Postcranial skeletal morphology in living and fossil African Suidae

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2 tables

This paper examines the postcranial adaptations and functional morphology of modern and fossil Afrotropical pigs, particularly as they relate to habitat preference. Pigs are large bodied dietary generalists (Hatley & Kappelman 1980). Fossil pigs are widespread and relatively common in the African fossil record, which gives us the opportunity to examine their skeletons in the past and in the present. In East Africa, where their fossil record is particularly good, their evolutionary history is relatively well known and is the basis for biostratigraphic correlations throughout the continent (Cooke 1967 *et seq*; Cooke and Wilkinson 1978; Harris & White 1979; Harris 1983).

The earliest known Suidae are from the Oligocene of Eurasia (Savage & Long 1986; Carroll 1988; Orliac *et al*. 2010a, 2010b; Bishop 2011; Gongora *et al.* this volume). Whereas all other even toed-ungulates (Mammalia: Artiodactyla) developed dentitions with selenodont cusps, only pigs, peccaries, and hippopotami retained bunodont dentition. Although there is some disagreement on taxonomy and evolutionary relationships, a consensus view holds that four extinct and three living genera occurred during the Pliocene and Pleistocene of Africa (Cooke & Wilkinson 1978; Cooke 1978a, b; Harris & White 1979; Bishop 2011; Gongara *et al.* this volume). There are three major radiations that took place: *Nyanzachoerus* → *Notochoerus*, *Kolpochoerus* → *Hylochoerus* (and *Potamochoerus*), and *Metridiochoerus* → *Phacochoerus* (Cooke 1978a,b; Harris & White 1979; White 1995). The earliest of these, *Nyanzachoerus* → *Notochoerus*, were archaic tetraconodont pigs and went extinct without issue. The outcome of the other radiations of suine pigs differs substantially. The modern survivor of the *Metridiochoerus* lineage is a derived genus, the warthog *Phacochoerus*. The bushpig *Potamochoerus*, a modern representative of the *Kolpochoerus* radiation, is a conservative representative of it, occuring rarely throughout the fossil record in a form very close to its modern appearance. The other taxon thought to have its genesis in that lineage, the (giant) forest hog, *Hylochoerus*, is derived in several aspects but has a poor fossil record. At times, some fossil sites preserve up to six sympatric and co-occurring suid taxa (Harris & White 1979; White 1985; Foley 1987).

African suids underwent several large adaptive radiations and during some time periods were highly diverse and speciose. Lengthening of the face, development of large upper and sometimes lower canines, and increased emphasis on the third molar as the most important functional dental element are recognised evolutionary trends in the African Suidae (Harris & White 1979; Harris 1983b; Savage & Long 1986). These trends manifested in each of the suid radiations to a greater or lesser extent. Changes in cranial anatomy had two modes. The first was functionally correlated with the dental changes and involved modifications in muscle position and thus their action related to mastication. The second suite of changes involved reinforcement or ornamentation of the skull akin to that underlying 'warts' and verrucosities in modern suids. This is thought to be sexually dimorphic and thus linked to both active and passive sexual display.

The postcranial anatomy of modern and fossil pigs is relatively poorly studied. Compared to other artiodactyls, or ungulates more generally, suoids have a relatively generalised postcranial skeleton. They lack many of the morphological specialisations linked with cursoriality in Bovidae and Equidae. Locomotor function and weight bearing relies on the third and fourth rays of both the forelimb and hindlimb, which remain unfused in modern African suids, although not in the hindlimb of modern peccaries. The second and fifth rays are retained in the skeleton, albeit reduced in both length and robusticity. Radius and ulna are unfused in most African suids although sometimes the ulna is relatively reduced in size and function and fused with the radius as, for example, in the more cursiorial, open-country preferring warthog.

Modern African pigs have marked habitat preferences, with warthogs (*Phacochoerus*) preferring open grassland habitats, bushpigs (*Potamochoerus*) preferring broken cover, bushland habitats, and the forest hog (*Hylochoerus*) living in dense forest as its name implies. Despite the generalised nature of their postcranial skeleton, both modern and fossil pigs exhibit specialisations related to differences in locomotion linked to their preferred habitats. The presence of morphological characters that relate to habitat preference allows us to separate their postcrania into open, closed, and intermediate habitat preferring groups (Pocock 1943; Kingdon 1979; McCrossin 1987; Pickford 1988; Van Neer 1989; Bishop 1994; Bishop *et al.* 1999). The morphological characteristics linked to habitat preference in modern pigs can be used to infer the habitat preferences of fossil pig taxa (Bishop 1994; Bishop *et al.* 1999).

The anatomy and dimensions of several bovid skeletal elements correlate well with locomotor habits associated with particular habitat types - open, closed, and intermediate - and with degree of cursoriality (Kappelman 1988, 1991; Kappelman *et al.* 1997; DeGusta & Vrba, 2005; Plummer *et al*. 2008; Bishop *et al*. 2011; Plummer *et al*. 2015). Locomotor adaptations related to habitat use distort the scaling relationships, based on elastic similarity, expected in some limb measurements; body size is not their sole determinant (McMahon 1975; Scott 1979, 1985). One possible explanation for this has to do with the different requirements for mobility and speed, which are the result of locomotor regimes specific to particular habitats (Scott 1985; Kappelman 1988). This may affect both size and shape in limb elements (Scott 1985). A distortion in the scaling relationship between limb length and body weight has been noted in the Suidae (Karp 1987). Joint stability and the range of rotation and movement of limbs in the parasagittal plane are linked to habitat preference and is examined here (Kappelman 1986). Predator avoidance, which has not been well studied in the Suidae, is thought to be a prime mover in cursorial strategies in the Bovidae. Crypsis as a predator avoidance strategy may also be linked to some long bone characteristics in the Suidae (Karp 1987). Differences in habitat preferences and locomotor regimes are suggested as partial explanations for the observed deviations from the predicted limb lengths. These differences can be used as tools to distinguish among modern suids of different habitat types (Bishop 1994, Bishop *et al.* 1999).

