# Chinese fossil Suoidea
## Systematics, Evolution, and Paleoecology

by

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*Academic dissertation*

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## Abstract

After nearly two centuries of accumulation, the collection of Chinese suoid fossils has become one of the best in the world. However, these fossils have not been well understood, and no comprehensive review of them has previously been undertaken.

New material from Guangxi, southern China includes the earliest fossil suoids known, and shows a surprising early diversity of this group. Altogether, five taxa are described from this collection. The presence of the earliest suid *Eocenchoerus* in this assemblage suggests that the origin of the Suidae is as early as that of the Tayassuidae. The earliest known tayassuid, an unidentified taxon from the same collection, supports the hypothesis that the New World tayassuids evolved from an Old World ancestor. Eocene suoids are now known both from southern China and from Thailand, suggesting that South Asia was the center of origin of suoids. The high diversity of late Eocene suoids indicates that the origin of the Suoidea was in the middle Eocene or earlier.

New material from the early Miocene of Shanwang helps to revise previously misidentified material, and establishes that the European genus *Hyotherium* was present in China, coexisting with *Sinapriculus*, a new genus, and with *Bunolistriodon*. New skull fossils from the late Miocene of the Hezheng area confirm the presence of *Microstonyx*, a typical European late Miocene suid. A review of the late Miocene suids from Xiaolongtan, southern China, reveals the presence of the European tetraconodont suid *Parachleuastochoerus* in the area.

A genus-level phylogenetic analysis of the Suoidea is undertaken. Twenty-eight genera are investigated, based on 82 characters. The strict consensus tree based on the 12 most parsimonious trees suggests a new classification of the Suoidea. The Tayassuidae and Suidae are two distinct groups and have been separated since the late Eocene. Unlike earlier suggestions in the literature, the primitive palaeochoerids and schizochoerids do not nest inside the Tayassuidae. The suggested Old World "tayassuids" are actually suids. Within the Suidae, five known subfamilies are well supported; Schizochoerinae, Listriodontinae, Kubanochoerinae, Tetraconodontinae, and Suinae. The subfamily Hyotheriinae could not be supported by any autapomorphy. The systematic positions of a few primitive suoids and suids remain unresolved.

A paleobiogeographically resolved range chart of 29 well-known taxa shows that China shares an unexpected number of suid genera with Europe. This is thought to reflect a free dispersal of land mammals between the two areas. The long-held belief in a close relationship between the suids of the Siwaliks and those of China was based on numerous misidentifications in previous studies.

Body mass analysis of Chinese suids of the middle and late Miocene indicates a stable environment in southern China, with small-sized suids suggesting a humid environment. In contrast, a sharp change is seen in northern China at about 8 Ma from arid to humid. This reversal is the opposite of that known from Europe, and is hypothesized to be the result of a regional development of the first summer monsoon system. This unexpected climatic trend in the latest Miocene of China was probably linked to a major phase of uplift in the Himalayas and the Tibetan plateau.

Key words: fossil Suoidea, systematics, biogeography, paleoecology, China

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**Reference**
**Papers I-VI**

## Original publications

This thesis is based on the following papers (I-VI), as well as some additional unpublished analyses:

I. Liu, L-P. 2001. Eocene suoids (Artiodactyla, Mammalia) from Bose and Yongle basins, China, and the classification and evolution of the Paleogene suoids. *Vertebrata PalAsiatica*, 39(2): 115-128.

II. Liu, L-P., M. Fortelius, and M. Pickford. 2002. New fossil Suidae from Shanwang, Shandong, China. *Journal of Vertebrate Paleontology*, 22(1): 152-163.

III. Pickford, M., and L-P. Liu. 2001. Revision of the Miocene Suidae of Xiaolongtan (Kaiyuan), China. *Bollettino della Società Paleontologica Italiana*, 40(2): 275-283.

IV. Liu, L-P., D. Kostopoulos, and M. Fortelius. Late Miocene *Microstonyx* reminds (Suidae, Artiodactyla) from Hezheng areas. *Geobios* (in press).

V. Zhang, Z-Q., A. Gentry, A. Kaakinen, L-P. Liu, J. P. Lunkka, Z-D. Qiu, S. Sen, R. Scott, L. Werdelin, S-H. Zheng, and M. Fortelius. 2002. Land mammal faunal sequence of the Late Miocene of China: new evidence from Lantian, Shaanxi Province. *Vertebrata PalAsiatica*, 40(3): 165-176.

VI. Fortelius, M., J. Eronen, J. Jernvall, L-P. Liu, D. Pushkina, J. Rinne, A. Tesakov, I. Vislobokova, Z-Q. Zhang, and L-P. Zhou. 2002. Fossil mammals resolve regional patterns of Eurasian climate change over 20 million years. *Evolutionary Ecology Research*, 4: 1005-1016.

# 1. Introduction

Compared to other mammalian fossils, such as primates, carnivores, proboscideans, horses, ruminants and rodents, suoids have received less attention from paleontologists, perhaps because their undifferentiated teeth make tooth-based species- or sometimes even genus-level identification difficult. Suoids have largely been ignored as stratigraphic indicators, with the notable exception of the Plio-Pleistocene of Africa, where the rapid evolution of grazing lineages offers a good biostratigraphic tool (Cooke and Wilkinson, 1978; Pickford, 1993). This lack of utilitarian interest is clearly indicated by the only comprehensive monograph published on fossil Suoidea (Stehlin, 1899-1900). There is, however, a body of continental or regional scale reviews from Europe (Pickford, 1993; Van der Made, 1996a, 1997a, 1997b), India (Pickford, 1988), and Africa (Pickford, 1986). As a country bearing rich and important fossils, China has not made its proper contribution to the knowledge of fossil Suoidea. This has been one of the most important reasons for me to choose this poorly resolved group as the topic of my PhD study. It is hoped that a review based on Papers I-VI and the new cladistic and body mass analyses herein will contribute to the understanding of systematics, biogeography and paleoecology of Chinese suoids.

### 1.2. Material

Most of the studied fossils are housed in the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP), Chinese Academy of Science, with the prefix "V" before specimen numbers (Papers I, II, III). The fossils described in Paper IV belong to the Hezheng Paleontology Museum, and specimen numbers are prefixed by "HMV". The comparative fossils from Europe and West Asia are studied from the personal cast collection of Prof. Mikael Fortelius and from the published literature, as indicated in the individual Papers.

Papers I, II, and IV describe new suid fossils from China. Paper III is a review of published material from southern China. My chief contributions to Paper V comprise collecting data and specimens in the field and studying the fossil material, especially of suids and equids. The analysis in Paper VI is based on the database "the Eurasian land mammal fossil database", which is coordinated by Prof. Mikael Fortelius. On behalf of IVPP and in collaboration with Dr. Zhang Zhaoqun, I have been responsible for compiling and updating the Chinese data.

# 2. The Suoidea

The Suoidea (pig-like animals) is a superfamily of the Artiodactyla (even-toed ungulates), which is further divided into four families Suidae (pigs), Tayassuidae (peccaries), Sanitheriidae (extinct) and Hippopotamidae (hippopotami) (McKenna and Bell, 1997). The sister relationship between Suidae and Tayassuidae is attested to on both morphological (Gentry and Hooker, 1988) and molecular grounds (Irwin and Arnason, 1994; Randi et al., 1996), but the closer relationships of Hippopotamidae and Sanitheriidae with suoids are in doubt. Van der Made (1999a) raised the Hippopotamidae to the superfamily Hippopotamoidea and moved it out of Suoidea, supporting the opinion of a closer relationship between hippopotami and anthracotherids (Colbert, 1935; Viret, 1961; Gentry and Hooker, 1988). Recently, molecular studies have indicated that hippopotami are embedded in a paraphyletic Artiodactyla, with cetaceans (whales and dolphins) as their sister clade (Irwin and Arnason, 1994; Randi et al., 1996; Nikaido et al., 1999). On the other hand, morphological phylogenetic studies are inconsistent with the hypothesis of a close relationship between hippopotami and cetaceans (Luckett and Hong, 1998; Luo and Gingerich, 1999; Thewissen et al., 2001). Although the taxonomic position of the hippopotami is still controversial, there is increasing accord that the Suoidea, including hippopotami, is a paraphyletic group. Opinions on the taxonomic position of sanitheres, another debated group, range from independent family status (Sanitheriidae; Pickford, 1993) to a genus of the Palaeochoerinae (Van der Made, 1997a). Acknowledging their uncertain status, and because neither group is represented in the fossil record of China, I exclude sanitheres and hippopotami from this work.

Pigs and peccaries occupy similar adaptive zones (sensu Simpson, 1944) in the Old and New World, respectively. The suoids are primarily omnivorous, and seem to be the most primitive living artiodactyls, retaining low-crowned cheek teeth with simple bunodont cusps, four distinct digits, separated foot bones, absence of frontal appendages, and a simple, non-ruminating stomach. Unlike the highly diverse ruminants, the suoids today form a small and simple group of artiodactyls, with only seven genera and 12 species worldwide (Table 1). Introduced to America, Australia, New Guinea and New Zealand by humans, the domestic pig (*Sus scrofa*) is one of the most common species of livestock in the world.

Table 1. The living suoids and their occurrences (Nowak, 1991; Macdonald, 1999).

| Family | Genus | Species | Main Distribution |
|---|---|---|---|
| Suidae | *Sus* | *S. scrofa* | Most of Eurasia , North Africa |
| | | *S. barbatus* | Malay Peninsula, Rhio Archipelago etc. |
| | | *S. celebensis* | Sulawesi and nearby small islands |
| | | *S. verrucosus* | Java, Madura and Bawean |
| | | *S. salvanius* | Himalayan foothills of Assam. |
| | *Potamochoerus* | *P. porcus* | Subsaharan Africa and Madagascar |
| | *Hylochoerus* | *H. meinertzhageni* | Central African Congo basin |
| | *Phacochoerus* | *P. aethiopicus* | Subsaharan Africa |
| | *Babyrousa* | *B. babyrussa* | Sulawesi, Togian,Sula and Bura islands |
| Tayassuidae | *Catagonus* | *C. wagneri* | Southern Bolivia, Paraguay, Northern Argentina |
| | *Tayassu* | *T. tajacu* | Arizona and Texas to N Argentina |
| | | *T. pecari* | SE Veracruz state, Mexico to N Argentina |

Perhaps reflecting their generalist adaptation and highly preservable and characteristic teeth, fossil suoids have a literature reading back to the early 19th century (e.g., Meisner, 1818; Cuvier, 1825; Clift, 1828; Croizet and Jobert, 1828). However, owing to a poor fossil record the early history of the group has remained obscure, and until the recent discoveries of Eocene suoid fossils from South Asia, the geological range of suoids was considered to be early Oligocene to Recent (Simpson, 1984). At present, the earliest known suoid fossils are from the late Eocene of China

(Tong and Zhao, 1986; Paper I) and Thailand (Ducrocq, 1994; Ducrocq et al., 1998). This very rare and incomplete material provides only a few pieces of the picture, but nonetheless opens an entirely new window on the early history of suoids (Ducrocq, 1994; Ducrocq et al., 1998; Paper I).

## 2.2. The history of Chinese fossil suoid research

The Chinese are among the earliest humans to have utilized mammalian fossils (dragon bone), a practice estimated to have begun as early as 500 B.C. Unfortunately, the scientific study of fossil suoids appeared quite late in China, and was originated by Europeans. W. Lockhart may have been the first to pay scientific attention to the Chinese dragon bone. He sent some mammalian fossils from Shanghai to England. When reported by a Mr. Davidson in 1853 in London, these Chinese mammalian fossils became known to the international scientific community (Schlosser, 1903). Koken (1885) is the first to have published a research paper dealing with Chinese suoid fossils. He studied mammalian fossils collected from China by German geographer and geologist Ferdinand von Richthofen during the 1870's. Two pig teeth, one M3 and a half m3, were recorded as *Sus* sp.. Later, Schlosser (1903) published his distinguished research based on Karl A. Haberer's Chinese collection assembled between 1899 and 1901. He is the first to have named Chinese suid fossil species, and of his nomina*, Sus. stehlini*, *S. hyotherioides*, *S. microdon*, and *S. giganteus*, the former two are still considered valid as *Chleuastochoerus stehlini, Hippopotamodon hyotherioides*, respectively. Purchased from pharmacy shops, the fossils recorded by Koken and Schlosser have no detailed locality information.

