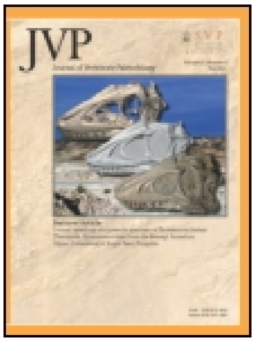

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NEW FOSSIL SUIDAE FROM SHANWANG, SHANDONG, CHINA

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ABSTRACT—The late Early Miocene locality of Shanwang, China is known for its rich and well preserved fossils. Here new suid material is described and previously published material is revised. *Hyotherium shanwangense*, sp. nov. is described based on a partial skull and includes the M3 from the site that was previously assigned to *Palaeochoerus* cf. *pascoei*. A right lower jaw is referred to *Sinapriculus linquensis*, gen. et sp. nov., a primitive suid. The type material of *Hyotherium penisulus* is assigned to Listriodontinae. The Chinese *Hyotherium* seems to lie close to the ancestry of tetraconodonts. The more primitive suid *Sinapriculus linquensis* may represent a survival of an earlier suid radiation in East Asia and the Shanwang suid community as a whole could be seen as a sample of a previously unsuspected East Asian early suid diversity. Such a view would be concordant with the record of late Eocene and early Oligocene suoids from China and Thailand.

INTRODUCTION

The Shanwang Miocene locality was first recorded by C. C. Young as Loc. 37 (Young, 1936, 1937) and since then it has attracted the attention of many researchers because of its abundant and well preserved fossils. Up to now, more than thirty genera of vertebrates have been published. Li et al. (1984) named the Shanwangian as a Chinese mammal stage and correlated it to the Orleanian, and later Qiu and Qiu (1990, 1995) included the Shanwangian among their Chinese land mammal ages. Previous mention of suids from Shanwang include *Hyotherium penisulus* and *Palaeochoerus* cf. *pascoei* (Chang, 1974), and these names have been included in Neogene mammalian fossil lists (Qiu and Qiu, 1990; Tong et al., 1995).

In 1998, the senior author was given three unpublished suid specimens from Shanwang for study. The fossils are an anterior part of a skull and two right lower jaws. The skull is crushed and it is difficult to reconstruct the original morphology, but the dentition is complete and the teeth are well preserved, and one of the lower jaws shows good occlusal fit with the skull. The material recorded by Chang (1974) included only one M3 and two m3s, all relatively undiagnostic. Her identifications were mainly influenced by comparison with the Siwalik fauna, which has since been revised by Pickford (1988). It is therefore necessary to study the newly discovered materials, and to critically re-examine the old collection.

The geology, stratigraphy and fauna of the locality were described in detail by Yan et al. (1983). According to their observation and subdivision, there are three fossil layers, Sw1, Sw2 and Sw4. Sw2 is the famous siliceous earth layer from which most material from Shanwang was collected, and the fossils from this layer are well preserved and black in color. In contrast, fossils found in other two layers are brownish yellow in color and tend to be broken. The new black fossils were collected from layer Sw2, while the previously collected brownish yellow fossil identified as *Palaeochoerus* cf. *pascoei* (Chang, 1974) was possibly collected from Sw4, above Sw2. Since there is no significant difference between the fossils from the various horizons, the Shanwang mammals are thought to represent a single fauna.

MATERIAL AND METHOD

Material

The Shanwang fossil collection is housed in the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP), Chinese Academy of Science, Beijing. The comparative fossils of *Hyotherium meisneri*, *H. soemmeringi* and *Conohyus* were studied in the personal cast collection of Mikael Fortelius, made from original specimens kept in the following Museum collections: SMNS (Staatliches Museum für Naturkunde, Stuttgart), BSP (Bayerische Staatssammlung für Paläontologie und historische Geologie, München), BMNH (The Natural History Museum, London), NMB (Naturhistorisches Museum, Basel). Other comparative material was studied mainly from figures in the published literatures.

Method

Logarithmic ratio diagrams were constructed according to Simpson's (1941) method, the measurements of European collections were made by Mikael Fortelius. The scatter diagrams employ data from Hellmund (1991) and Van der Made (1994). The terminology we use in this paper (Fig. 1) mainly follows Pickford (1988), largely based on and Hünermann (1968).

SYSTEMATIC PALEONTOLOGY

Order ARTIODACTYLA Owen, 1848
Superfamily SUOIDEA Cope, 1887
Family SUIDAE Gray, 1821
Subfamily HYOTHERIINAE Cope, 1888
SINAPRICULUS, gen. nov.

Type Species—*Sinapriculus linquensis*, sp. nov.
Diagnosis—As for the type species.
Etymology—From Latin apriculus, diminutive of aper, wild boar; and Sin-, latinized prefix indicating China. The gender is masculine.

SINAPRICULUS LINQUENSIS, sp. nov.
(Figs. 2, 3)

Holotype—A female right lower jaw with i2–m3 (IVPP, V11941).

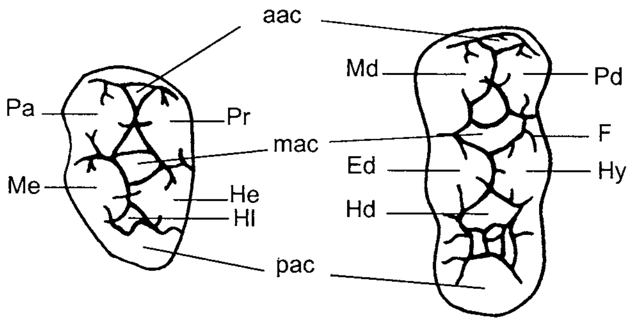


FIGURE 1. Topography of the last right molars in Suidae. **Pr**, Protocone; **Pd**, Protoconid; **He**, Hypocone; **Hy**, Hypoconid; **Pa**, Paracone; **Me**, Metacone; **Md**, Metaconid; **Ed**, Entoconid; **Hl**, Hypoconule; **Hd**, Hypoconulid; **aac**, anterior accessory cusp; **mac**, median accessory cusp; **pac**, posterior accessory cusp; **F**, Furchen.

Diagnosis—A medium size hyotheriine differing from other hyotheriines in having the following special character states: symphysis very long, diastemata well developed between i3/c, c/p1, and p1/p2, mandible shallow and thick, canine vertically upward, p3 and p4 slightly longer than m1.

Locality—Shanwang, Shandong Province, China.

Age of Type Locality—Late Early Miocene, type Shanwangian.

Etymology—Linqu is the county in which the locality occurs.

Description—The lower jaw is long and shallow (Table 1), with a long symphysis extending back to the level of p3 (Fig. 2). There are long diastemata developed between i3/c (8.3 mm), c/p1 (5.5 mm), p1/p2 (11.1 mm) and even a short one between p2/p3 (2.2 mm) (Fig. 3). The length of the symphysis (about 63 mm) is nearly half of the distance from i1 to the end of m3 (133 mm); the height of the lower jaw in the only place where it can be measured below the p2 is about 35mm. Two mental foramina are situated beneath the diastema between p1/p2, a third foramen occurs beneath the talonid of p3. The teeth are worn to the extent that the Furchen are no longer present. Inferred from the thick and smooth enamel of the teeth, the Furchen are very week or lack. Except beneath p1 and p2, the base of the lower jaw is missing.

