



## A new species of *Chleuastochoerus* (Artiodactyla: Suidae) from the Linxia Basin, Gansu Province, China

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### Abstract

The Linxia Basin, Gansu Province, China, is known for its abundant and well-preserved fossils. Here a new species, *Chleuastochoerus linxiaensis* sp. nov., is described based on specimens collected from the upper Miocene deposits of the Linxia Basin, distinguishable from *C. stehlini* by the relatively long facial region, more anteromedial-posterolaterally compressed upper canine and more complicated cheek teeth. A cladistics analysis placed *Chleuastochoerus* in the subfamily Hyotheriinae, being one of the basal taxa of this subfamily. *Chleuastochoerus linxiaensis* and *C. stehlini* are considered to have diverged before MN 10. *C. tuvensis* from Russia represents a separate lineage of *Chleuastochoerus*, which may have a closer relationship to *C. stehlini* but bears more progressive P4/p4 and M3.

**Key words:** Linxia Basin, upper Miocene Liushu Formation, Hyotheriinae, *Chleuastochoerus*, phylogeny

### Introduction

*Chleuastochoerus* Pearson 1928 is a small late Miocene-early Pliocene fossil pig (Suidae). Isolated teeth of *Chleuastochoerus* were first reported by Schlosser (1903) under the name “*Sus stehlini*.” Cranio-mandibular specimens and postcranial skeletal elements of this small suid were subsequently recovered from the upper Miocene “*Hipparion* Red Clays” of northern China and a new genus *Chleuastochoerus* was established, primarily based on primitive features of the teeth and a distinctive snout and zygomatic structure (Pearson 1928). In general, this genus is characterized by the “supra-canine arch-niche” (a bony arch above the upper canine, with a niche in front of the upper canine to accommodate the lower canine when the mouth is closed), and the “pre-zygomatic plate” (a shelf-like expansion of the anterior end of the zygomatic arch). Despite the presence of notable range of metric variation, Pearson (1928) was against splitting all the material of this small suid into different species, and she included all the material into a single species, *Chleuastochoerus stehlini*. Later studies were mostly simple reports of new records and did not venture beyond Pearson’s study (Young & Liu 1948; Liu & Zhou 1959; Chow *et al.* 1965; Liu *et al.* 1978; Tang *et al.* 1985). *Chleuastochoerus* was long thought to be endemic to northern China. Beginning in the early 1990s, however, *Chleuastochoerus* specimens began to be reported from southern China (van der Made & Han 1994; Pan *et al.* 2006), Vietnam (Covert *et al.* 2001), and Asiatic Russia (Vislobokova 2009b). Of these new findings, only those from Russia include cranio-mandibular material that clearly shows *Chleuastochoerus* characteristics. The specimens from southern China and Vietnam are fragmentary, including only isolated teeth, to be certain of their identity (Pickford & Liu 2001; Liu *et al.* 2004). Therefore, the geographic range of *Chleuastochoerus* may be limited to northern China and the southwestern part of Asiatic Russia.

Pearson (1928) did not discuss the systematic affinities of *Chleuastochoerus*, and only mentioned that this genus might be a terminal taxon of an unknown lineage that derived independently of *Hyotherium* von Meyer 1834 from some Oligocene *Palaeochoerus* Pomel 1847. Since Pearson (1927) had already included *Palaeochoerus* into Suidae based on the comparison of primitive suids and tayassuids, *Chleuastochoerus* was also included in Suidae.