Beginning in 1918, mammalian fossils accumulated quickly through a series of systematic excavations in northern China (Qiu et al., 1987), resulting in the first period (1920s-1940s) of extensive research on Chinese suids. Classical works on Chinese suids appeared at this time, including the first monograph on Chinese fossil suoids (Pearson, 1928). Disrupted by the Japanese invasion (1937-1945), the research work stagnated and remained limited through the 1950s. From the 1960s, activities started anew, and the collections of fossil material increased rapidly. Suoid fossils have been found from the Eocene to the Pleistocene (Table 2), but most of the published studies are merely descriptions of new material. In recent years, a few studies have addressed systematic questions (Qiu et al., 1988; Van der Made, 1996a; Paper I), but all have been limited in scope.

Table 2. Summary of the study of Chinese suoid fossils (the Pleistocene suids are not reviewed or completely listed).

| Locality | Collection | Description/Discussion | Age | Age Reference |
|---|---|---|---|---|
| *Odiochoerus uniconus* Tong & Zhao, 1986 | | | | |
| Tianyang | GXM. F0844 | Tong & Zhao, 1986; Paper I | Late Bartonian | Tong et al., 1995 |
| *Siamochoerus viriosus* Liu, 2001 | | | | |
| Yongle | V7881,V7881.1 | Paper I | Late Bartonian | Tong et al., 1995 |
| *Huaxiachoerus guangxiensis* Liu, 2001 | | | | |
| Bose | V7883, V7883.1 | Paper I | Late Bartonian | Tong et al., 1995 |
| Tayassuidae gen. et sp. indet. | | | | |
| Bose | V7882 | Paper I | Late Bartonian | Tong et al., 1995 |
| *Eocenchoerus savagei* Liu, 2001 | | | | |
| Bose | V7884, V7885 | Paper I | Late Bartonian | Tong et al., 1995 |
| cf. *Hyotherium* sp. | | | | |
| Puzhen | V2690.1 | (Chow & Wang), 1964 | MN4 | Qiu & Qiu, 1990 |
| *Sinapriculus linquensis* Liu et al., 2002 | | | | |
| Shanwang | V11941 | Paper II | MN5 | Qiu & Qiu, 1990 |
| *Hyotherium shanwangense* Liu et al., 2002 | | | | |
| Shanwang | V11942.1-2 | Paper II | MN5 | Qiu & Qiu, 1990 |
| Shanwang | V4693 | (Chang),1974; Paper II | MN5 | Qiu & Qiu, 1990 |
| *Bunolistriodon* indet. | | | | |
| Shanwang | V4691.1-2 | (Chang),1974; Paper II | MN5 | Qiu & Qiu, 1990 |
| Dongshapo | V2804 | (Liu & Li), 1963a | MN6 | Liu & Li, 1963a |
| Guanghe | BPV 819, 1500-1502 & 1504 | Guan & Zhang, 1993 | MN6-8 | Guan & Van der Made, 1993 |
| Gen. et sp. indet. | | | | |
| Xiaodian | No specimen number | (Gu), 1980; Pickford, 1987; Qiu & Qiu, 1990 | MN5 | Qiu & Qiu, 1990 |
| *Bunolistriodon intermedius* Liu and Li, 1963b | | | | |
| Koujiacun | 59003 | Liu & Li, 1963b | MN6 | Qiu & Qiu, 1990 |
| Tongxin | V9519-9525 | Ye et al., 1992 | MN6 | Qiu & Qiu, 1990 |
| Tongxin | BPV1670, BPV928-930, 952 | Guan & Van der Made, 1993 | MN6 | Qiu & Qiu, 1990 |
| *Listriodon splendens* von Meyer, 1846 | | | | |
| Tunggur | AMNH 26504<br>AMNH 26517 | (Colbert), 1934; (Chen), 1986, Van der Made, 1996a | MN8 | Qiu & Qiu, 1990 |
| Lengshuigou | V3204, V3205, V3204.1-9, V3205.1-3, V3206 | (Li & Wu), 1978; (Chen), 1986; Van der Made, 1996a | MN7 | Qiu & Qiu, 1990 |
| Xin'an | V8283, V8282, V8284-8286 | (Chen), 1986; Van der Made, 1996a | MN7-8 | Chen, 1986 |
| Erlanggang | V5152.1-5, V5152.6-11 | (Yan), 1979; (Chen), 1986; (Van der Made, 1996a) | MN8 | Qiu & Qiu, 1990 |
| *Listriodon* sp. | | | | |
| Tongxin | No specimen number | Guan, 1988 | MN6 | Guan, 1988 |
| Guanghe | No specimen number | Guan, 1988 | MN6-8 | Guan &Van der Made, 1993 |
| *Kubanochoerus minheensis* Qiu et al., 1981 | | | | |
| Minghe | V6021, V6022 | Qiu et al., 1981; Qiu et al., 1988; Van der Made, 1996a | MN6-8 | Qiu & Qiu, 1990 |

| | | | | |
|---|---|---|---|---|
| *Kubanochoerus gigas* (Pearson), 1928 | | | | |
| Yongdeng | No specimen number | (Pearson), 1928; Qiu & Qiu, 1990; Van der Made, 1996a | MN8 | Qiu & Qiu, 1990 |
| Koujiacun | 59002, 59001 | (Liu & Li), 1963b; Guan & Van der Made, 1993 | MN6 | Qiu & Qiu, 1990 |
| Tongxin | V8501, V8502 | (Qiu et al.), 1988; Chen, 1986 | MN6 | Qiu & Qiu, 1990 |
| Tongxin | BPV901-911, BPV921-924, BPV1671 | Guan & Van der Made, 1993 | MN6 | Qiu & Qiu, 1990 |
| ?Shanxi | V2861.1-4, V2862, V2863 | (Liu & Li), 1963b | ? | Liu & Li, 1963b |
| Guanghe | BPV802 | Guan & Zhang, 1993 | MN6-8 | Guan &Van der Made, 1993 |
| Junggar | V8614 | Ye, 1989 | MN6-8 | Ye et al., 2000 |
| Tunggur | No specimen number | Qiu & Qiu, 1990 | MN8 | Qiu & Qiu, 1990 |
| *Miochoerus youngi* Chen, 1997 | | | | |
| Xin'an | V7235, V7235.1 | Chen, 1997 | MN7-8 | Chen, 1986 |
| *Propotamochoerus* cf. *palaeochoerus* | | | | |
| Lingyanshan | No specimen number | (Bi et al.), 1977 | MN8 | Qiu & Qiu, 1990 |
| *Parachleuastochoerus sinensis* Pickford & Liu, 2001 | | | | |
| Kaiyuan | V8092.1-7, V8093 | (Dong),1987; Paper III | MN9 | Paper III |
| *Propotamochoerus parvulus* (Chang), 1974 | | | | |
| Kaiyuan | V4690.1-2 | (Chang), 1974; (Dong),1987; Paper III | MN9 | Paper III |
| *Propotamochoerus hyotherioides* (Schlosser), 1903 | | | | |
| Shanxi? | No specimen number | (Schlosser), 1903; | ? | Pearson, 1928 |
| Baode & Yushe | No specimen number | (Pearson), 1928; | ? | Pearson, 1928 |
| Kaiyuan | V4691.1-3, V8092.3 | (Chang), 1974; (Dong),1987;(Paper III) | MN9 | Paper III |
| *Chleuastochoerus stehlini* (Schlosser), 1903 | | | | |
| Shanxi &Henan | No specimen number | (Schlosser), 1903 | MN12-13 | Paper IV |
| Baode, Jingle Wuxiang&Xin'an Qingyang | No specimsen number | Pearson, 1928 | MN12-13 | Paper IV |
| Yushe | V518 | Young & Peiho, 1948 | Pliocene | Young&Peiho,1948 |
| Lantian | V3090, V3171 | Liu et al.,1978;PaperV | MN12-13 | Paper V |
| Binxian | SV83007-83020 | Tang et al., 1985 | MN12-13 | Paper IV |
| *Microstonyx major* (Gervais), 1848-1952 | | | | |
| Shanxi, Henan | No specimen number | (Schlosser) 1903 | MN12-13 | Paper V |
| Shanxi | No specimen number | (Pearson) 1928 | MN12-13 | Paper V |
| Lantian | V3136 | (Liu et al.) 1978 | MN12-13 | Paper V |
| Binxian | SV83007-83006 | (Tang et al.) 1985 | MN12-13 | Paper V |
| Hezheng | HMV0976-0977<br>HMV1032-1033<br>HMV0567 | Paper IV | MN12-13 | Paper IV |
| *Yunnanochoerus lufengensis,* (Han), 1983 | | | | |
| Lufeng | V6891 | (Han), 1983<br>Van der Made & Han, 1994 | MN11 | Qiu and Qiu, 1990 |
| *Propotamochoerus wui* Van der Made & Han, 1994 | | | | |
| Lufeng | V9942.1, V9942 | Van der Made & Han, 1994 | MN11 | Qiu & Qiu, 1990 |
| Lufeng | V4493 | Van der Made & Han, 1994 | MN11 | Qiu & Qiu, 1990 |
| *Sus subtriquetra* Xue, 1981 | | | | |
| Youhe | 75Wei③1.1-1.3 | Xue, 1981 | MN15 | Qiu & Qiu, 1990 |

|  |  |  |  |  |
|---|---|---|---|---|
| *Potamochoerus chienxianensis* Li, 1963 |  |  |  |  |
| Qingxian |  | Li, 1963 | ? | Li, 1963 |
| *Sus xiaozhu* Han et al., 1975 |  |  |  |  |
| Liucheng | V5188 | Han et al., 1975 | Early Pleist. | Han et al., 1975 |
| Longgudong | V5107 | Xu et al., 1974 | Early Pleist. | Xu et al.,1974 |
| Dongpaoshan | BV011-015 | Wang et al., 1982 | Early Pleist. | Wang et al., 1982 |
| Liucheng | V5821 | Han, 1987 | Early Pleist. | Han, 1987 |
| Daxin | V6248 | Han, 1982 | Early Pleist. | Tong et al., 1995 |
| Wushan | CV937.1-15 | Huang & Fang, 1991 | Early Pleist. | Huang&Fang,1991 |
| *"Dicoryphochoerus" ultimus* Han, 1987 |  |  |  |  |
| Liucheng | V5819 | Han, 1987 | Early Pleist. | Han, 1987 |
| Wushan | CV936.1-3 | Huang & Fang, 1991 | Early Pleist. | Huang&Fang,1991 |
| *Sus bijiashanensis* Han et al., 1975 |  |  |  |  |
| Liuzhou | V5189<br>V6249 | Han et al., 1975;<br>Han, 1982 | Early Pleist. | Tong et al., 1995 |
| *Potamochoerus nodosarius* Han, 1987 |  |  |  |  |
| Liucheng | V5820 | Han, 1987 | Early Pleist. | Han, 1987 |
| *Sus liuchengensis,* Han, 1987 |  |  |  |  |
| Liucheng | V5823 | Han, 1987 | Early Pleist. | Han, 1987 |
| Wushan | CV938.1-26 | Huang & Fang, 1991 | Early Pleist. | Huang&Fang,1991 |
| *Sus houi* Qi et al., 1999 |  |  |  |  |
| Zuozhen | HZ 9-14 | Qi et al., 1999 | Pleistocene | Qi et al., 1999 |
| *Sus offecinalis* Koenigswald, 1933 |  |  |  |  |
| Unknown | No number | Koenigswald, 1933 | ? | Koenigswald, 1933 |
| *Sinohus minimus* Koenigswald, 1933 |  |  |  |  |
| Unknown | No number | Koenigswald, 1933 | ? | Koenigswald, 1933 |
| *Sus peii* Han, 1987 |  |  |  |  |
| Liucheng | V5189 | Han, 1987 | Early Pleist. | Han, 1987 |
| Wushan | CV939.1-33 | Huang & Fang, 1991 | Early Pleist. | Huang&Fang,1991 |
| *Sus australis* Han, 1987 |  |  |  |  |
| Liucheng | V5824 | Han, 1987; Xu et al., 1974 | Early Pleist. | Han, 1987 |
| Zuozhen | HZ1, HZ 6-8 | Qi et al., 1999 | Pleistocene | Qi et al., 1999 |
| *Sus jiaoshanensis* Zhao, 1980 |  |  |  |  |
| Wuming | GXM. F0133 | Zhao, 1980 | Early Pleist. | Tong et al., 1995 |
| *Sus lydekkeri* Zdansky, 1928 |  |  |  |  |
| Zhoukoudian 1 | No specimen number | Zdansky, 1928 | Mid. Pleist. | Tong et al., 1995 |
| Nihewan | No specimen number | Chardin & Piveteau, 1930 | Early Pleist. | Qiu & Qiu, 1990 |
| Zhoukoudian 1 | No specimen number | Young, 1932 | Mid. Pleist. | Tong et al., 1995 |
| Zhoukoudian 9 | No specimen number | Chardin, 1936 | Early Pleist. | Tong et al., 1995 |
| Zhoukoudian 13 | No specimen number | Chardin & Pei, 1941 | Mid. Pleist. | Tong et al., 1995 |
| *Sus scrofa* Serres, 1839 |  |  |  |  |
| Yuanmo | V4040 | You & Qi, 1973 | Early Pleist. | You & Qi, 1973 |
| Yanjinggou | No specimen number | Matthew & Granger, 1923 | Early Pleist. | Tong et al., 1995 |
| *Potamochoerus* sp. |  |  |  |  |
| Zuozhen | HZ 2-5 | Qi et al., 1999 | Pleistocene | Qi et al., 1999 |