The i2 is narrow and high crowned, similar to the corresponding tooth in *Hyotherium* species, but the mesial and distal ribs are not as strongly developed. The i3 is low crowned and more asymmetrical, with a weak medial rib. The tip of i3 reaches the basal part of i2.

The canine is slender and short, and set almost vertically in the lower jaw. In lateral view it is triangular without sharp ridges and it has a verrucosic cross section (the posterior surface is transverse to the tooth row and narrower than the lingual surface). The posterior surface is narrow and concave at the base where is not worn away by the upper canine, the others are slightly convex. There are at least two small wear facets at the apex of the tooth, in addition to the large posterior one.

The p1 is double-rooted (although the roots are partly fused) and asymmetrical, with a long posterior ridge and a short steep anterior one, the main cusp being situated above the anterior root. A shallow concave facet is situated on the posterior ridge.

The p2 is more symmetrical than p1, with the main cusp centrally positioned above the two roots and it possesses a blade-like anterior ridge. The posterior surface is blunt, with some small tubercles and a small talonid.

The p3 is a larger copy of p2, with a distinct talonid. The tooth is long and narrow and the anterior cingulum forms a small cusp. There are distinct anterior and posterior wear facets.

The p4 is moderately inflated, and the crown is heavily worn. The stout main cusp lies to the lingual side, owing to the presence of a well-developed Innenhügel. There is a large talonid and the anterior and posterior wear facets are also large and clearly in a single plane of occlusal movement.

The first and second molars are rectangular in occlusal out-

FIGURE 2. V11941, holotype right lower jaw of *Sinapriculus linquensis*, gen. et sp. nov. with i2–m3, right lateral view (**A**) and occlusal view (**B**). Scale bar equals 20 mm.

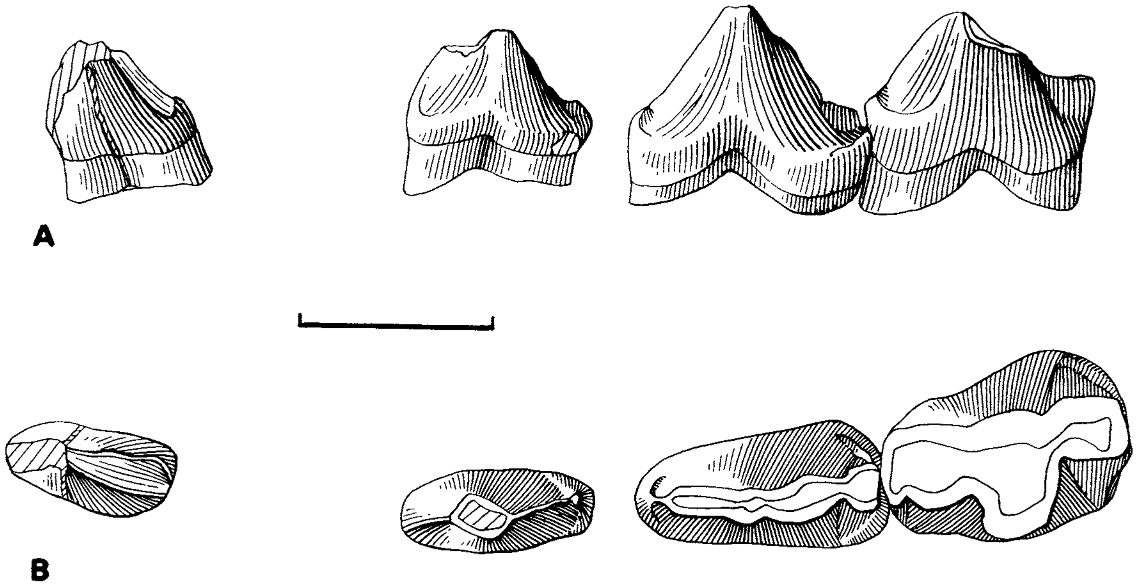


FIGURE 3. The left labial (**A**) and occlusal (**B**) views of the V11941 specimen's premolars. Scale bar equals 10 mm.

line. The bases of the four main cusps fuse with each other, and the grooves between them are quite shallow. The accessory cusps are present in their usual locations (anterior, central, posterior), but are smaller than in *Hyotherium*. At this wear stage no trace of Furchen remains.

The m3 is like the anterior molars, but it possesses a *Hyotherium*-like talonid: a central positioned posterior accessory cusp is flanked by beaded buccal and lingual cingula, and connects to the hypoconulid by a middle ridge.

Discussion—Van der Made (1996) applied Matthew's (1924) nomen Palaeochoerinae at the family level as Palaeochoeridae for the Old World primitive pig-like genera which in recent decades have mostly been referred to the Tayassuidae. The known genera *Odoichoerus* (Tong et al., 1986), *Taucanamo*, *Yunnanochoerus*, *Schizochoerus*, *Propalaeochoerus* and *Palaeochoerus* are classified in the new family (Van der Made, 1996). We agree that the Old World primitive suoids differ substantially from Neogene and Recent New World peccaries, but the establishment of a new family for the forms will remain controversial as long as Eocene and Oligocene Old World suoids remain poorly understood. Recent studies on newly found Eocene pig-like mammals from Thailand (Ducrocq, 1994; Ducrocq et al., 1998) will greatly help us to understand the early evolution of these suoids, but it is not the purpose of this paper to enter into this matter. We prefer to retain Palaeochoerinae as a subfamily of Tayassuidae for the time being in order to accord with the majority of published papers.

The vertical canine and the molars lacking Furchen (or having very shallow ones) could be taken to align the specimen with the Tayassuidae, but the presence of a true central accessory cusp in the molars (rather than a ridge from the hypoconid), the strong middle rib on the lower incisor, and the relatively long talonid of m3 (rather than a mere posterior accessory cusp) differentiate the specimen from the tayassuid genera *Propalaeochoerus* and *Palaeochoerus* that are closest to the Shanwang specimen in terms of general size and shape. *Odoichoerus* and *Taucanamo* are much smaller and their dentitions are simpler. *Yunnanochoerus* and *Schizochoerus* are very different from the Shanwang fossil because of their highly lophodont molars.

Ducrocq et al. (1998) described the new species *Siamochoerus banmarkensis* from Krabi, Late Eocene of southern Thailand. It is obviously more primitive than *Sinapriculus*, having p4 with weakly developed talonid, molars without real accessory cusps, a simple talonid on m3. The peculiar pig-like species *Egatochoerus jaegeri* from Krabi cannot be related directly to other Old World suoids (Ducrocq, 1994).