Bishop (1994; Bishop *et al.* 1999) studied postcrania of modern suoids, examining a total sample of 70 individual modern skeletons from the collections of the American Museum of Natural History (AMNH), the National Museum of Natural History (USNM), the Cleveland Museum of Natural History (CMNH), the Field Museum of Natural History (FMNH), the National Museums of Kenya (KNM), the British Museum of Natural History (BMNH) and the Koninklijk Museum voor Midden-Afrika (KMMA). Modern suoid postcrania are not particularly well represented in museum osteological collections, and so the sample size was not as large as would be optimum for this analysis. Two species were not included in the analysis because of a lack of postcrania: *Catagonus wagneri* and *Porcula salvania*. Bias in museum collections adversely affects the study of distal skeletal elements. Sample sizes of carpals, tarsals, metacarpals, and metatarsals are greatly reduced by the lack of preparation, and in some cases failure to collect these elements. Often distal limb elements remain articulated by their tendons, which also hinders detailed research.

There were only eight modern suid species of the true pigs (Suidae) available for study (Table 2.1). If the analysis had concentrated solely on these species, the possibility of correlation within habitat categories due to phylogenetic relationship would have existed.

Taxonomic bias within habitat categories is a problem of studies with the Bovidae, where often all species of the same tribe have the same habitat preference (Plummer *et al*. 2008, 2011). The addition of the peccaries, or New World pigs (Tayassuidae), was intended to eliminate this possibility while increasing the number of species in each habitat category. Large fossil postcrania of extinct Suidae far exceeded their modern descendants in body size. In order to represent the full range of body sizes for suids, while remaining constant to the basic artiodactyl body plan, the common and pygmy hippopotami (Hippotamidae) were included in preliminary analyses, described below.

Modern pigs and peccaries were attributed to one of three broadly defined habitat types on the basis of the ethological literature: open (savannas, grasslands), intermediate (bush woodland, swamp, ecotone), and closed (continuous tree canopy, including forest) (Table 2.1). Differences in locomotor regime, which are associated with these three substrate types, have morphological correlates that are described below (for complete methodology, see Bishop 1994).

Modern suoids - hindlimb

Femur

The cross-sectional areas of the femur taken immediately below the lesser trochanter versus on the lesser trochanter itself show differences that are related to habitat preference. The more cursorial, open habitat forms show less of a discrepancy between the two cross-sectional areas, with the area at the base of the trochanter relatively larger. The cross-sectional area of the femoral shaft appears to be more consistent along its length in the open habitat forms, with the area below the lesser trochanter being almost equivalent to the midshaft cross-sectional area. There is more constriction in the midshaft area (relative to the proximal end) in the closed and intermediate habitat forms. This is also is true distally because the open country animals have less of a discrepancy between cross-sectional area at the base of the lesser trochanter and the cross-sectional area distally, at the attachment for the gastrocnemius, the extensor of the foot immediately proximal to the femoral condyles.

In the open country pigs and peccaries, the midshaft medio-lateral (M-L) dimension is wider than the antero-posterior (A-P) dimension, whereas in intermediate and closed habitat forms the A-P dimension is the larger. The more robust M-L midshaft in the open-country bovids may be linked with increased rigidity in the medio-lateral plane (Kappelman 1988). In the intermediate habitat animals, the distal femur is relatively narrow compared to the proximal articular end. Open country animals have a relatively wider proximal femur. A counterintuitive result is that the greater trochanter height is shorter relative to the functional length of the femur in the open country animals, contrary to the observation in bovids (Gentry 1970). There was a wider range of variation in trochanter height in the open country animals, but the functional implications of this are not understood.

In open country forms, the proximal part of the patellar groove is relatively narrower, and the distal part relatively wider. The reverse is the case for the closed country animals, and the mixed habitat animals have an intermediate morphology. A relatively wide patellar fossa is recognized as an anatomical characteristic of cursorial bovids (Gentry 1970). For both the medial and lateral condyles, the relatively longest (A-P) condyles are found in intermediate habitat forms, whereas the most compressed are found in the closed habitat species. Open country bovids have more elliptically shaped distal femora, a characteristic associated with cursoriality and in increased length of the moment arm for the quadriceps (Kappelman 1988).

Tibia

Many of the muscles that are responsible for the movement of the hindlimb during locomotion originate or insert on the tibia. Among these are *biceps femoris*, which abducts the thigh and flexes the shank, *semitendinosus*, which also flexes the shank, *semimembranosus*, the extensor of the thigh, *sartorius* and *gracilis*, the adductors of the femur and thigh and the digital extensors, flexors, and *peroneus longus*. Thus, the muscular forces exerted on and through it are complicated.

In open country preferring pigs and peccaries, the lateral condyle of the tibia is relatively narrower. The difference between the areas of the articular surfaces of the medial and lateral condyles is greatest in the intermediate habitat forms, which have relatively larger lateral condyles. The tibial midshaft of open country animals is relatively broad compared to the width at of the proximal articulation. They also have antero-posteriorly deep midshaft when the midshaft A-P is compared to the proximal articulation A-P. When considered as a cross-sectional area, the proximal tibia is proportionally much smaller than the midshaft area in the open-country forms. In the distal tibia, the open habitat forms have a marked central constriction, narrowing the tibial shaft. This forms a more stable joint at the distal articulation with the astragalus. Also, as previously documented by Van Neer (1989), the distal epiphysis is more narrow in the open country forms, a morphology that also relates to stability in the parasagittal plane and resistance to mediolateral forces.