## 3. Systematic paleontology

In contrast to extant suids and peccaries (tayassuids), two distinct groups differing either in teeth or cranial and postcranial morphology, the classification of fossil suoids has been debated for a long time. The key discrepancy lies in the taxonomic status of the primitive suoids, including "Palaeochoerinae". The dental characters used to define the

"Palaeochoerinae" are plesiomorphic (primitive), and equally support their assignment either to Tayassuidae (Van der Made, 1990; Van der Made and Han, 1994; Pickford, 1993) or to Suidae (Pickford, 1988). Another ambiguous group is the Old World Miocene taxa *Taucanamo, Schizochoerus* and *Yunnanochoerus.* They were generally considered to be peccaries rather than suids (Pickford, 1993; Van der Made, 1990; Van der Made and Han, 1994). However, other authors have realized that the differences between the primitive Old World "peccary" and the New World peccary are very clear. Dechaseaux (1959) compared the skull of the Old World taxon *Doliochoerus* (*Propalaeochoerus*) with the New World taxa *Perchoerus* and *Tayassu*, and rejected any close relationship. Tong and Zhao (1986) compared the dentition of the Old World "peccary" with the New World peccary and inferred that the Old World peccary-like suoids are not typical peccaries. Wright (1998) mentioned that the alliance between the Old World "tayassuids" and North American tayassuids is not based on synapomorphy. Recently, a resurrected family Palaeochoeridae was suggested to resolve the discrepancies (Van der Made, 1996b, 1997a), and the Old World *Taucanamo-Schizochoerus-Yunnanochoerus* group is included as a subfamily Schizochoerinae (Van der Made, 1997a). This classification seems to be a good way to avoid contradictions, but has not been demonstrated by a phylogenetic analysis.

## 3.2. Cladistic analysis

Gentry and Hooker (1988) undertook a phylogenetic analysis of fossil artiodactyls, but only dealt with family-level relationships among suoids. We (Paper II) also only focused on the inner relationships within the genus *Hyotherium.* A phylogenetic study of the relationships of Suoidea is therefore particularly desirable.

In order to test the validity of the current classification of the Suoidea (Van der Made, 1997a, 1997b), I herein analyze a data matrix that includes a variety of suoids. The analysis is run at the generic level for a manageable number of taxa. Genera with multiple species are defined by their most primitive member, but their advanced members are used to obtain more information if this is unavailable from the former. Since the postcranial material is extremely poor, the analysis is limited to dental and cranial characters. Twenty-eight genera are used in the analysis, with all suoids from China included, even those with very poor information, especially the Eocene genera that consist of only a few isolated teeth. Other suoids from Europe, America and South Asia are also selected to check their relationship with the Chinese suoids, but advanced suoids from Africa and the Siwaliks are not incorporated in this analysis because they do not affect the basal relationships. Three genera, *Diacodexis*, *Gobiohyus*, and *Archaeotherium*, were chosen to form the outgroups. They are all primitive artiodactyls and do not cluster within Suoidea (Gentry and Hooker, 1988), and moreover, are represented by relatively complete fossils. Furthermore, *Archaeotherium* belongs to the entelodonts, which was suggested to be the sister group of Suoidea by Gentry and Hooker (1988).

### 3.2.1 Taxa analyzed

Abbreviations
BNHM: Beijing Natural History Museum.

1) *Diacodexis*: The character states in our analysis are assigned according to Coombs & Coombs (1982), Thewissen et al. (1983), Krishtalka and Stucky (1985), Rose

(1982, 1996), and Stucky (1998). This genus has not been recorded from China. It is thought to be the oldest artiodactyl (Rose, 1996).

2) *Gobiohyus*: The type material is from Inner Mongolia (Matthew and Granger, 1925). It is a common member of the Chinese late Eocene fauna. Its character states are assigned from the following literature: Coombs & Coombs (1977), Coombs and Coombs (1982), Matthew and Granger (1925), Krishtalka and Stucky (1985).
3) *Archaeotherium*: An entelodont with peculiar processes on the skull and mandible. Isolated teeth are found from China. Its character states are based on Effinger (1998).
4) *Perchoerus*: The earliest peccary fossil found in North America. It is treated as the ancestor of the modern peccary (Woodburne, 1969). Scott (1940) and Pearson (1927) provided detailed descriptions.
5) *Tayassu*: Extant peccary from North America. Characters are according to Herring (1972) and personal observations from the IVPP living mammal collection.
6) *Egatochoerus*: A late Eocene suoid found in Thailand. Represented by few upper molars and a mandible (Ducrocq, 1994).
7) *Odiochoerus*: A monospecific genus based on a part of a mandible from the late Eocene of southern China (Tong and Zhao, 1986).
8) *Huaxiachoerus*: A monospecific genus from southern China named by myself (Paper I).
9) Gen. et sp. indet.: A single upper molar found in the late Eocene of southern China, and assigned to Tayassuidae (Paper I).
10) *Eocenchoerus*: An ambiguous suid collected from southern China (Paper I).
11) *Siamochoerus*: A genus with two species, found in Thailand (Ducrocq et al., 1998) and southern China (Paper I).
12) *Palaeochoerus*: A well-known European genus from the Oligocene. Hellmund (1992) recently contributed a review of the group.
13) *Taucanamo*: A European small suoid; Chen (1984), Pickford and Moyá-Solá (1994), Pearson (1927) (*Choerotherium* in Pearson's paper), and Fortelius et al. (1996) have discussed this taxon in-depth.
14) *Conohyus*: A well-recorded genus from the Siwaliks and Europe; the character states in my matrix basically follow Colbert (1933), Chen (1984), Pickford (1981), Van der Made (1999b), and Pearson (1927) (*Hyotherium simorrense* in her paper).
15) *Sinapriculus*: A genus with a single species recorded from northern China (Paper II).
16) *Hyotherium*: A multispecific genus found in Europe and China but not from the Siwaliks (Paper II). Hellmund (1991) and Pearson (1927) (the skull she assigned to *Palaeochoerus* from St. Gérand-le-Puy, belongs to *Hyotherium* (Hellmund, 1991)) provided detailed descriptions of the dental and skull.
17) *Listriodon*: A well-known lophodont suid from China and Europe. The character states are based on Chen (1984), Van der Made (1996a) and personal observations on the IVPP fossil collections.
18) *Bunolistriodon*: A sublophodont suid described by Pickford and Moyá-Solá (1995), Van der Made (1996a, 1997b), and Guan and Van der Made (1993).
19) *Kubanochoerus*: A giant suid found in Asia and Africa. Qiu et al. (1988), Van der Made (1996a, 1997b), and Guan and Van der Made (1993) made detailed descriptions. I have studied the fossil collection in IVPP and BNHM.

20) *Miochoerus*: A small suid from the Middle Miocene of China. It coexisted with Listriodon. Chen (1997) described a well-preserved mandible.
21) *Yunnanochoerus*: A suoid recorded from the late Miocene of southern China by Han (1983) and Van der Made and Han (1994).
22) *Schizochoerus*: The type species *S. vallesensis* is known from a variety of localities in Europe, mainly Spain (Crusafont and Lavocat, 1954). Pickford (1976) described a new species, *S. gandakasensis,* from the Potwar Plateau, Pakistan. My understanding of this genus is based on Pickford (1976, 1978), and Pickford and Ertürk (1979).
23) *Chleuastochoerus*: A well-known Chinese endemic suid from the Hipparion fauna. Pearson (1928) published a detailed study of this suid and the IVPP has rich collection of fossils of this suid.
24) *Parachleuastochoerus*: A suid once only known from Europe (Pickford, 1981), but recently is confirmed as occurring in southern China (Paper III).
25) *Microstonyx*: A large suid found in the Eurasian Hipparion fauna. Pearson (1928), Thenius (1972), Kostopoulos et al. (2001), Kostopoulos (1994), and Paper IV presented detailed comparisons and descriptions.
26) *Propotamochoerus*: A cosmopolitan taxon in the Old World; Van der Made et al. (1999), Hellmund (1995), Thenius (1972), and Pickford (1988) provided the skull and dental characters.
27) *Hippopotamodon*: A large-sized suid recorded from the Siwaliks. The character states listed are based on the studies of Pickford (1988) and I (Paper IV).
28) *Sus*: Extant suid living in the northern of Old World. Skulls are easily obtained from the IVPP collection.

### 3.2.2 Nomenclature for suoids and the data matrix:

The naming of the four main cusps of the molar follows Osborn's system. These are the protocone, paracone, metacone, and hypocone in the upper tooth and the protoconid, metaconid, hypoconid, and entoconid in the lower tooth (Osborn, 1907). The accessory cusplets follow the same system as I used in Paper II. The nomenclature for the cristae follow that of Coombs and Coombs (1977) (Figure 1). A total of 83 characters of the teeth and skull are included, and their states are as follows:

1. *Parastyle*: **(0)** absent; **(1)** present.
2. *Postprotocrista*: **(0)** present; **(1)** absent.
3. *Hypocone*: **(0)** absent; **(1)** metaconule and hypocone both present; **(2)** only one cusp in the hypocone position.
4. *Upper molar labial cusps connected by centrocrista*: **(0)** yes; **(1)** no.
5. *Labial cingulum on upper molar*: **(0)** strong; **(1)** weak; **(2)** absent.
6. *Lingual cingulum on upper molar*: **(0)** present; **(1)** absent.
7. *The protocone on molar*: **(0)** medially located; **(1)** shifting anteriorly but still posterior to the paracone; **(2)** as anterior as the paracone.
8. *Paraconule*: **(0)** a cusplet on the preprotocrista; **(1)** displaced toward protocone; **(2)** displaced toward anterior cingulum; **(3)** lost.
9. *The cusplet between the posterior main cusps on upper molar*: **(1)** absent; **(2)** present.
10. *Upper molar middle accessory cusp*: **(0)** absent; **(1)** a crest from the metaconule (hypocone); **(2)** incipient; **(3)** distinct; **(4)** disappear because of lophodont protocone and paracone.

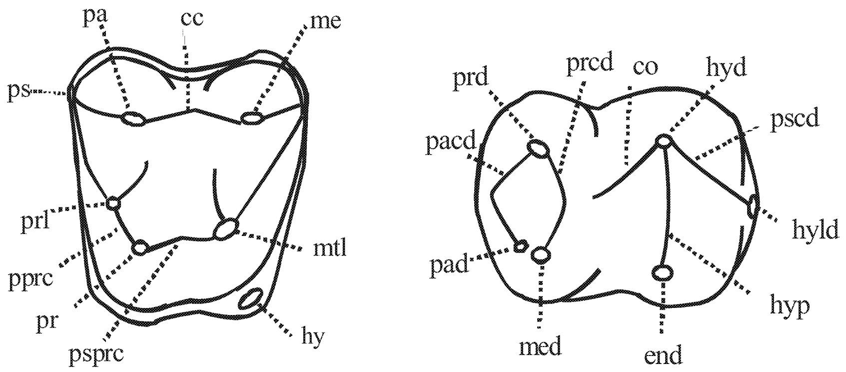

Figure1. Diagrammatic occlusal views of upper and lower molar of a composite early artiodactyl after Coombs and Coombs (1977). Abbreviations: cc-centrocrista, co-cristid obliqua, end-entoconid, hy-hypocone, hyd-hypoconid, hyp-hypolophid, hyld-hypoconulid, me-metacone, med-metaconid, met-metaconule, pa-paracone, pacd-paracrista, pad-paraconid, pprc-preprotocrista, pr-protocone, prcd-protocrista, prd-protoconid, prl-paraconule, ps-parastyle, pscd-postcristid, psprc-postprotocrista.