## References

- Boisserie, J.-R., Lihoreau, F. & Brunet, M. (2005) The position of Hippopotamidae within Cetartiodactyla. *Proceedings of the National Academy of Sciences, USA*, 102, 537–541  
<http://dx.doi.org/10.1073/pnas.0409518102>
- Boisserie, J.-R., Lihoreau, F., Orliac, M., Fisher, R. E., Weston, E.M. & Ducrocq, S. (2010) Morphology and phylogenetic relationships of the earliest known hippopotamids (Cetartiodactyla, Hippopotamidae, Kenyapotaminae). *Zoological Journal of the Linnean Society*, 158, 325–366.  
<http://dx.doi.org/10.1111/j.1096-3642.2009.00548.x>
- Chen, G.F. (1997) A new suid from the Middle Miocene of Xinan, Henan. In: Tong, Y.S., Zhang, Y.Y., Wu, W.Y., Li, J.L. & Shi, L.Q. (Eds.), *Evidence for Evolution - Essays in Honor of Prof. Chungchien Young on the Hundredth Anniversary of His Birth*. China Ocean Press, Beijing, pp. 129–136.
- Chow, M.Z., Huang, W.B., Zhang, Y.P., Tang, Y.J. & Huang, X.S. (1965) Observations on the younger Cenozoic of SW Shansi. *Vertebrata Palasiatica*, 9, 256–269.
- Covert, H.H., Hamrick, M.W., Dzanh, T. & McKinney, K.C. (2001) Fossil mammals from the Late Miocene of Vietnam. *Journal of Vertebrate Paleontology*, 21, 633–636.  
[http://dx.doi.org/10.1671/0272-4634\(2001\)021\[0633:fmftlm\]2.0.co;2](http://dx.doi.org/10.1671/0272-4634(2001)021[0633:fmftlm]2.0.co;2)
- Damuth, J. (1990) Problems in estimating body masses of archaic ungulates using dental measurements. In: Damuth, J. & MacFadden, B.J. (Eds.), *Body Size in Mammalian Paleobiology*. Cambridge University Press, Cambridge, pp. 229–253.
- 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., 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.  
<http://dx.doi.org/10.1111/j.1755-6724.2004.tb00669.x>
- 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.
- Fortelius M. (1990) Problems with using fossil teeth to estimate body sizes of extinct mammals. In: Damuth, J. & MacFadden, B.J. (Eds.), *Body Size in Mammalian Paleobiology*. Cambridge University Press, Cambridge, pp. 207–228.
- 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. & Hooker, J.J. (1988) The phylogeny of the Artiodactyla. In: Benton, M.J. (Ed.), *The Phylogeny and Classification of the Tetrapods*. Clarendon Press, Oxford, pp. 235–272.
- Ginsburg, L. (1974) Les tayassuidés des Phosphorites du Quercy. *Palaeovertebrata*, 6, 55–85.
- Goloboff, P.A., Farris, J.S. & Nixon, K. (2008) TNT, a free program for phylogenetic analysis. *Cladistics*, 24, 774–786.  
<http://dx.doi.org/10.1111/j.1096-0031.2008.00217.x>
- Hellmund, M. (1991) New and old finds of Suina (Artiodactyla, Mammalia) from Oligo-Miocene localities in Germany, Switzerland and France I. *Hyotherium meissneri* (Suidae) from the Lower Miocene of Ulm-Westtangente (Baden-Württemberg). *Stuttgarter Beiträge zur Naturkunde, Serie B*, 176, 1–69.
- Hellmund, M. (1992) New and old finds of Suina (Artiodactyla, Mammalia) from Oligo-Miocene localities in Germany, Switzerland and France II. Revision of the genera *Palaeochoerus* Pomel 1847 and *Propalaeochoerus* Stehlin 1899 (Tayassuidae). *Stuttgarter Beiträge zur Naturkunde, Serie B*, 189, 1–75.
- 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 Chinese). In: Dong, W. (Ed.), *Proceedings of the Tenth Annual Meeting of the Chinese Society of Vertebrate Paleontology*. China Ocean Press, Beijing, pp. 85–94.
- Liu, H.Y. & Zhou, B.X. (1959) Pliocene mammals of Lushi, Henan. *Palaeovertebrata et Paleoanthropologie*, 1, 73–78.
- Liu, L.P. (2003) *Chinese fossil Suoidea: Systematics, Evolution and Paleocology*. PhD Thesis, University Helsinki, Helsinki, 34 pp.
- Liu, L.P., Fortelius, M. & Pickford, M. (2002) New fossil Suidae from Shanwang, Shandong, China. *Journal of Vertebrate Paleontology*, 22, 152–163.  
[http://dx.doi.org/10.1671/0272-4634\(2002\)022\[0152:nfsfss\]2.0.co;2](http://dx.doi.org/10.1671/0272-4634(2002)022[0152:nfsfss]2.0.co;2)
- Liu, L.P., Kostopoulos, D.S. & Fortelius, M. (2004) Late Miocene *Microstonyx* Remains (Suidae, Mammalia) from Northern

