Chapter 1
Experimental Comparative Anatomy in Physical Anthropology: The Contributions of Dr. William L. Hylander to Studies of Skull Form and Function

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1.1 Introduction

Two important events occurred during the 74th Annual Meeting of the American Association of Physical Anthropology (AAPA) held in Milwaukee, WI (USA), in the spring of 2005. On the one hand, it was the 75th anniversary of the AAPA and a special symposium was held discussing the scientific impact of its founders and early contributors. On the other hand, colleagues and friends of Professor William Hylander gathered to present their most recent work and pay tribute to Dr. Hylander's lifetime contribution to studies of skull functional morphology in primates. Although these two important events were coincidental, they both reminded us of a critical event in the history of physical anthropology: that is, the rise of what Washburn defined as the "New Physical Anthropology" (Washburn, 1951a, b), which advocated for the use of an experimental approach in physical anthropology.

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Our goal in this chapter is to briefly review the historical context that led to Washburn's important, albeit at the time controversial, call for a comparative experimental anatomy and to show how that call was answered by the functional morphologists interested in the evolution of the skull and feeding apparatus of primates and other mammals. In particular, the contribution of Bill Hylander to this important area of research will be reviewed and some directions for the future, which build on Bill's pioneering work, will be discussed.

1.2 Experimental Comparative Anatomy in Physical Anthropology

In 1951, Sherwood Washburn published two seminal essays in which he explicitly urged physical anthropologists to adopt a laboratory-based methodology to address questions of human evolution (Washburn, 1951a, b). The view espoused in these papers is considered a paradigm shift from the typological approach that characterized physical anthropology at the time to a more multidisciplinary approach where experiments played a major role (Stini, 2005). Washburn's (1947; Mednick and Washburn, 1956) approach using laboratory-based data to resolve conflicts in scenarios of human evolution was not always well received by his peers at the time. Indeed, one famous contemporary of Washburn questioned him about the validity of using rats to understand the human phenomenon (Washburn, 1983; Marks, 2000). Moreover, many of his peers saw the experimental method as a major threat because "they thought it was destroying the evidence" (DeVore, 1992:417).

At the time Washburn made the call for a "modern, experimental, comparative anatomy" (Washburn, 1951a:67), there was little activity of that type in the field of physical anthropology. The pioneering studies of Hildebrand (1931) and Elftman and Manter (1935) represent some of the few laboratory-based studies of mastication and locomotion, respectively, completed at the time. Despite the scarcity of such studies in 1951, Washburn foresaw the relevance of these types of data for the evaluation of functional and evolutionary hypotheses in physical anthropology. In addition, he understood the burgeoning technological revolution that would make the experimental approach possible.

The term "experimental comparative anatomy" is cumbersome and on the surface seems too vague to have any meaning. But what Washburn meant is very clear. He meant to expand the available tools for assessing the functional significance of a given morphological trait by controlled, laboratory-based testing of hypotheses derived from comparative anatomy. He wanted anthropologists to go beyond the "opinions," theoretical models, and simple correlations that dominated comparative anatomy at the time.

By the late 1960s and 1970s, there was a rapidly growing trend in the use of laboratory-based methods to study the functional morphology of primates. Much of this was directed toward a better understanding of the primate postcranium and began incorporating the newest techniques available (see Fleagle, 1979; Jouffroy, 1989; Churchill and Schmitt, 2003; Schmitt, 2003; Lemelin and Schmitt, 2007 for historical accounts). But the focus of this chapter is the parallel development of laboratory-based studies of primate craniofacial biology.

In order to fully explore the ways in which laboratory-based studies have influenced our understanding of primate craniofacial anatomy and evolution, it is worth beginning by discussing the foundations of experimental comparative anatomy. In a seminal paper in 1977, Rich Kay and Matt Cartmill formalized the methodological principles that had guided studies of functional morphology for many decades. They laid out four clear steps for making inferences about behavior in fossil animals. Kay and Cartmill (1977) stressed that any trait which we wished to use as a surrogate for a behavior had to be present in extant animals and its function had to be known. But they did not discuss in detail how to determine the function of a trait.