11. *The length of M3*: **(0)** shorter than that of M2; **(1)** longer than that of M2.
12. *Metacone on M3*: **(0)** smaller than other main cusps; **(1)** same size as other main cusps.
13. *Talon cusp (posterior accessory cusp) on M3*: **(0)** absent; **(1)** cingulum swells but without an obvious cusp; **(2)** a simple cusplet present; **(3)** complicated cusplets present.
14. *Talon cusp on M3*: **(1)** labially placed; **(2)** medially placed; **(3)** lingually placed.
15. *Hypoconule on M3*: **(0)** absent; **(1)** present.
16. *Morphological dissimilarity between the two anterior premolars and the two posterior ones*: **(0)** absent; **(1)** present; **(2)** strong.
17. *Hypocone on P4*: **(0)** absent; **(1)** incipient; **(2)** distinct.
18. *Metacone on P4*: **(0)** absent; **(1)** incipient; **(2)** as large as paracone.
19. *Paracone on P4*: **(0)** larger than protocone; **(1)** close to protocone; **(2)** smaller than protocone.
20. *Crest on the sagittal groove of P4*: **(0)** absent; **(1)** incipient; **(2)** well-developed crest.
21. *P4*: **(0)** bunodont; **(1)** sublophodont; **(2)** lophodont.
22. *P3 and P2 molarized*: **(0)** no; **(1)** yes.
23. *The upper canine*: **(0)** downward; **(1)** slightly splayed; **(2)** strongly splayed; **(3)** splayed upward.
24. *Sexual dimorphism of the upper canine*: **(0)** weak; **(1)** strong.
25. *The sexual bimodality of the upper canine*: **(0)** absent; **(1)** weak; **(2)** strong.
26. *I3*: **(0)** smallest; **(1)** largest; **(2)** absent.
27. *The two I1*: **(0)** form a v-shaped ridge; **(1)** form a straight transverse ridge.
28. *The I1*: **(0)** simple peg-like tooth; **(1)** with a lingual pillar.
29. *The I1*: **(0)** hypsodont; **(1)** brachydont.
30. *The i2*: **(0)** larger than i1; **(1)** similar to i1.
31. *The i3*: **(0)** smallest incisor; **(1)** largest incisor in mesiodistal length.
32. *Lower male canine*: **(0)** oval section; **(1)** verrucose section; **(2)** scrofic section.

33. *Lower male canine*: **(0)** rooted; **(1)** rootless.
34. *p1*: **(0)** present; **(1)** absent.
35. *p3 longer than m1*: **(0)** yes; **(1)** no.
36. *The talonid cusp on p3*: **(0)** absent; **(1)** incipient single cusplet; **(2)** distinct single cusplet; **(3)** two cusplets; **(4)** distinct and very high (hypoconulid almost to the height of main cusp).
37. *Hypertrophy of p3 and p4*: **(0)** absent; **(1)** weakly present; **(2)** strongly present.
38. *Entoconid in p4*: **(0)** absent; **(1)** present.
39. *p4 hypoconid*: **(0)** absent; **(1)** present but small; **(2)** distinct but low (below the half of main cusp's height); **(3)** distinct and very high (over half of the main cusp's height); **(4)** almost to the level of the main cusp.
40. *p4 metaconid*: **(0)** absent; **(1)** present but fused with protoconid; **(2)** separated from protoconid; **(3)** well separated from protoconid by deep groove.
41. *Entoconid on lower molar*: **(0)** small; **(1)** normal size as other main cusps.
42. *Paraconid on lower molar*: **(0)** distinct; **(1)** close to metaconid; **(2)** fused to metaconid.
43. *Paracristid*: **(0)** high; **(1)** low; **(2)** very low and week.
44. *Cristid obliqua*: **(0)** present; **(1)** absent.
45. *Hypoconid and entoconid*: **(0)** connected by hypolophid; **(1)** without hypolophid connection; **(2)** cusp with tendency to lophodonty; **(3)** cusp sublophodont; **(4)** cusp lophodont.
46. *Protoconid and metaconid*: **(0)** with protocristid connection; **(1)** without protocristid connection; **(2)** cusp with lophodont tendency; **(3)** cusp sublophodont; **(4)** cusp lophodont.
47. *Hypoconulid in lower molar*: **(0)** none; **(1)** incipient; **(2)** distinct.
48. *M3 hypoconid*: **(0)** present; **(1)** reduced.
49. *M3 elongation*: **(0)** third lobe single cusp; **(1)** third lobe single cusp with a hypoconulid between it and the rear cusp pair; **(2)** with elongate hypoconulid; **(3)** third lobe double cusps; **(4)** fourth lobe double cusps.
50. *Lower molar central accessory cusps*: **(0)** none; **(1)** incipient; **(2)** distinct.
51. *Lower molar anterior lobe higher than posterior*: **(0)** strongly present; **(1)** weakly present; **(2)** absent.
52. *Transverse valley on molar*: **(0)** narrow valley and shallow floor; **(1)** narrow valley and deep floor; **(2)** wide valley and deep floor.
53. *Posterior orbital bar*: **(0)** absent; **(1)** partly developed (with a long zygomatic process); **(2)** complete.
54. *Dentary and zygomatic protuberances*: **(0)** absent; **(1)** present.
55. *Tympanic process of squamosal dorsoventrally elongated and external auditory meatus dorsally opened*: **(0)** no; **(1)** yes.
56. *Ossified tympanic bulla*: **(0)** absent; **(1)** present.
57. *Tympanic bulla*: **(0)** vertical axis is not longer than other axis; **(1)** vertical axis is longer than other axis.
58. *Glenoid fossa level*: **(0)** near to the occlusal plane; **(1)** above palatine level.
59. *Angular process of mandible downturned*: **(0)** yes; **(1)** no.
60. *Sagittal crest on skull*: **(0)** sharp ridge; **(1)** absent but parietal crests close to each other; **(2)** absent and parietal crests well-separated; **(3)** parietal crests far-separated.
61. *Frontal horn in male*: **(0)** absent; **(1)** present.
62. *Orbital protuberance*: **(0)** absent; **(1)** present; **(2)** strong.

Figure 2. The strict consencus tree. Autapomorphies support the monophyletic groups as: 49:6(1),30(1), 33(1),42(2),55(1),56(1); 46:43(2); 45:17(1); 43:59(1); 42:19(2); 41:52(1); 40:52(2); 39:28(1),58(1),64(1), 76(1); 37:24(1),25(2),80(1); 36:7(2),15(1),81(1); 34:16(1),37(1); 33:12(1),20(1),65(1),74(2); 32:20(2), 57(1),68(3),69(1),72(1); 31:65(2),81(2); 30:27(1),29(1),68(1); 29:21(1); 28:61(1),62(2).

63. *Insicive foramen*: **(0)** open; **(1)** covered by nasal cavity.
64. *Posterior glenoid process*: **(0)** present; **(1)** absent.
65. *Upper canine alveolar crest*: **(0)** absent; **(1)** weak; **(2)** strong.
66. *Posterior palatine foramina*: **(0)** near the palato-maxillary suture; **(1)** forward to the level of P2.
67. *The facial part of the lacrimal*: **(1)** present; **(2)** absent.
68. *Lacrimal foramen*: **(1)** absent; **(2)** one; **(3)** two.
69. *Jugal process*: **(0)** short; **(1)** long and robust.
70. *"Furchen"*: **(0)** absent; **(1)** weak; **(2)** medium; **(3)** strong.
71. *The anterior border of orbit*: **(0)** before M3; **(1)** M3 level; **(2)** behind M3.
72. *The direction of jugal process*: **(0)** backward or downward; **(1)** forward.
73. *Prezygomatic shelf*: **(0)** absent; **(1)** weak; **(2)** medium and behind the infraorbital foramen; **(3)** extends over the infraorbital foramen; **(4)** extends over the canine.
74. *Fossa infraorbitalis*: **(0)** absent; **(1)** incipient; **(2)** obvious; **(3)** very deep.
75. *Diastemata inside tooth row*: **(0)** absent; **(1)** short; **(2)** long.
76. *Occipital condyles*: **(0)** around the palate level; **(1)** higher than palate level.
77. *Zygoma*: **(0)** no obvious laterally extended; **(1)** slight laterally extended; **(2)** strong laterally extended.
78. *Masseter fossa*: **(0)** limited to the angular process of the mandible; **(1)** extends forward to the middle of horizontal ramus.
79. *The process on the zygomatic arch*: **(0)** absent; **(1)** present.
80. *Pterygoid process*: **(0)** weak; **(1)** robust.
81. *Preorbital fossa*: **(0)** absent; **(1)** sallow; **(2)** deep.

The data matrix consists of 28 genera and 81 characters (Appendix 1). The phylogenetic relationships of suiforms is evaluated through MP procedures using the computer package PAUP 4.0* BETA5 (Swofford, 2000). All characters are unweighted and unordered. Maximum parsimony is the criterion to find the shortest trees. Addition sequence is random with the ALLSWAP option. Heuristic search (2000 replicates) finds 12 MP trees, which differ at three unresolved polychotomies. The first is the relationship between *Egatochoerus*, *Huaxiachoerus* and all other ingroup members; the second is the relationship between *Hyotherium*, *Sinapriculus,* and later “true suids”; and the third is the relationship between *Microstonyx*, *Propotamochoerus* and *Hippopotamodon*. The strict consensus tree of the 12 MP trees (Figure 2) rooted by outgroup, shows the following monophyletic lineages: a) the superfamily Suoidea (without considering sanitherids); b) the unidentified tayassuid found from China (Paper I) with the American *Perchoerus* and *Tayassu*; c) *Sinapriculus*, *Palaeochoerus* and all other old world true suids; d) *Taucanamo*, *Schizochoerus* and *Yunnanochoerus*; e) Tetraconodontinae with *Conohyus* and *Parachleuastochoerus*; f) Listriodotinae with *Listriodon* and *Bunolistriodon* ; g) Suinae, nesting *Chleuastochoerus*, *Sus*, *Microstonyx*, *Propotamochoerus*, and *Hippopotamodon*; e) Dicoryphochoerini grouping *Microstonyx*, *Propotamochoerus*, and *Hippopotamodon*. The description of the strict consensus tree based on the data matrix (Appendix I) is shown in Appendix II.

### 3.3. Suggested classification based on the cladistic analysis

The cladogram from the cladistic analysis supports the separation of Tayassuidae from palaeochoerids, but the palaeochoerids themselves do not form a monophyletic group. That means the Palaeochoeridae have no place in a natural classification, and thus, we have to caution against the use of the family Palaeochoeridae. *Schizochoerus*, *Taucanamo* and *Yunnanochoerus*, are distinct from the "true suids", but their close relationship with palaeochoerids (Van der Made, 1996b, 1997a) or Tayassuidae (Pickford, 1988; Pickford, 1993) is rejected. Instead, they are nested within the "true suids", so their taxonomic position needs to be reevaluated. *Taucanamo*, *Schizochoerus* and *Yunnanochoerus* form a monophyletic group. Van der Made (1997a) provided a subfamily name for this group, Schizochoerinae. I adopt this subfamily name in my classification, but put it inside Suidae rather than Palaeochoeridae or Tayassuidae (Table 3, Figure 2).

Table 3. A primary classification of Suoidea.

| Superfamily | Family | Subfamily | Genus |
|---|---|---|---|
| Suoidea | Indet. | | *Huaxiachoerus*<br>*Egatochoerus*<br>*Siamochoerus*<br>*Odiochoerus* |
| | Suidae | Indet. | *Eocenchoerus*<br>*Palaeochoerus*<br>*Sinapriculus*<br>*Hyotherium*<br>*Miochoerus* |
| | | Schizochoerinae | *Taucanamo*<br>*Schizochoerus*<br>*Yunnanochoerus* |
| | | Listriodontinae | *Listriodon*<br>*Bunolistriodon* |
| | | Kubanochoerinae | *Kubanochoerus* |
| | | Tetraconodontinae | *Conohyus*<br>*Parachleuastochoerus* |
| | | Suinae | *Chleuastochoerus*<br>*Microstonyx*<br>*Propotamochoerus*<br>*Hippopotamodon*<br>*Sus* |
| | Tayassuidae | | Gen. et sp. indet.<br>*Perchoerus*<br>*Tayassu* |

Most of the taxonomic classification of "true suids" is supported by my results except the subfamily Hyotheriinae. The Hyotheriinae of Van der Made (1997b), including *Aureliachoerus*, *Xenohyus*, *Hyotherium*, and *Chleuastochoerus*, is rejected, since *Chleuastochoerus* belongs to another monophyletic group. The Hyotheriinae as defined by Pickford (1993) to group *Aureliachoerus* and *Hyotherium*, could not be supported unambiguously, and there is no autapomorphy for *Hyotherium*. I leave it as an ambiguous genus inside Suidae. Listriodontinae is accepted, either with Kubanochoerini as a tribe (Van der Made, 1997b) or leaving this in a separate subfamily Kubanochoerinae (Pickford, 1993). I prefer the latter, because of the presence in Kubanochoerinae of unique autapomorphies, such as a frontal bone horn in the males and the strong orbital protuberance, which are not found in the Listriodontinae. Tetraconodontinae, not surprisingly, is a monophyletic group including *Conohyus* and *Parachleuastochoerus*. *Miochoerus* was suggested as the earliest suine (Chen, 1997). My cladogram does not confirm this hypothesis unconditionally, since *Miochoerus* lies outside the clade of Suinae and Tetraconodontinae, but there is also no robust reason to reject it (no autapomorphy for *Miochoerus*) either.