Hellmund (1992) erected the genus *Dubiotherium* for *Palaeochoerus waterhousi*. The holotype of *D. waterhousi* is a mandibular fragment with p2–m3. He argued that the genus is more similar to *Hyotherium* than to the tayassuids, and considered it to be a suid. Van der Made (1994) discussed the status of this taxon and referred it to the Tayassuidae, i.e., the Palaeochoeridae sensu Van der Made (1996), and considers *Dubiotherium* to be a synonym of *Palaeochoerus* (Van der Made, pers. comm., Nov. 1999). We agree that *Dubiotherium* (whatever its formally valid name turns out to be) is more like a tayassuid than a primitive suid, because of the relatively simple talonid of m3 (lacking the ridge between the second lobe and talonid) and the simple premolars (without talonid on p3 and weak talonid on p4), and the absence of well developed accessory cusps in the molars.

The Shanwang specimens are comparable with *Dubiotherium* in shape and size (Table 1). In both forms the m1 is also relatively short and the molars are simple. The Shanwang specimen differs, however, in having a longer p3 (near p4 size), p2, p3 and p4 with a well-developed talonid, m3 with a ridge between the second lobe and talonid, diastema between p2 and p3 and well developed accessory cusps in the molars. These characters do not occur in *Dubiotherium* and other tayassuids, which suggests that our material represents a primitive suid.

Of the primitive suid taxa *Hyotherium* is the best known. The Shanwang lower jaw cannot be referred to *Hyotherium* for the following reasons: (1) the more vertically placed canine; (2) the weaker Furchen on the main cusps in the molars; (3) the shallower mandible; (4) the more developed diastemata in the premolar row; (5) the longer p3 and p4. These differences also differentiate our material from other known early suids. Considering the fact that our material has important differences from the known primitive suids, we think that it represents a new genus for which we propose the name *Sinapriculus*. This form retains characters typical of tayassuids (vertical canine, shallow molar Furchen and simple talonid in m3), possibly reflecting a phylogenetic position close to the origin of the family Suidae.

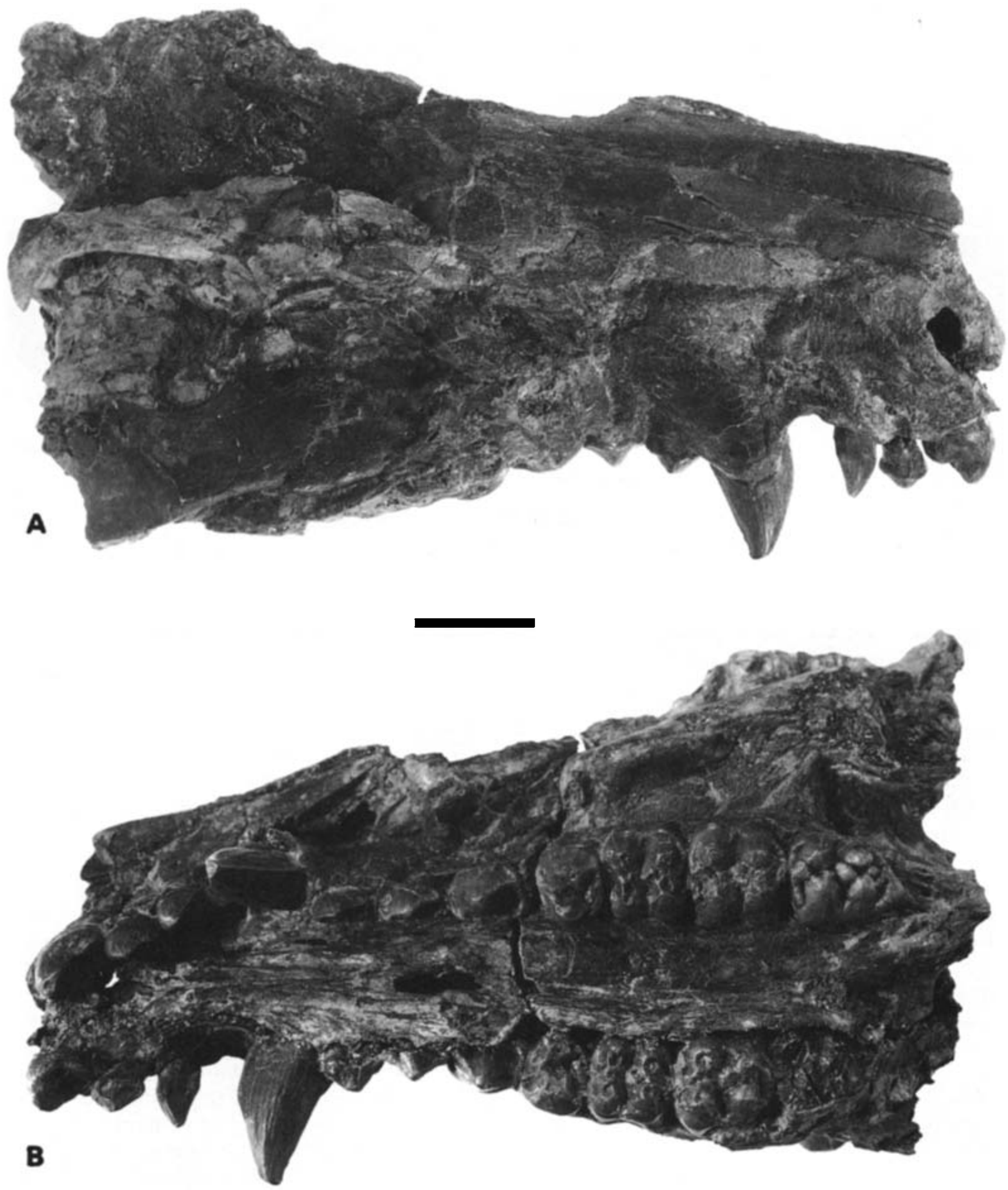


FIGURE 4. V11942.1, holotype skull of *Hyotherium shanwangense*, sp. nov., dorsal view (**A**) and ventral view (**B**). Scale bar equals 20 mm.

TABLE 1. Measurements of right lower jaw of *Sinapriculus linquensis* (in mm). Abbreviations: L1 = basal length, L2 = occlusal length of the crown, mesiodistal dimension of incisors; W1 = maximum width, anterior width of molars, buccolingual dimension of the incisors, W2 = posterior width of molars, W3 = width of talon(id), H1 = preserved labial height of anterior cusps of molars, H2 = preserved labial height of posterior cusps of molars, H3 = preserved labial height of talon(id).

