



Foraging behavior of *Chleuastochoerus* (Suidae, Artiodactyla): A case study of skull and mandible morpho-functional analysis

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The skull and mandible of a Late Miocene fossil pig, *Chleuastochoerus*, are compared morphologically with those of extant pigs and peccaries, and subjected to a functional analysis. The presence of a rostral bone in the skull and relatively strong rostral muscles indicates that *Chleuastochoerus* possessed considerable digging ability, though the relatively narrow occipital surface and the shortness of the skull would have restricted the range of motion through which the skull could be swung. The distinctive pre-zygomatic plate and over-canine arch-niche may have played a role in protecting the skull and canines during digging. The massive masticatory muscles, reconstructed based on well-developed parietal and zygomatic crests, would have enabled the mouth to close quickly and contributed to moving the mandible both longitudinally and laterally. The configuration of the cranio-mandibular joint and its relatively high position show clearly that *Chleuastochoerus* was capable of both crushing and grinding movements during mastication. The comparatively simple structure of the crown surfaces of the cheek teeth suggests that the food of *Chleuastochoerus* may have been softer than that of extant suids. The diet of *Chleuastochoerus* is postulated to fall between those of true forest pigs and open habitat pigs, and the habitat of *Chleuastochoerus* to be relatively humid forest edge or nearby areas of open steppe.

Suidae, Late Miocene, Linxia Basin, morpho-functional analysis, foraging behavior

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Foraging behavior and adaptations for feeding in the context of habitat condition have been widely studied in living suids (Ewer, 1958a; Skinner et al., 1976; Kingdon, 1979, 1997; Groves, 1991; d' Huart, 1991), but have been little explored in their fossil relatives. This study focuses on the foraging behavior of *Chleuastochoerus*, a small Asian endemic Late Miocene fossil pig. Isolated teeth of *Chleuastochoerus* were first reported in 1903 from North China, under the genus name *Sus* (Schlosser, 1903). Several craniomandibular specimens of this small suid were subsequently recovered

from the Upper Miocene “*Hipparion* Red Clays” of North China and the new genus *Chleuastochoerus* was established, based primarily on primitive features of the teeth and a distinctive snout and zygomatic structure (Pearson, 1928). In general, this genus is characterized by a bony arch above the upper canine, with a niche in front of the upper canine to accommodate the lower canine when the mouth is closed (we name this structure the “over-canine arch-niche”), and a shelf-like expansion of the anterior end of the zygomatic arch (which we name “the pre-zygomatic plate”). Later studies of this genus were mostly simple reports of new discoveries (Young et al., 1948; Liu et al., 1959; Chou et al.,

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1965; Liu et al., 1978; Tang et al., 1985; Van der Made et al., 1994; Covert et al., 2001; Pan et al., 2006). No extensive morpho-functional or ecological analysis of this genus was ever performed (Pearson, 1928; Vislobokova, 2009). *Chleuastochoerus* was long thought to be endemic to northern China. Beginning in the early 1990s, however, *Chleuastochoerus* began to also be reported from South China (Van der Made et al., 1994; Pan et al., 2006), Vietnam (Covert et al., 2001), and Asiatic Russia (Vislobokova, 2009). Of these new finds, only those from Russia include craniomandibular materials that clearly show *Chleuastochoerus* characters. The specimens from southern China and Vietnam are too incomplete, being limited to isolated teeth, for their identification as *Chleuastochoerus* to be certain. Therefore, the geographic range of *Chleuastochoerus* may be limited to northern China and the southwestern part of Asiatic Russia.

In recent years, abundant specimens of *Chleuastochoerus* have been found in the Linxia Basin, Gansu Province, China. These new finds have included skulls and mandibles of juveniles and adult males and females, and even a nearly complete skeleton. These new specimens provide an opportunity for more detailed studies of the genus. A special effort to reconstruct some critical aspects of the musculature of *Chleuastochoerus*, and analyze the functional morphology of this taxon, has been made by the senior author of the present paper during her doctoral dissertation research. This paper is a component of that broader study, focusing on foraging behavior and some aspects of the ecology of *Chleuastochoerus*.

1 Materials

The following specimens of *Chleuastochoerus* were studied (IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences; H MV, Hezheng Paleozoological Museum).

Adult skulls: IVPP V 18061, IVPP V 18062, H MV 0569, H MV 1439, H MV 1870;

Adult mandibles: IVPP V 18065-18069, H MV 0564, H MV 0565-0566, H MV 1439;

Juvenile skulls and mandibles: IVPP V 18063, IVPP V 18064.1-2, H MV 0575.

All the specimens studied were collected from the Linxia Basin, Gansu Province, China, and are housed in either the Hezheng Paleozoological Museum or the Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences. The Linxia Basin contains 700–2000 m of Cenozoic deposits. The currently accepted lithostratigraphical subdivisions of the Linxia Cenozoic deposits (Deng et al., 2004a, 2004b; Deng, 2005; Deng et al., 2013), in ascending order, are as follows. Oligocene: Tala and Jiaozigou formations; Miocene: Shangzhuang, Dongxiang, Hujialiang, and Liushu formations; Pliocene: Hewangjia and Jishi formations; Early Pleistocene: Wucheng For-

mation. All of the *Chleuastochoerus* specimens are from the middle-upper part of the Liushu Formation, which consists of light yellowish brown carbonate-cemented siltstones with thin intercalated mudstones and marls. The formation contains abundant fossils of the *Hipparion* fauna and has been dated to 11–6.4 Ma.

