J.T., Zhu, Y.M., Zhou L.P., Cerling, T.E. & Fortelius, M. (2009) Strengthened East Asian summer monsoons during a period of high-latitude warmth? Isotopic evidence from Mio-Pliocene fossil mammals and soil carbonates from northern China. *Earth and Planetary Science Letters*, 277, 443–452.
<http://dx.doi.org/10.1016/j.epsl.2008.11.008>
- Pitra, C., Fickel, J., Meijaard, E. & Groves, C. (2004) Evolution and phylogeny of old world deer. *Molecular Phylogenetics and Evolution*, 33, 880–895.
<http://dx.doi.org/10.1016/j.ympev.2004.07.013>
- Rössner, G.E. (1995) Odontologische und schadelanatomische Untersuchungen an *Procervulus* (Cervidae, Mammalia). *Münchener Geowissenschaftliche Abhandlungen*, 29 (A), 1–127.
- Stehlin, H. (1928) Bemerkungen über die Hirsche von Steinheim am Aalbuch. *Eclogae geologicae Helveticae*, 21, 245–256.
- Teilhard de Chardin, P. & Trassaert, M. (1937) The Pliocene Camelidae, Giraffidae, and Cervidae of South Eastern Shansi. *Palaeontologia Sinica*, 1, 1–56. [New Series C]
- Thenius, E. (1948) Zur Kenntnis der fossilen Hirsche des Wiener Beckens, unter besonderer Berücksichtigung ihrer stratigraphischen Bedeutung. *Annalen des Naturhistorischen Museums in Wien*, 56, 262–308.
- Tütken, T., Vennemann, T.W., Janz, H. & Heizmann, E.P.J. (2006) Palaeoenvironment and palaeoclimate of the Middle Miocene lake in the Steinheim basin, SW Germany: A reconstruction from C, O, and Sr isotopes of fossil remains. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 241, 457–491.
<http://dx.doi.org/10.1016/j.palaeo.2006.04.007>
- Vislobokova, I.A. (1983) *The fossil deer of Mongolia*. Sciences Press, Moscow, 80 pp.
- Vislobokova, I.A. (1990) Fossil deer of Eurasia. *Transactions of the Paleontological Institute*, 240, 1–206.
- Vislobokova, I.A. (2005) The importance of Late Miocene faunal exchanges between Eastern Mediterranean areas and Central Europe. *Annales de Paléontologie*, 91, 241–255.
<http://dx.doi.org/10.1016/j.anpal.2005.04.001>
- Vislobokova, I.A. (2006) Associations of ruminants in Miocene ecosystems of Eastern Alpine Region. *Paleontological Journal*, 40, 438–447.
<http://dx.doi.org/10.1134/S0031030106040101>
- Wang, L.H. & Zhang, Z.Q. (2011) A new species of *Euprox* (Cervidae, Mammalia) from the Middle Miocene of Damiao, Nei Mongol, China. *Vertebrata Palasiatica*, 49, 365–376.
- Wang, X.M., Xie, G.P. & Dong, W. (2009) A new species of crown-antlered deer *Stephanocemas* (Artiodactyla, Cervidae) from the Middle Miocene of Qaidam Basin, northern Tibetan Plateau, China, and a preliminary evaluation of its phylogeny. *Zoological Journal of the Linnean Society*, 156, 680–695.
<http://dx.doi.org/10.1111/j.1096-3642.2008.00491.x>
- Zdansky, O. (1925) Fossile Hirsche Chinas. *Palaeontologia Sinica*, 2, 1–94. [Series C]
- Zhang, Z.Q. (2006) Chinese Late Neogene land mammal community and the environmental changes of East Asia. *Vertebrata Palasiatica*, 44, 133–142.