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The action of the masticatory muscles and cranial changes in pigs as results of domestication

Alexandru Dinu
Department of Anthropology, University of Wisconsin, Madison, US
adinu@wisc.edu

ABSTRACT – *The comparative study of wild boar and domestic pig skulls suggests that a change in feeding habits under human control may have been a factor influencing the action of the masticatory and neck muscles in reshaping the cranial region. This paper offers both an anatomical and an osteological comparative morphological argument supporting this hypothesis.*

IZVLEČEK – *Komparativen študij lobanj divjega in domačega prašiča sugerira oceno, da je bila sprememba prehranjevalnih navad pod človeškim nadzorom lahko dejavnik, ki je vplival na delovanje žvekalnih in vratnih mišic pri preoblikovanju lobanjskega predela. Članek ponuja anatomski in osteološki komparativno morfološki dokaz, ki podpira to oceno.*

KEY WORDS – *differential feeding; masticatory muscles; biomechanical stress*

Introduction

The domestication of animals is one of the most important and debated chapters in archaeological and zoo-archaeological research. Researchers are trying to answer a number of questions: why domestication; why certain species; how it happened, when and where first; what may be considered as markers of domestication; and what actually is the definition of a domestic animal. Although metrics have played a significant role in making a differentiation between wild and domestic samples, it may be that such measurements alone offer a false image (*Zeder 2006*). In offering answers to questions such as those above, zoo-archaeology has increasingly looked to other sciences, especially genetics (*Albarella, Dobney, and Rowley-Conwy 2006; Berry 1969; Larson et al. 2005; Larson et al. 2007; Mignon-Grasteau et al. 2005; Vila, Seddon, and Ellegren 2005*).

The present study attempts to explore aspects of pig domestication less investigated by zoo-archaeologists: the relationship between the action of the masticatory muscles and the reshaping of the skull. The author suggests that a drastic change in pig feeding habits due to human control, may have been an important factor in triggering cranial morphological changes; therefore, in the absence in an archaeological record of other measurable elements (as teeth), the angle of the ascending ramus of the mandibula, of the zygomatic arch, and of the occipital, may assist in differentiating between wild and domestic individuals.[1]

Materials

This study considered more than 500 pig skull fragments, and skulls found at the locations listed below. Due to space restrictions, photos of only some of these materials are shown here.

❶ Contemporary domestic pig and wild boar skulls from: the National Museum of Natural History 'Grigore Antipa' (20); University of Bucharest the Fa-

1 All anatomical terms used in this study are in conformity with the latest revised edition of Nomica Anatomica Veterinaria prepared by International Committee on Veterinary Gross Anatomical Nomenclature (I.C.V.G.A.N.) 2005.

culty of Veterinary Medicine – Laboratory of Comparative Anatomy (8); The National History Museum – New Center for Pluridisciplinary Research (8). In Bucharest, Romania.

❷ Contemporary wild boar skulls and skull fragments obtained by the authors in the village of Dubova (8), region of Danube Iron Gates, Romania.

❸ Contemporary domestic pig skulls obtained by the authors from the villages of Varteju (2), Frasinet (3), Rotunda (1), and Topoloveni (2), Romania.

❹ Mesolithic pig remains from the sites of Ostrovul Banului (4), Ostrovul Corbului (5), Cave Climente II (10), Icoana (212) and Schela Cladovei (20) region of Danube Iron Gates; The Institute of Archaeology 'V. Parvan'. In Bucharest, Romania.

❺ Neolithic pig remains from Cuina Turcului (8), Veterani (25); The Institute of Archaeology 'V. Parvan'. In Bucharest, Romania.

❻ Neolithic pig remains from Chitila (5), Mariuta (8), Poduri (2), Vitanesti (6), Bordusani (29) and Insuratei (2); The National History Museum – New Center for Pluridisciplinary Research. In Bucharest, Romania.

❼ Neolithic pig remains from the sites of Cascioarele (98) and Varasti (23); The Center for Anthropological Research 'Francisc Rainer'. In Bucharest, Romania.

What is different?

Considering wild pig habitats and behaviour, feeding habits, and the nature and quality of its food compared to that of the domestic pig, the problem presented in this study can be divided into two inextricably related aspects: the action of the neck muscles, and the action of the masticatory muscles. The present study considers only the latter; the action of the neck muscles will be considered in future research.