2 Comparative morphology and functional analysis

2.1 Foraging behavior

The skull of *Chleuastochoerus* is less elongated than in extant suids (pigs), and its dorsal profile has only a slight posterodorsal inclination unlike in extant suids and tayassuids (peccaries). The anterior tips of the premaxillae bear a pair of flat or slightly concave facets. In extant suoids, the rostral bone (os rostri) contacts the premaxillae and nasal septum, so the paired facets on the premaxillae indicate the presence of a rostral bone in *Chleuastochoerus* (Herring, 1972a) (Figure 1). The over-canine arch-niche of *Chleuastochoerus* looks like that of tayassuids, but the wall of the niche is much thicker and stronger. In both *Chleuastochoerus* and tayassuids the lower canine fits into the niche in front of the upper canine. In extant suids no such niche is present, and the upper and the lower canines both project out of the oral cavity when the mouth is closed. The prezygomatic plate of *Chleuastochoerus* is unique, and significantly enlarges the attachment area available for the facial muscles. In suids and tayassuids there is only weak facial crest. The occipital region in *Chleuastochoerus* is relatively low and faces posteroventrally. Its external lateral crest is strong, and divides the occipital region into a lateral temporal part and a posterior part. In extant suids the occipital region is usually very high, facing primarily backward, and the external lateral crest is very weak so that the temporal and the posterior parts of the occipital region come close to one broad, posteriorly facing plane. The paroccipital process of *Chleuastochoerus* is small and short, directed downward, and situated far from the tympanic bulla. In extant suids, this process is long, directed antero-downwardly, and close to the tympanic bulla. The glenoid of *Chleuastochoerus* is convex longitudinally and slightly concave transversely, with a triangular depression posteriorly; the condyle of the mandible is enlarged and has a triangular posterior facet. The glenoid is slightly above the level of the basioccipital, and far above the level of the tooth row and the base of the paroccipital process. The cranio-mandibular joint of extant suids is very similar to that of *Chleuastochoerus*. In tayassuids well-developed pre- and post-glenoid processes are present, and the glenoid is situated far below the basioccipital but only slightly above the tooth row and at about the same level as the base of the paroccipital process.

Since the rough facets on the premaxillae prove that *Chleuastochoerus* does have a rostral bone, this genus presumably

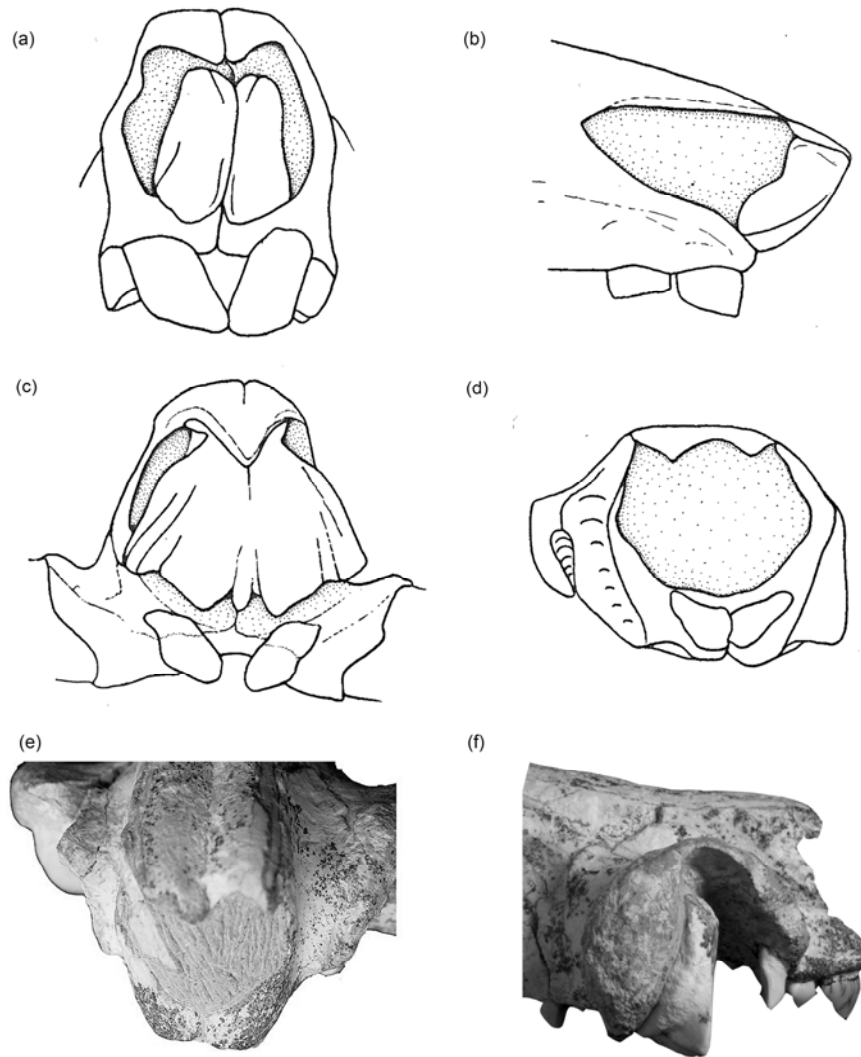


Figure 1 Snouts of *Sus* ((a), (b)), *Hylochoerus* (c) and *Chleuastochoerus* ((d)–(f)). (a), (c)–(e) anterior views; (b), (f) lateral views. (a)–(c) are from Herring (1972a), (d) from Vislobokova (2009).

also had a fleshy snout disc as in extant suids. In view of the small size of the facets, we infer that the rostral bone was probably relatively narrow. The broad pre-zygomatic plate notably enlarges the attachment areas available for several muscles. In living suoids, the rostral muscles (*M. levator rostri*, *M. dilatator naris*, *M. depressor rostri*) originate from this area (Figure 2). In suids the origins of the rostral muscles are more superiorly and posteriorly located (*M. levator rostri* arises from the maxillary, lachrymal and jugal bones above the facial crest, and *M. dilatator naris lateralis* from the facial crest), and are relatively large in *Sus* (Figure 2(d), (h)) and *Potamochoerus* (Figure 2(c), (g)). In tayassuids all these muscles appear to originate from the maxillary bone below the facial crest (Figure 2(b), (f)). Woodburne (1968) drew the origins of *M. levator rostri* and *M. dilatator naris* above the facial crest, but Herring (1972a) reported finding no individuals in which this was the case. In *Chleuastochoerus*, the attachment areas for *M. levator rostri* and *M. depressor rostri* are undoubtedly enlarged by the pre-zygo-