Treated simply, at least two comparative approaches can be used to assess function based on studying morphological traits: (1) an approach capitalizing on convergence or divergence to relate organismal form with presumed functions (Brooks and McLennan, 1991) and (2) an "argument from design" that applies theoretical principles of engineering and design to interpret organismal function based on form (Rudwick, 1964; Lauder, 1996). Both approaches have their strengths and flaws that have been reviewed elsewhere (Bock and von Walhert, 1965; Bock, 1977; Fleagle, 1979; Homberger, 1988; Lauder, 1995, 1996), so we will just briefly touch on them here. The central point here is that conclusions derived from traditional comparative anatomy or engineering-style "argument from design" studies must be viewed not as end-results, but rather as hypotheses to be tested. In many instances, those tests are best accomplished in the laboratory.

Laboratory-based hypothesis testing is exactly what Washburn had in mind and what Hylander and his contemporaries have been pursuing for the past 30 years. But they represent the leaders of a small group within physical anthropology. In spite of the theoretical strengths and observed success of an experimental comparative approach, few physical anthropologists test their functional models with experimental data. There are a lot of reasons for the lack of rigorous testing using laboratory data. Many anthropologists misunderstand how the experimental approach can be used to test functional hypotheses. Too often, criticisms are made about small sample sizes, unnatural laboratory conditions, and the highly technical aspect of the methods used in the laboratory. These concerns inhibit the willingness of physical anthropologists to collect experimental data and the acceptance of such data when they are presented. In the absence of experimental data, confirmation of a functional model can only be achieved via traditional comparative anatomy (e.g., the prediction that long legs are mechanically critical for leaping primates is confirmed by the observation that other leaping animals have long legs). This mode of checking functional models may lead to correct conclusions; but as Bock (1977), Homberger (1988), and others have noted, this is not always the case. Lauder (1996:56) points out that such conclusions are based on untested assumptions and that:

> ...in our desire to draw conclusions about biological design and to support theoretical views of how organism are built, we have been too willing to make assumptions about the relationship between structure and mechanical function...[and]... we have not often

> conducted the mechanical and performance tests needed to assess the average quality of organismal design.

Similarly, Fleagle (1979:316) noted that “Regardless of how mechanically plausible and convincing [functional] explanations may be, they can be rigorously tested only by in vivo studies”. The work of Bill Hylander and his colleagues represents an ideal combination of basic design principles (e.g., beam theory to describe the jaw) and experimental analyses. His approach has led to a better understanding of both structure–function relationships and the evolution of primate craniofacial function and is a model for how to proceed in testing morphological hypotheses with laboratory data.

There are three possible outcomes when using an experimental approach to determine structure–function relationships. The first possibility is that a given hypothesis developed from comparative data or engineering principles will be supported. This is a common, although not universal, outcome.

A second possible outcome is that a mechanical hypothesis relating a specific structure to a particular function may be found to be in error; however, the underlying correlation between structure and behavior still exists. In this case, experimental studies can yield a better understanding of the underlying causal relationship between a trait and its function, and may lead to novel areas for investigation. One good example of how laboratory studies may clarify or change conclusions based on the measurements of morphology is the debate over adaptations to tree gouging in primates. Prior to any laboratory work, researchers measuring jaws and teeth, especially the highly modified incisors of many gouging primates, argued that tree gouging induced large forces on the masticatory system (e.g., Szalay and Seligsohn, 1977; Rosenberger, 1992; Dumont, 1997; Spencer, 1999). This conclusion seems logical, but in vivo work on marmosets has shown that this is not the case and that, in fact, the forces generated during gouging can be seen as being relatively low (Vinyard et al., 2001, in press). This does not invalidate the correlation between chisel-like incisors and gouging behavior in callitrichids. But the finding of relatively low bite forces during gouging in callitrichids is unexpected and it opens up new areas of research into structural modifications of the bones and muscles of the skull that may not be related to force production but instead allow for the use of large gapes in primates (Williams et al., 2002; Taylor and Vinyard, 2004; Perry, 2006).