Elements	i2	i3	C	p1	p2	p3	p4	m1	m2	m3
L1	5.2	5.3	–	7.4	8.7	11.5	11.8	12.2	13.4	21.5
L2	5.6	6.8	9.1	8.6	9.7	13.6	13.3	12.9	14.5	21.0
W1	8.0	5.0	5.8	3.7	4.1	6.2	8.4	10.8	11.9	12.3
W2								11.6	12.1	10.9
W3										8.1
H1	11.3	7.1	15.5	5.5	6.6	9.1	6.5	4.4	5.7	6.2
H2								4.4	5.2	6.0
H3										6.0

FIGURE 5. V11942.2, holotype right lower jaw with left i1, i2 and right i1–m3 of *Hyotherium shanwangense*, sp. nov., right lateral view (**A**) and occlusal view (**B**). Scale bar equals 20 mm.

HYOTHERIUM H. v. Meyer, 1834
HYOTHERIUM SHANWANGENSE, sp. nov.
(Figs. 4–6)

Palaeochoerus cf. *pascoei*, Chang Yuping, 1974

Holotype—The anterior part of a male skull with the full dentition lacking only the right M3 (IVPP, V11942.1) and a right lower jaw that probably belongs to same individual (IVPP, V11942.2).

Referred Material—A right M3 (IVPP, V4693).

Diagnosis—A medium sized species of the genus. Distinguished from other known species by p1 incisiform, p4 unicuspid and somewhat inflated in the manner of tetraconodonts, with a posterobuccal bulge, upper molars lacking buccal cingulum. The cheek tooth series is continuous from P1 to M3

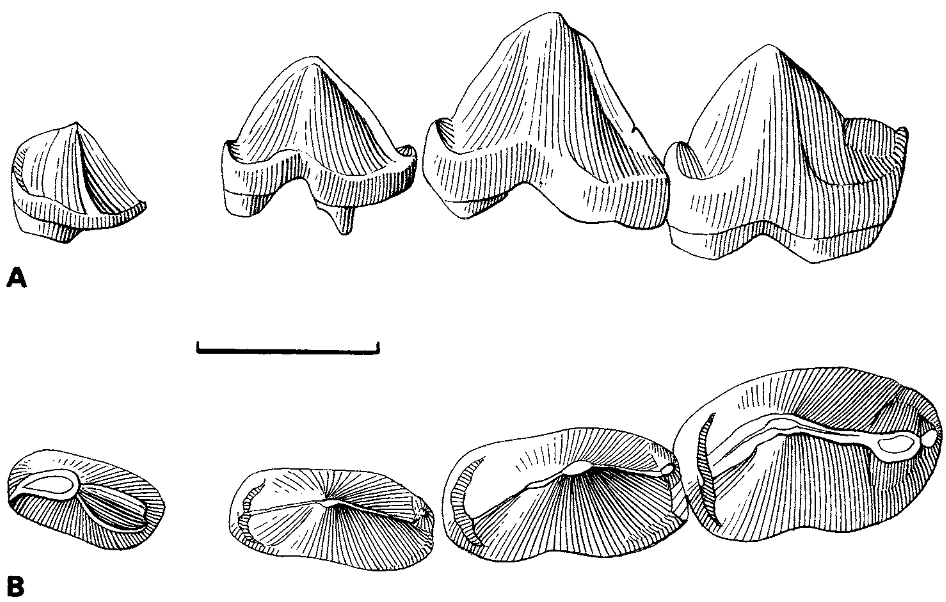


FIGURE 6. The left labial (**A**) and occlusal (**B**) views of the V11942.2 specimen's premolars. Scale bar equals 10 mm.

TABLE 2. Measurements (in mm) of the dentition of *H. shanwangense*. Abbreviations as in Table 1.

Element	Number	L2	W1	W2	W3	H1	H2	H3
I1	2	11.7–#	7.7–8.0	–	–	12.4–12.6	–	–
I2	2	8.1–8.3	5.9–#	–	–	6.7–7.0	–	–
I3	2	8.1–8.0	5.2–#	–	–	8.7–8.8	–	–
C	2	14.2–14.0	11.1–11.0	–	–	13.5–#	–	–
P1	2	11.5–11.9	4.9–5.1	–	–	6.3–#	–	–
P2	2	11.4–12.1	#–6.5	–	–	7.1–7.3	–	–
P3	2	12.3–13.9	10.8–10.9	–	–	10.5–9.9	–	–
P4	2	11.1–11.3	#–13.3	–	–	8.2–8.3	–	–
M1	2	14.2–14.7	#–15.0	#–16.7	–	6.6–6.5	6–5.8	–
M2	2	17.1–16.7	#–17.3	#–17	–	7.3–7.5	7.6–7.7	–
M3	1	19.4	15.7	13.8	6.4	7.5	6.9	5.6
i1	2	4.9–5.1	7.6–7.9	–	–	13.8–14.9	–	–
i2	2	5.4–5.6	7.8–7.8	–	–	14.7–14.5	–	–
i3	1	8.4	5.6	–	–	7.2	–	–
C	1	12.1	8.9	–	–	22.1	–	–
p1	1	8.7	4.4	–	–	6.9	–	–
p2	1	11.0	5.3	–	–	7.6	–	–
p3	1	13.0	7.1	–	–	10.2	–	–
p4	1	13.8	9.2	–	–	10.3	–	–
m1	1	14.4	10.7	12.2	–	5.6	6.5	–
m2	1	16.2	12.8	12.8	–	7.1	6.2	–
m3	1	23.4	12.6	11.4	7.9	6.9	6.2	#

= cannot be measured.

and p2 to m3, with no gaps between adjacent or occluding teeth.

Locality—Shanwang, Shandong province, China.

Age of Type Locality—Late Early Miocene, type Shanwangian.

Etymology—shanwangense, from Shanwang.

Description

Skull—The skull is preserved from the snout to the posterior part of the orbits, and is crushed and deformed obliquely, the left side of the face being pushed down over the palate (Fig. 4). The choana opens at the rear of M3, the anterior end of the zygomatic arch arises behind the middle of P4. The crowded incisors and very short diastema between the I3 and the canine make the snout relatively short. The canine is strong and moderately splayed out on the better preserved left side. Above it there is a canine flange. Anterior to the upper canine is a shallow depression which houses the lower canine when the jaw is closed.

I1 is the largest and most asymmetric of the incisors, the distal facet being larger than the mesial one. The lingual surface is concave while the labial surface is convex. A thick cingulum borders the lingual face, and the medial ridge is high and strong. As in *Hyotherium soemmeringi* there is a small distal cusplet separated from the main cusp by a shallow groove. No trace is found to show the closed connection of the pair I1.

I2 has the same basic structure as I1 but is much smaller and more symmetrical, and the medial ridge is not as strongly elevated as in I1.

I3 is similar to I2, but is less elongated and higher. The cingulum is weaker than in the other incisors, and the posterior surface is abraded by occlusion with the lower canine.

The upper canine is strong and moderately splayed outside. The transverse section is oval with sharp anterior and posterior ridges, the labial side is larger. The anterior wear facet formed by occlusion with the lower canine is vertical and transverse to the tooth row; the posterolingual side has an oblique, trough-like wear facet made by p1.