Fibula

The fibula's main function in locomotion is for muscle attachment (for the digital flexors and extensors, and for *peroneus longus*) rather than as a bodyweight stress transmitter, so functional differences may relate to factors other than body weight. The proximal epiphysis of the fibula is much longer in the A-P dimension (relative to the M-L) in the open country forms. Expressed relative to the maximum length of the fibula, the midshaft M-L dimension is largest in the open-country specimens. The M-L dimension of the proximal epiphysis is smallest in relation to the midshaft M-L in the open country forms, also emphasizing midshaft robusticity. Distally, the M-L dimension of the malleolus is relatively larger in the open country forms (and see Van Neer 1989). This, like the features in the distal tibia and astragalus, may be linked with increased joint stability and confinement of movement to the parasagittal plane.

Astragalus

The suid astragalus does not conform to the elastic or geometric theories of scaling with body weight (Karp 1987). This suggests that aspects of joint stability and the overall length and proportions of this tarsal can be related to habitat preference. Most differences can be related to joint stability, particularly in the astragalus-calcaneum articulation. Open country forms have posterior calcaneal facets that are more square, rather than triangular. This represents a constraint to the motion of this joint in open country animals, which confines movements of the metapodials and digits to a parasagittal plane. In open-habitat animals, the articulation at the posterior calcaneal facet is relatively long, increasing the range of motion in the parasagittal plane.

The radius of the arc transcribed by the calcaneum on the astragalus is smallest relative to the arc travelled by the tibia on the astragalus in open country animals. The diameter of the lateral portion of the tibial trochlea is closest to the diameter of its medial portion in open country animals, whereas intermediate and closed habitat forms show a more marked disparity of the medial and lateral (larger) aspects of the trochlea. The former condition is linked with cursoriality in increasing the stability of the tibio-astragalar joint during running. In open country forms, the medial and lateral breadth of the tibial trochlea is most similar in country animals, indicating less difference between the two halves of the trochlea. This is a convergence toward the more cursorially adapted bovid form, which constrains movement to the parasagittal plane.

The breadth of the tibial and tarsal trochlea is most similar in the open habitat forms, again a convergence to the bovid condition. In terms of the radius (e.g., the A-P range of movement) in the proximal tibial articulation versus the distal tarsal articulation, both laterally and medially, the least disparity occurs in the open country forms, indicating that range of motion is equally large for the proximal and distal attachments of the astragalus. This ensures that the distalmost hindlimb has a wide arc of motion in the parasagittal plane.

Calcaneum

The length of the calcaneum does not conform to the predictions of the elastic theory, but is more in accordance with the geometric theory (Karp 1987). Open country forms have a relatively broader calcaneal tuberosity. Because the calcaneum is the insertion for the major extensors of the foot, *gastrocnemius* and *soleus mm*., this robusticity is associated with the speed adapted for a cursorial regime. With motion confined to the parasagittal plane, the calcaneum of open-country forms is relatively slender posterior to sustentaculum tali. The relative length of the calcaneal tuberosity reflects the effort arm for the action of the extensors of the foot. It is smaller in the open-country pigs and peccaries. The anterior, articular portion of the calcaneum is relatively longer in the open country forms.

The sustentaculum tali is relatively long and narrow in the open country animals, also representing a limit of inversion and eversion for the feet, and confinement to forward rather than side to side motion. Morphology of the coracoid process, which differentiates bushpigs from warthogs (Van Neer 1989), also distinguishes open from mixed country species. The coracoid of the intermediate habitat species is more robust medio-laterally, and longer anteroposteriorly. Finally, the distal calcaneum articulates both with the astragalus and with the cuboid. In open habitat animals, the cuboid facet is relatively narrow and long, where it is broader in the pigs and peccaries that prefer intermediate to closed habitats. This is interpreted as another instance of lower-limb excursion and mobility being limited to the parasagittal plane in the open habitat species.

Third Metatarsal

These observations focus on suids alone, because the fusion of the third and fourth metatarsals in peccaries makes inter-family comparisons difficult. The articular surfaces of the open country suids' metatarsals are consistently narrowest, which supports the hypothesis that ecomorphic adaptations to cursoriality in open country are linked to joint stability and a reduction of medio-lateral mobility (Kappelman 1988). The relatively narrowest proximal articular facets were in the open country animals, whereas closed country forms had far wider facets.

The relatively deepest posterior proximal metatarsal facet in the third metatarsal was found in the forms that preferred intermediate habitat types. The posterior process of the proximal metatarsal, which articulates with the cuboid and with the fourth metatarsal, is much narrower relative to the proximal articular facet in the open country suids and peccaries, indicating that they have a very gracile process compared with those of the forest species. Many of the characteristics that distinguished best among the different habitat types were those concerned with the morphology of the distal articulation of the metatarsal. The distal trochlea of the third metatarsal was narrowest (M-L relative to A-P) in the open country animals. The least discrepancy in the A-P depth of the trochlea between the raised central flange and its narrowest portion is in the closed country animals, consistent with more distal joint mobility in these animals for coping with varied substrate. The placement of the central flange varied among the three habitat-preference types, with it being placed closest to the middle of the trochlea in the open habitat animals. The distal trochlea itself was most cylindrical and had less A-P constrictions in the open country forms. The lateral aspect of the trochlea is relatively more flared than the medial side in the open country forms, providing less scope for medio-lateral motion along the metatarsal phalangeal joint.

Fourth Metatarsal

The morphologies found in the third metatarsal are echoed here. As was the case for the third metatarsal, the proximal articulation of the fourth metatarsal was relatively narrowest in the open country specimens. Similarly, proximal posterior process of the fourth metatarsal was most gracile in the open country suids and peccaries. The area of the proximal articular surface was largest relative to the midshaft cross-sectional area in the open habitat specimens. Finally, as was the case in the third metatarsal, the flange on the trochlea is more centrally located in the open adapted species.