A final potential outcome is that experimental data change our perception of both structure–function correlations and causal relationships. Understanding the mechanics of phase II during the power stroke of mastication, which began with Hiiemae and Kay (1972, 1974a, b) and was further investigated by Hylander and Crompton in the late 1980s (Hylander and Crompton, 1986; Hylander et al., 1987), represents a perfect example. Prior to the work of Hylander and Crompton, it was assumed that powerful grinding occurs during phase II. This is a heavily embedded assumption in comparative studies of the primate molar dentition. For example, certain occlusal facets on the molar teeth are identified as “phase II facets,” and pitting and abrasions observed on the occlusal surfaces have been linked to forceful contact between the teeth and food during phase II (Kay, 1977, 1987; Grine, 1986). More recently, in a combined video and electromyographic study designed to confirm Hylander's earlier work, Wall et al. (2006) found in baboons that there is negligible force produced by the major jaw adductors during phase II and that mandibular movements were minimal during phase II as compared to phase I. Their results showed that phase II movement is likely trivial for breaking down food. Instead, most food breakdown on the phase II facets probably takes place late in phase I movement, in association with crushing of the food object (see also Hiiemae, 1984; Teaford and Walker, 1984; Teaford, 1985). Additional work to characterize phase II jaw movements in other primate species is underway, but the experimental data clearly suggest the need for an alternative functional explanation for the structure and microwear patterns on the phase II facets of primates.

1.3 The Experimental Approach and Contributions of Bill Hylander

Clearly, the experimental approach is a critical tool for physical anthropologists. Despite the obvious relevance of this approach to the study of primate craniofacial biomechanics, little laboratory-based research was conducted before Bill Hylander began his career. Bill was a graduate student at the University of Chicago in the 1960s. He returned to graduate school after practicing dentistry for several years. His goal was to combine his knowledge of the functional anatomy of the teeth and jaws with the study of the evolution of the primate skull. In the 1970s, he pioneered the experimental approach to understanding the functional anatomy of the skull in primates.

As a graduate student, Bill was interested in developing biomechanical models explaining craniofacial form and function that could ultimately be tested with experimental data. In his thesis, Bill evaluated competing hypotheses to explain the functional anatomy of the Eskimo skull (Hylander, 1972). Specifically, he wanted to know which of the features seen in the cranium and mandible were related to the aspects of tooth use and diet and which could be explained as cold adaptations. This work was eventually published in an edited volume (Hylander, 1977a) in the same year that Bill published his first in vivo bone strain paper (Hylander, 1977b). Bill developed a biomechanical model to explain such features as a robust mandible, high temporal lines, and large bicondylar dimensions as structures that aid in the generation and dissipation of high vertical bite forces.

In another study that demonstrates his knack for critically evaluating competing hypotheses, Bill published a seminal analysis of the human mandible as a lever system (Hylander, 1975). A number of workers had claimed that the jaw functioned as a mechanical link, and thus generated no reaction force at the temporomandibular joint (TMJ). Bill showed that the mandible does function as a third-class lever, and that many aspects of mandibular morphology can be explained in this context.

Since then Bill has made an enormous and fundamental contribution to studies of primate skulls and teeth. Bill has published over 75 research articles, including papers in many edited volumes. A Science Citation search indicates that since 1980, Bill's work has been cited more than 933 times in published articles. His research has been continuously funded by the National Science Foundation, National Institutes of Health, and private foundations for more than 30 years.

Although Bill is probably best known for his work documenting and interpreting the functional significance of in vivo patterns of bone strain in the primate skull (Hylander, 1977b, 1979a, b, c, 1984; Hylander and Johnson, 1992, 1997a, b; Hylander and Ravosa, 1992; Hylander et al., 1991a, b, 1998; Ravosa et al., 2000; Ross and Hylander, 1996 and many others), he has made seminal contributions in the areas of theoretical jaw mechanics (Hylander, 1975b), jaw kinematics (Hylander, 1978; Hylander and Crompton, 1986; Hylander et al., 1987), bone biology (Bouvier and Hylander, 1981, 1996; Hylander et al., 1991b; Hylander and Johnson, 2002), muscle function (Hylander and Johnson, 1985, 1994; Hylander et al., 2000, 2005), and comparative morphometrics (Hylander, 1972, 1975a, 1977, 1985, 1988; Kay and Hylander, 1978). Along the way, he has trained a number of graduate and post-doctoral students who have published extensively in these areas.

Because of the massive volume of Bill's work, it is impossible to review it entirely in this short contribution. Furthermore, we feel that simply reiterating all that Bill has done cannot do justice to how influential his thinking has been on the field of primate craniofacial function and biology. As an alternative approach, we consider what we think are three key articles and discuss how they have molded thinking on mammalian craniofacial biology and the evolution of the primate masticatory system. Other authors might have chosen different articles, but to our way of thinking the work we describe below exemplifies not only the scope of Bill's career but also raise important issues that will remain at the forefront of research on craniofacial functional anatomy for decades to come. We will discuss the implications of Bill's pioneering studies on understanding bone mechanical properties, the scaling of craniofacial structures in primates, and muscle activity during mastication.