P1–2 are low and elongate teeth with one main cusp. The lingual cingulum encloses a posterolingual basin with no trace of a cusplet. There is a straight and sharp ridge on the posterior ridge and a sharp anterior ridge that is deflected towards the lingual side. P1 is more asymmetrical, with the cusp placed anterior to middle of the tooth. P2 is more symmetrical, with the main cusp at midpoint.

P3 is large, high and stout compared with P2 and has a cingulum-enclosed basin at the distal lingual corner, as typically seen in other *Hyotherium* species. The main cusp has a slightly inflated appearance.

P4 is a short and broad tooth with the two buccal cusps close together, separated only at their tips. The protocone has a rounded crescent-shaped cross-section. A strong and high ridge descends from the top of the protocone to the anterior cingulum, and another low ridge from the posterior cingulum ends to the base of the protocone. There is no cusplet in the sagittal groove. The anterior and posterior cingula are well developed, but there is no buccal cingulum and the lingual cingulum is only expressed at the distal corner of the tooth.

M1/2 are square in occlusal outline and are bunodont, with four main cusps. The anterior and central accessory cusps are well developed, the posterior one is very weak. The anterior accessory cusp is fused to the anterior cingulum, and the hypocone is connected by a ridge to the distal cingulum. There is no buccal or lingual cingulum except for a trace at the lingual mouth of the median valley. The teeth and roots expand from the crown tip to the cervix and below. The main cusps show pairwise shallow fusion, suggesting an incipient lophodonty.

M3 is similar to M1/2, but has a well-developed hypoconule just before the ridge from the hypocone to the posterior cingulum. The posterior cingulum has a row of tubercles and is enlarged on the lingual side to form a small talon.

Mandible—The diastemata in the lower jaw are short, 3.5 mm between i3 and the canine, 4.6 mm between the canine and p1, and 4.5 mm between p1 and p2 (Fig. 5). Wear facets are present on each of the premolars. Only the anterior part of the symphysis is preserved. The bone is damaged around the canine alveolus but it seems that the canines would have been moderately splayed outside. The ascending ramus departs from the body just distally to m3; in side view the m3 is not hidden by it.

The incisors form a tight battery, with i1 and i2 forming an arc in which the occlusal surfaces of all four teeth are level with each other. The i1 is high crowned and symmetrical. There are prominent mesial, medial and distal ridges on the lingual surface. The medial one is the strongest.

The i2 is similar to i1 but is higher and more asymmetric. The distal part is narrower than the mesial part.

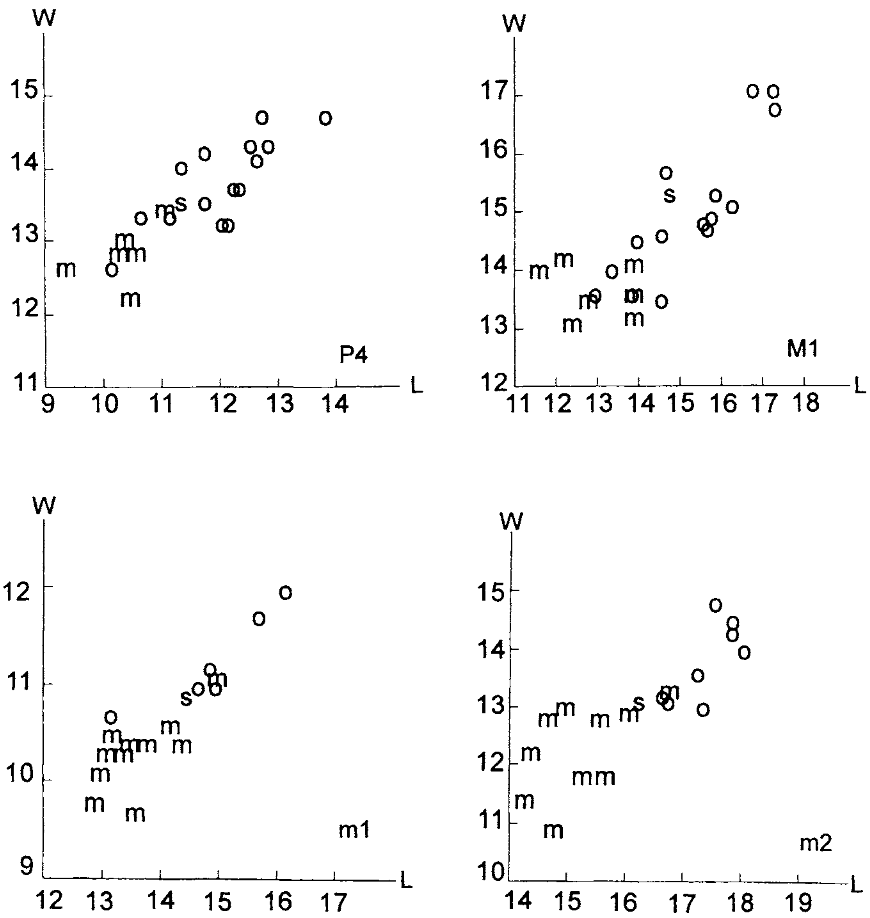


FIGURE 7. Bivariate scatter plots of *H. meisneri* (**m**), *H. soemmeringi* (**o**), and *H. shanwangense* (**s**) of upper teeth P4, M1, lower teeth m1 and m2. L = occlusal length of tooth, W = anterior width of tooth.

The i3 is half the height of i1/i2 and is more asymmetric, with the medial ridge located near the distal ridge.

The lower canine is strong and high, with a scrofic cross section (the posterior surface is oblique to the toothrow and is about as long as the lingual face, and much longer than the labial face).

The p1 is more like an incisor than a premolar in shape (Fig. 6). Its structure is similar to i3 but it is more laterally compressed and has two roots. The tip has a wear facet caused by contact with the upper canine. The p1 is the last tooth to erupt in the lower jaw, its lower part is still hidden in the jaw and the blade-like posterior ridge is fresh and sharp.

The p2/p3 each have one main central cusp with sharp anterior and posterior ridges. There is no clear cusplet where the cingulum joins the anterior ridge and the ridge itself is only very slightly deflected towards the lingual side.

The p4 is a simple, stout tooth with a single main cusp and a distinct small talonid flanked by faint buccal and lingual cingulum. There are well-developed anterior and posterior wear facets, all corresponding to occlusal movement in a single plane. The tooth has no Innenhügel and is slightly inflated, faintly suggesting affinities to tetraconodonts.

The m1/m2 are simple and bunodont, the closely spaced cusps (and roots) flare out towards the base, and the Furchen are moderately deep. As in the upper molars there is a slight tendency for pairwise fusion of the main cusps suggesting incipient lophodonty.

The m3 is similar to the other molars but it has a talonid. The centrally positioned posterior accessory cusp flanked by buccal and lingual cingula to the posterior main cusps and connected to the well developed hypoconulid by a strong ridge in the midline. The sagittal ridge is clearly separated from the buccal and lingual cingula by deep grooves.