Modern Suoidea – forelimb

Humerus

Although the functional morphology of the forelimb is dominated by locomotor considerations, for suoids, other non-locomotor functions include kneeling behavior of warthogs while feeding. This may more properly be called non-standard use of the forelimb in locomotion, because warthogs will shuffle around on their "wrists" while feeding. This behaviour might affect forelimb morphology in some forms.

Forest animals have the widest proximal epiphysis, whereas the broadest humeral head is found in the open country adapted pigs and peccaries, for which limb excursion would be expected to be high. A broad and flat humeral head may serve to limit lateral excursion of the humerus during fast locomotion. The least robust greater tuberosities are also found in the open habitat forms. Overall, the area of the proximal end of the humerus is largest, relative to the cross-sectional area at midshaft in the open country animals.

The greatest discrepancy between the mediolateral dimensions of the shaft at the base of the deltoid tuberosity and distally, at its narrowest point, is found in the open country suids. The increase may be in the relative size of the tuberosity, which is the insertion for the deltoid muscle, an important flexor of the humerus. The greater development of this muscle attachment may be a function of cursoriality. The midshaft A-P dimension is largest relative to its the M-L dimension in forest animals. Intermediate and open-habitat specimens may have increased buttressing in the mediolateral plane.

The open habitat suoids have the widest trochlea relative to their overall distal width. This broader articular surface may be to provide confinement of motion to the parasagittal plane. Although the trochlea is broad, the distal end is deepest (A-P) relative to its breadth in the open country animals. This is because the medial epicondyle, on which originates *pronator teres* and flexors of the carpals and digits, is most robust in open country animals. Morphological differences in the distal trochlea of the humerus may relate to stability of that joint in cursorial animals, with a more cylindrical trochlea in the open country forms. This also suggests greater joint stability in the mid-sagittal plane and is similar to the condition in antelopes.

Radius

The radius and ulna are variably fused in the suoids, so consistent and verifiable observations are difficult. The widths of the medial and lateral portions of the glenoid facet, which articulate with the trochlea of the humerus, are most similar in intermediate and open habitat animals. The proportion of the lateral facet width to that of the whole glenoid is smallest in the open country animals, whereas the medial portion is smallest in the forest forms. This implies less motion mediolaterally about the humero-radial joint in open-country forms. The radius is longest relative to its minimum breadth in the open species, suggesting that relative elongation of the limbs is a characteristic of cursorial species (Scott 1985; Karp 1987).

Relative to the mediolateral dimension of the midshaft the distal radius of open country animals was most flared mediolaterally. Relative to the proximal articulation, however, the greatest flare is in the forest species. The area of the distal shaft cross section is smallest relative to the area of the carpal articulation in the open country animals (see also Van Neer 1989). Because the carpal articulation is set in a depression on the distal end of the radius, less articular surface implies a more limited range of motion in that joint for the open-country species.

The carpal articulation of the open country animals is the widest, relative to their A-P depth. This may be due to limiting mediolateral displacement along this joint. The depth of the distal carpal facet articular surface is smallest relative to distal A-P flare in the mixed country animals, and larger in closed and open country forms. Robusticity in the distal radius, both articular and non-articular, may be due to forces other than standard locomotion, because it is upon this radio-carpal-metacarpal joint that warthogs rest during their "kneeling" feeding behavior.

Ulna

Examination of the ulna is subject to the same difficulties as that for the radius, and for similar reasons. As a proportion of the overall length of the radioulna, the ulna is shortest in the closed country animals. This has the additional implication that the radius projects less inferiorly in intermediate and open-country animals. Relative to the length of the radioulna, and to the length of the ulna alone, the olecranon process is shortest in the open country animals. The short olecranon process, which is the effort arm for the triceps muscle, an extensor of the forelimb, in cursorial animals may relate to the overall greater length of the ulna in the open-country forms (Karp 1987). Olecranon length is largest, and it is most gracile, in open country forms. The open country taxa have the deepest semilunar notch, relative to its width. A deeper articulation with the humerus is consistent with the greater stability of articular surfaces in more cursorial animals.

Third Metacarpal

Open country suoids have relatively long third metacarpals, suggesting that cursoriality in pigs is associated with elongated distal segments as is the case for antelopes (Plummer and Bishop 1994). The posterior metacarpal facet, the posterior articulation between the two metacarpals, is more anteroposteriorly deep (relative to its height) in the open habitat forms. This may restrict the motion of the two elements against each other during locomotion on a relatively even, open substrate.

Relative to the distal epiphysis cross sectional area, the proximal epiphysis cross sectional area is largest in the open habitat animals. This has been a persistent pattern in the open-country taxa, to have relatively large proximal epiphyses. The midshaft antero-posterior dimension is smallest relative to its mediolateral dimension in the forest animals, making them more prone to mediolateral bending. Extra breadth in the open and intermediate country animals may be related to increased bone buttressing in the medio-lateral plane, and the relatively high bending stresses in unfused metapodials (as opposed to a single cannon bone, as in bovids) (Karp 1987).

Distally, the cross-section of the shaft is smallest relative to that at the trochlea in the open country animals. The articular surface is relatively expanded, and that the flanges are relatively high in the open country animals. An interpretation of decreased joint mobility outside of the parasagittal plane for open country animals is reinforced by the central position of the bony flange or central ridge on the trochlea. This limits rotation of the proximal phalanges more effectively for cursorial locomotion.