- China. *Geobios*, 37, 49–64.  
<http://dx.doi.org/10.1016/j.geobios.2003.01.007>
- Liu, T.S., Li, C.K. & Zhai, R.J. (1978) Pliocene vertebrates of Lantian, Shensi. *Professional Papers of Stratigraphy and Paleontology*, 7, 186–188.
- McKenna, M.C. & Bell, S.K. (1997) *Classification of Mammals Above the Species Level*. Columbia University Press, New York, 640 pp.
- Orliac, M.J. (2006) *Eurolistriodon tenarezensis* sp. nov. from Montréal-du-Gers (France): implication for the systematics of the European Listriodontinae (Suidae, Mammalia). *Journal of Vertebrate Paleontology*, 26, 967–980.  
[http://dx.doi.org/10.1671/0272-4634\(2006\)26\[967:etsnfm\]2.0.co;2](http://dx.doi.org/10.1671/0272-4634(2006)26[967:etsnfm]2.0.co;2)
- Orliac, M.J. (2009) A differentiation of bunodont Listriodontinae (Mammalia, Suidae) of Africa: new data from Kalodirr and Moruorot, Kenya. *Zoological Journal of the Linnean Society*, 157, 653–678.  
<http://dx.doi.org/10.1111/j.1096-3642.2008.00525.x>
- Orliac, M.J. (2013) The petrosal bone of extinct Suoidea (Mammalia, Artiodactyla). *Journal of Systematic Palaeontology*, 11, 925–945.  
<http://dx.doi.org/10.1080/14772019.2012.704409>
- Orliac, M.J., M.J., Antoine P.-O. & Duranthon, F. (2006) The Suoidea (Mammalia, Artiodactyla), exclusive of Listriodontinae, from the early Miocene of Béon 1 (Montréal-du-Gers, SW France, MN4). *Geodiversitas*, 28, 685–718.
- Orliac, M.J., M.J., Antoine P.-O. & Ducrocq, S. (2010) Phylogenetic relationships of the Suidae (Mammalia, Cetartiodactyla): new insights on the relationships within Suoidea. *Zoologica Scripta*, 39, 315–330.  
<http://dx.doi.org/10.1111/j.1463-6409.2010.00431.x>
- Pan, Y.R., Liu, J.H. & Dong, W. (2006) Artiodactyla. In: Qi, G.Q. & Dong, W. (Eds.), *Lufengpithecus huidienensis Site*. Science Press, Beijing, pp. 195–228.
- Passey, B.H., Ayliffe, L.K., Kaakinen, A., Zhang, Z.Q., Eronen, J., 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>
- Pearson, H.S. (1923) Some skulls of *Perchoerus* (*Thinohyus*) from the White River and John Day formations. *Bulletin of the American Museum of Natural History*, 48, 61–96.
- Pearson, H.S. (1927) On the skulls of Early Tertiary Suidae, together with an account of the otic region in some other primitive Artiodactyla. *Philosophical Transactions of the Royal Society, London, Series B*, 215, 389–462.
- Pearson, H.S. (1928) Chinese fossil Suidae. *Palaeontologia Sinica, Series C*, 5, 1–75.
- Pickford, M. (1986) A revision of the Miocene Suidae and Tayassuidae (Artiodactyla, Mammalia) of Africa. *Tertiary Research Special Paper*, 7, 1–83.
- Pickford, M. (1988) Revision of the Miocene Suidae of the Indian Subcontinent. *Münchener Geowissenschaftliche Abhandlungen, Reihe A, Geologie und Paläontologie*, 12, 1–91.
- Pickford, M. (1993) Old World Suid systematics, phylogeny, biogeography and biostratigraphy. *Paleontologia i Evolucio*, 26/27, 237–269.
- Pickford, M. & Liu, L.P. (2001) Revision of the Miocene Suidae of Xiaolongtan (Kaiyuan), China. *Bullettino della Società Paleontologica Italiana*, 40, 275–283.
- Schlosser, M. (1903) Die fossilen Säugethiere Chinas nebst einer Odontographie der recent Antilopen. *Abhandlungen der (königlich) Bayerischen Akademie der Wissenschaften*, 22, 89–92.
- Schmidt-Kittler, N. (1971) Die obermiozäne Fossilagerstätte Sandelzhausen 3. Suidae, Artiodactyla, Mammalia. *Mitteilungen der Bayerischen Staatssammlung für Paläontologie und historische Geologie*, 11, 129–170.
- Simpson, G.G. (1945) The principles of classification and a classification of mammals. *Bulletin of the American Museum of Natural History*, 85, 1–350.
- Tang, Y.J., Liu, Z.Q., Chen, D. & Chen, L.Q. (1985) The fossil Suidae from Late Miocene of Binxian, Shaanxi. *Vertebrata Palasiatica*, 23, 60–68.
- Thenius, E. (1969) Artiodactyla (Paarhufer). In: Thenius, E. (Ed.), *Phylogenie der Mammalia Stammesgeschichte der Säugetiere (einschließlich der Hominiden)*. Walter de Gruyter & Co, Berlin, pp. 415–442.
- van der Made, J. (1996) Listriodontinae (Suidae, Mammalia), their evolution, systematics and distribution in time and space. *Contribution to Tertiary and Quaternary Geology*, 33, 3–254.
- van der Made, J. (1997a) Systematics and stratigraphy of the genera *Taucanamo* and *Schizochœrus* and a classification of the Palaeochoeridae (Suoidea, Mammalia). *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen*, 100, 127–139.
- van der Made, J. (1997b) On *Bunolistriodon* (= *Eurolistriodon*) and *kubanochoeres*. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen*, 100, 141–160.
- van der Made, J. (2010) The pigs and “Old World peccaries” (Suidae and Palaeochoeridae, Suoidea, Artiodactyla) from the Miocene of Sandelzhausen (southern Germany): phylogeny and an updated classification of the Hyotheriinae and Palaeochoeridae. *Paläontologische Zeitschrift*, 84, 43–121.  
<http://dx.doi.org/10.1007/s12542-010-0051-3>
- van der Made, J. & Han, D.F. (1994) Suoidea from the Upper Miocene hominoid locality of Lufeng, Yunnan Province, China.

*Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen*, 97, 27–82.

- Viret, J. (1961) Artiodactyla. In: Piveteau, J. (Ed.), *Traité de Paléontologie*. Masson, Paris, pp. 887–930.
- Vislobokova, I.A. (2009a) A new species of *Megacerini* (Cervidae, Artiodactyla) from the Late Miocene of Taralyk-Cher, Tuva (Russia), and remarks on the relationships of the group. *Geobios*, 42, 397–410.  
<http://dx.doi.org/10.1016/j.geobios.2008.12.004>
- Vislobokova, I.A. (2009b) The first record of *Chleuastochoerus* (Suidae, Artiodactyla) in Russia. *Paleontological Journal*, 43, 686–698.  
<http://dx.doi.org/10.1134/s0031030109060136>
- Woodburne, M.O. (1968) The cranial myology and osteology of *Dicotyles tajacu*: the collared peccary, and its bearing on classification. *Memoirs of the Southern California Academy Sciences*, 7, 1–48.
- Wright, D.B. (1998) Chapter 26. Tayassuidae. In: Janis, C., Scott, K.M. & Jacobs, L.J. (Eds.), *Evolution of Tertiary Mammals of North America II*. Cambridge University Press, Cambridge, pp. 389–401.
- Young, C.C. & Liu, P.T. (1948) Note on a mammalian collection probably from the Yushe Series (Pliocene), Yushe, Shansi, China. *Contributions from the Institute of Geology*, 8, 273–291.
- Zhang, Z.Q. (2006) Chinese Late Neogene land mammal community and the environmental changes of East Asia. *Vertebrata Palasiatica*, 44, 133–142.