It is obvious that there is a major difference between the skull shapes of wild and domestic pigs (Figs. 1, 2). Especially when looked at akrokranion (*von den Driesch 1976*), in wild pigs no areas of the occipital bone or tuberculum nuchale can be seen, which otherwise are perfectly visible in a domestic pig skull (Figs. 1, 2). This is because the angle of the occipital and of the ascending ramus of the mandibula in domestic pigs is much closer to 90° compared to those in wild pigs; in other words, if the snout is oriented towards 2π (1, 0) in a trigonometric circle, the orientation of the occipital and the ascending ramus of the mandibula of a domestic pig follows a trajectory most likely from the 3rd quadrant to the 1st quadrant closer to $\pi/2$, while in the wild pig this orientation tends to be from the 4th quadrant to the 2nd quadrant, more likely towards $2\pi/3$. In some cases, the skull of an old domestic pig may display morphological changes more closer than its wild cousin, but such cases are extremely rare; usually domestic pigs are sacrificed at a younger age.

What could have caused these differences? It may be that such changes occurred during the process of domestication; however, it would be incorrect to say that humans deliberately selected pigs having a less sharp mandibular and occipital angle. During the process of domestication, humans may have selected animals that were less aggressive, smaller, and easier to manage; such action constitutes direct human involvement, whereas the reshaping of the skull of the selected animals as in the case presented here is a side-effect of domestication, totally independent of human intentions.

The starting point for this analysis lies in the fact that there is a marked difference in the feeding behaviour of wild and domestic pigs. Generally, the mammalian masticatory apparatus is similar (*Turnbull 1970*). Under human control, however, pigs chew on softer food, and generally, their feeding behaviour has drastically changed. It has been accept-

Fig. 1. Differential angle of the occipital. Far left: wild pig from Dubova, Iron Gates; Next three, domestic pigs. Skulls collected by the author.

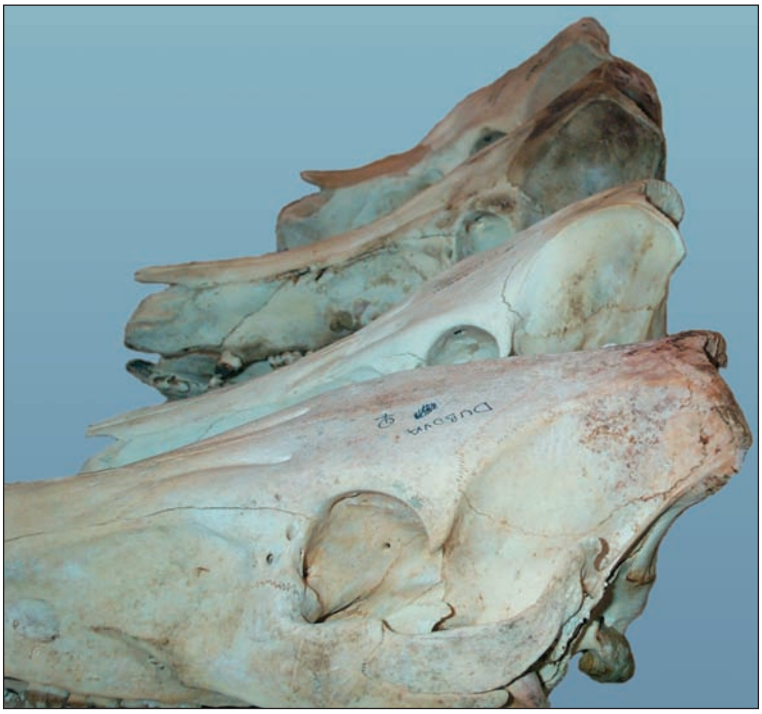

Fig. 2. Same pig skulls as in Figure 1, lateral view.

ed that during the process of mastication: "*Masticatory muscle activation and coordination determine the direction of the jaw movement, control occlusal force, and deform the skull in a variety of ways.*" (*Herring 2006*).

Basically, the study considers the action of Wolff's Law (*Chamay and Tschantz 1972; Dowthwaite 2007; Enlow 1968; Forwood and Tuner 1995; Rubin, McLeod, and Bain 1990; Vainionpaa et al. 2007; Wolff 1892(1986)*). Generally stated, as the law of bone transformation (or remodelling), it holds that bone is not what it appears to be: hard, inflexible, and immutable. On the contrary, bone is responsive to biomechanical stress, and changes according to changing needs not only as material build-up, but also in shape.