matic plate: *M. levator rostri* originates from the preorbital fossa, which is above the pre-zygomatic plate, and *M. depressor rostri* originates from a depression on the anterior part of the ventral surface of the pre-zygomatic plate (Figure 2(a), (e)). The anterior end of the pre-zygomatic plate is very thin and maybe cannot be an attachment area. However, we found a small, deep depression in the anteroinferior part of the preorbital fossa. This depression occupies about half the size of the preorbital fossa and could potentially have served as an attachment area for *M. dilatator naris*. As a result, we postulate that the preorbital fossa contained the origins of both *M. levator rostri* and *M. dilatator naris*. This would imply that *M. dilatator naris lateralis* was extremely massive in *Chleuastochoerus*, possibly larger than in any other known suoid. The relatively broad occipital region in living suids suggests that the muscles (*M. splenius*, *M. complexus*, etc.) that swing the skull mainly in the horizontal plane are enlarged and have long moment arms. In contrast, these muscles were probably relatively weak and provided

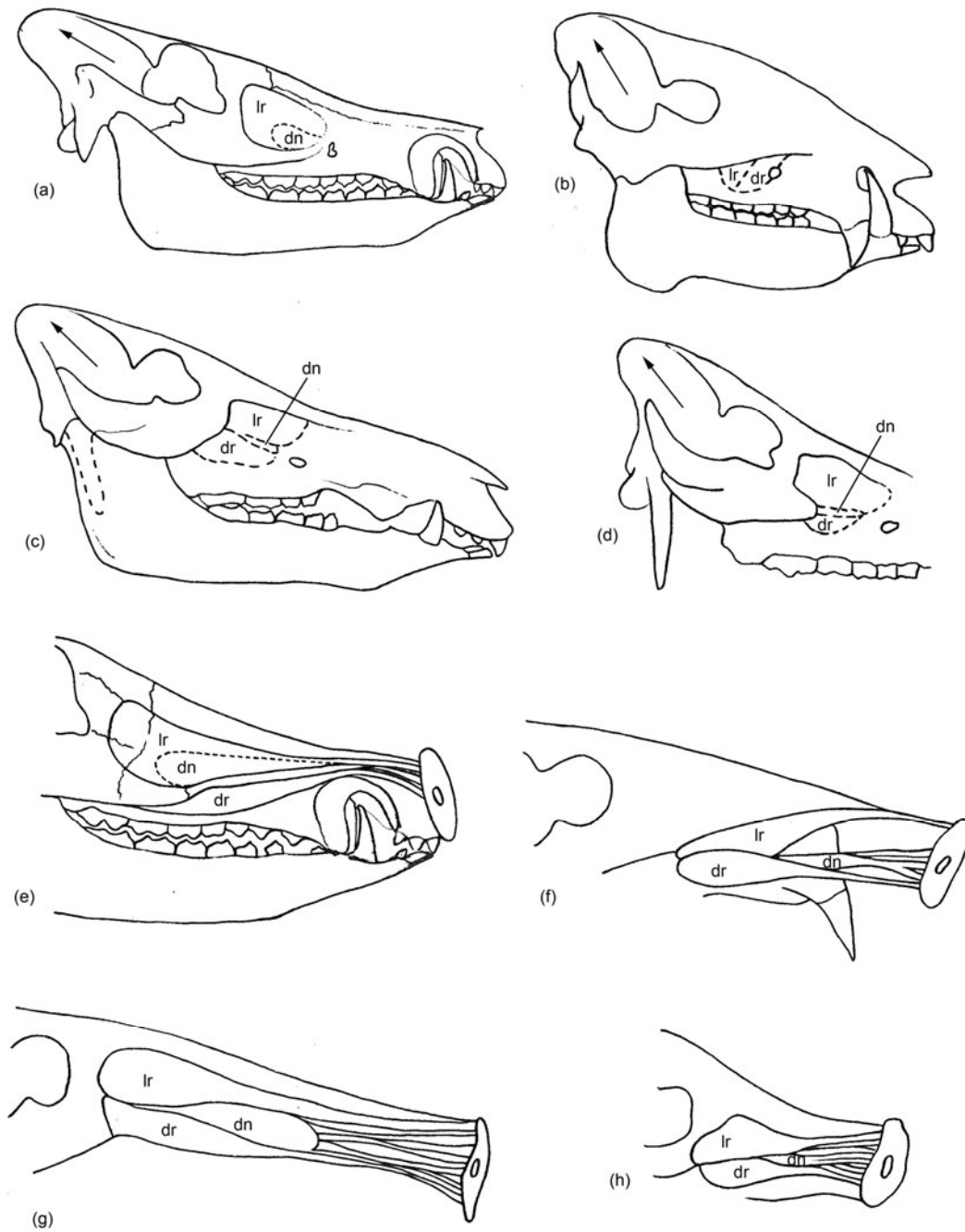


Figure 2 Rostral muscles and orientation of *M. temporalis* in *Chleuastochoerus* ((a), (e)), *Dicotyles* ((b), (f)), *Potamochoerus* ((c), (g)) and *Sus* ((d), (h)). lr, *M. levator rostri*; dn, *M. dilatator naris lateralis*; dr, *M. depressor rostri*; (b), (c) modified from Herring (1972b); (d), (f)–(h) modified from Herring (1972a).

with relatively short moment arms in *Chleuastochoerus*, because of the narrowness of the occipital region in this taxon.