#### APPENDIX 1. List of the characters used in the data matrix.

1. Nasal bone—shape of the anterior part of the nasal bone: (0) long and sharp; (1) short and rounded. (Orliac *et al.* 2010, char 1; Orliac 2013, char 31)
2. Premaxilla—extension of the premaxilla anterior to the canine fossa: (0) weak; (1) important. (Orliac *et al.* 2010, char 2; Orliac 2013, char 32)
3. Premaxilla/Maxilla—relative width of the ante- and post- canine part of the palate: (0) ante-canine part slenderer than the postcanine part; (1) ante-canine part wider or of same width compared to the post-canine part. (Orliac *et al.* 2010, char 3; Orliac 2013, char 33)
4. Premaxilla/Maxilla—ante-canine constriction: (0) absent; (1) present. (Orliac *et al.* 2010, char 4; Orliac 2013, char 34)
5. Maxilla—canine niche: (0) absent; (1) present. (Orliac *et al.* 2006, char 37; Orliac *et al.* 2010, char 5; Orliac 2013, char 35)
6. Maxilla—canine niche, shape: (0) high, posterior face straight, and dorsal part close to the nasal lateral wall; (1) low, posterior face inflated, dorsal part far away from the lateral wall of the nasal. (Orliac *et al.* 2010, char 6; Orliac 2013, char 36)
7. Maxilla—*crista alveolaris*: (0) absent; (1) present. (Liu 2003, char 65; Orliac *et al.* 2010, char 7; Orliac 2013, char 37)
8. \*Maxilla—position of the upper canine: (0) at the posterior part of the alveolus (including canine niche or *crista alveolaris*); (1) in the middle; (2) at the anterior part.
9. Maxilla—position of the infraorbital foramen: (0) anterior to the level of P4; (1) at the level of the P4 or posteriorly to it. (Boisserie *et al.* 2005, char 10; Orliac *et al.* 2010, char 8; Orliac 2013, char 38)
10. Maxilla/lacrymal/jugal—preorbital fossa: (0) absent; (1) present. (Liu 2003, char 81; Orliac *et al.* 2010, char 9; Orliac 2013, char 39)
11. \*Maxilla/jugal—prezygomatic plate: (0) absent; (1) present.
12. Jugal/Squamosal—shape of the zygomatic arch: (0) constant height; (1) anterior part slenderer; (2) anterior part wider. (Orliac *et al.* 2010, char 10; Orliac 2013, char 40)
13. Jugal—prominence on the jugal: (0) absent; (1) present. (Gentry & Hooker 1988, char 69; Liu 2003, char 54; Orliac *et al.* 2010, char 11; Orliac 2013, char 41)
14. Jugal/lacrymal/frontal—location of the anterior border of the orbit: (0) anterior to the level of M3; (1) at the level of the M3 or posteriorly to it. (Liu 2003, char 71; Orliac *et al.* 2010, char 12; Orliac 2013, char 42)
15. Jugal—infraorbital fossa: (0) absent; (1) present. (Liu 2003, char 74; Orliac *et al.* 2010, char 13; Orliac 2013, char 43)
16. \*Lacrymal foramen: (0) one in each orbit; (2) two.
17. Frontal—prominence on the frontal: (0) absent; (1) present. (Liu 2003, char 61; Orliac *et al.* 2010, char; Orliac 2013, char 44)
18. Frontal/nasal—supraorbital sulcus, divergence: (0) anterior to the anterior margin of the orbit; (1) posterior to the anterior margin of the orbit. (Orliac *et al.* 2010, char 15; Orliac 2013, char 45)
19. Squamosal—articular joint height relative to the occlusal plane: (0) articular joint not elevated; (1) articular joint elevated above the occlusal plane. (Gentry & Hooker 1988, char 79; Liu 2003, char 58; Orliac *et al.* 2010, char 16; Orliac 2013, char 46)
20. Squamosal—suprameatic process: (0) absent; (1) present. (Gentry & Hooker 1988, char 70; Orliac *et al.* 2010, char 17; Orliac 2013, char 47)
21. Squamosal/jugal—posterior extension of the ventral margin of the jugal: (0) anterior to the glenoid surface; (1) posterior to the glenoid surface. (Boisserie *et al.* 2005, char 28; Orliac *et al.* 2010, char 18; Orliac 2013, char 48)
22. Maxilla/palatine—width of the palate at M2-3: (0) wide; (1) narrow. (Orliac *et al.* 2010, char 19; Orliac 2013, char 49)
23. Palatine—ectopterygoid crest of the palatine bone: (0) parallel and close to one another, their spacing being less than