Functional Design of Cranial Muscles: Comparative and Physiological Studies in Pigs

SUSAN W. HERRING

Department of Oral Anatomy, University of Illinois at the Medical Center, Chicago, Illinois 60680

SYNOPSIS. The adaptive significance and evolutionary history of the internal architecture of the masseter muscle in suid artiodactyls are investigated. Hypotheses are developed on the basis of anatomical and physiological studies in the pig, Sus scrofa, and used to make predictions about the expected anatomy in the giant forest hog, Hylochoerus meinertzhageni and the warthog, Phacochoerus aethiopicus. The hypotheses are then tested by anatomical examination of these animals. In the pig, pinnation of the masseter serves to increase masticatory force and to partition the muscle into three semi-independent parts: vertical anterior fibers, which are used especially to close from wide gape; a central pinnate portion, which is used for all activities; and horizontal fibers covering the jaw joint, which are used especially for anterior translation of the condyle. In the giant forest hog and warthog the structure of the masseter is more uniform and the physiological cross section is larger than in the pig. These changes are interpreted as correlates of decreased emphasis on gape and increased emphasis on masticatory force in the African suids. In order to clarify the evolutionary sequence, masseteric architecture in the suids is compared with that of tayassuids and the hippopotamus.

INTRODUCTION

In mammalian anatomy, truly parallel-fibered muscles exist mainly in textbooks. In fact, muscle fibers almost never run directly from bony origin to bony insertion; they normally attach at one or both ends to tendinous tissue and are at least slightly angled to the long axis of the muscle. Sometimes the pattern of internal tendons is amazingly complicated. The concern of this paper is to examine the architecture of complex muscles in terms of function, and to use this information in arriving at an evolutionary explanation for species-specific differences in pinnation pattern.

The analysis of musculoskeletal anatomy has been one of the most successful endeavors of functional morphology, and has led to great insights into the evolution of vertebrate feeding and locomotor adaptations. The traditional muscle-bone analysis generally proceeds by determining muscular lines of action and moment arms and using these in free-body diagrams. It is well-known to the practitioners of this art that the technique does not address some important points of muscle function, such as fiber type, position along length-tension curve, and nonsynchronous contraction of fibers, all of which could have major biomechanical effects. The problem is at its worst in the case of multipinnate muscles, where even the simple procedure of determining a line of action is probably not valid. Since the functional significance of complex muscular architecture is not understood, it is difficult to progress to the mechanical analysis; a physiological analysis of the muscle must come first.

Providing that the function of a trait such as complex muscle structure can be clarified, it becomes possible to construct hypotheses about its selective value, i.e., its status as an adaptation. The most direct way to test such hypotheses is by detailed field observations that assess not only the operation of the trait but also its value in differential reproduction, as exemplified by Sherman’s (1977) study on the evolution of alarm calls in ground squirrels. A less direct test can be made by tampering with the trait involved and studying survival, as has been done for rodent ears by Webster and Webster (1971). Unfortunately, the assessment of adaptive value of specific internal architecture in muscles resists either of these approaches, since the operation of the architecture is not readily observable in the wild nor modifiable by surgical procedures. A third, even less di-

---

FIG. 1. Lateral views of the left masseters of Sus (S), with parts of the skull shown for reference; Hylochoerus (H), and Phacochoerus (P). One-half actual size.

rect method for testing hypotheses of adaptation remains, however, and this is by prediction. A hypothesis constructed by analysis of the anatomy and function of a trait in one animal can be used to generate predictions about the anatomy of the trait in another animal where the function is known. Of necessity, such investigations are conducted on taxa, rather than individuals, which means that the trait’s value in differential reproduction can never be measured. Nonetheless, correct predictions can be taken as evidence that the hypothesized adaptive role of the trait is indeed something which has been selected for, although not necessarily related to taxonomic evolution in the animals. This latter method of testing hypotheses is what is usually called “comparative” and has been used implicitly for years by functional morphologists. An important consideration in the comparative method is the selection of animals to be used. Comparisons based on anatomical details cannot be made if the animals are wildly dissimilar, because it will be impossible to sort out all the factors influencing the trait. On the other hand, a certain amount of diversity is necessary for an adequate test of the prediction.