Fourth Metacarpal

Proximally, the carpal facet is broader in the M-L aspect relative to the A-P aspect in the open country animals. This is contrary to the case with the metatarsals, when the open country animals have the narrowest carpal facets, and may be due to differences in morphology or action along the podial-metapodial joint in the fore- and hindlimb. The broader facet in the metacarpal is consistent with limitation of mediolateral motion of the metapodials during cursorial locomotion.

Distally, a relatively wide internal to external (in this case medial to lateral) trochlea is present in the open country animals. This result was also found in the fourth metatarsal, and was interpreted as increasing joint stability. Finally, the cross section through the distal shaft, above the trochlea, was widest in the A-P direction relative to the M-L in the open country forms. This result may be related to greater stress transmission through a deep trochlea, or to non-locomotor parameters.

Considered as a whole, the morphological characteristics of the suoid skeleton showed several interesting characteristics in relation to their relationships to particular habitat preference categories. The intermediate forms sometimes exhibited morphology which differed from that of open and closed habitat animals not by being intermediate, but by being extreme. This may indicate that the exploitation of intermediate and ecotonal habitats requires specialized adaptations in the suids, where in the bovids this habitat preference is associated with "intermediate" morphology (Kappelman 1988). Since the intermediate species had a mosaic of characteristics, another possibility is that different aspects of forest-adapted or open-adapted locomotor patterns are the optimum choice for exploiting bushland, intermediate habitat types.

In general, the variation in morphologies between the different habitat categories was more pronounced in hindlimb than forelimb elements. This might be related to the observation of Scott (1979) that in some bovid tribes the hindlimb is more important in locomotion than the forelimb. Thus hindlimb morphology would be more likely to manifest morphological adaptations to locomotion in particular habitat types. In examination of the forelimb it should also be kept in mind that non-locomotor habits, such as metacarpal "kneeling" in the warthog, may have morphological consequences (Kingdon 1979). It has often been noted that cursorial forms have relatively long limbs (e.g. Smith & Savage 1956; Hildebrand 1974). However, in artiodactyls, limb lengths, especially of proximal bones, correlate highly with body weight (Scott 1979, 1985; Karp 1987).

Evaluation of functional explanations for the habitat specific differences in postcranial limb morphology is hampered by the lack of ethological and physiological data on the locomotor habits of suids. However, a pig-like body plan can possess modifications to particular habitat preferences in ways which predictable. The analyses in Bishop (1994) demonstrate that these skeletal characteristics can be used to estimate habitat preferences in extinct suid taxa.

Fossil pig skeletons

Although pig fossil remains are relatively common in the geological and archaeological record, only partial skeletons that occur with the diagnostic cranial and dental elements can be assigned confidently to taxa. Bishop (1994; Bishop *et al.* 1999) examined partial skeletons of extinct pigs which had been assigned to fossil taxa and had good stratigraphic provenance. Using ecomorphological analysis, partial skeletons of *Nyanzachoerus devauxi*, *Nyanzachoerus kanamensis*, *Notochoerus euilus*, *Metridiochoerus modestus*, and *Kolpochoerus* (*limnetes*) *heseloni* were examined to determine their habitat preferences as determined by postcranial morphology.

Nyanzachoerus devauxi

A partial skeleton of this small, primitive suid has been recovered from the base of the Lothagam sequence (KNM-LT 22970). The specimen is likely to be older than 5.5 Ma (Hill *et al*. 1992; Feibel 2003). Two elements, a tibia and a humerus, were sufficiently complete to analyze. Both are grouped with intermediate, mixed habitat species, leading to the conclusion that this species preferred intermediate habitats.

Nyanzachoerus kanamensis

Several specimens and partial skeletons have been assigned to this taxon. They derive from Kanapoi (Cooke & Ewer 1972) and from the Koobi Fora Region (Harris 1983). KNM-ER 3412 is a partial skeleton assigned to *Ny. kanamensis* (Harris 1983). It derives from area 116, and is most likely dated at approximately 3.0 Ma (Brown & Feibel 1986; Feibel *et al*. 1989). Five skeletal elements are sufficiently complete for analysis. The third metatarsal gives an indication of open habitat preference. However, this result can be discounted due to directionality of error in the DFA models (Bishop 1994). The partial astragalus is assigned to closed habitat preference group. Three skeletal elements, the calcaneum and the third and fourth metacarpals, discriminate with the intermediate habitat animals. The most accurate of the models is for the complete third metacarpal. If this is relied upon, the skeleton's assignment is to an intermediate habitat preference.

On the basis of associated tooth fragments KNM-KP 215 is attributed to *Ny. pattersoni* by Cooke and Ewer (1972), and this taxon was sunk into *Ny. kanamensis* by Harris and White (1979). There are four hindlimb elements complete enough for study: a fourth metatarsal, a calcaneum, an astragalus, and a tibia. The metatarsal is incomplete and could only be analyzed in the model with 3 variables, which has a relatively low success rate. The determination of an open habitat preference for this element is thus less sound. Analysis of all but the metatarsal indicate an intermediate habitat preference, which is the more robust assignment for this specimen (Table 2.2). Although some bones from some partial skeletons known to belong to *Ny. kanamensis* yield anomalous results, most of the evidence points to an intermediate habitat preference for this tetraconodont species. The Kanapoi specimens are not radiometrically dated.

***Nyanzachoerus* indet.**

Several specimens are likely to belong to the genus *Nyanzachoerus*. An additional specimen from Kanapoi, KNM-KP 246, is unpublished, but has an accession designation of *Ny. kanamensis*. This is a nearly complete humerus that discriminates with the open habitat specimens. The full discriminant model for humeri is very robust. However, the specific designation is not definite, and the specimen is mentioned here for completeness. It is possible that the humerus belongs to *Ny. jaegeri,* also found at Kanapoi (Cooke & Ewer 1972).