During the process of domestication, changes in the feeding pattern of herbivores did not occur to an extended degree; sheep, goats, horses, and cows were still herded and grazed on pastureland. Pigs, on the other hand, may have been subject to a more drastic change from an early stage (*Minagava, Akira, and Naotaka 2005; O'Regan and Kitchener 2005*) if kept in an enclosure at site. Generally considering the action of the Law of Bone Remodelling (Wolff) when there was a change in the pattern of stress developed by the mastication muscles on the cranium, the bones reacted accordingly. In domestic pigs, the muscles of the head, and especially those associated with mastication, are used less intensively, triggering a similar response from the cranial skeleton. The reshaping of the skull from wild to domestic is visible mainly at the level of the maxillary complex, especially in the angle of the temporal and zygomatic bones, in the angle of the ascending ramus of the mandibula, and in the cranium, especially in the angle of the occipital. At the frontal level (face), the anterior height increases.

Previous studies

There have been many studies of the process of mastication in fields such as biochemistry, physiology, and orthodonty (*Fisher, Godfrey, and Stephens 1976; Freeman, Teng, and Herring 1997; Herring 1980, 1985; 1992; 1993; 2006; Herring, Anapol, and Wineski 1991; Herring, Peterson, and Huang 2005; Herring et al. 2001; Herring and Scapino 2004; Herring et al. 1996; Herring and Wineski 1986; Kakizaki et al. 2002; Langenbach et al. 2002; Lieberman et al. 2004; Liu et al. 2004; Popowics and Herring 2007; Rafferty et al. 2007; Sato et al. 2005; Sun, Liu, and Herring 2002; Teng, Herring and Ferrari 1996*). The subject of such research constitutes the bones and muscles included in this study, but for purposes totally unrelated to animal domestication. Rather, it is directed to a better understanding of human disorders and treatment. Pigs have become an increasingly important component in such research, providing extremely valuable information on the biomechanics of muscle and the skeleton (*Larsson et al. 2005; Lieberman et al. 2003; Liu et al. 2004; Rafferty et al. 2007; Risinger and Gianelly 1970; Sato et al. 2005; Sun, Liu, and Herring 2002; Usui et al. 2004; Zhang, Peck, and Hannam 2002*).

With regard to the cranial muscle-bone relation, such studies indicate extremely intensive strain activity in the region of the zygomatic-squamosal (zygomatic process of the temporal bone) – upper ascending mandibular ramus, mainly as a result of the action of the masseter and temporalis muscles during food processing (*Freeman, Teng and Herring 1997*). In fact, the masseter muscle appears to be the key force for the entire mechanism triggered by the process of mastication: "*If there is a unifying theme in this analysis of masticatory biomechanics, it is the* *masseter muscle. The masseter muscle is directly responsible for bending the zygomatic bone in plane, and the load transmitted from the zygomatic bone to the squamosal bone is responsible for the out-of-plane bending of the squamosal. By moving the mandible to the opposite side, the masseter is indirectly responsible for the strain patterns in the zygomatic flange and probably the premaxilary bone. In conjunction with the temporalis muscle, the masseter twists the braincase and tenses the braincase sutures. Reaction forces from masseteric contraction compress the mandibular condyle, and occlusal forces produced by masseteric contraction bend the snout dorsally. The pull of the masseter, in combination with the bite force, twists the body of the mandible.* (*Herring et al. 2001.219*).

According to some, the mechanical requirements of feeding delineate skull design (*Mayer and Lehr Jr. 1988*). The wild pig has a diet rich in coarse foods; among the muscles of the head, masticatory muscle contraction causes both jaw movement and tissue deformation, suggesting that mastication is a forceful cranial activity that produces obvious loads on the craniofacial components, especially on the jaw joint. The masseter muscle, the largest jaw adductor, is the major source of masticatory loads. Its activity in both pars profunda and pars superficialis was found to be highly correlated with condylar neck and squamosal bone strains. These results suggest that bone strains are driven by different mechanical regimes (*Herring 1992; Herring et al. 2001; Liu et al. 2004a; Liu and Herring 2000*), in other words, by differential feeding.