The rostral bone, the rostral muscles, and the occipital region that we discussed above are closely related to one of the most important behaviors of extant suoids, namely digging. The rostral bone supports the fleshy terminal snout disc, which can be used as a strong digging tool. It is believed that a narrow rostral bone (in extant *Sus* (wild boar), *Potamochoerus* (bush pig), and *Dicotyles* (peccaries)) can

serve as an incisive tool for digging or other manipulatory activities, whereas taxa with a wide one (in extant *Phacochoerus* (warthog) and *Hylochoerus* (giant forest hog)) are “probably less proficient in precise manipulations or in applying a large force to a small area” (Herring, 1972a). *Chleuastochoerus* was previously thought to lack a rostral bone, primarily because the anterior end of the premaxilla was short and rounded off whereas the anterior end of the nasal was situated posterior to that of the premaxilla (Pearson, 1928). In *Sus* the premaxilla is long and sharp, the

nasal reaches almost as far forward as the premaxilla, and the rostral bone is interposed between the tips of the nasal and the maxilla. However, our observations suggest that the position of the tip of the nasal may not be a reliable indicator of whether a rostral bone was present, because the rostral bone does not always contact the nasal. More important evidence is provided by the rough facet on the premaxilla of *Chleuastochoerus*, which shows that the rostral bone articulated with the premaxilla. Although we have not yet found a rostral bone in *Chleuastochoerus*, we believe that one was present. The rostral muscles are better developed in extant suids than in other artiodactyls. They help to “maintain the integrity of rhinarial structures during wrenching” and “cause alterations in rhinarial form centering around the nostrils” (Herring, 1972a). The muscles of the occipital region provide the force needed for powerful digging movements, and the force usually operates on the neck like a wedge. In extant suids, the relatively large muscles of the occipital region and their long moment arms increase the amount of torque that can be exerted about a given joint’s center of rotation, and the elongated skull increases the length of the arc traversed by the snout when the head is swung through a given angle. In *Chleuastochoerus* the occipital surface is considerably narrower than in extant suids, and the skull is much shorter. For these reasons, both the force and the range of the swing of the skull would have been relatively smaller in *Chleuastochoerus* than in extant suids.

The digging ability of extant suoids varies. *Sus* and *Potamochoerus* are considered strong diggers with sensitive snouts (Herring, 1972a; Kingdon, 1979, 1997). *Phacochoerus* and *Hylochoerus* are believed to engage in digging less commonly (Frädrich, 1965; Dorst et al., 1970; Field, 1970; Herring, 1972b), and the rooting behavior of these suids has been claimed to be scraping rather than true digging (Herring, 1972a) because it involves use of the strongly developed tusks. *Dicotyles* (the collared peccary) has been observed to spend considerable time digging (Eddy, 1961), although it has been stated that “most of the foraging time is spent moving the snout about near the ground but not actually digging with it” (Herring, 1972a). Nevertheless, analysis of stomach contents shows that the diet of *Dicotyles* includes a small proportion of roots and invertebrates, implying at least some digging activity (Herring, 1972a; Everitt et al., 1981).

Being equipped with a narrow rostral bone and strong rostral muscles, *Chleuastochoerus* was undoubtedly a strong digger like *Sus* and *Potamochoerus*. However, the relatively narrow occipital region and short skull length would have restricted the swing range of the skull, and the relatively small canines probably could not be used for scraping because of their more downwardly direction. We suggest that *Chleuastochoerus* engaged in digging, like *Sus* and *Potamochoerus*, but that digging behavior in *Chleuastochoerus* was mainly effected by the rostral bone and the rostral mus-

cles and involved a smaller range of head motion than the two modern genera. When digging, the lower and upper canines would have been tightly locked and housed inside the thick over-canine arch-niche, which may have helped protect the canines and shield them from stresses during rooting. Similarly, the pre-zygomatic plate may have not only enlarged the attachment area for the rostral muscles, but also reinforced the skull and protected the lateral parts of the head. When digging, stresses on the skull would have been directed mainly antero-posteriorly and the pre-zygomatic plate would have played a role of massive counterforts, absorbing some of the pressure (Vislobokova, 2009).

Differences in the position and morphology of the cranio-mandibular joint are known to influence the movements of the mandible. The strong pre- and post-glenoid processes of tayassuids suggest that mandibular movement is restricted in a way that maintains accurate occlusion between the lower and upper canines (Herring, 1972b). In suids, by contrast, the absence of pre- and post-glenoid processes implies that jaw movements are less strongly constrained. A superiorly positioned cranio-mandibular joint is a common feature in herbivorous and omnivorous mammals, and is claimed to help equalize the occlusal pressure along the tooth row and enhance the mechanical advantage of the masseter and medial pterygoid muscles (Moss, 1968). The relatively ventral cranio-mandibular joint in tayassuids has been suggested to allow the lower canine to move more dorsoventrally as opposed to anteroposteriorly, helping to increase the effective gape and prevent collisions between the canines during jaw elevation and depression (Herring, 1972b). Because of the constraints on the motion of the mandible, grinding mastication is relatively weak in tayassuids and the chewing stroke is essentially vertical. In extant suids, transverse mastication occurs in every genus (Field, 1970), and crushing and grinding are both important components (Herring, 1985). Crushing movements are approximately vertical, and significant dorsoventral pressure can be brought to bear because of the relatively vertical position of M. temporalis and the massive M. masseter. Since *Chleuastochoerus* has a relatively dorsal cranio-mandibular joint and no structures that would have tightly restricted mandibular movement, mastication in *Chleuastochoerus* probably involved both crushing and grinding as in extant suids.

2.2 Masticatory mechanism

The dentition of *Chleuastochoerus* is generally *Sus*-like, but simpler and more primitive. The incisors of *Chleuastochoerus* are clearly primitive. The I1s are the broadest and highest, but are still smaller and simpler than those of many other suoids, including even the primitive Middle Miocene *Hyotherium*. The I2 and I3 are markedly lower, smaller and simpler than the I1. The i1 and i2 are brachyodont and the i3 is significantly reduced. In extant suoids, the medial incisors are robust. The lateral incisors are reduced in *Sus*, *Potamo-*