KNM-KP 243A and B are assigned to *Ny. kanamensis* (Cooke & Ewer 1972). This determination was made on the basis of their similarity to KNM-KP 215, which had associated dentition, and is thus not definite. Because of the possibility that this skeleton belongs to *Ny. jaegeri*, which is also found at Kanapoi, this specimen will be considered as

Nyanzachoerus indet. here. Two bones, a tibia and a third metatarsal, yield disparate results of closed and open habitat types, respectively

A partial skeleton from Lothagam, KNM-LT 436, is also problematic. KNM-LT 436 is a partial skeleton, which is stratigraphically associated with *Ny. syrticus* and its presumed daughter species *Ny. kanamensis.* These are the only two taxa known from this stratum or from any African site of similar age (Harris & White 1979; Hill *et al*. 1992). The post-crania are extremely elongate and the specimen was initially thought to be a bovid. Analysis of the numerous postcranial elements shows a range of results for the six elements sufficiently complete for study. Analyses of the complete tibia and third metatarsal indicate intermediate habitat preference.

Notochoerus euilus

One remarkably complete skeleton of this taxon is known from the Koobi Fora region, KNM-ER 3541 (Harris 1983). The specimen was recovered in Area 117, beneath the Tulu Bor Tuff and is assigned a date of 3.43 Ma here on the basis of this stratigraphic placement (Feibel *et al*. 1989). All of its bones are fragmentary but seven are complete enough for analysis. Three of these, a tibia, a radius, and a third metacarpal, are assigned to an intermediate habitat type. The remaining four, a humerus, an ulna, a fourth metacarpal, and a femur, are assigned to closed habitat preference. The strongest discriminant function that was applied to these elements is that for the humerus. This would suggest that a closed habitat was preferred by this taxon.

Kolpochoerus (*limnetes*) *heseloni*

Two partial skeletons of *Kolpochoerus* (*limnetes*) *heseloni* are available. One from the Chemeron Formation of the Tugen Hills succession, KNM-TH 18934, was recovered from site K099. The site is stratigraphically below a tuff in the Kapthurin River which is dated at 2.8 Ma (Deino *et al.* 2006). Dentally, this specimen is a primitive example of this species, with relatively low crowned teeth and limited expansion of the talon/id. Three bones are relatively complete, a humerus, radius, and ulna. The humerus and ulna are both classified with closed habitat preference specimens, but the radius sorts with the mixed country suoids. The discriminant function for the radius has slightly less reliable statistics, so an attribution to closed habitat preference is indicated here.

The second *K. heseloni* skeleton, KNM-ER 4567, is from Area 8 of the Koobi Fora Region near Ileret. These sediments are dated to approximately 1.5 Ma (Brown & Feibel 1986; Feibel *et al.* 1989). Thus, this specimen derives from 1.3 Ma later in time than the one from the Tugen Hills. During this period, *K. heseloni* dental evolution is characterized by increased hypsodonty (Harris & White 1979). Four distal forelimb elements were analyzed, a radius, an ulna, and third and fourth metacarpals. The ulna, which is partial, was classified with a closed habitat preference. The remaining bones were all complete, and discriminated with the intermediate habitat suoids.

Kolpochoerus majus

One partial skeleton from Olorgesailie, KNM-OG 1521, has been attributed to *Kolpochoerus majus*. The stratigraphic provenance is LS 10 = T10, dated at 0.662 Ma (Potts *et al.* 2004). Although a radiometric date is not available for this particular individual, the taxon occurs widely during the Pleistocene. Eight elements are complete enough for analysis. A partial fourth metacarpal gives an intermediate habitat preference classification. The remaining skeletal elements, a partial astragalus, and complete third and fourth metatarsals, complete tibia, and complete fourth and two complete third metacarpals are assigned a closed habitat preference. The reduction of reliability for the partial metapodial discriminant functions would suggest that an intermediate habitat classification is more likely for this specimen.

Metridiochoerus modestus

Although an extremely common genus during the Pleistocene (and less so during the later part of the Pliocene), there is only one partial skeleton that can be assigned with confidence to the genus *Metridiochoerus*. This is a partial skeleton of *M. modestus*, KNM-ER 90 4883, which was recovered by the Koobi Fora Field School east of Lake Turkana. There are numerous postcranial fragments, but only one skeletal element is sufficiently complete for analysis. This complete humerus is classified as closed habitat adapted. Although the smallest of the metridiochoeres, *M. modestus* possesses extremely hypsodont third molars in a warthog-like cranium (Harris and White 1979). Forest-adapted limb morphology is unexpected in a species of the hypsodont genus *Metridiochoerus.*

Discussion

Whether due to differences in discriminant function analysis model success or in locomotor adaptations (and by inference past habitats), in several cases limb elements from one skeleton yielded a range of habitat type results (Bishop 1994). It is interesting to note that these instances were most noticeable in the most archaic genus *Nyanzachoerus*. In most cases, these discrepancies were reconcilable by comparing the relative likelihood that particular models would yield correct results, and choosing the result that had the highest probability of correctness (See Table 2.2 for summary of results).

The recurrent trend in suid dental evolution, an increase in third molar hypsodonty, is not invariably associated with open-habitat adaptation in the limb bones. The postcrania of *No. euilus*, a hypsodont suid, indicate a preference for closed habitats. A relatively late example of *Kolpochoerus* (*limnetes*) *heseloni*, KNM-ER 4576, which has an extremely elaborated lower third molar, has postcrania that are classified with intermediate and closed habitat forms. It is interesting to note that despite the advanced level of hypsodonty shown by later examples of *Kolpochoerus* (*limnetes*) *heseloni*, there is no indication of postcranial adaptations for open habitat exploitation or cursoriality. Different postcranial adaptations for earlier and later *K. heseloni* may indicate a gradual change in habitat preference for the species, from closed toward more mixed-country habitats (Bishop *et al.* 2006). It is also possible that past habitat structure differed in ways that required a mosaic of postcranial adaptations, and thus what are discrepancies in these results are actually representative of past environmental conditions and the unique suite of adaptations now extinct suids possessed as adaptations to these.