The current classifications, focusing on the systematic position of primitive suoids, are unacceptable. A primary classification (Table 3) based on the present phylogenetic analysis is proposed herein. In order to minimize modification to the current classifications, many taxa are treated as ambiguous (indet.) rather than members of new groups. Suoidea includes all the ingroup taxa, which are united by the absence of a lingual cingulum on the upper molars (6-1), i2 similar to i1 (30-1), rootless lower male canine (33-1), paraconid fused to metaconid (42-2), tympanic process of squamosal dorsoventrally elongated and external auditory meatus opening dorsally (55-1), and presence of ossified tympanic bulla (56-1). Inside Suoidea, *Huaxiachoerus*, *Egatochoerus*, *Siamochoerus* and *Odiochoerus* are placed in an unresolved group. *Perchoerus*, Tayassuidae indet. and *Tayassu* are placed in Tayassuidae, on the basis of the incipient metaconule in P4 (17-1). Suidae was expanded to include *Eocenchoerus* and Schizochoerinae, as defined by the absence of the angular process of the mandible (59-1). *Taucanamo*, *Schizochoerus* and *Yunnanochoerus* are grouped in the Schizochoerinae by their deep transverse valley floor of the molar (52-1). *Bunolistriodon* and *Listriodon* are grouped into the Listriodontinae by the sublophodont morphology of P4 (21-1), and Kubanochoerinae is defined by the presence of the frontal bone horn in males (61-1) and strong orbital protuberances (62-2). The Kubanochoerinae and Listriodontinae differ other suids by more characters, such as a branchydont I1 (29-1), a transverse ridge forming by two I1 (27-1), and the absence of a lacrimal foramen (68-1). *Conohyus* and *Parachleuastochoerus* share a morphological dissimilarity between the two anterior premolars and the two posterior ones (16-1), and the inflation of the main cusps of p3 and p4 (37-1), which are well-known unique characters for Tetraconodontinae. The larger subfamily Suinae consists of *Chleuastochoerus*, *Microstonyx*, *Hippopotamodon*, *Propotamochoerus* and *Sus*, united by an unreduced metacone on M3 (12-1), well developed crest on the sagittal groove of P4 (20-1), a more or less developed upper canine alveolar crest (65-1), and an obvious fossa infraorbitalis (74-2).

## 4. Biogeography

The study of Chinese suoids was once overly dependent on Pilgrim's (1926) influential early work on the Siwaliks, regarded as geographically close to the supposed origin, divergence and dispersion center of suoids (Pilgrim, 1925). The confusing wealth of synonyms that characterized Pilgrim's work (Pickford, 1988) and the fact that direct comparison of specimens was hardly ever possible added to the confusion. Before a series of recent review works (Papers II, III and IV), the fossil suoids of China were considered much more closely related to those of the Siwaliks than to those of Europe, a view that gave rise to many misidentifications conforming to this expectation. The relationship between European and Chinese suoids was, by a similar but opposite reasoning, considered distant and shared taxa were neither expected nor recognized.

A paleobiogeographically resolved range chart of 29 well-known taxa is shown in Figure 3. The Tayassuidae are represented only by an unidentified taxon from southern China. Although the hypothetical link between the unidentified taxon and living tayassuids is based on limited data, finding the origin of the Tayassuidae among primitive Old World suoids should not come as a surprise. *Eocenchoerus* clusters in the suids (Figure 2, Table 3), supporting the origin of the Suidae as early as the Bartonian (late Eocene) independently of the Tayassuidae (Paper I). Overall, southern China (South Asia) is the strongest candidate to be the center of origin of the Suoidea. Five primitive taxa reveal a diverse suoid fauna in the late Eocene, suggesting an origin in the middle Eocene or earlier (Paper I).

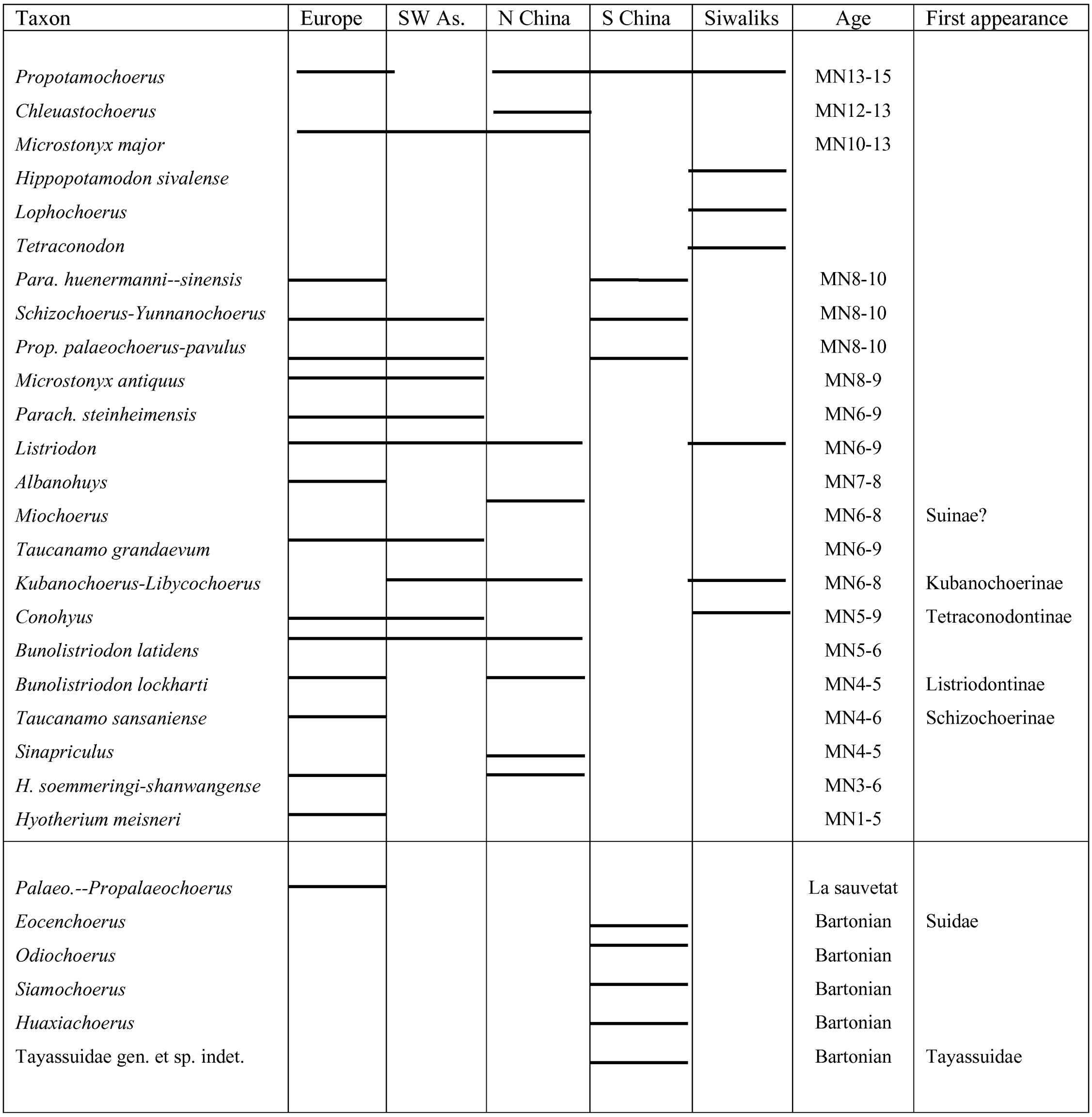

Figure 3. Chronological range chart of Eurasian Suoidea.

The small early-middle Miocene European suoids *Albanohyus* and *Taucanamo* are geographically distant from China and the Siwaliks, suggesting a European origin and dispersal to West Asia. Occurrences of *Hyotherium* and *Microstonyx* have recently been confirmed from China, but they seem to have been much rarer than in Europe and are absent from the Siwaliks (Paper II and IV), suggesting European origins for these taxa.

*Bunolistriodon, Listriodon* and *Kubanochoerus* are thought to be of African origin (Pickford, 1988), dispersing into China at the end of the early Miocene and having become dominant there in the middle Miocene (Paper II). The Tetraconodontinae (*Parachleuastochoerus*) seem to have dispersed to China from a European lineage. *Miochoerus*, is close to the ancestor of suines, indicating an early origin of the Suinae in China in the middle Miocene.

The geographic distributions of Eocene and Oligocene taxa, which are only found in a limited area, are difficult to assess, but indicate restriction of suoids at this time to tropical South Asia. Miocene suoids are well represented and more diverse in all the study areas (Figure 3). A total of 23 Miocene taxa are listed, 17 recorded in Europe, ten in West Asia, 13 in China, and six in the Siwaliks. Since ten taxa from China are also found in Europe, and seven in West Asia, west-east mammalian contact was obviously open, without major biogeographic barriers. Conversely, the fact that Siwalik taxa are not found in China, either in the north or south, except for the cosmopolitan *Propotamochoerus* and *Kubanochoerus* (including *Libycochoerus* of African origin; Van der Made, 1996a), suggest strong biogeographic isolation of the Siwaliks from China (Paper IV), and strengthen the case for isolation of southern China from the Siwaliks (Qiu and Qiu, 1990). Fossil suids show a relatively high diversity in southern China during the early late Miocene (Van der Made and Han, 1994; Paper III), in agreement with the tropical or subtropical forest environments indicated by micromammals (Qiu, 1995). In contrast, no fossil suids have been recovered from the synchronous (Bahean Land Mammal Age) mammalian assemblage of northern China (Paper V). The difference between the southern and northern China, shown both by suids and by other mammals (Qiu and Qiu, 1990; Qiu, 1995), indicates a strong ecological contrast between the two areas.

## 5. Suoid Paleoecology

Suoids constitute a relatively common and ecologically diverse group, and are characterized by broad dietary and environmental adaptations, so little can be concluded for a specific fossil taxon from comparison with living species, and taxon-based paleoecology has not been attempted for this group. Fortelius et al. (1996) introduced body mass as a criterion to study suoid paleoecology in relation to environmental change during the early and middle Miocene in Europe and West Asia. Their work showed that changes in suoid body mass matched general environmental trends recognized from other sources. They also showed that the timing of origination and extinction events was suggestively synchronous with known episodes of physical change (Fortelius et al., 1996). The robustness of the body mass analysis allows me to extend their discussion by adding data for Asian fossils. The result is compared with the analysis of Eurasian rainfall distribution using the hypsodonty proxy (Paper VI).

### 5.2. Body mass analysis of the Eurasian middle and late Miocene suids

In my analysis I exclude East Europe, and merge Central Europe with the similar but less well-sampled Southwestern Europe. I recognize four "provinces": (1) Main Europe (Central and Southwestern Europe); (2) West Asia (Anatolia, and Iran); (3) Northern China; (4) Southern China. The body sizes of suids found from the four provinces are estimated by their upper M2 length (Table 4), with the equation "body mass= $10^{1.08}\times(\mathrm{LM2})^{2.99}$" (Fortelius, 1990).

Based on Table 4, a size distribution and transformation figure (Figure 4) is constructed. Thirty taxa are divided into four classes (1-4). Fortelius et al. (1996) considered size classes 1 and 2 as predominantly associated with forest or closed environments and size classes 3 and 4 as associated mainly with open habitats.