1.3.1 Bone Mechanical Properties

One area that Bill focused on is the mechanical determinants of bone size and shape. In 2002, he published a paper with his long-time associate Kirk Johnson, which summarizes his research on this topic and places these results within the context of the functional adaptation/optimal strain environment model of bone remodeling (Hylander and Johnson, 2002; see also Bassett, 1968; Hylander and Johnson, 1997a, b; Lanyon and Rubin, 1985; Pauwels, 1980; Rubin, 1984). Briefly, the phrase "functional adaptation" describes the supposition that normal, day-to-day loading conditions play an important role in maintaining bone mass and geometry (e.g., Hert et al., 1971; Bouvier and Hylander, 1981; Lanyon and Rubin, 1985;

Carter, 1987). Lanyon and Rubin, (1985) argue that functional adaptation maintains bone strain magnitudes within a physiological range of values (usually understood to be between 2,000 and 3,000 με), in order to maintain this optimal strain environment. Under this model, bone models or remodels in response to altered loads in order to maintain the optimal strain environment. One prediction based on the observation of functional adaptation to a narrow range of physiological strains in long bones is that bones should be optimized for resisting routine, physiological loads and should, by definition, exhibit a maximum of strength with a minimum of material for load-bearing purposes. This putative relationship is widely accepted among physical anthropologists (see Lanyon and Rubin, 1985 and Churchill and Schmitt, 2003 for a review of engineering models and bone strength in general biology and anthropology, respectively), but has rarely been tested experimentally. In several studies where it has been tested in the experimentally, significant questions have arisen (Lanyon and Rubin, 1985; Demes et al., 2001).

Hylander and Johnson (2002) bring an enormous amount of data on strain patterns within the jaws and face of primates to test the predictions of the functional adaptation hypothesis. Their evidence unequivocally shows that functional adaptation is not the only mechanism acting to determine the size and shape of bones in the skull. Although some regions (e.g., the anterior root of the zygoma) probably respond to the functional loads incurred during mastication and other feeding behaviors, many bony regions appear grossly over-designed or under-designed for their purported load-resisting function during feeding. The problem that Hylander and Johnson (2002) lay out with respect to the distribution of bone and bone strains is that it is not possible to predict strain from bone geometry (see also Daegling, 1993). The good news is that high strain regions are generally correlated with strong bone (either due to type, amount, or distribution). The bad news is that it is difficult to predict high strain regions simply by proximity to muscle or teeth. Furthermore, low strains are a bad indicator of underlying bone geometry. Several implications follow from these profound findings. Most critically for physical anthropologists, the data suggest that bone size and shape within the skull is not "largely or exclusively determined by or associated with routine and habitual forces associated with mastication, incision, or isometric biting"... and that "reconstructing the masticatory behavior and biomechanics of primates from the fossilized remains of the craniofacial skeleton is extremely problematic, particularly when done in the complete absence of a detailed understanding of the biomechanical environment of the craniofacial region of living primates" (Hylander and Johnson, 2002:43–44). Hylander and Johnson (2002) go on to cite numerous studies published since 1955, which have made this unwarranted assumption. It would seem that though Washburn's call for an experimental approach was heeded by a number of anthropologists that went on to collect in vivo data, those data are not always incorporated into comparative studies.

The importance of the results presented in Hylander and Johnson (2002) is not just about the inability to link bone structure and function in the absence of experimental data. They also provide a testable alternative to explain bone deposition and maintenance in regions where strains do not match bone mass or geometry. They reason that heredity must play an important role in maintaining bone mass in such regions as the browridge.