Food consistency affects the duration of muscle burst activities differently in different muscle groups. Studies considering the muscles for closing the jaws (masseter), for opening them (digastric), for extending the tongue (genioglossus), and for retracting the tongue (styloglossus) (*Fehrenbach and Herring 2002; Ghetie 1971; Sinelnikov 1988*) suggest that the duration of burst activity is longer for hard food than soft food in the masseter and styloglossus; no difference with regard to differential food was detected in the digastric and genioglossus (*Kakizaki et al. 2002*). Significant mandibular morphological differences in pigs (as well as in rats), fed on soft and hard diets were also indicated in other studies (*Kiliaridis, Engstrom, and Thilander 1985; Larsson et al. 2005; Yamamoto 1996*).

Due to the closing jaw group action during mastication, the zygomatic arch is distorted on both sides of the skull, the largest strain being in the suture (*Herring et al. 1996*), compressive in the vertical part and tensile in the horizontal part; all parts of the zygomatic bone show tension aligned with the pull of the masseter (rostrodorsal); the squamosal is bent out-of-plane, with the lateral surface becoming more convex. The axis of tension on the lateral surface is caudodorsal. These strains can be explained as a result of the masseter's backward and downward pull on the zygomatic, which is braced at its sutures with the maxillary and squamosal bone, suggesting that the squamosal and the region of the occipital-parietal-nuchal crest is affected upwards and forwards. Studies of strain in the zygomatic arch have indicated that the most likely cause of bending of the squamosal during mastication is the inward pull of the masseter. Condylar strain results from the downward force exerted by the articular eminence on the condyle when the upward-acting jaw adductors contract (*Fisher, Godfrey, and Stephens 1976; Herring 1992; 2006; Herring, Anapol, and Wineski 1991; Herring, Peterson, and Huang 2005; Herring et al. 2001; Liu and Herring 2000*). Strains in all brain case bones and sutures are produced by the action of the masseter, temporalis, both pterygoids, and the neck extensors. The overall loading patterns in the skull of the pig especially may produce drastic bone alterations (*Herring et al. 2001.Fig. 7*).

As a skull grows from infancy to adulthood, the normal forces of mastication in the skull bones produce differential strains (*Langenbach and van Eijden 2001; Langenbach et al. 2002*). These strains cause the skull to grow in such a way as to minimize the strains, and to make them less variable over the skull as the skull matures. This result is very much dependent upon the type of force magnitude applied to the masseter, temporalis and medial pterygoid muscles. The variance of the strain magnitude decreases from infant to adolescent to adult, thus indicating that as the animal matures, the bones distribute the induced strain across the skull in a manner which minimizes strain variances (*Fisher, Godfrey and Stephens 1976*).

Generally, there is a differential fiber structure between the masticatory muscles of wild and domestic animals (*Essen-Gustavson and Lindholm 1984; Fiedler et al. 1998; Ruunsen and Eero 2004*). Could this be a result of a differential mastication process triggering differential biochemical reactions, as shown by some studies (*Luck et al. 2005*)? In the mandible, the orientation of the compressive axis is similar to the vector of the masseter muscle, suggesting that the masseter muscle might be particularly important in engendering the reaction force. The masseter is not the only source of maxillary strain, but no other muscle plays such a significant role. It is possible that the maxillary strain, which is very similar to that of the neighbouring zygomatic bone, directly reflects the pull of the masseter muscle transmitted through the zygomatico-maxillary suture.

The pterygoid has also been subject of a number of studies (*Herring, Grimm, and Grimm 1984; Herring and Scapino 1973*). The strain caused by this muscle is located mainly on the mandibular condyle, which is generally affected significantly by strains from both masseter and pterygoid, although the later action is lesser compared to the former. Nevertheless, the pterygoid does cause a significant and different bone strain in the mandibula. The lateral pterygoid is extremely important in protrusive movements, but less important for loading.

The muscles

This study considers only the possible effect of the masticatory muscle in reshaping the cranial area. Although there are many muscles involved to one degree or another in the process of mastication (*Daumas, Xu, and Bronlund 2005; Fehrenbach and Herring 2002; Ghetie 1971, Gorniak 1985*), we have focused on the two muscles whose action elevates the mandible: 1) the masseter, which is the largest, most powerful, and most active masticatory muscle, and, 2) the temporalis, which, due to its origin, is the masticatory muscle directly related to the cranial region.