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REFERENCES

- Bishop, L.C. (1994) Pigs and the ancestors: hominids, suids and environments during the Plio-Pleistocene of East Africa. Ph.D. Dissertation, Yale University. Ann Arbor, MI: University Microforms International.
- Bishop, L.C., Hill, A., & Kingston, J. (1999) Paleoecology of Suidae from the Tugen Hills, Baringo, Kenya. In Andrews, P. & Banham , P. Late *Cenozoic Environments and Hominid Evolution: a tribute to Bill Bishop*.Geological Society, London. 99-111.
- Bishop, L.C., King, T., Hill, A., & Wood, B. (2006) Palaeoecology of Kolpochoerus heseloni (= K. limnetes): a multiproxy approach. *Transactions of the Royal Society of South Africa* **61** (2): 81-88.
- Bishop, L.C., Plummer, T.W., Hertel, F. & Kovarovic, K. (2011) Paleoenvironments of Laetoli, Tanzania as determined by antelope habitat preferences. In T. Harrison *Paleontology and Geology of Laetoli: Human Evolution in Context. Vol. 2: Fossil Hominins and the Associated Fauna*, Springer Netherlands. 355-366.
- Brown, F.H., & Feibel, C.S. (1986). Revision of lithostratigraphic nomenclature in the Koobi Fora region, Kenya. *Journal of the Geological Society, London* **143**: 297-310.
- Carroll, R.L. (1988). *Vertebrate paleontology and evolution.* New York: W.H. Freeman. 507-512.
- Cooke, H.B.S. (1967). The Pleistocene sequence in South Africa and problems of correlation. Background to evolution in Africa. In Bishop, W.W. & Clark, J.D. Chicago: University of Chicago Press. 175-184.
- Cooke, H.B.S. (1978a). Pliocene Pleistocene Suidae from Hadar, Ethiopia. *Kirtlandia*. **29**: 1-63.
- Cooke, H.B.S. (1978b). Suid evolution and correlation of African hominid localities: an alternate taxonomy. *Science* **201**: 460-463.
- Cooke, H.B.S., & Ewer, R.F. (1972). Fossil Suidae from Kanapoi and Lothogam, Northwestern Kenya. *Bulletin of the Museum of Comparitive Zoology* **143**(3): 149-296.
- Cooke, H.B.S., and Wilkinson, A.F. (1978). Suidae and Tayassuidae. Inn Maglio, V.J. & Cooke, H.B.S. *Evolution of African mammals*. Cambridge: Harvard University Press. 435 482.
- DeGusta, D., & Vrba, E. (2005). Methods for inferring paleohabitats from the functional morphology of bovid phalanges. *Journal of Archaeological Science* **32**: 1099-1113.
- Deino, A. L., Kingston, J. D., Glen, J. M., Edgar, R. K., & Hill, A. (2006). Precessional forcing of lacustrine sedimentation in the late Cenozoic Chemeron Basin, Central Kenya Rift, and calibration of the Gauss/Matuyama boundary. *Earth and Planetary Science Letters* **247**: 41-60.
- Feibel, C. S. (2003). Stratigraphy and depositional history of the Lothagam sequence. In Leakey, M.G & Harris, J.M. *Lothagam: The Dawn of Humanity in Eastern Africa.* Columbia University Press, New York, 17-29.
- Feibel, C.S., Brown, F.H., and McDougall, I. (1989). Stratigraphic context of hominids from the Omo group deposits: Northern Turkana Basin, Kenya and Ethiopia. *American Journal of Physical Anthropology* **78**: 595-622.
- Foley, R. (1987). *Another Unique Species*. New York: John Wiley and Sons.
- Gentry, A.W. (1970). The Bovidae (Mammalia) of the Fort Ternan fossil fauna. In (ed.) Leakey, L.S.B. & Savage, R.J.G. *Fossil vertebrates of Africa. Volume 2.* New York: Academic Press. 243-322.