In this paper I have employed a comparative approach to the study of internal design of the masseter muscle in three genera of pigs (Suidae, Artiodactyla). The following stages were involved: (1) anatomical description of the masseter of the pig, Sus scrofa; (2) physiological studies, mainly electromyography, to elucidate the function of the pig masseter; (3) formulation of a hypothesis of the adaptive significance of the anatomy of the masseter; (4) predictions of masseteric anatomy in two other suids, the warthog Phacochoerus aethiopicus and the giant forest hog Hylochoerus meinertzhageni, based mainly on field descriptions of diet and jaw movements; and (5) testing these predictions by anatomical investigation of the masseters of these species.

STUDIES ON SUS SCROFA

The pig masseter is a large muscle which originates from the zygomatic arch and inserts on the lateral surface of the mandibular angle (Fig. 1). Most fasciculi arise and insert on a branching system of internal tendons (Fig. 2S). Although the masseter
Fig. 2. Internal aponeuroses of the left masseter, oriented as in Figure 1. S—Sus (modified from Herring and Scapino, 1973); H—Hylochoerus; P—Phacochoerus. Aponeuroses of origin are shown in the left column, and the attachments to the zygomatic arch are filled in. Aponeuroses of insertion are shown in the right column, and the attachments to the mandibular angle are hatched. Origin and insertion systems interdigitate.

is an indivisible mass with all fibers running inferiorly, posteriorly and medially, there are several gradual changes along an anteroposterior axis. First, the muscle is thickest anteriorly and tapers posteriorly to a thin edge. Second, the internal tendons of the anterior part are interdigitating septa oriented in an oblique plane, but these give way in the posterior part to broad parasagittal aponeuroses. Third, the anterior fasciculi are comparatively long and vertical (with respect to the tooth row) but the posterior fasciculi are short and near-horizontal (anteroposteriorly) (Fig. 2).
Sarcomere lengths also differ between anterior and posterior fasciculi (Herring et al., 1979). With the jaws near occlusion, sarcomeres near the anterior border of the muscle are short, 2.4-2.5 µm, but from the middle of the muscle to the posterior border, sarcomere length ranges between 2.9 and 3.0 µm. With the jaws near maximum gape (25° angle between upper and lower toothrows), sarcomeres are longest anteriorly (3.7 µm) and progressively shorter posteriorly, reaching 3.3 µm at the posterior border. The sarcomeres in the posterosuperior corner (the fibers which cover the jaw joint) are even shorter, becoming as small as 2.6 µm.

All these anteroposterior transitions are gradual and do not correspond exactly to the change in orientation of the internal tendons. There is no consistent anteroposterior variation in angle of pinnation, but these angles are all less than 25°, indicating that all fibers can contribute effectively to the production of axial force (Benninghoff and Rolihäuser, 1952).

The anatomical differences between anterior and posterior fasciculi have several functional implications. Assuming that one or both jaw joints serve as the fulcrum for jaw movement, the most anterior fibers will have the longest moment arm. For a given point of origin, verticality of fiber orientation is also associated with increased moment arm. At the same time, features that promote mechanical advantage have a deleterious effect on the degree of stretch required when the jaw is opened (Herring and Herring, 1974). Thus we see the bulk of masseteric volume oriented relatively vertically in the anterior part of the muscle, but with relatively long fasciculi to compensate for increased stretch. Since the sharp change in orientation of the internal tendons is not correlated with any sharp change in fasciculus orientation, the obliquely positioned anterior septa are probably associated with the efficient packing of a large number of long fibers. Sarcomere length is related to the isometric force produced by the muscle;
force is diminished when sarcomeres shorten beyond the point of maximum overlap of thick and thin filaments. At sarcomere lengths longer than the point of maximal overlap, force may also diminish, but more often force increases because of passive tension generated by stretched connective tissue (e.g., Benninghoff and Rollhäuser, 1952). The sarcomere length at which maximal overlap occurs is variable, but a value of about 3.0 μm has been found for several mammalian muscles (Tabary et al., 1976; Muhl and Grimm, 1977). Applying this figure to the data on sarcomere lengths, it appears that the vertical fibers of the anterior border will produce submaximal force when the jaws are closed but supramaximal force when they are opened. In contrast, the horizontal fibers covering the joint will produce maximal force when the jaws are closed but submaximal force when they are opened. The remainder of the muscle will work at high force levels in either jaw position. These considerations suggest that, given equal fiber activation, the vector of masseteric pull will not be that expected by adding all the individual fiber directions. Instead, the vector will be more vertical than expected when the jaws are opened and more anterior than expected when the jaws are closed.