Southern China has only a brief period with suoids and shows no major change in body size or diversity. Unlike other studied areas, it is the only province dominated by suoids of smaller size during early late Miocene (class 2), reflecting its relatively stable humid environment (Qiu, 1995) as opposed to the harsher and more arid conditions of most of Eurasia at the time (Fortelius et al., 1996; Paper VI).

Table 4. Body mass estimation of Eurasian middle and late Miocene suids, based on upper M2 length. (The numbers in parentheses are estimated from lower m2.)

| Taxon/Locality | Reference | N | LM2(mm) | Mass (kg) |
|---|---|---|---|---|
| Class 1: 1-20kg | | | | |
| *Albanohyus pygmaeus* (LaGrive) | Fortelius et al., 1996 | 4 | 9.2 | 9 |
| *Taucanamo grandaevum* (Steinheim) | Fortelius et al., 1996 | 4 | 9.9 | 11 |
| *Taucanamo sansaniense* (Sansan) | Fortelius et al., 1996 | 8 | 10.4 | 13 |
| *Taucanamo inonuensis* (Inönü I) | Fortelius et al., 1996 | 1 | 11.0 | 16 |
| “Gen. indet. cf. *Taucanamo* (Candir) | Fortelius et al., 1996 | 1 | (11) | 16 |
| Class 2: 21-80 kg | | | | |
| *Yunnanocherus* (southern China) | Han, 1983 | 1 | (13.3) | (28) |
| *Schizochoerus* sp. (lower Sinap) | Fortelius et al., 1996 | 1 | 14.7 | 37 |
| *Parachleuastochoerus* (various locs) | Fortelius et al., 1996 | 4 | 14.9 | 39 |
| *Chleuastochoerus* (northern China) | Pearson, 1928 | 18 | 16.3 | 51 |
| *Miochoerus youngi* (northern China) | Chen, 1997 | | (16) | (48) |
| *Propotamochoerus wui* (southern China) | Van der Made & Han, 1994 | 26 | 17.2 | 60 |
| *Hyotherium soemmeringi* (various locs) | Fortelius et al., 1996 | 9 | 17.5 | 63 |
| *Hyotherium shanwangense* (northern China) | Paper II | 2 | 16.9 | 56 |
| *Conohyus simorrensis* (various locs) | Fortelius et al., 1996 | 3 | 18.1 | 69 |
| *Parach. steinheimensis* (Steinheim & China) | Fortelius et al., 1996 | 2 | 18.4 | 73 |
| Class 3: 81-200kg | | | | |
| *Bunolistriodon* sp. nov. (Pasalar) | Fortelius et al., 1996 | 2 | 19.6 | 88 |
| *Listriodon* cf. *splendens* (Pasalar) | Fortelius et al., 1996 | 21 | 19.8 | 91 |
| *Listriodon xianensis* (northern China) | Chen, 1986 | 8 | 23.2 | 145 |
| *Bunolistriodon latidens* (Inönü) | Fortelius et al., 1996 | 2 | 21.4 | 110 |
| *Schizochoerus vallesiensis* (Middle Sinap) | Fortelius et al., 1996 | 1 | 21.7 | 120 |
| *Propo. palaeochoerus* (various locs) | Fortelius et al., 1996 | 21 | 22.0 | 120 |
| “*Postpotamochoerus*” (Samos) | Fortelius et al., 1996 | 1 | 23 | 140 |
| *Propo. provincialis* (various locs) | Fortelius et al., 1996 | | 23.9 | 160 |
| “Suinae sp.” (Karain) | Fortelius et al., 1996 | 1 | (25) | 180 |
| *Microstonyx major* (northern China) | Paper IV | 7 | 25.2 | 186 |
| Class 4: 201-1000kg | | | | |
| *Microstonyx major* (various locs) | Fortelius et al., 1996 | 12 | 30.5 | 330 |
| *Kubanochoerus robustus* (Belometchetskaia) | Fortelius et al., 1996 | 1 | 34.7 | 480 |
| *Hippopotamodon sivalense* (Siwaliks) | Pickford, 1988 | 6 | 35.3 | 510 |
| *Kubanochoerus khinzikebirus* (Inönü) | Fortelius et al., 1996 | 1 | 41.8 | 850 |

In contrast, northern China shows a sharp change between the middle and late Miocene. The suids suddenly change from dominance of large-sized species (class 3-4) to dominance of medium-sized species (class 2). Although the time of reversal of the trend cannot be provided by suoids, Paper V indicates a clear faunal change at about 8 Ma (the beginning of the late Miocene) in northern China, with replacement of the bovid- and horse-dominated Bahe fauna by the more diverse assemblage of the Baodean. Subsequently, northern China appears to have reverted to a condition characterized by high diversity and the occurrence of forest forms. This unexpected reversal, firstly discovered through our hypsodonty proxy (Paper VI), is fully supported by the medium-sized suid assemblage. We (Paper VI) have hypothesized that it could be explained as a regional effect of the intensification of the monsoon circulation suggested by Ding et al (1999) and An et al. (2001), thought to be directly linked to a major phase of uplift in the Himalayas (Amano and Taira, 1992) and the Tibetan Plateau (An et al., 2001).

The trends in northern China show further discrepancies from those of Europe and West Asia. In the middle Miocene, Europe and West Asia show only a minor decline in diversity, and are still dominated by small- to medium-sized suoids. Northern China, on the other hand, has hardly any small- to medium-sized suoids in the middle Miocene, indicating an earlier expansion of open country habitats at the beginning of the middle Miocene, some five million years before the abrupt decline of forest forms seen in Europe in the early late Miocene.

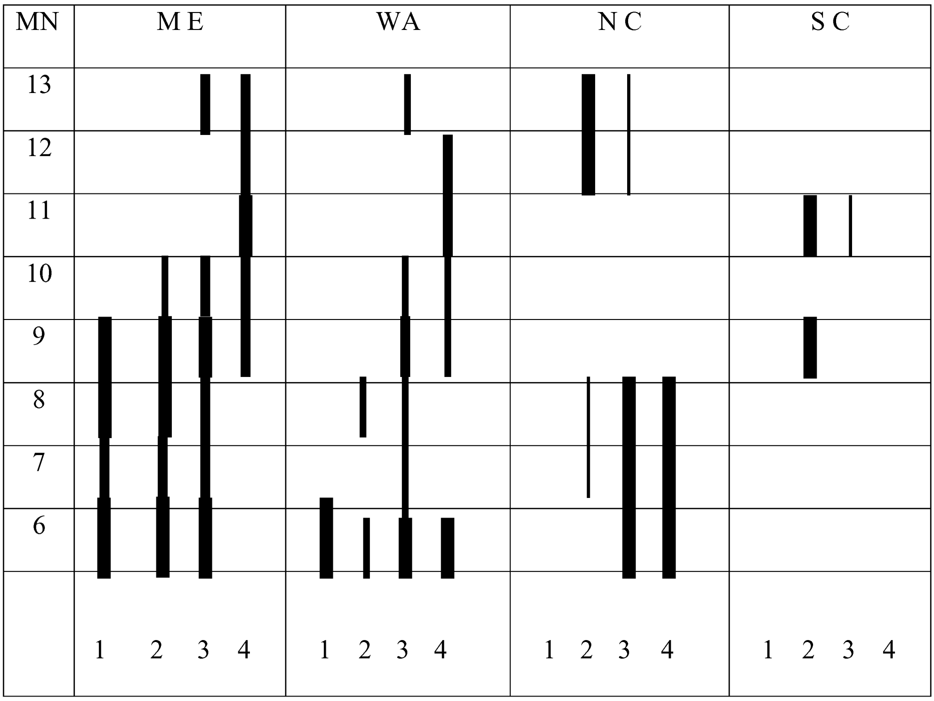

Figure 4. The suoid body mass (1-4 classes) change and their distribution during middle-late Miocene. ME= Main Europe; WA= West Asia; NC = Northern China; SC= Southern China.

## 6. Conclusions

I summarize my understanding of Chinese Suoidea as follows, based on the original papers and the further analysis introduced in this summary:

1) Suidae and Tayassuidae are two distinct groups, including fossil as well as living animals. Their earliest fossils, *Eocenchoerus* and Tayassuidae gen. et sp. indet. respectively, are found in southern China from strata correlated with the late Bartonian (late Eocene). (Paper I)

2) The diverse suoids from the late Eocene of South Asia (southern China and Thailand) suggests an origin of Suoidea in middle Eocene or earlier time in this region. (Paper I)

3) The phylogenetic analysis indicates that the Old World "palaeochoerids" or "tayassuids" from the Oligocene and Miocene of Eurasia are actually suids. The family Palaeochoeridae could not be supported. (Summary)

4) Suidae can be divided into five well-defined subfamilies: Schizochoerinae, Listriodontinae, Kubanochoerinae, Tetraconodontinae, and Suinae. The systematic position of a few primitive taxa remains unresolved. (Summary)

5) The expected close relationship between the Siwaliks and China must be rejected after a series of review works. The similarity between European and Chinese suid assemblages instead indicates free communication between these regions. A strong ecological contrast is seen between southern and northern China. (Papers II, III, IV)

6) Comparison of suid body mass change and distribution shows that southern China retained a relatively stable humid environment when most of Eurasia changed to harsher and more arid conditions during the late Miocene. (Summary)

7) An expansion of open habitats in northern China at the beginning of the middle Miocene occurred 5Ma earlier than in Europe and West Asia, as indicated by dominance of suids of large size. (Summary)

8) A continuous rock sequence in the Bahe formation indicates a sharp faunal change at 8 Ma, which conforms to a reversal of the body size of suids from large to medium. (Paper V, Summary)

9) The obvious decrease of suoid body mass in the later late Miocene of northern China supports a reversal to more humid conditions, and is thought to present a regional effect of the intensification of the summer monsoon. Both the global aridity and the regional humidity in China are thought to directly link to a major phase of uplift in the Himalayas and the Tibetan Plateau. (Summary, Paper VI)

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Appendix 1: The data matrix used in the cladistic analysis.

| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 31 | 32 | 33 | 34 | 35 | 36 | 37 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Diacodexis* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | - | 0 | 0 | 0 | 0 | - | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Gobiohyus* | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 2 | 0 | 1 | 0 | 0 | - | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | ? | ? | ? | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Archaeotherium* | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | - | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | ? | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Egatochoerus* | 0 | 1 | 2 | 0 | 1 | 1 | 1 | 1 | 2 | 1 | ? | ? | ? | ? | ? | 0 | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | 1 | ? | 1 | 1 | 1 | 0 |
| *Odiochoerus* | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | 0 |
| Tayassuidae indet. | 0 | 1 | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| *Huaxiachoerus* | 0 | 1 | 2 | 0 | 1 | 1 | 1 | 1 | 2 | 0 | 0 | 0 | 0 | - | 0 | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| *Siamochoerus* | 0 | 1 | 2 | 1 | 1 | 1 | 1 | 1 | ? | 0 | 1 | 0 | 0 | - | 0 | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | 1 | 0 | 0 |
| *Eocenchoerus* | 0 | 1 | 2 | 1 | 2 | 1 | 1 | 1 | 2 | 0 | 1 | 0 | 2 | 1 | 0 | ? | 0 | 0 | 1 | 0 | 0 | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| *Perchoerus* | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | - | 0 | 0 | 1 | 2 | 1 | 0 | 0 | 3 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | ? | 0 | 1 | 1 | 0 |
| *Tayassu* | 0 | 1 | 2 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 0 | 0 | 0 | - | 0 | 0 | 2 | 2 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 2 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 3 | 0 |
| *Palaeochoerus* | 0 | 1 | 2 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 1 | 0 | 0 | - | 0 | 0 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 0 |
| *Sinapriculus* | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | 0 | ? | ? | ? | ? | 0 | 0 | ? | ? | ? | ? | ? | ? | 0 | 1 | 0 | ? | ? | 0 | 0 | 1 | 0 |
| *Hyotherium* | 0 | 1 | 2 | 1 | 1 | 1 | 1 | 2 | 2 | 2 | 1 | 0 | 2 | 1+2+3 | 0 | 0 | 0 | 1 | 2 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 2 | 1 | 0 | 1 | 1 | 0 |
| *Kubanochoerus* | 0 | 1 | 2 | 1 | 1 | 1 | 1 | 2 | 2 | 3 | 1 | 0 | 1 | 3 | 0 | 0 | 0 | 1 | 2 | 0 | 0 | 0 | 2 | 1 | 2 | 0 | 1 | 1 | 1 | 1 | 0 | 2 | 1 | 0 | 1 | 1 | 0 |
| *Bunolistriodon* | 0 | 1 | 2 | 1 | 1 | 1 | 1 | 3 | 2 | 3 | 1 | 0 | 1 | 3 | 0 | 0 | 0 | 1 | 2 | 0 | 1 | 0 | 2 | 1 | 2 | 0 | 1 | 1 | 1 | 1 | 0 | 2 | 1 | 0 | 1 | 1 | 0 |
| *Listriodon* | 0 | 1 | 2 | 1 | 1 | 1 | 1 | 3 | 2 | 4 | 1 | 0 | 1 | 3 | 0 | 0 | 0 | 2 | 2 | 0 | 2 | 0 | 2 | 1 | 2 | 0 | 1 | 1 | 1 | 1 | 0 | 2 | 1 | 1 | 1 | 1 | 0 |
| *Miochoerus* | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | 0 | ? | ? | ? | ? | ? | 0 | ? | ? | ? | ? | ? | ? | 0 | 1 | 0 | ? | ? | 0 | 1 | 2 | 0 |
| *Conohyus* | 0 | 1 | 2 | 1 | 1 | 1 | 2 | 2 | 2 | 3 | 1 | 0 | 2 | 2 | 1 | 2 | 0 | 1 | 2 | 0 | 0 | 0 | 1 | 1 | 2 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 2 | 2 |
| *Parachleuastochoerus* | 0 | 1 | 2 | 1 | 1 | 1 | 2 | 2 | 2 | 3 | 1 | 0 | 2 | 2 | 1 | 1 | 0 | 1 | 2 | 0 | 0 | 0 | 1 | 1 | 2 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 2 | 1 |
| *Taucanamo* | 0 | 1 | 2 | 1 | 1 | 1 | 1 | 1 | 2 | 2 | 1 | 0 | 2 | 2 | 0 | 0 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | ? | ? | ? | 0 | 1 | 1 | 0 | 1 | 0 | 0 |
| *Schizochoerus* | 0 | 1 | 2 | 1 | 1 | ? | 1 | 2 | 2 | 2 | 1 | 0 | 2 | 2 | 0 | 0 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | ? | ? | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 0 |
| *Yunnanochoerus* | 0 | 1 | 2 | 1 | ? | 1 | ? | 2 | 2 | 2 | ? | 0 | 2 | 2 | 0 | 0 | ? | ? | ? | ? | ? | 0 | ? | ? | ? | ? | ? | ? | ? | ? | ? | 1 | 1 | 0 | ? | 0 | 0 |
| *Chleuastochoerus* | 0 | 1 | 2 | 1 | 1 | 1 | 2 | 2 | 2 | 3 | 1 | 1 | 2 | 3 | 1 | 0 | 0 | 2 | 2 | 1 | 0 | 0 | 1 | 1 | 2 | 0 | 0 | 1 | 0 | 1 | 0 | 2 | 1 | 0 | 1 | 2 | 0 |
| *Propotamochoerus* | 0 | 1 | 2 | 1 | 2 | 1 | 2 | 2 | 2 | 3 | 1 | 1 | 2 | 3 | 1 | 0 | 0 | 2 | 2 | 2 | 0 | 0 | 2 | 1 | 2 | 0 | 0 | 1 | 0 | 1 | 0 | 2 | 1 | 0 | 1 | 2 | 0 |
| *Microstonyx* | 0 | 1 | 2 | 1 | 2 | 1 | 2 | 2 | 2 | 3 | 1 | 1 | 2 | 3 | 1 | 0 | 0 | 2 | 2 | 2 | 0 | 0 | 1 | 1 | 2 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 2 | 0 |
| *Hippopotamodon* | 0 | 1 | 2 | 1 | 2 | 1 | 2 | 2 | 2 | 3 | 1 | 1 | 2 | 3 | 1 | 0 | 0 | 2 | 2 | 2 | 0 | 0 | 2 | 1 | 2 | 0 | 0 | 1 | 0 | 1 | 0 | 2 | 1 | 0 | 1 | 2 | 0 |
| *Sus* | 0 | 1 | 2 | 1 | 2 | 1 | 2 | 2 | 2 | 3 | 1 | 1 | 3 | 3 | 1 | 0 | 0 | 2 | 2 | 2 | ? | 0 | 3 | 1 | 2 | 0 | 0 | 1 | 0 | 1 | 0 | 2 | 1 | 0 | 1 | 4 | 0 |

| 38 | 39 | 40 | 41 | 42 | 43 | 44 | 45 | 46 | 47 | 48 | 49 | 50 | 51 | 52 | 53 | 54 | 55 | 56 | 57 | 58 | 59 | 60 | 61 | 62 | 63 | 64 | 65 | 66 | 67 | 68 | 69 | 70 | 71 | 72 | 73 | 74 | 75 | 76 | 77 | 78 | 89 | 80 | 81 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | - | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | ? | ? | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | - | ? | 0 | ? | 0 | 0 | 0 | 0 | 0 | 0 | ? | ? | 0 | 0 | 0 | 0 | 0 | 0 | 1 | ? | 0 | 0 | 0 | 0 | 0 |
| 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | - | 0 | 0 | 0 | 2 | 1 | 0 | 0 | - | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | ? | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 |
| 0 | 2 | 1 | 1 | ? | ? | ? | ? | ? | ? | 0 | 0 | 0 | ? | 0 | ? | ? | ? | ? | ? | ? | 0 | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | 0 | ? | ? | ? | 0 | 0 | ? | ? | ? | ? | ? | ? |
| 0 | 2 | 0 | 1 | 2 | 1 | 0 | 1 | 0 | 2 | 0 | ? | 1 | 1 | 0 | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | 0 | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | 0 | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | 0 | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | 0 | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | 0 | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| 0 | 2 | 1 | 1 | 2 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | 0 | ? | ? | ? | 0 | ? | ? | ? | ? | ? | ? | ? |
| ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | 0 | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | 0 | ? | ? | ? | 0 | ? | ? | ? | ? | ? | ? | ? |
| 0 | 2 | 3 | 1 | 2 | 2 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | ? | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 1 | 3 | 3 | 1 | 2 | 2 | 0 | 1 | 1 | 2 | 0 | 1 | 1 | 2 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 2 | - | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 2 | 1 | 1 | 2 | 2 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | ? | 0 | 0 | ? | ? | 0 | 0 | 0 | 0 | 0 | 0 | 0 | ? | 0 | 0 | 0 | ? | 0 |
| 0 | 2 | 1 | 1 | 2 | 2 | 1 | 1 | 1 | 2 | 0 | 1 | 1 | 1 | 0 | ? | 0 | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | 1 | ? | ? | ? | 0 | 1 | ? | ? | 0 | ? | ? | ? |
| 0 | 2 | 1 | 1 | 2 | 2 | 1 | 1 | 1 | 2 | 0 | 1 | 2 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 2 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| 0 | 3 | 1 | 1 | 2 | 2 | 1 | 1 | 1 | 2 | 0 | 1 | 2 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 2 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 2 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 |
| 0 | 3 | 2 | 1 | 2 | 2 | 1 | 3 | 3 | 2 | 0 | 1 | 2 | 1 | 0 | 0 | 0 | 1 | 1 | ? | ? | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | ? | 1 | ? | 0 | 1 | ? | ? | 1 | 1 | ? | 0 | 0 | 0 | ? | 0 |
| 0 | 3 | 2 | 1 | 2 | 2 | 0 | 4 | 4 | 2 | 0 | 1 | 2 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 2 | 2 | 1 | 0 | 0 | 0 | 1 | 0 |
| 0 | 3 | 1 | 1 | 2 | 2 | 1 | 1 | 1 | 2 | 0 | 1 | 2 | 2 | 0 | ? | 0 | ? | ? | ? | ? | 1 | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | 1 | ? | ? | ? | 0 | 0 | ? | ? | ? | ? | ? | ? |
| 0 | 3 | 0 | 1 | 2 | 2 | 1 | 1 | 1 | 2 | 0 | 1 | 2 | 2 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 2 | 0 | 2 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | ? |
| 0 | 3 | 1 | 1 | 2 | 2 | 1 | 1 | 1 | 2 | 0 | 1 | 2 | 2 | 0 | ? | 0 | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | 2 | ? | ? | ? | 0 | 1 | ? | ? | ? | ? | ? | ? |
| 0 | 2 | 1 | 1 | 2 | 2 | 0 | 2 | 2 | 1 | 0 | 1 | 1 | 2 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | ? | ? | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 2 | 1 | 1 | 2 | 2 | 0 | 3 | 2 | 1 | 0 | 1 | 0 | 2 | 2 | ? | 0 | ? | ? | ? | ? | ? | ? | ? | ? | 0 | ? | 0 | 0 | ? | ? | ? | 0 | ? | ? | ? | 0 | 1 | ? | ? | ? | ? | ? | ? |
| ? | ? | ? | 1 | 2 | 2 | 0 | 3 | 2 | 1 | 0 | 1 | 0 | 2 | 2 | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | 0 | ? | ? | ? | 0 | 1 | ? | ? | ? | ? | ? | ? |
| 0 | 3 | 1 | 1 | 2 | 2 | 1 | 1 | 1 | 2 | 0 | 2 | 2 | 2 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 1+2 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 2 | 0 | 2 | 1 | 0 | 2 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 1 |
| 0 | 3 | 1 | 1 | 2 | 2 | 1 | 1 | 1 | 2 | 0 | 3 | 2 | 2 | 0 | 0 | 0 | 1 | 1 | ? | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 2 | 0 | 1 | 3 | 1 | 2 | 1 | 1 | 2 | 0 | 0 | 1 | 2 | 0 | 0 | 1 | 2 |
| 0 | 3 | 1 | 1 | 2 | 2 | 1 | 1 | 1 | 2 | 0 | 3 | 2 | 2 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 3 | 0 | 0 | 0 | 1 | 2 | 0 | 1 | 3 | 1 | 2 | 2 | 1 | 3 | 0 | 2 | 1 | 2 | 0 | 0 | 1 | 2 |
| 0 | 3 | 1 | 1 | 2 | 2 | 1 | 1 | 1 | 2 | 0 | 3 | 2 | 2 | 0 | 0 | 0 | 1 | 1 | ? | 1 | 1 | 3 | 0 | 0 | 0 | 1 | 2 | 0 | ? | ? | ? | 2 | 1 | 1 | 1 | 0 | 1 | ? | 1 | 0 | 0 | 1 | 2 |
| 0 | 4 | 1 | 1 | 2 | 2 | 1 | 1 | 1 | 2 | 0 | 3+4 | 2 | 2 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 2 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 3 | 1 | 3 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 |