choerus and tayassuids, and absent in *Phacochoerus* and *Hylochoerus*. The upper canine of *Chleuastochoerus* is specialized. This short and robust tooth is directed mainly downward-forwardly and slightly outward, but never upward. The orientation of the upper canine in *Chleuastochoerus* resembles the tayassuid condition. The upper canine is usually large in extant suids, especially in *Phacochoerus* and *Hylochoerus*, and extends laterally before curving upward. The lower canine of *Chleuastochoerus* is also more tayassuid-like and locks tightly against the upper canine when the mouth is closed. In *Chleuastochoerus* the upper and lower canines are both sharp, but nevertheless fit inside the oral cavity as in tayassuids. However, the upper canine of *Chleuastochoerus* is less sharp than in tayassuids, and the anterior surface of this tooth bears a wear facet that is notably broad. In suids, both the upper and the lower canines project out of the oral cavity, but they are not arranged as tightly as in tayassuids, and the upper canine is not sharp. The premolars of *Chleuastochoerus* are relatively large, sharp, and not reduced in number, more similar to the condition in *Sus*. The molars of *Chleuastochoerus* are much simpler than those of other taxa, and their relatively low crowns bear only a small number of simple accessory cusps and furrows; the third molar of *Chleuastochoerus* is not as elongated as in extant suids. *Sus* has large, sectorial premolars and complicated molars, with numerous accessory cusps and large occlusal surfaces covered by thick, rough enamel. In *Phacochoerus* and *Hylochoerus* the premolars are small and often reduced in number, and the molars are elongated. The molars of *Hylochoerus* have sharp hills and valleys, forming transverse lophs, whereas those of *Phacochoerus* are hypsodont and have a large number of cusps that are uniform in size and arranged in longitudinal rows (Figure 3).

The relatively brachyodont and bunodont molars of *Chleuastochoerus* undoubtedly indicate that this animal was omnivorous like extant suids. However, variations in tooth structure among extant suids indicate specialization for different diets: for example, the large mesial incisors of *Sus* and *Potamochoerus* are thought to play a major role in tearing food. The sharpening of both the upper and the lower canines in tayassuids and the restricted size of the wear facet on the upper canine prove that both canines are used during biting, and that the mandible moves mainly vertically and only slightly transversely during jaw closure. In suids, by contrast, jaw movement may be less restricted given that both canines project out of the oral cavity and are not as closely appressed when the jaws are closed as in tayassuids, and that the upper canine does not become sharp (Herring, 1972b). *Sus* uses its large, sectorial premolars to prepare large pieces of food for ingestion, and its complicated molars for grinding. The specialized dental characters of *Phacochoerus* and *Hylochoerus* have been considered generally analogous to those seen in folivorous monkeys, suggesting that these suids are more herbivorous than *Sus* (Herring,

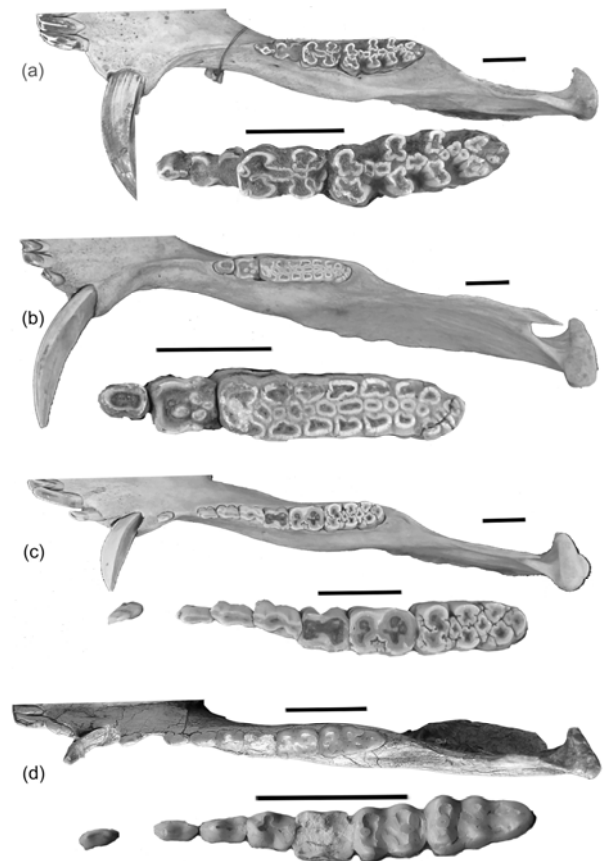


Figure 3 Left mandibles of *Hylochoerus* (a), *Phacochoerus* (b), *Sus* (c), and *Chleuastochoerus* (d) in occlusal view. Scale bars equal 3 cm.

1980). *Hylochoerus* has been reported to eat herbaceous plants and possibly invertebrates (Ewer, 1958b, 1970), and *Phacochoerus* is believed to rely more on grazing (Field, 1970). It is reasonable to postulate that the simple and small incisors of *Chleuastochoerus* may have been less efficient at tearing food. The jaw probably moved both vertically and transversely given the broad wear facet on the anterior surface of the upper canine, implying that the canines could be used for taking in and tearing food as well as for display and combat. The relatively large, sharp premolars could also have been used for breaking down large pieces of food, whereas the relatively simple, low-crowned molars suggest that *Chleuastochoerus* differed from *Sus* and *Potamochoerus* in preferring softer food.

Besides dental morphology, the position and size of the masticatory muscles are important factors that influence mastication. The masticatory muscles of extant suids include the jaw elevator muscles and jaw dilator muscles. M. temporalis and M. masseter are very important jaw elevator muscles. In extant suids M. temporalis originates from the rough part of the temporal fossa and inserts on the medial and lateral surfaces of the jaw, on and around the anterior part of the coronoid process of the mandible. This muscle functions chiefly to raise the lower jaw, closing the mouth. M. masseter is extremely massive in extant suids. This

muscle is divided into two or three layers, but the boundaries between the layers are not clear. *M. masseter* originates from the zygomatic arch and inserts on nearly the whole lateral surface of the broad part of the ascending ramus of the mandible, from the angle of the mandible to the coronoid fossa that lies below the coronoid process (Sisson et al., 1953; Herring, 1972b; Kneepkens et al., 2010).