These findings are set in context when the total contribution of the masseter in pig mastication is considered. The following results are deduced from a combination of electromyography (EMG) and mechanical analysis. EMG, when combined with motion studies, can give information about the timing of a muscle's activity with respect to a movement. The technique cannot indicate whether the muscle is a prime mover or whether it is lengthening or shortening. Nor can EMG accurately reflect force, because the linear relationship between force and integrated EMG (Lenman, 1969) is disrupted by nonisometric contractions (all movements), fatigue, and differential contraction of fibers. A rough approximation of all the forces on a bone can be made, however, if EMG of all the muscles is combined with motion analysis and a consideration of length-tension relations (e.g., Goslow et al., 1977). In this way the contribution of a given muscle to a given movement may be estimated. Length-tension relations are not known for pig masticatory muscles, or indeed for any multipinnate muscles, although some preliminary work on other mammals has begun (Nordstrom and Yemm, 1974; Thexton and Hiemae, 1975). Even so, overall EMG and mechanical analysis of the muscles involved in pig feeding implicate the masseter in two activities (Herring and Scapino, 1973): the provision of elevator force during closing and the production of lateral deviations of the jaw. In the latter role it acts in combination with other muscles on the same side pulling anteriorly (medial and lateral pterygoids) and muscles on the opposite side pulling posteriorly (temporalis, zygomaticomandibularis) to produce a movement toward the opposite side. Clearly, the more horizontal the vector of the masseter, the more effective it will be for this function. Lateral deviations occur twice in each pig masticatory cycle, during crushing when the jaw swings from the midline toward the chewing side, and during the power stroke when it swings from the chewing side to the opposite side (Herring, 1976). Both phases take place with the teeth in or near occlusion. The change in vector indicated by the sarcomere measurements fits well with these observations; jaw closing will be promoted by the vertical vector associated with an open position, while lateral deviations always occur at closed positions when the vector is more horizontal.

One final line of inquiry, using EMG in a more critical way, further buttresses these conclusions. Although fine-wire EMG electrodes are commonly used to assess the activity of whole muscles, they probably record from only a limited volume. Their ability to represent whole muscles presumably stems from the extensive overlap of motor unit territories in many muscles, so that even a small area contains fibers from a representative cross section of motor units. If, however, different parts of a complex muscle are able to fire nonsynchronously, the motor unit territories must be more restricted and fine-wire elec-
trodes can be used to record differential activity within the muscle. Accordingly, EMG was recorded simultaneously from several sites in the pig masseter during mastication (Herring et al., 1979). As expected, this study revealed that all muscle fibers are not, in fact, equally activated. The pattern of differential activity suggests a division of the muscle into three semi-independent parts: anterior border, posterosuperior corner (fibers over TMJ), and the remaining central portion. During closing, only the vertical fibers of the anterior border are strongly active, while the horizontal fibers over the TMJ are silent, so the vector produced must be even more vertical than previously supposed. The horizontal posterosuperior fibers are active only during lateral deviations and only on the side opposite to the direction of movement. Thus it seems that the alteration of the muscle vector from relatively vertical to relatively anterior is restricted to transverse movements. The central part of the masseter is active during both closing and lateral deviations.