Comparison and Discussion—The Shanwang material described above is considered to belong to the Hyotheriinae, a primitive subfamily of the Suidae, because of the simple bunodont dentition, splayed-out canines, P4 without accessory ridge in the sagittal groove and the simple talonid on m3. According to Van der Made (1998), the known genera of Hyotheriinae are *Hyotherium*, *Xenohyus* and *Aureliachoerus*.

Aureliachoerus is a small suid recorded from Europe, similar in age to the Shanwangian. Ginsburg (1974) and Van der Made (1998) cited it as a genus independent from *Taucanamo*. The Shanwang specimen differs from *Aureliachoerus* by its more elongated premolars and larger size. *Xenohyus* is a poorly known genus from the Early Miocene of Europe. Pickford and Morales (1989) and Pickford (1993) assigned it to Tayassuidae on the basis of dental and cranial characters, contra Van der Made (1989–1990) and Ginsburg (1980) who considered it to be a suid. Bouvrain and De Bonis (1999) think it is a special form and its systematic position remains unclear. In any case the enlarged incisors and reduced premolars of *Xenohyus* are clearly different from the Shanwang material.

Overall, our new material is much closer in size (Table 2) and morphology to *Hyotherium* species than to other hyotheriine genera, especially in having a full set of elongated pre-

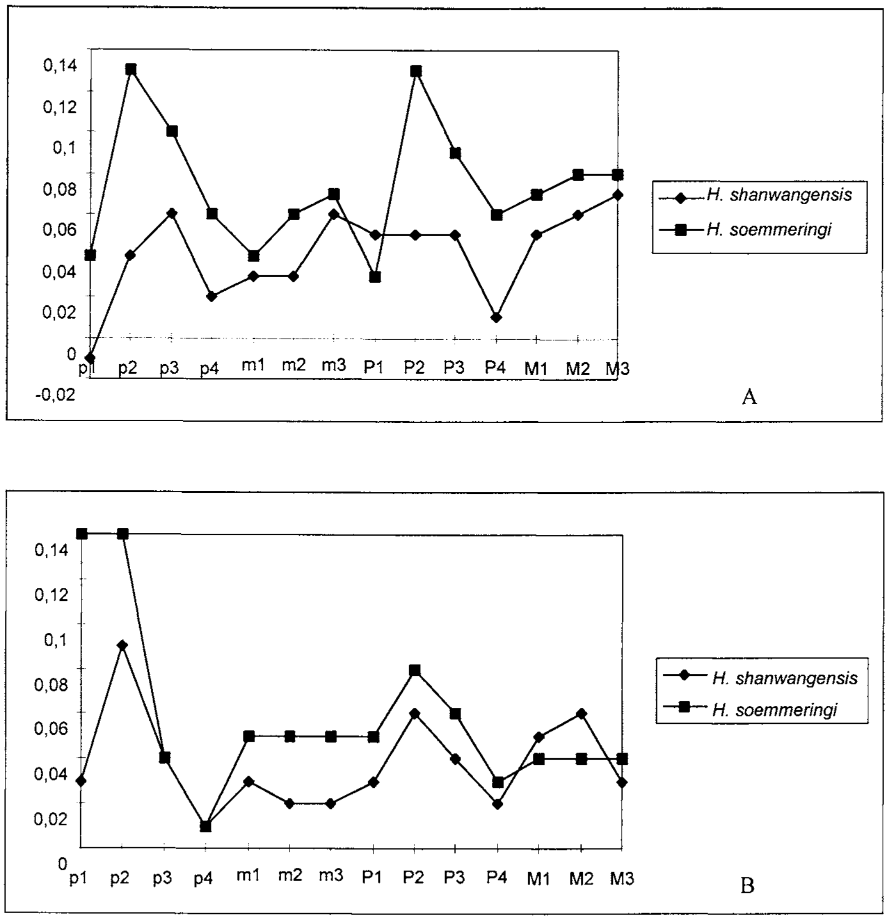


FIGURE 8. Dental proportions of *H. shanwangense* and *H. soemmeringi*. The values shown represent the difference between the log transformations of the means for the species with *H. meisneri* as the standard. **A**, length; **B**, width.

molars. *Hyotherium* was previously recorded from Shanwang as *Hyotherium penisulus* (Chang, 1974), a species based on two broken lower jaws, each with a complete m3 and one with a broken m2 as well. However, the size and morphology of these teeth recall bunodont listriodontines rather than hyotheriines, as discussed below.

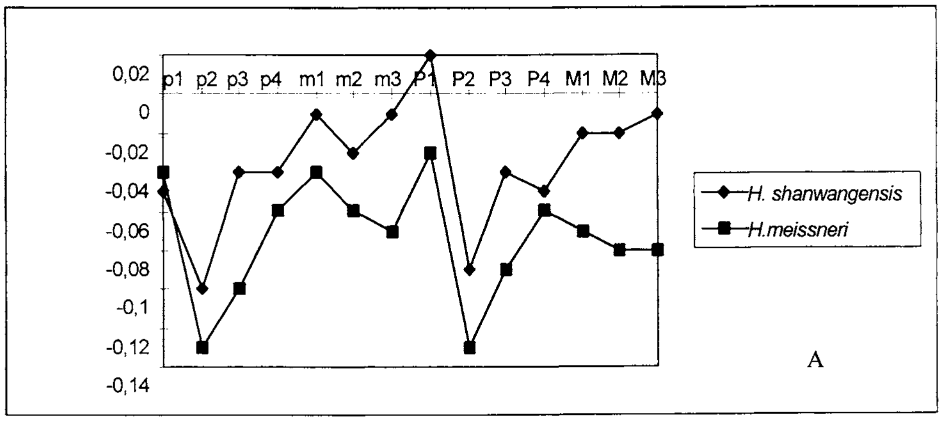
Isolated teeth from Thailand have been assigned to *Hyotherium* sp. (Pope and Bernor, 1990) but these are now known to represent *Conohyus thailandicus* (Ducrocq et al., 1997). *Hyotherium pilgrimi* was named by Pickford (1988) when he revised the Indian Suidae. This species is 20% larger than *H. soemmeringi*, and is thus considerably larger than the Shanwang material. Its size, its longer talon of M3 and the small enamel ridge leading into the sagittal valley in P4 indicate that it differs from other species of *Hyotherium*, perhaps enough for it to be assigned to a different genus.

Hyotherium is well known from Europe and includes the species *H. meisneri*, *H. soemmeringi*, and perhaps *H. major*. *H. meisneri* and *H. soemmeringi* have been redescribed and discussed in detail (Schmidt-Kittler, 1971; Hellmund, 1991) and may be regarded as well established species in the genus. Ginsburg (1974) and Hellmund (1991) synonymized *H. major* with *H. meisneri*, but Van der Made (1994) insisted that *H. major* is a valid species because of its smaller size, the linear molar measurements being on average 93% of those of the check teeth of *H. soemmeringi* (the corresponding figure for *H. meisneri* relative to *H. soemmeringi* is 88%). Since *H. major* seems to differ from *H. meisneri* only in size, and marginally at that, and because the two species overlap in geography and time range, we include it in *H. meisneri*.