The skull of *Chleuastochoerus* lacks a sagittal crest but has clearly convergent parietal crests, a relatively large temporal fossa, and an occipital region that slants strongly posteriorly. Accordingly, the area of origin of *M. temporalis* appears to have been large and to have taken the form of a longitudinally elongated rectangle (Figure 4(a)), making the muscle fibers more oblique in orientation. In extant suids

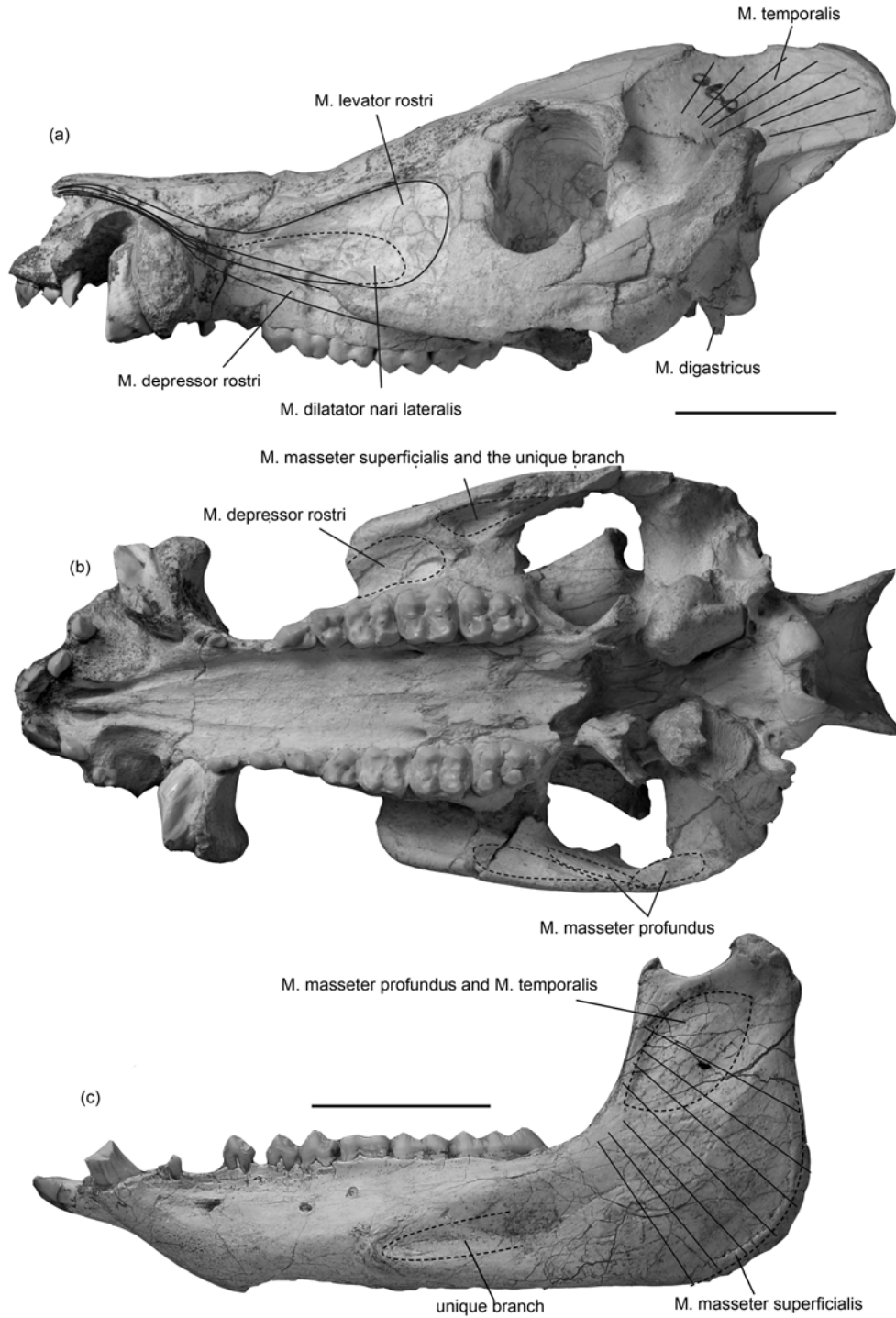


Figure 4 Rostral and masticatory muscles of *Chleuastochoerus*. (a) lateral view of skull; (b) ventral view of skull; (c) lateral view of mandible. Scale bars equal 5 cm.

the facial region is elongated and the parieto-occipital region is relatively short, so *M. temporalis* is smaller (in the domestic pig, *M. temporalis* accounts for only about 26.3% of the total mass of the masticatory muscles, *M. masseter lateralis superficialis* for 33.5%, and *M. masseter lateralis profundus* for 17.7% (Vislobokova, 2009), whereas in *Chleuastochoerus* *M. temporalis* was very massive and may have equaled *M. masseter* in volume), and the orientation of the fibers gradually shifts to more vertical (Figure 2). In many early suoids the parietal crests converge strongly (*Hyotherium* has a sagittal crest), resulting in a relatively large temporal fossa and implying the existence of a correspondingly large *M. temporalis*. This feature is somewhat reminiscent of the condition in carnivores, which have a strong sagittal crest and massive *M. temporalis*. Carnivores can close the mouth quickly in order to catch fast-moving prey, and in early suoids the strongly convergent parietal crests and massive *M. temporalis* with obliquely oriented fibers may have facilitated similarly rapid jaw closure.

As described above, the pre-zygomatic plate in *Chleuastochoerus* has notably enlarged the attachment area available for some of the facial muscles. The relatively broad ventral surface of the zygomatic arch bears distinct crests and pits that indicate the attachment of *M. masseter* (Figure 4(b)). *M. masseter superficialis* is quite wide, originates from the posterior part of the pre-zygomatic plate, and terminates near the border of the mandibular angle. The border of the mandibular angle extends posteriorly to a point below the glenoid, so that the line of action of *M. masseter superficialis* arises from a point between the middle of the pre-zygomatic plate (near level of the anterior border of M3) and the most prominent part of the mandibular angle. The line of action intersects the long axis of the skull at a 45° angle, enabling the muscle to exert a strong forward pull on the mandible. In extant suids the zygomatic arch is very thin, with a sharp ventral edge, so *M. masseter* arises mainly from the medial surface of the arch. In *Sus*, the ventral end of the very long paroccipital process extends far below the palate and reaches the horizontal ramus of the mandible. This causes *M. digastricus* to exert a backward traction on the mandible, as well as pulling the mandible downward to open the mouth. In *Chleuastochoerus*, however, the paroccipital process is very short, so that *M. digastricus* (which extends from the free end of the paroccipital process to the middle of the medial surface of the horizontal ramus of the mandible) is directed from supra-posterior to infra-anterior. The main function of *M. digastricus* in this taxon is to help open the mouth, and only very limited backward traction can be produced. Perhaps this can explain the massive size of *M. masseter superficialis* in *Chleuastochoerus*.