In sum, the experimental evidence indicates that the vector and action line of the pig masseter can be altered by differential contraction of fibers and different length-dependent contributions to force.

**Adaptive Significance and Predictions**

Pinnation serves to increase the number of fibers in a given volume of muscle. Low pinnation angles further indicate that the added fibers will act reasonably close to the axis of movement. The end result should be improved force output. High force output suggests an ability to process very resistant foods, an adaptation which is supported by the robust construction of the molars and a high proportion of items such as tubers and acorns in the winter diet of wild boar (Henry and Conley, 1972; Pine and Gerdes, 1973). Given that the attachment positions of the fasciculi are dictated by force requirements, the differences in fasciculus length can be ascribed to the demands of gape (Herring and Herring, 1974). *Sus* is not reported to have an open-mouth display and fights with side-ways slashing rather than biting, so the gape requirement may have to do with the necessity of fitting large hard food items in the premolar and molar regions. The significance of the differences in fasciculus orientation and sarcomere length appears to be the specialization of vertical fibers for forceful rotational (closing) jaw joint movements and of horizontal fibers for forceful translational (protrusive and transverse) movements. The transverse movements are particularly associated with grinding mastication, which is presumably necessary for foods of a tough or fibrous nature.

With the proviso that only one function, feeding, in a domestic animal has been studied, two factors seem especially important—diet and gape. Elevating force and grinding mastication will be correlated with resistance to diet, while gape is involved in ingestion of large particles, display and combat. Sarcomere measurements and EMG are impossible at this stage for wild animals, but three pertinent anatomical measurements can be made: (1) physiological cross section, which is related to total possible force and expected to covary with harshness of diet; (2) fasciculus length, which is related to excursion and expected to increase for large gape; and (3) fasciculus orientation, which is expected to be vertical when rotational jaw movements prevail or when leverage is important, and expected to be horizontal for gape or for translational movements.

Both the warthog (*Phacochoerus*) and the giant forest hog (*Hylochoerus*) are more herbivorous than the pig. The diet of the forest hog is poorly known, but includes herbaceous plants and possibly invertebrates (Ewer, 1958, 1970). In contrast, warthogs rarely browse and prefer grasses, including some coarse varieties (Field, 1970). The different structure of the cheek teeth in the three suid genera also points to specialization for different diets (Fig. 4). In *Sus* the premolars are large, sectorial, and used to prepare large food items for ingestion, while the molars have large crushing surfaces complicated by many small cuspules. In *Hylochoerus* and *Phacochoerus* the premolars are reduced both in number and in size, probably in
Fig. 4. Occlusal views of the left mandibular halves of Sus (S), Hylochoerus (H), and Phacochoerus (P). The cheek teeth of each are enlarged and inset. To scale; teeth shown actual size.

combination with the ingestion of small particles only, and the third molars are elongated. In Hylochoerus the molar cusps are arranged in lophs, resulting in sharp hills and valleys. These features are generally analogous to those found in folivorous, as opposed to frugivorous, monkeys (Kay, 1978). In Phacochoerus the hypso-
thornt third molars show a great proliferation of equal-sized cusps, which are arranged in longitudinal rows. The multitude of enamel crests produced after slight wear is suitable for shredding mineral-containing grasses. The movements of mastication have been reported for both forest hog and warthog by Ewer (1958, 1970) and strongly resemble those described for pig, except that the transverse movements are more extensive, particularly in warthog. Behaviors requiring wide gape have not been described for either warthog or giant forest hog; both fight by frontal wrestling and upward slashing with the canines.

The following predictions of masseteric anatomy can now be made for forest hog and warthog. First, since wide gape is not required, fasciculi should be shorter than in the pig. Sarcomere lengths of the anterior border and central part of the muscle should be more similar than in Sus. Masticatory force should be increased in the warthog (but not forest hog) with, therefore, an enlarged physiological cross section or more vertical fasciculus orientation. At the same time both warthog and forest hog should have short horizontal fasciculi to produce transverse grinding movements. Sarcomere lengths in the postero-superior corner should be optimal in closed positions, as in the pig.