Figure 7 are bivariate plots of dental dimensions of *Hyotherium shanwangense*, *H. meisneri* and *H. soemmeringi*. The Shanwang material is mostly intermediate in size between the two European species.

Figures 8 and 9 show logarithmic ratio diagrams illustrating the relative proportions of the toothrow in the three taxa. The difference between *H. soemmeringi* and *H. shanwangense* appears greater than the difference between *H. meisneri* and *H. shanwangense*, except in the upper molars. Compared with *H. soemmeringi*, *H. shanwangense* has relatively shorter premolars, especially the second and fourth upper and lower ones (Fig. 8A). Compared with *H. meisneri* the main difference in proportions seems to be that the second premolars are relatively broader (Fig. 9B). There is no indication that the faintly tetraconodont-like shape of the posterior premolars is accompanied by proportional enlargement.

Non-metric characters of the three species are presented in Table 3. The Shanwang specimen shows some important morphological differences with the European taxa, especially the stout and inflated morphology of the single-cusped p4, the close approximation of the two main cusps of P4, the lack of cingula on the upper check teeth, the incisiform p1, and the short diastemata. It is impossible to know whether these characters were universal for the Shanwang population, but they are quite distinct and we failed to find any specimen with them in the two European species. Because of the significant nature of the dif-



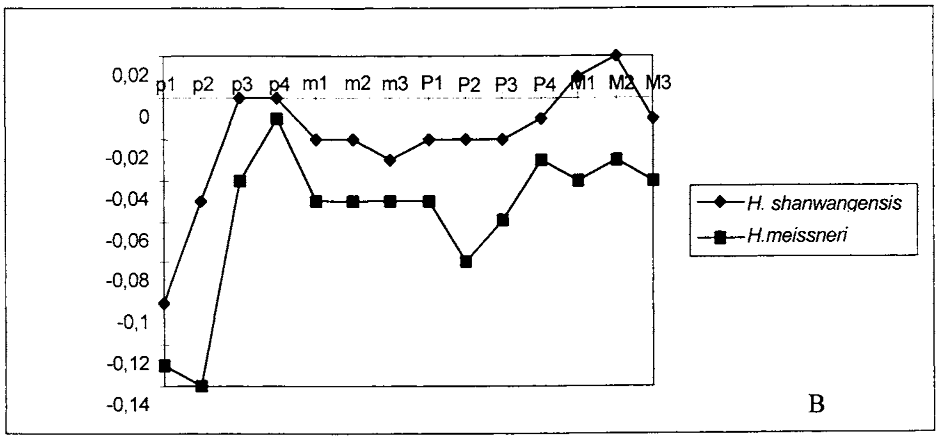


FIGURE 9. Dental proportions of *H. shanwangense* and *H. meisneri*. The values shown represent the difference between the log transformations of the means for the species, with *H. soemmeringi* as the standard. **A**, length; **B**, width.

ferences we feel justified in assigning the Shanwang specimen to a new species of *Hyotherium*.

Chang (1974) referred a right M3 from Shanwang to the Siwalik species *Palaeochoerus* cf. *pascoei*. *Palaeochoerus pascoei* has since been synonymized with *Conohyus sindiensis* by Pickford (1988). Chang's specimen is closely similar to our new material in size and morphology of the cingulum and talon, and is distinct from *Conohyus*. We refer this tooth to *Hyotherium shanwangense*.

The main characters of the posterior premolars and molars (the unicuspid p4, the weak separated labial cusps on P4, and none of labial cingula on molars) that set the Shanwang specimen apart from European *Hyotherium* are suggestive of tetraconodont affinities, although the indications are in our opinion too weak to be recognized taxonomically. There is no indication of the specialized anterior premolars or the wrinkling of the enamel that characterizes tetraconodonts, nor is there any indication in the ratio diagrams of the relative enlargement of the posterior premolars. Nevertheless it remains an intriguing possibility that this species might be close to the so far unknown origin of the Tetraconodontinae. Another genus closed to hyotheriines and tetraconodonts is *Parachleuastochoerus*, a small suid from Spain which Golpe (1972) originally considered to be a hyotheriine. Pickford (1981) noticed its tetraconodont-like

TABLE 3. Summary of the morphological differences between the dentition of various species of *Hyotherium*.

Characters	Species		
	H. soemmeringi	*H. meisneri*	*H. shanwangense*
distal cusp in I1	present	absent	present
medial ridge in I1	high	low	high
diastema between the incisors	short	none	none
diastema between I3 and canine in male skull	longer than canine length	longer than canine length	shorter than canine length
anterior ridge deflected lingually in P1-P3	strong	weak	strong
the labial main cusps of P4	far apart	far apart	close together
bucco-medial cusplet in upper molars	developed	none	none
buccal cingulum in upper molars	strong in the posterior part	strong in the posterior part	none
morphology of p1	premolariform	premolariform	incisiform
apex of p4	two or three cusplets	two cusplets	single main cusp

TABLE 4. List of the transformation series used in the analysis.

0. The distal cusp in I1: 0 (absent), 1 (present)
1. Sexually dimorphic canine shape: 0 (absent), 1 (present)
2. The direction of the upper canine: 0 (vertically downward); 1 (splayed outwards)
3. P3 metacone: 0 (absent); 1 (present)
4. P4 metacone relative to paracone: 0 (undeveloped); 1 (developed)
5. P4 protocone: 0 (large and robust); 1 (reduced)
6. The ridge connecting protocone to paracone and metacone on P4: 0 (absent); 1 (present)
7. The anterior and central accessory cusps in molars: 0 (incipient cusp fused to main cusps); 1 (independent cusps)
8. The buccal cingulum on the upper molars: 0 (developed outside metacone); 1 (absent outside metacone)
9. The talon of M3: 0 (absent); 1 (present)
10. Furchen in the molars: 0 (absent or very weak); 1(moderately developed)
11. The main cusp in p4: 0 (bi- or tricuspid); 1 (unicuspid)
12. The position of the posterior choana: 0 (behind M3); 1 (in front of M3)
13. The talonid of m3: 0 (only posterior accessory cusp); 1 (with developed hypoconulid between the second lobe and posterior accessory cusp)

morphology even though these features are developed more slightly than in other tetraconodonts, and he reassigned it to Tetraconodontinae. The Shanwang specimen is even more like a hyotheriine than the Spanish one, and if the conservative *Parachleuastochoerus* is close the origin of Tetraconodontinae, then the tetraconodont-like *H. Shanwangense* might indicate the possible origins of the subfamily Tetraconodontinae.