1.3.2 Scaling in Craniofacial Structures

The second paper we want to review is entitled "Mandibular Function and Biomechanical Stress and Scaling," and was published by Bill Hylander over 20 years ago (Hylander, 1985). This paper is important because it lays out a very explicit methodology for examining the relationship between mechanical loads and the form of the masticatory apparatus across several primate species. Bill makes the important observation that animals do not walk on their faces, and that therefore gravity or a surrogate for gravity, such as body mass, is not a directly relevant independent variable in the functional analyses of size and shape of the masticatory apparatus. There is no a priori reason to predict geometric similarity of masticatory structures. There is, however, ample experimental evidence that predicts strong mechanical influences on the size and shape of masticatory structures. Hylander's (1985) call to develop mechanical predictions of how various features of the masticatory apparatus should scale had a strong influence on studies of craniofacial biomechanics (Daegling, 1993; Daegling and McGraw, 2001; Ravosa, 1996a, b; Ross, 2001; Vinyard and Ravosa, 1998). Here Hylander develops independent variables with specific mechanical relevance to the question at hand, rather than relying on the ones that may be less relevant but are easy to measure (e.g., mandibular length is not always the most relevant mechanical variable).

Moreover, Hylander (1985) advice is much more far-reaching. He pointed out the need for more data on muscle cross-sectional area and to develop explicit models of bone size and scaling under masticatory stress regimes. More recently, Lucas (2004) has developed a set of scaling predictions based on food material properties. Future work should focus on testing various aspects of Lucas's (2004) model, and should incorporate appropriate independent variables into analyses. For example, analysis of moment arms may reveal interesting results about bite force generation when scaled relative to some other estimate of muscle force (e.g., mass or cross-sectional area). These muscle data are now available for many primate species (Anapol et al., Chapter 10; Perry and Wall, Chapter 11) and are relatively easy to collect for others that remain undocumented.

1.3.3 EMG of Mastication

The third paper, Hylander et al. (2005), summarizes much of what we know about the activity of the temporalis muscle during mastication in primates and represents close to 15 years of EMG data collection by Hylander and his colleagues. This paper, in addition to Hylander and Johnson (1994), Hylander et al. (2000), Vinyard et al. (2005, 2006), and Wall et al. (2006, Chapter 6), provide up-to-date information on timing differences and working-side versus balancing-side muscle activity for a wide array of primates and treeshrews as an outgroup species. One important focus of Bill's EMG work (Hylander and Johnson, 1994; Hylander et al., 2000, 2004) has been to evaluate the link between the late peak in activity of the balancing-side deep masseter and wishboning of the mandibular symphysis in anthropoids. Research is underway to extend our understanding of interspecific variation in EMG patterns both by studying other primate species (e.g., *Propithecus verreauxi*, *Eulemur fulvus*, *Saimiri sciureus*, and *Cebus apella*) and looking at specific regions within the temporalis, medial pterygoid, and masseter muscles in representative species. One basic comparison that would be useful for understanding the relationship between EMG, muscle force, and interspecific variation is to compare variability in EMG variables during incision, puncture-crushing, and rhythmic chewing (i.e., tooth-tooth contact) cycles to look for patterns with mechanical significance. For example, do animals avoid unpredictable loads of the symphysis and corpus during the early part of food breakdown (puncture-crushing) as compared to the later part (rhythmic chewing)? If they do, we would expect animals to avoid high peaks in favor of multiple, lower-amplitude peaks.

1.4 Conclusion

Bill's career is hardly at an end. He is an emeritus professor and is currently working on generating testable hypotheses about important features of the primate masticatory apparatus. One of his current projects is to quantify the relationship between canine length, mandible length, maximum passive gape, and muscular development in catarrhine primates. Hylander and Vinyard (2006) find that short canines are correlated with small gape. They suggest that canine reduction, such as that seen in the earliest hominins, is a functional requirement to minimize canine interference associated with decreased gape.

In this chapter, we tried to highlight the role that Bill, his colleagues, and his students have played in advancing our understanding of the biomechanics and evolution of craniofacial structures in primates. The field of physical anthropology owes Bill a tremendous debt of gratitude not only for the specific data he generated concerning primate skull anatomy but also for the model he provides as an experimentalist and for the platform from which much current and future work is and will be built. It is often tedious, difficult, and time-consuming to collect in vivo data, especially on primates. Bill Hylander spent more than 30 years collecting the bone strain, kinematic, and EMG data that have so enriched our understanding of the function, biology, and evolution of the primate craniofacial region. This work represents, we hope, only a beginning for our field. The students that Bill trained and, in turn, the students that they will train need to keep on building on the remarkable dataset that Bill created, because it is the only way to fully understand craniofacial morphology in primates and other mammals.

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