We suspect that a unique division of *M. masseter* is present in *Chleuastochoerus*, in addition to the divisions present in typical suoids. The lateral surface of the horizontal ramus of the mandible bears a rough bulge situated in front of a narrow depression (Figure 4(c)), and these features

could indicate a muscle attachment area. The inferred position and the orientation of this muscle support the interpretation that it might be an anteroventrally descending unique branch of *M. masseter*, or a ventral branch of *M. platysma* (the ventral branch of *M. platysma* has been mentioned terminates on the body of the mandible (Herring, 1972a; Kneepkens et al., 2010)). The former possibility implies that *M. masseter* may have provided stronger traction for the jaw to move posteriorly, perhaps compensating for the weakness of the backward traction exerted by *M. digastricus*. The latter possibility implies that more musculature was available to pull the mandible together with the skull postero-downwardly, increasing the digging ability of *Chleuastochoerus*.

2.3 Diet

The Old World pigs were said to thrive best in moist areas with dense cover and soft soils, but *Phacochoerus* has adapted to arid habitats in Africa (Kingdon, 1979, 1997). *Sus* and *Potamochoerus* are strong diggers. *Sus* is adapted to a wide range of habitats that from a moist forest habitat to an arid habitat, so its food also has a big range. *Sus* in Africa adapts to the humid forest habitat and feeds on seeds, bulbs, roots, fallen fruits, snails, insect larvae, and other invertebrates, and occasionally small vertebrates. *Potamochoerus* are divided into two groups, *Potamochoerus larvatus* (true forest bush pig) and *Potamochoerus porcus* (savannah-adapted). *Potamochoerus larvatus* is adapted to a wide range of forest and woodland habitats. Its food is highly variable according to local and seasonal conditions, but may include roots, tubers, bulbs, corms, fallen fruits, herbage, and some fungi, larvae, beetles, snails, amphibians and reptiles. *Potamochoerus porcus* usually lives in areas of savannah that are near river courses and swamp forest margins. Its diet consists mainly of underground roots and tubers, but includes some fallen fruits and invertebrates. *Hylochoerus* is forest glade grazer, being mainly adapted to forest/grassland mosaic habitats. *Hylochoerus* feeds on grasses, sedges and herbs, and masticates less thoroughly than *Phacochoerus*. *Phacochoerus*, the only genus mainly adapted to arid environments, is also mainly a grazer. *Phacochoerus* inhabits arid and open areas, including savannah and open-woodland, and feeds on grasses, mats, seed heads, and in the dry season also leaf bases and rhizomes, occasionally fallen fruits, faeces and animal foods (Kingdon, 1979, 1997).

Comparisons to extant taxa indicate that *Chleuastochoerus* undoubtedly had considerable digging ability. Also, the teeth of *Chleuastochoerus* are similar to those of *Sus* and *Potamochoerus*, suggesting that *Chleuastochoerus* also resembled these two suids in its dietary preferences. However, the seemingly limited range of head motion and relatively primitive and simple teeth suggest that *Chleuastochoerus* may have been less effective at digging than *Sus*

and *Potamochoerus*, and that its typical food may have been somewhat softer. It is possible that *Chleuastochoerus* ate proportionally more overground food than *Sus* and *Potamochoerus* do today. *Chleuastochoerus* was obviously a stronger digger than *Hylochoerus* or *Phacochoerus*, taxa whose teeth are highly specialized for grazing. It is likely that *Chleuastochoerus* would have eaten more underground food and less herbage than *Hylochoerus* and *Phacochoerus*. Moreover, the strongly convergent parietal crests and massive, obliquely directed M. temporalis of *Chleuastochoerus* would have facilitated a rapid closure of the mouth, potentially allowing capture of fast moving animals such as insects or small vertebrates. In short, the diet of *Chleuastochoerus* may have been intermediate in composition between those of true forest suids (*Sus*, *Potamochoerus*) and open habitat suids (*Hylochoerus*, *Phacochoerus*) today, perhaps most closely resembling that of the savannah-adapted *Potamochoerus*. It is possible that the diet of *Chleuastochoerus* consisted of a substantial amount of roots, tubers, corms, bulbs, seeds, fallen fruits and leaves, fungi, and a small amount of herbage, insect larvae, snails, beetles, and occasionally small vertebrates like amphibians and reptiles.

2.4 Ecology

Chleuastochoerus fossils were abundant in the Late Miocene *Hipparion* fauna of northern China. This genus has been reported to be rarely found at localities that have also yielded the contemporaneous taxa *Propotamochoerus* and *Microstonyx* (Pearson, 1928), which are closely related to the extant *Potamochoerus* and *Sus*. Since *Potamochoerus* and *Sus* usually occupy true forest habitats, *Propotamochoerus* and *Microstonyx* have been postulated to live in woodland or small wood islands, whereas *Chleuastochoerus* would have occupied neighboring areas of open savannah (Pearson, 1928). However, *Chleuastochoerus* and *Microstonyx* occur together in deposits in the Linxia Basin of Gansu Province (Liu et al., 2004), and have been postulated to have lived in a close forest habitat based on body size (Liu, 2003).