The Phylogenetic Relationship of *Hyotherium shanwangense*

It seems probable that *H. meisneri* and *H. sommeringi* form an evolutionary lineage that shows minor size increase. The description of a new Asian taxon demands analysis of the phylogenetic relationships within the genus *Hyotherium*. Here we present an analysis using the Hennig 86 computer program.

Table 4 lists the characters used in the systematic analysis. The characters are identified by a sequential numbering system (0: primitive character state; 1: derived character state; ?: state unknown due to incomplete material). All transformation series are polarized between primitive and derived using outgroup comparison method (Nelson, 1978). The taxa included in the analysis are *H. shanwangense*, *H. meisneri*, and *H. soemmeringi*. The poorly known *Aureliachoerus*, *Xenohyus*, *Dubiotherium*, *Siamochoerus* and *Sinapriculus* did not yield enough relevant characters, and they are therefore excluded from this analysis. *Propalaeochoerus* and *Palaeochoerus* are commonly considered to be close to the ancestry of the Suidae and are therefore selected as the outgroup. Due to lack of complete material, only dental characters are included in the matrix (Table 5).

The result of the analysis is the single most parsimonious tree given by the Hennig 86 and shown in Figure 10 (tree length = 12, CI = 100, RI = 100). In the cladogram, *Hyotherium soemmeringi* and *Hyotherium shanwangense* are sister taxa, their ancestor is the sister taxon of *Hyotherium meisneri*. *Hyotherium* as a whole differs from *Palaeochoerus* and *Propalaeochoerus* in the following synapomorphies: (1.1) the sexually dimorphic canine shape; (2.1) the splayed-out canine; (4.1) the metacone developed on P4; (5.1) the reduced protocone on P4; (6.1) the ridge connecting the protocone to the paracone and metacone on P4; (7.1) the independent anterior and central accessory cusps in molars; (9.1) the presence of a talon in M3; (10.1) the presence of moderately developed Furchen in the molars; (13.1) with developed hypoconulid in m3. The number of synapomorphies of *Hyotherium* will decrease in the complete analysis if *Aureliachoerus*, *Xenohyus*, *Dubiotherium*, *Siamochoerus* and *Sinapriculus* are included.

Subfamily LISTRIODONTINAE Simpson, 1945

Material—left m2–m3 (IVPP, V4692.1), right m3 (IVPP, V4692.2).

Locality—Shanwang, Shandong Province, China.

Discussion—Chang (1974, Pl. I, figs. 6, 7) erected the species *Hyotherium penisulus* based on two mandibular fragments, each with a worn m3. Examination of her figures suggests that both specimens belong to a bunodont listriodontine, perhaps the genus *Bunolistriodon* in the conventional sense (Fortelius et al., 1996a, b). Unfortunately, we could not find out the specimens. Without study of the original specimens it would be unwise to speculate in detail on the status of this material, but it seems

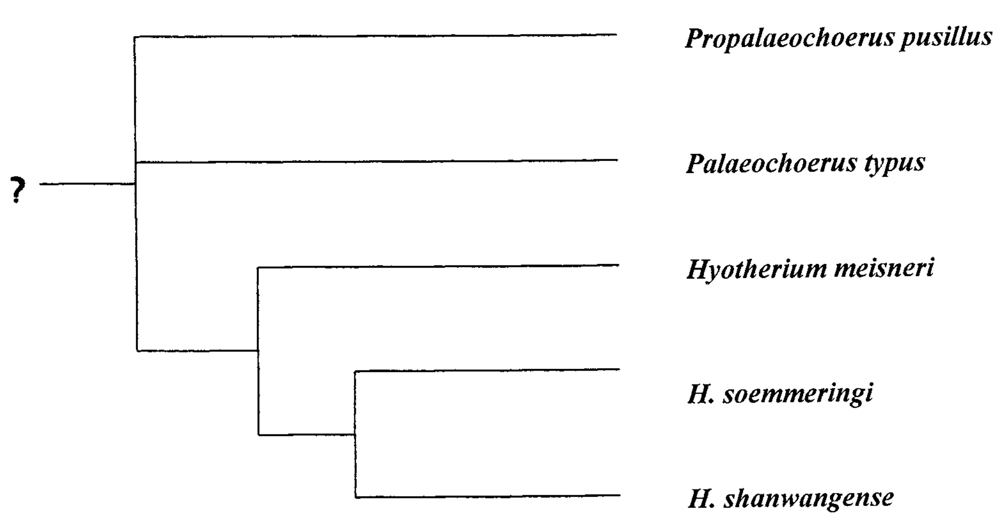


FIGURE 10. Result of the phylogenetic analysis within the genus *Hyotherium*.

TABLE 5. Cladistic data matrix from the coding list.

Taxon	0123456789	0123
Propaleochoerus pusillus	0000000000	00?0
Palaeochoerus typus	?000000000	0000
Hyotherium meisneri	0110111101	1011
Hyotherium soemmeringi	1111111101	1011
Hyotherium shanwangense	1110111111	1111

worth noting that the general morphology of the teeth is closer to the robust and angular *B. lockharti* than to the *B. latidens* group, which is characterized by relatively narrower molars. Compared with *Bunolistriodon intermedius* from Tongxin (Ye et al., 1992), the Shanwang listriodont appears decidedly less lophodont. Normally, it is considered that *B. intermedius* in China and *B. guptai* in India (Savage and Russell, 1983) appeared in Asia later than in Europe, but the Shanwang listriodont proves that the subfamily was present in Asia as early as it was in Europe.

CONCLUSIONS

The suid fossils found in Shanwang belong to three taxa: *Sinapriculus linquensis*, gen. et sp. nov., *Hyotherium shanwangense*, sp. nov. and an indeterminate bunodont listriodont.

The new genus *Sinapriculus* is interpreted as one of the most primitive known true suids (Hyotheriinae). The diastemata between the premolars seen in *Sinapriculus* do not occur in *Palaeochoerus* or *Hyotherium*. The assumption that the *Palaeochoerus-Hyotherium* lineage evolved in Europe during the Early Miocene might be a misconception due to the generally plesiomorphic nature of these forms, and the true origin of the Suidae could have occurred earlier in East Asia. Indeed, the discovery of late Eocene suoids from Thailand (*Siamochoerus banmarkensis* and *Egatochoerus jaegeri*) and early Oligocene (or late Eocene, cf. Ducrocq et al., 1998) from China (*Odoichoerus uniconus*) suggest that the Suoidea might have an East Asian origin. Under such a scenario the split between the various suoid lineages could have occurred well before the early Miocene.

The autapomorphic characters of the premolar of *Hyotherium shanwangense* suggest that the species might be close to the origin of the Tetraconodontinae. The listriodont from Shanwang is the earliest known from China, and it attests to the presence of this subfamily in eastern Asia as early as its earliest record in Europe—middle Orleanian (MN4). The possibility that much, if not most, of the early evolution and radiation of suoids occurred in the Oligocene and early Miocene of East Asia appears increasingly probable. The suid community of Shanwang provides evidence of a previously unsuspected early diversity of the family in East Asia.

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