❶ The masseter has two heads:

- **a.** the superficial head or pars superficialis originates on the anterior-interior two thirds portion of the lower border of the zygomatic arch and inserts on the mandibular angle (*Fehrenbach and Herring 2002; Ghetie 1971*).
- **b.** the deep head or pars profunda originates on the medial-posterior interior one third and medial portion of the zigymatic, and inserts on the masseteric fossa (*Fehrenbach and Herring 2002; Ghetie 1971*).

Main action: for the most part, during mastication the two heads of the masseter have a different function. Basically, during the power stroke, the deep head is most active on the balancing side of the jaw and serves to retrude the balancing mandibular condyle; the superficial head is the most active on the working side, and serves to generate occlusal force. The action of the superficial head will be considered in this paper.

❷ The temporalis, despite its name, originates in the temporal fossa or planum parietale and inserts on the internal side of the coronoid process of the mandibula. According to some authors, the insertion occupies the entire rostral region down to the 3rd molar (*Ghetie 1971.508*). Main action: a complete contraction of the temporalis elevates the mandible.

Other muscles important in assisting mastication are:

❶ Pterygoid. It has two branches:

- A. the medial pterygoid originates from the pterygoid fossa on the medial surface of the lateral pterygoid plate of the sphenoid, and inserts on the interior medial surface of the angle of the mandibula. Main action: the contraction of the medial pterygoid raises the mandibula. However, the muscle is weaker than the masseter muscle in this action.
- B. the lateral pterygoid has two heads
  - a. The superior head originates from the inferior surface of the greater wing of the sphenoid and,
  - b. The inferior head originates from the lateral surface of the lateral pterygoid plate of the sphenoid.

Both heads unite and insert on the anterior surface of the neck of the mandibular condyle and the pterygoid fovea. Main action: the inferior head of the muscle has a slight tendency to depress the mandibula. When both medial and lateral branches contract, a protrusion of the mandible occurs. If only one lateral pterygoid muscles contracts, a lateral deviation of the mandible occurs.

❷ Buccinator (main action: pulls the angle of the mouth laterally and shortens the cheek both vertically and horizontally, keeping the food pushed back on the occlusal surface of the teeth).

❸ Muscles that, due to their origin, may have played a role in reshaping the bones to which they are attached, such as the zygomaticus major (main action: elevates the angle of the upper lip) and zygomaticus minor (main action: elevates the upper lip) (*Fehrenbach and Herring 2002; Ghetie 1971*). These muscles, as well as the muscles of the neck, will be considered in future research.

Among the muscles involved in mastication, some authors have pointed out the particular importance

Fig. 3. Left: skull of wild pig. Right: skull of domestic pig. A: mandibular angle. B. temporal process of the zygomatic bone. C: zygomatic process of the temporal bone. D: the ascending ramus of mandibula. E: the horizontal ramus (the body) of mandibula. F: fossa temporalis (planum parietale). Schematic representation of: (red) masseter pars superficialis; (green) masseter pars profunda (zygomaticomandibularis), and (yellow) temporalis.

of the masseter and temporalis: *"Masticatory muscles, through their direct action on bony attachments and their indirect action in loading the teeth and the jaw joints, constitute the major biomechanical challenge to the skull. Direct effects of a muscle attachment are sensitive to the particular muscles used and to the pattern of muscle coordination. For example, the temporalis and masseter twist the pig braincase in opposite directions, and because these muscles usually act in opposite-side 'couples', the effect is exaggerated rather than cancelled."* (*Herring 2007*).

It must be clearly underlined, however, that the line of action in the jaw muscles is extremely difficult to determine. The muscles extend over complex skull surfaces, and the fibres do not run exactly from bone to bone, but rather between internal tendons. The pig's masseter superficial head in particular, has fibres that run in different directions: more vertically in the anterior part, and more horizontally in the posterior part (*Susan W. Herring, personal communication*). In both muscles, the elevation of the mandible is a result of the average line of action generated by these fibres.

The sum of these lines of action in both the masseter and temporalis are always divergent in all mammals due to general skull morphology (*Daumas, Xu and Bronlund 2005*). The purpose of this study is not to identify these lines of action, but to see if, due to their general direction – the result of these lines of action – the chewing force differentially applied for harder of softer foods may affect jaw deformation (*Langenbach and van Eijden 2001; Langenbach et al. 2002*) in the case of wild pigs and domestic pigs.