- Gongora, J., Groves, C.P., & Meijaard, E. (this volume) Evolutionary relationships and taxonomy of Suidae and Tayassuidae. In Melletti, M. & Meijaard, E. *Ecology, Evolution and Management of Wild Pigs and Peccaries. Implications for Conservation.* Cambridge University Press.
- Grubb, P. (1993). The Afrotropical Suids *Phacochoeros*, *Hylochoerus*, and *Potamochoerus*. In Oliver, W. L. R. (1993). *Pigs, peccaries, and hippos: status survey and conservation action plan*. IUCN (World Conservation Union), Gland, Switzerland: 66-75.
- Harris, J.M. (1983b). Family Suidae. In Harris , J.M. *Koobi Fora Research Project. Volume II.* Oxford University Press. 215-302.
- Harris, J.M. & White, T.D. (1979). Evolution of the Plio Pleistocene African Suidae. *Transactions of the American Philosophical Society* **69** (2): 1-128.
- Hatley, T., & Kappelman, J. (1980). Bears, pigs, and Plio Pleistocene hominids: a case for the exploitation of belowground food resources. *Human Ecology* **8**: 371-387.
- Hildebrand, M. (1974). *Analysis of vertebrate structure.* New York: John Wiley and Sons.
- Hill, A., Ward, S., & Brown, B. (1992). Anatomy and age of the Lothagam mandible. *Journal of Human Evolution* **22**: 439 451.
- Kappelman, J. (1986). Plio Pleistocene marine continental correlation using habitat indicators from Olduvai Gorge, Tanzania. *Quaternary Research* **25**: 141-149.
- Kappelman, J. (1988). Morphology and locomotor adaptations of the bovid femur in relation to habitat. *Journal of Morphology* **198**: 119-130.
- Kappelman, J. (1991). The paleoenvironment of Kenyapithecus at Fort Ternan. *Journal of Human Evolution* **20**: 95-129.
- Karp, L.E. (1987). Allometric effects and habitat influences on the postcranial skeleton of suids and tayassuids. Unpublished M.S. Thesis. Rutgers, the State University of New Jersey.
- Kingdon, J. (1979). *East African mammals. Volume IIIB. Large mammals*. Chicago: University of Chicago Press.
- McCrossin, M.L. (1987). Post cranial remains of fossil Suidae from the Sahabi Formation, Libya. In Boaz, N.T. *Neogene paleontology and geology of Sahabi.* New York: Alan R. Liss. 267-286.
- McMahon, T.A. (1975). Allometry and biomechanics: limb bones in adult ungulates. *American Naturalist* **109**: 547-563.
- Orliac, M.J., Antoine, P.O., & Ducrocq, S. (2010a). Phylogenetic relationships of the Suidae (Mammalia, Cetartiodactyla): new insights on the relationships within Suoidea. *Zoologica Scripta* **39**: 315-30.
- Orliac, M.J., Antoine, P.O., Roohi, G., & Welcomme, J.L. (2010b) Suoidea (Mammalia, Cetartiodactyla) from the Early Oligocene of the Bugti Hills, Balochistan, Pakistan. *Journal of Vertebrate Paleontology* **30**:1300-305.
- Pickford, M. (1986). A revision of the Miocene Suidae and Tayassuidae, (Artiodactyla, Mammalia) of Africa. *Tertiary Research Special Paper. Number 7*. 1 83.
- Plummer, T., Bishop, L.C. & Hertel, F. (2008) Habitat preference of extant African bovids based on astragalus morphology: operationalizing ecomorphology for palaeoenvironmental reconstruction. *Journal of Archaeological Science* **35**: 3016-3027.
- Plummer T.W., Ferraro J.V., Louys J., Hertel, F., Alemseged, Z., Bobe, R., & Bishop, L.C. (2015) Bovid ecomorphology and hominin paleoenvironments of the Shungura Formation, lower Omo River Valley, Ethiopia. *Journal of Human Evolution* **88**: 108-126.

- Pocock, R.I. (1943). The external characteristics of a forest hog (*Hylochoerus*) and of a babirusa (*Babirussa*) that died in the Society's gardens. *Proceedings of the Zoological Society, London*, *Series B*, **112**: 36-42.
- Potts, R., Behrensmeyer, A. K., Deino, A., Ditchfield, P., & Clark, J. (2004). Small mid-Pleistocene hominin associated with East African Acheulean technology. *Science* **305**: 75-78.
- Savage, R.J.G. & Long, M.R. (1986). *Mammal evolution*. London: Facts on File.
- Scott, K.M. (1979). Adaptation and allometry in bovid postcranial proportions. Unpublished Ph.D. Thesis, Yale University.
- Scott, K. (1985). Allometric trends and locomotor adaptations in the Bovidae. *Bulletin of the American Museum of Natural History* **179**: 197-288.
- Smith, J.M., & Savage, R.J.G. (1956). Some locomotory adaptations in mammals. *Journal of the Linnean Society (Zoology)* **42**: 603-622.
- Van Neer, W. (1989). Contribution to the Archaeozoology of Central Africa. *Annales Sciences Zoologiques*. Musée Royal de L'Afrique Centrale, Tervuren, Belgium. **259**.
- White, T.D. (1985). African suid evolution: the last six million years. *South African Journal of Science* **81**: 271.
- White, T.D. (1995). African Omnivores: Global climate change and Plio Pleistocene hominids and suids. In Vrba, E.S., Denton, G.H., Partridge, T.C. & Burckle, L.H. *Paleoclimate and evolution with emphasis on human origins.* New Haven: Yale University Press. 369- 384.

Taxon	Habitat	Average Weight
Babyrousa babyrussa	Forest	80 kg
*Catagonus wagneri**	Bushland/ Intermediate	35 kg
Hylochoerus meinertzhageni	Forest	200 kg
Phacochoerus aethiopicus/africanus	Grassland	M 90 kg F 60 kg
Potamochoerus porcus	Bushland/ Intermediate	70 kg
Sus barbatus	Forest	50 kg
Sus celebensis	Forest	55 kg
*Porcula salvania**	Bushland/ Intermediate	7 kg
Sus scrofa	Bushland/ Intermediate	100 kg
Tayassu pecari	Forest	38 kg
Pecari tajacu	Grassland	22 kg

Taxon	Habitat Preference	Approximate specimen age(s)
Nyanzachoerus devauxi	Bushland/ Intermediate	Older than 5.5 Ma
Nyanzachoerus kanamensis	Bushland/ Intermediate	3.0 Ma
Notochoerus euilus	Forest / Closed	3.43 Ma
Kolpochoerus (*limnetes*) *heseloni*	Bushland/ Intermediate	2.8 Ma and 1.5 Ma
Kolpochoerus majus	Forest / Closed	0.662 Ma
Metridiochoerus modestus	Forest / Closed	Not known

Table 2.1. List of species, habitat types and average weights for pig and peccary species. Weights and habitat type information from Dorst and Dandelot 1972, Karp 1987, and various authors in Bongo 18 (1991) and the IUCN Status Survey and Conservation Action Plan (1993). *not analysed due to small sample size. For a complete list of specimens, see Bishop 1994.

Table 2.2. Partial skeletons of extinct African suid taxa discussed in this chapter.