# Appendix 2: The description of the strict consensus tree.

```
P A U P *
Version 4.0b10 for 32-bit Microsoft Windows

Data matrix has 28 taxa, 81 characters
Valid character-state symbols: 0123456
Missing data identified by '?'
Gaps identified by '-'

>Heuristic search completed
>   Total number of rearrangements tried = 207522393
>   Score of best tree(s) found = 206
>   Number of trees retained = 12
>   Time used = 00:13:48.0

Tree description:

  Unrooted tree(s) rooted using outgroup method
  Optimality criterion = parsimony
    Character-status summary:
      Of 81 total characters:
        All characters are of type 'unord'
        All characters have equal weight
        18 characters are parsimony-uninformative
        Number of parsimony-informative characters = 63
    Gaps are treated as "missing"
    Multistate taxa interpreted as uncertainty
    Character-state optimization: Accelerated transformation (ACCTRAN)

Strict consensus tree (rooted using default outgroup)

Tree length = 200
Consistency index (CI) = 0.7100
Homoplasy index (HI) = 0.2900
CI excluding uninformative characters = 0.6723
HI excluding uninformative characters = 0.3277
Retention index (RI) = 0.8098
Rescaled consistency index (RC) = 0.5750

Character change lists:

Character                   CI  Steps                Changes
------------------------------------------------------------------------------

1 (parastyle)           1.000      1          node_51 0 ==> 1 Gobiohyus
2 (postprotocrista)     1.000      1          node_51 0 ==> 1 node_50
3 (hypocone)            0.667      1          node_51 0 --> 1 node_50
                                   1          node_50 1 --> 2 node_49
```

```
                                   1         node_44 2 ==> 1 Perchoerus
4 (upper molar labial ) 0.500      1         node_50 0 ==> 1 Archaeotherium
                                   1         node_49 0 ==> 1 node_48
5 (labial cingulum on ) 0.667      1         node_50 0 ==> 1 node_49
                                   1         node_43 1 ==> 2 Eocenchoerus
                                   1         node_33 1 ==> 2 node_32
6 (lingual cingulum on) 1.000      1         node_50 0 ==> 1 node_49
7 (the protocone on mo) 1.000      1         node_51 1 ==> 0 Diacodexis
                                   1         node_37 1 --> 2 node_36
8 (paraconule)          0.750      1         node_51 0 ==> 1 node_50
                                   1         node_39 1 ==> 2 node_38
                                   1         node_30 2 ==> 3 node_29
                                   1         node_41 1 ==> 2 node_40
9 (the cusplet between) 0.500      1         node_50 2 ==> 1 Archaeotherium
                                   1         node_45 2 ==> 1 node_44
10 (upper molar middle) 0.667      1         node_43 0 ==> 2 node_42
                                   1         node_39 2 ==> 1 Palaeochoerus
                                   1         node_38 2 ==> 3 node_37
                                   1         node_29 3 ==> 4 Listriodon
                                   1         node_46 0 ==> 1 node_45
                                   1         node_49 0 ==> 1 Egatochoerus
11 (The length of M3)   0.333      1         node_51 0 ==> 1 Gobiohyus
                                   1         node_49 0 --> 1 node_48
                                   1         node_46 1 --> 0 node_45
12 (metacone on M3)     1.000      1         node_35 0 ==> 1 node_33
13 (talon cusp on M3)   0.750      1         node_46 0 ==> 2 node_43
                                   1         node_39 2 ==> 0 Palaeochoerus
                                   1         node_37 2 ==> 1 node_30
                                   1         node_32 2 ==> 3 Sus
14 (talon cusp on M3)   0.667      1         node_43 1 --> 2 node_42
                                   1         node_42 2 --> 3 node_39
                                   1         node_35 3 --> 2 node_34
15 (Hypoconule on M3)   1.000      1         node_37 0 --> 1 node_36
16 (heteromorphy betwe) 1.000      1         node_35 0 --> 1 node_34
                                   1         node_34 1 --> 2 Conohyus
17 (metaconule in P4)   1.000      1         node_46 0 --> 1 node_45
                                   1         node_45 1 --> 2 Tayassu
18 (metacone on P4)     0.500      1         node_43 0 ==> 1 node_42
                                   1         node_29 1 ==> 2 Listriodon
                                   1         node_35 1 ==> 2 node_33
                                   1         node_46 0 ==> 2 node_45
19 (paracone on P4)     1.000      1         node_51 0 ==> 1 node_50
                                   1         node_43 1 ==> 2 node_42
20 (crest on the saggi) 1.000      1         node_35 0 --> 1 node_33
                                   1         node_33 1 --> 2 node_32
21 (P4)                 1.000      1         node_30 0 --> 1 node_29
                                   1         node_29 1 --> 2 Listriodon
22 (P3 and P2 molarize) 1.000      1         node_45 0 ==> 1 Tayassu
23 (the upper canine)   0.600      1         node_39 0 ==> 1 node_38
                                   1         node_37 1 ==> 2 node_30
                                   1         node_33 1 --> 2 node_32
                                   1         node_31 2 --> 1 Microstonyx
                                   1         node_32 2 --> 3 Sus
```

```
24 (sexual dimorphism ) 1.000      1          node_38 0 ==> 1 node_37
25 (the sexual bimodal) 1.000      1          node_51 1 ==> 0 Diacodexis
                                   1          node_38 1 ==> 2 node_37
26 (I3)                 0.667      1          node_51 0 --> 1 node_50
                                   1          node_46 1 --> 0 node_43
                                   1          node_45 1 --> 2 Tayassu
27 (The two I1)         1.000      1          node_37 0 ==> 1 node_30
28 (The I1)             1.000      1          node_42 0 ==> 1 node_39
29 (The I1)             1.000      1          node_37 0 ==> 1 node_30
30 (the i2)             1.000      1          node_50 0 --> 1 node_49
31 (the i3)             1.000      1          node_50 0 ==> 1 Archaeotherium
32 (lower male canine)  0.500      1          node_50 0 ==> 1 node_49
                                   1          node_39 1 ==> 2 node_38
                                   1          node_31 2 ==> 1 Microstonyx
                                   1          node_35 2 ==> 1 node_34
33 (lower male canine)  1.000      1          node_50 0 --> 1 node_49
34 (p1)                 0.250      1          node_29 0 ==> 1 Listriodon
                                   1          node_31 0 ==> 1 Microstonyx
                                   1          node_45 0 ==> 1 Tayassu
                                   1          node_49 0 ==> 1 Egatochoerus
35 (p3 longer than m1)  0.333      1          node_50 0 ==> 1 node_49
                                   1          node_38 1 ==> 0 Sinapriculus
                                   1          node_35 1 ==> 0 node_34
36 (The talonid cusp i) 0.667      1          node_39 0 ==> 1 node_38
                                   1          node_37 1 ==> 2 node_36
                                   1          node_32 2 ==> 4 Sus
                                   1          node_46 0 --> 1 node_45
                                   1          node_45 1 --> 3 Tayassu
                                   1          node_49 0 ==> 1 Egatochoerus
37 (Hypertrophy of p3 ) 1.000      1          node_35 0 --> 1 node_34
                                   1          node_34 1 --> 2 Conohyus
38 (entoconid in p4)    1.000      1          node_45 0 ==> 1 Tayassu
39 (p4 hypoconid)       0.800      1          node_51 0 ==> 1 Gobiohyus
                                   1          node_50 0 ==> 2 node_49
                                   1          node_38 2 ==> 3 node_37
                                   1          node_32 3 ==> 4 Sus
                                   1          node_45 2 ==> 3 Tayassu
40 (p4 metaconid)       0.500      1          node_51 0 --> 1 Gobiohyus
                                   1          node_50 0 --> 1 node_49
                                   1          node_30 1 ==> 2 node_29
                                   1          node_34 1 ==> 0 Conohyus
                                   1          node_46 1 ==> 3 node_45
                                   1          node_47 1 ==> 0 Odoichoerus
41 (entoconid in lower) 1.000      1          node_51 1 ==> 0 Diacodexis
42 (paraconid on lower) 1.000      1          node_51 1 ==> 0 Diacodexis
                                   1          node_50 1 --> 2 node_49
43 (paracristid)        1.000      1          node_51 1 ==> 0 Diacodexis
                                   1          node_47 1 ==> 2 node_46
44 (cristid obliqua)    0.333      1          node_50 0 ==> 1 Archaeotherium
                                   1          node_42 0 ==> 1 node_39
                                   1          node_29 1 ==> 0 Listriodon
45 (hypoconid and ento) 0.667      1          node_51 0 --> 1 node_50
                                   1          node_48 1 --> 0 Siamochoerus
```

```
                                   1          node_30 1 --> 3 node_29
                                   1          node_29 3 --> 4 Listriodon
                                   1          node_42 1 --> 2 node_41
                                   1          node_41 2 --> 3 node_40
46 (protoconid and met) 0.667      1          node_50 0 ==> 1 Archaeotherium
                                   1          node_47 0 --> 1 node_46
                                   1          node_39 1 --> 0 Palaeochoerus
                                   1          node_30 1 --> 3 node_29
                                   1          node_29 3 --> 4 Listriodon
                                   1          node_42 1 ==> 2 node_41
47 (hypoconulid in low) 0.500      1          node_50 0 --> 1 node_49
                                   1          node_39 1 ==> 2 node_38
                                   1          node_45 1 ==> 2 Tayassu
                                   1          node_47 1 ==> 2 Odoichoerus
48 (m3 hypoconid)       1.000      1          node_50 0 ==> 1 Archaeotherium
49 (m3 elongation)      0.750      1          node_48 0 --> 1 node_47
                                   1          node_39 1 ==> 0 Palaeochoerus
                                   1          node_35 1 --> 2 node_33
                                   1          node_33 2 --> 3 node_32
50 (lower molar centra) 0.500      1          node_49 0 ==> 1 node_48
                                   1          node_39 1 --> 2 node_38
                                   1          node_38 2 --> 1 Sinapriculus
                                   1          node_41 1 ==> 0 node_40
51 (lower molar anteri) 0.500      1          node_48 0 ==> 1 node_47
                                   1          node_37 1 ==> 2 node_36
                                   1          node_42 1 ==> 2 node_41
                                   1          node_45 1 ==> 2 Tayassu
52 (vally on molar)     1.000      1          node_42 0 --> 1 node_41
                                   1          node_41 1 --> 2 node_40
53 (posterior orbital ) 0.667      1          node_51 0 --> 1 node_50
                                   1          node_50 1 --> 2 Archaeotherium
                                   1          node_42 1 --> 0 node_39
54 (dentary and zygoma) 1.000      1          node_50 0 ==> 1 Archaeotherium
55 (tympanic process o) 1.000      1          node_50 0 --> 1 node_49
56 (Ossified tympanic ) 1.000      1          node_50 0 --> 1 node_49
57 (tympanic bulla)     1.000      1          node_33 0 ==> 1 node_32
58 (glenoid fossa leve) 1.000      1          node_42 0 ==> 1 node_39
59 (angular process of) 1.000      1          node_46 0 --> 1 node_43
60 (sagittal crest on ) 0.750      1          node_29 0 ==> 1 Listriodon
                                   1          node_35 0 ==> 2 node_33
                                   1          node_32 2 ==> 3 node_31
                                   1          node_31 3 ==> 1 Propotamochoerus
61 (frontal born horn ) 1.000      1          node_30 0 ==> 1 Kubanochoerus
62 (orbital protuberla) 1.000      1          node_29 0 ==> 1 Listriodon
                                   1          node_30 0 ==> 2 Kubanochoerus
63 (insicive foramen)   1.000      1          node_45 0 ==> 1 Tayassu
64 (posterior glenoid ) 1.000      1          node_42 0 --> 1 node_39
65 (upper canine alveo) 1.000      1          node_35 0 ==> 1 node_33
                                   1          node_32 1 ==> 2 node_31
66 (posterior palatine) 1.000      1          node_45 0 ==> 1 Tayassu
67 (the facial part of) 1.000      1          node_45 1 ==> 2 Tayassu
68 (lacrimal foramen)   1.000      1          node_37 2 ==> 1 node_30
                                   1          node_33 2 ==> 3 node_32
```

```
69 (jugal process)      1.000      1          node_33 0 ==> 1 node_32
70 ("Furchen")          0.750      1          node_39 0 ==> 1 node_38
                                   1          node_30 1 ==> 0 node_29
                                   1          node_36 1 ==> 2 node_35
                                   1          node_32 2 ==> 3 Sus
71 (the anterior borde) 0.500      1          node_38 0 ==> 1 node_37
                                   1          node_30 1 ==> 2 Kubanochoerus
                                   1          node_31 1 ==> 2 Microstonyx
                                   1          node_42 0 --> 1 node_41
72 (The direction of j) 1.000      1          node_33 0 ==> 1 node_32
73 (prezygomatic shelf) 0.750      1          node_37 0 --> 1 node_36
                                   1          node_33 1 ==> 2 Chleuastochoerus
                                   1          node_31 1 ==> 3 Microstonyx
                                   1          node_31 1 ==> 2 Propotamochoerus
74 (fossa infraorbital) 1.000      1          node_29 0 ==> 1 Listriodon
                                   1          node_35 0 ==> 2 node_33
                                   1          node_31 2 ==> 3 Microstonyx
75 (diastemata inside ) 0.182      1          node_51 0 --> 1 Gobiohyus
                                   1          node_50 0 --> 1 Archaeotherium
                                   1          node_39 0 --> 1 node_38
                                   1          node_38 1 --> 0 Hyotherium
                                   1          node_29 1 ==> 2 Listriodon
                                   1          node_36 1 --> 0 Miochoerus
                                   1          node_31 1 ==> 2 Microstonyx
                                   1          node_31 1 ==> 0 Propotamochoerus
                                   1          node_34 1 --> 0 Conohyus
                                   1          node_41 0 --> 1 node_40
                                   1          node_45 0 --> 1 Tayassu
76 (Occipital condylus) 1.000      1          node_42 0 --> 1 node_39
77 (zygoma)             0.667      1          node_35 0 ==> 1 node_33
                                   1          node_32 1 --> 2 node_31
                                   1          node_31 2 --> 1 Hippopotamodon
78 (masseter fossa)     1.000      1          node_33 0 ==> 1 Chleuastochoerus
79 (the process on the) 1.000      1          node_50 0 ==> 1 Archaeotherium
80 (pterygoid process)  1.000      1          node_38 0 ==> 1 node_37
81 (preorbital fossa)   1.000      1          node_37 0 --> 1 node_36
                                   1          node_32 1 ==> 2 node_31
```