As can be seen (Figs. 1, 2, 3) and explained earlier in this paper, there is a marked difference between the angle of the ascending ramus of the mandibula, zygomatic, fossa temporalis, and the occipital when wild and domestic specimens are compared. The 'V' formed by the orientation of the vectorial forces developed by the action of masseter and temporalis follow the same pattern. Evidently, if the angle of the mandibula and of the temporal fossa is closer to 90°, the smaller the angle of 'V' becomes. Might a decrease in this angle result in differential chewing (crushing) forces? It must be underlined that in Figure 3 the anatomical locus of the muscles is not represented, but rather a schematic representation of the masticatory muscles orientation. For instance, in reality, the superficial head of the masseter is much larger, superimposing on most of the deep head.

Considering the drastic differences shown in Figure 3, it may be assumed that, over time, a more refined diet, and therefore less muscle activity, could have triggered an alteration in the mandibular angle, the angle of the zygomatic arch, and the angle of the parietal fossa. Human control of pig diets may explain such a drastic change in the vectorial forces acting on the remodeling of the skull bones. Of course, the contribution of all the other muscles of the head and neck to this process of morphological change must also be taken into account.

The bones

In order to verify the assumption stated above, we compared a number of samples of known wild and known domestic pig, to both Mesolithic and Neolithic pig remains. The latter, even if subject of previous metric studies for establishing the status of wild or domestic, were considered simply as 'unknown', the present research not being interested in evaluating metric caractheristics.

First, in Figures 4, 5, 6, the angle of the ascending ramus of the mandibula of a modern domestic pig was compared to the angle in Neolithic pigs from Bordusani, Cascioarele, and Insuratei.

It is obvious that in the three cases, the mandibular angle in the Neolithic samples and modern do-

Fig. 4. The angle of the madibula of a modern domestic pig and a Neolithic Bordusani pig.

Fig. 5. The angle of the madibula of a modern domestic pig and a Neolithic Cascioarele pig.

mestic samples are identical, and that they were subject to the same feeding patterns, generating the same pattern of mechanical strain.

In Figures 7 and 8, the planum parietale of a modern wild boar is compared to remains from the Neolithic site of Varasti and the Mesolithic site of Icoana.

The temporalis muscle, which follows perfectly in the planum parietale (fossa temporalis), due to its origin and insertion, is set at an angle following the ascending ramus of the mandibula. The angle of this alignment has two points of conjuncture: it contributes to the increase or the decrease of the mastication force, and is in direct relationship with the angle of the occipital. In the two cases presented above, the morphology and the angle are identical, suggesting identical action of the mastication muscles, generating the same type of stress on the skull bones. The most probable cause is identical feeding patterns.

In Figures 9 and 10, the temporal process of the zygomatic bone of a modern wild boar is compared to an example from the Mesolithic layer site of Schela Cladovei.

The morphology and angle match perfectly, obviously both subject to the same type of biomechanical strain.

In Figures 11 and 12, two zygomatic processes in the temporal bone of a modern wild pig are compared with Mesolithic remains from Icoana and Schela Cladovei.

Again, the morphology and angle are identical, both obviously subject to the same type of biomechanical

Fig. 6. A pig mandibula ascending ramus from the Neolithic site of Insuratei compared to a modern domestic example.

strain. As the jaw opens, the muscles that open the jaw shorten and become less forceful. Meanwhile, they have to stretch the muscles which close the jaw. A function of the coupling between head and jaw movements is to extend the gape of the jaw, the extension forward contributing to the extended opening of the jaw. The forward extension of the head involves neck muscle action (*Koolstra and von Eijden 2004*).

The neck muscles

Although the action of the neck muscles will be addressed in future research, it may be useful to note a few aspects here. Wild pigs make strenuous and constant use of the head and neck for rooting and for penetrating forest undergrowth and thicket, as well as for fighting. In the absence of support offered

Fig. 7. The parietal fossa, nuchal crest, and zygomatic process of the temporal bone of a pig skull from Varasti compared to a modern wild pig skull from Dubova.

Fig. 8. Fragment of occipital-temporal-parietal fossa from Mesolithic Icoana compared to a modern wild pig skull from Dubova. The morphology and angle match perfectly.

by the cervical ligament, this peculiar behaviour redistributes the function and pressure of the muscles of the neck and head. In addition, the weight of the head is redistributed to the neck muscles.