The climate of North China has been interpreted as surprisingly humid during the Late Miocene, when Europe was experiencing arid conditions, based on the hypsodonty of Neogene herbivores. The relatively humid Late Miocene climate of North China may have been partly caused by the intensification of monsoon circulation that resulted from the uplift of the Tibetan Plateau, and the “*Hipparion* Red Clay” of North China was apparently deposited under these humid conditions (Fortilius et al., 2002). Moreover, the composition of the Late Miocene mammalian faunas of North China has been interpreted as indicating regional differentiation between a close and humid environment in the east and an open and arid one in the west, which was closely related to the intensification of the summer monsoon (Zhang, 2006). On the other hand, the Linxia Basin strata dating to the

middle-late Late Miocene are thought to have been deposited in an open but humid environment, based on a ceno-gram analysis of their fossil mammal fauna (Deng, 2009).

The inferred foraging behavior and diet of *Chleuastochoerus* provided a possibility for us to reconsider the deductions about the Late Miocene climate of North China given above. Since *Chleuastochoerus* had considerable digging ability, it would presumably have preferred to live in areas in which the ground was soft and wet enough for digging to be feasible. Furthermore, the diet of *Chleuastochoerus* was probably intermediate in composition between those of true forest pigs (*Sus* and *Potamochoerus*) and open habitat pigs (*Hylochoerus* and *Phacochoerus*), perhaps most closely resembling the diet of *Potamochoerus porcus* that are adapted to savannah conditions. We postulate that the habitat of *Chleuastochoerus* may also have been similar to *Potamochoerus porcus*. *Sus* and *Potamochoerus* mainly live in humid and close environment, except *Potamochoerus porcus* is savannah-adapted. By contrast, *Hylochoerus* favors forest and grassland mosaics habitats, and *Phacochoerus* inhabits arid regions and open savannahs. *Chleuastochoerus* may have been adapted to relatively humid but open environments, like forest edges, or may have lived near river courses and swamp forest margins like modern savannah-adapted *Potamochoerus porcus*. The proportions of the limb bones of *Chleuastochoerus* also suggest adaptation to a relatively open habitat. All of the limb bones are distinctly slender, the hind limb is much longer than the forelimb, and the lateral digits are significantly reduced. The limb bones of *Chleuastochoerus* are most similar in their proportions to those of *Phacochoerus*, which is a capable sprinter and lives in savannah habitats (Kingdon, 1979, 1997). Moreover, the fact that *Sinohippus* and *Tapirus* occur together with *Chleuastochoerus* in the Linxia Basin implies the presence in the Late Miocene of North China of some shrubs that were suitable food for generalized browsers (Hou et al., 2007; Deng et al., 2008). *Sinohippus* is a brachyodont equid thought to have lived near the forest edge and fed on soft leaves (Hou et al., 2007), whereas *Tapirus* has been reported to feed on low-cellulose foliage such as leaves, fresh sprouts, small branches, and, in Central American tapirs, some fruit (Janis, 1984; Deng et al., 2008). In addition, stable carbon isotope analysis of the tooth enamel of the Chinese Late Neogene mammals also shows that northern China was covered during the Late Miocene, pre ~7 Ma, in steppes dominated by C3 grasses instead of savannas dominated by C4 plants; then between 7 Ma to the Early Pliocene, there were still nearly pure C3-Plant ecosystems in the southern Chinese Loess Plateau, and the Chinese Loess Plateau was characterized by a pattern of northward-increasing C4 vegetation (Hou et al., 2006; Passey et al., 2009). For those basins from where *Chleuastochoerus* fossils were collected, Linxia Basin, which resides on the western margin of the Chinese Loess Plateau and was rich in *Chleuastochoerus* fossils, was dominated by C3

vegetation for most of the Late Neogene; and a small component of C4 vegetation was found in the diet of the herbivores from Lantian and Baode; the C4 signal is greatest at Yushe but there is less *Chleuastochoerus* fossils found from this area. The sum of the available evidence suggests that *Chleuastochoerus* occupied relatively humid forest edges or nearby areas that were basically steppe-like but nevertheless contained a diversity of vegetation types, perhaps near river courses and swamp forest margins.

3 Conclusions

Though *Chleuastochoerus* is only a small endemic suid form, its occurrence in the Late Miocene of northern China has its own significance. The rough facets on the dorsal surface of the anterior end of the premaxilla of *Chleuastochoerus* imply the presence of a relatively narrow rostral bone while the peculiar pre-zygomatic plate provides enlarged areas of origin for some of the rostral muscles, indicating that *Chleuastochoerus* had considerable digging ability. However, the relatively weak musculature of the occipital region and the relatively short and flat skull suggest the range of skull motion during digging was smaller in *Chleuastochoerus* than is the case in extant suids with strong digging capabilities (*Sus*, *Potamochoerus*). The distinctive over-canine arch-niche and pre-zygomatic plate would have helped to protect the canine and the lateral side of the head, respectively, during digging. The strongly convergent parietal crests and relatively large, obliquely-directed *M. temporalis* would have enabled rapid closure of the mouth. The massiveness of *M. masseter*, together with the presence of a unique muscle slip inserting on the mandible, indicates that the mandible could be moved forcefully in both the lateral and posterior directions. The relatively high position of the cranio-mandibular joint, and the fact that this joint does not appear to have been strongly restricted in its movements, suggest that mastication in *Chleuastochoerus* involved both crushing and grinding as in extant *Sus* and *Potamochoerus*. The dentition of *Chleuastochoerus* also resembles those of *Sus* and *Potamochoerus* except that the incisors and cheek teeth are simpler in *Chleuastochoerus*, suggesting that this taxon may have eaten softer food than the two living genera. Based on comparisons to modern forms, the diet of *Chleuastochoerus* was probably intermediate in composition between those of extant true forest suids and open habitat suids, consisting of roots, tubers, corms, bulbs, seeds, fallen fruits and leaves, and fungi, some herbage, insect larvae, snails, and beetles, and occasionally small vertebrates like amphibians and reptiles. *Chleuastochoerus* is postulated to have inhabited relatively humid forest edge environments or nearby areas of open steppe that contained a diversity of vegetation, adding fresh evidence that the area of the Linxia Basin was open but still relatively humid in the middle-late Late Miocene.

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