**Comparative Anatomy of the Masseter**

Comparisons among the suids are facilitated by an overall similarity. Body size is comparable, although warthogs are somewhat smaller than wild boar and giant forest hogs. Masticatory movements are qualitatively, if not quantitatively similar. The proportions of the masticatory muscles are also similar: (1) the masseter is about 40% by weight of the total adductor mass (slightly less in Sus, slightly more in Phacochoerus); and (2) the temporalis plus zygomaticomandibularis amount to about 43%, although the zygomaticomandibularis contributes more to the total in forest hog and especially warthog than in pig (Herring, 1971). Any differences in masseter morphology are therefore likely to be related to the remaining variables, diet and gape.

The internal aponeuroses of the three suid masseters are shown in Figure 2. All have parasagittal sheets posteriorly and oblique interdigitating septa anteriorly, but the proportions of these sections are altered. In the pig the parasagittal sheets occupy more than half the expanse of the muscle in lateral view. In the giant forest hog only about a third of the muscle is so occupied, and in the warthog less than a fourth. The remaining area is taken up by the oblique septa. In the forest hog there are about the same number of septa as in the pig, but they are larger and extend all the way to the anterior border of the muscle. In the warthog the number of septa is increased and a very regular arrangement achieved. There are correlated changes in the angulation of the fasciculi in the sagittal plane (Fig. 3). In Sus horizontal fasciculi (oriented at 45° or less to the tooth row) are found throughout the posterior half of the masseter, but in *Hylochoerus* and *Phacochoerus* such fibers are progressively restricted to the posterosuperior corner. The average inclination over the entire muscle is 49° in Sus, 64° in *Hylochoerus* and 69° in *Phacochoerus*. There are also differences in relative fasciculus length. The longest fasciculi measured about 40 mm in all genera, and these were found antero-superiorly in each case. In the pig no fasciculi in the anterior half of the muscle were less than 69% of the longest, and even in the posterior region none was below 44%. In forest hog and warthog, lengths decreased more rapidly and some posterior fasciculi were less than 30% of the longest. The average lengths were 69%, 61% and 64% of the longest fasciculus in pig, forest hog and warthog, respectively. These average lengths were divided into muscle weights to calculate a crude approximation of physiological cross sections. The results were 26.6 cm² for a female wild boar, 32.0 cm² for a female giant forest hog, and 34.9 cm² for a large male warthog. All three animals were about the same body weight, roughly 95 kg.
To a considerable extent, the regional specialization seen in the pig masseter is lost in the African genera. Both the long vertical anterior fibers and the horizontal posterior fibers found in *Sus* have given way to a relatively homogeneous pattern of vertical fibers of intermediate or short lengths. At the same time the physiological cross section of the muscle has been increased. Although the result is similar in the warthog and the forest hog, the changes in muscle architecture are not the same. A comparison of these findings with the predictions of the previous section reveals only partial success. The expectation of diminished gape requirements leading to shorter fasciculi was borne out for both genera. Modifications for increased masticatory force were predicted only for warthog, but were found for both warthog and giant forest hog. These included both larger cross section and more vertical fasciculus orientation. Since the prediction of low force for giant forest hog was based on uncertain knowledge of diet, it seems likely that this was the source of the error and that the giant forest hog actually eats a fair proportion of resistant foods. The most interesting discrepancy between observed and predicted anatomy is the failure to find increased numbers of short horizontal fasciculi to correlate with translational movements in the African genera; in fact, the proportion of horizontal fasciculi is reduced, with orientations of less than 45° being restricted to the immediate vicinity of the jaw joint. The experimental results reported above for *Sus* implicated only fibers in this same posterosuperior corner in translational movements, but it seemed reasonable to suppose that the greater lateral excursions that have been reported in *Hylochoerus* and *Phacochoerus* would require increased force along an anterior vector. Evidently this is not the case and some revision is in order. One possibility is that greater excursions do not involve greater force, i.e., work is done on the food mainly via vertical elevating force, and the force for lateral deviations is little more than is required to move the weight of the jaw. This idea strikes me as implausible since the enamel crests on the teeth would seem to demand forceful lateral movements for effective grinding. Another possibility is that some muscle other than the masseter has increased its horizontal component, but examination of the other masticatory muscles gives no hint of this (Herring, 1971). A third possibility is that the increase in masseteric size, with all added fibers having some anterior com-
ponent, is sufficient to provide additional force along anterior as well as vertical axes. If so, then the question arises as to why these intermediate fibers do not suffice for *Sus*—why are the fasciculi in the center of the muscle oriented at 45° in *Sus* and 60° in the other genera? The only answer that occurs is that the need for gape is once again a determining factor—that in the pig these fasciculi are long as well as horizontal, indicating greater suitability for stretching.