Three layers of paired muscles directly link the skull either to the cervical and thoracic vertebrae or to the shoulder griddle (*Dutia 1991; Fehrenbach and Herring 2002; Ghetie 1971; Richmond and Vidal 1988*). These include the large muscles of the neck that act across three or more neck joints (example of extensors: splenius, longissimus capitis, biventer cervicis and complexus; example of flexors: obliquus capitis inferior and superior), as well as short suboccipital muscles that act specifically in the region of the upper cervical joints (rectus capitis posterior and rectus capitis anterior muscles). Of extreme importance to the subject presented here is the trapezius muscle, having an origin that extends from the occipital to the 10th thoracic vertebra (*Ghetie 1971*); the role of its action in relation to the morphology and angle of the occipital is obvious.

Fig. 9. The temporal process of zygomatic bone from Mesolithic Schela Cladovei compared to a modern wild pig skull from Dubova. The morphology and the angle match perfectly, obviously both subject to the same type of biomechanical strain.

It has also been pointed out by some authors that among domesticated animals, the pig has the most developed iliocostalis cervicis muscle (*Ghetie 1971*), which originates on the first rib, attaches in its trajectory to all the cervical transverse processes, and inserts on the atlas wing. In addition, each neck vertebra is linked to its neighbors by short intervertebral muscles that attach to the transverse and spinous processes (*Dutia 1991*).

Movements of the head on the neck are achieved by the coordinated realignment of the cervical and thoracic vertebrae, and involve simultaneous movements around many vertebral joints. The forward extension of the head involves neck muscle action (*Koolstra and von Eijden 2004*). The articulation between the skull and the first cervical vertebra (the atlanto-occipital joint) allows a large amount of extension and flexion typical of wild pig feeding and fighting behaviour, but much reduced in domestic pigs.

Fig. 10. The same bone shown in Figure 11, from a different angle.

Discussion and conclusion

There are certain aspects of pig domestication that are very difficult to address. For instance, one pig-keeping practice, still found in some parts of the world, is to let the animals roam freely (Fig. 13).

This practice may result in both a continuation of feeding associated with wild boar feeding habits, and in hybridization (Fig. 14).

At this point, it is impossible to say if such practices were present during the early period of domestication. Although they may have been present, it is impossible to asses how widespread they were. It may be that the nature of the environment, unfriendly neighbours, or other social and political circumstances greatly influenced patterns of animal husbandry. Moreover, the fact that there is historical and contemporary evidence for such practices does not mean that they originated in the Neolithic, or that people from widely separated geographical regions followed the same patterns of husbandry. It may be that keeping pigs on site was practiced in order to protect wealth, to insure food storage on the hoof, or as a disposal of kitchen garbage.

However, the problem of hybridization is a very serious issue. The skull of the resulting individuals strongly retains the characteristics of the wild boar. Detecting hybrid specimens in the archaeological record may be extremely difficult. The measurement of the mandibular angle may offer answers, but there are some uncertainties; for instance, how a mandibular angle in a hybrid individual can be differentiated from the mandibular angle of an individual entirely controlled by humans, but still at an earlier stage of domestication. Despite such problems, it appears that the cranial morphological changes associated with the domestication of pigs were rapid, and due primarily to changes in the biomechanics of mastication.

Fig. 11. Mesolithic squamosal (zygomatic process of the temporal bone) from Icoana compared to a contemporary wild pig skull from Dubova.

Fig. 12. Mesolithic squamosal (zygomatic process of the temporal bone) fragment from Schela Cladovei compared to a modern wild pig from Dubova.

The data included in this paper represents only a small fraction from an impressive number of studies on pig; the studies listed here were totally unrelated

Fig. 13. Domestic pigs left to roam freely on the island of Ostrovul Mare, region of the Iron Gates, southwestern Romania.

Fig. 14. Hybrid wild and domestic pigs in Dobrogea, southeastern Romania, not far from the Danube Delta.

to archaeological questions such as animal domestication, but, used in conjunction with archaeological data, may be of great help in producing clues to this process. Therefore, the present author suggests that restricting zoo-archaeological research to traditional methods of analysis such as metrics, morphology, and economic patterns, may lead to an incomplete, or even erroneous picture of what, and how, animal domestication occurred.

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