In summary, this comparative test of the adaptive importance of internal architecture of the masseter in suids has supported the influence of gape on fiber length and orientation and the influence of diet on physiological cross section and fiber orientation but has denied the influence of grinding mastication on fiber orientation.

**Evolution of Pinnation in the Suid Masseter**

To decide which of the observed architectures is primitive, I used outgroup comparisons. The sister group of the Suidae is the Tayassuidae, or peccaries, and the Hippopotamidae are the next closest living relatives of both groups. The masseters of the collared peccary *Dicotyles tajacu* and the hippo *Hippopotamus amphibius* are both of simple construction with parasagittal sheets situated as in the posterior half of the *Sus* masseter (Fig. 5). The posterosuperior corner, with its horizontal fibers, is absent, as are the obliquely oriented tendinous septa. The fasciculi are generally vertical and extremely long in these animals, both of which are adapted for wide gape (Herring, 1975). For example, the collared peccary is about half the size of the suids examined in this study, yet the fasciculi of its masseter averaged 33% longer. Thus it appears that in these animals the masseter is adapted for gape by lengthening fibers rather than reorienting them (but see Herring and Herring, 1974, for other ways in which orientation affects gape). Assuming that the peccaries and hippos represent the primitive condition, the addition of posterosuperior fasciculi covering the joint is a shared derived feature in the suids. Its functional significance is surely the development of anteroposterior jaw movements, which are not permitted by the carnivore-like structure of the joint in peccaries and hippos. Similarly, the oblique septa constitute a derived suid character which is less advanced in *Sus* than the other suids, since the septa have not completely replaced the long vertical fibers. Based on the physiological cross sections, the function of the interdigitating oblique septa is to increase the number of fibers housed in a given volume of muscle, and because fiber length is thus decreased it works at the expense of gape. The pinnation patterns of giant forest hog and warthog, although achieving the same result, are different and therefore probably independently derived from a *Sus*-like pattern, a finding which corresponds to current ideas of suid phylogeny (Cooke, 1978). Although in *Sus*, pinnation serves to differentiate the masseter functionally as well as to increase masticatory force, in *Hylochoerus* and *Phacochoerus* increasing masticatory force seems to be the only important factor.

The evolutionary sequence seems therefore to have been (1) the development of horizontal fibers covering the joint in conjunction with translatory movements of the condyle (all suids); (2) development of oblique pinnation compartments in the center of the muscle as a means for increasing vertical and probably also anterior force for mastication, but leaving long anterior fibers for providing vertical force when the jaws are opened (*Sus*); and (3) replacement of long anterior fibers by pinnation compartments as wide gape becomes less important and masticatory force more important (independently in *Hylochoerus* and *Phacochoerus*).

**Acknowledgments**

The original research was supported in part by NIH Grant DE-3806 (NIDR-PHS/DHEW). A. F. Grimm, S. E. Herring and R. P. Scapino were my collaborators on various aspects of the study. Wet specimens of the African suids were obtained from the American Museum of Natural History, courtesy of R. Van Gelder, and dry specimens were from the Field Mu-
seum of Natural History, courtesy of P. Freeman. I thank William Winn for the photography, and J. Cracraft, W. S. Greaves and K. Hiiemae for reading the manuscript.

REFERENCES


