Histomorphological Variation in the Appendicular Skeleton

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Abstract: Densities of osteons and osteon fragments at the midshafts of the femur, tibia, fibula, humerus, radius, ulna and clavicle are examined in a sample of contemporary human males and females (n = 39; 23 female, 16 male), with comparative data derived from one specimen each of *Gallus gallus* and *Felis silvestris catus*. Results demonstrate that there are significant differences in mean complete and fragmentary osteon densities among bones and between the sexes. We suggest that these patterns are less a simple reflection of the so-called "Wolff's law," but instead represent not only remodeling in response to loading, but also underlying intrinsic developmental parameters specific to each bone. Given the diversity of locomotor patterns of the three species, and the resulting differences in loading environments of their limbs, this histomorphological pattern suggests that remodeling is an inherently complex phenomenon, subject to local intrinsic developmental factors in addition to mechanical loading.

Key Words: *Homo sapiens, Felis silvestris catus, Gallus gallus*, Wolff.

INTRODUCTION

The emergence and development of the mammalian skeleton is an exceedingly complex process, largely under genetic control, but with some influence by each bone's mechanical environment [1, 2]. However, in recent years several aspects of that process have become significantly clarified. Among the most important is an accumulation of evidence suggesting that osteoblast behavior is highly conserved [3-5]. Despite an enormous range of body mass, actual microstrain experienced by mammalian bones has been found to fall within a very narrow range [6-11]. This raises the strong possibility that osteoblast response protocols are highly conserved, and do not vary substantially from one mammal to another. Such a view has also received strong support from studies of limb bud dynamics [4, 5]. These suggest that differences in the structure and form of the skeleton can be traced to early initial differences in the disposition of positional information (PI). Thus, morphological differences between species owe their existence almost exclusively to differences in pattern formation rather than to species-specific programmatic differences in the anabolic behavior of these cells (including osteoblasts). There are some obvious areas where this is probably not entirely the case, such responses to loading within epiphyseal plates. However, it is still very likely that throughout the metamorphosis of each skeletal anlagen into its adult structure, the location, speed, and composition of bone deposition depend primarily upon the inherent "programming" of osteoblasts provided by their PI, and that these protocols are very probably highly conserved among mammals. Thus, it is changes in the form and composition of anlagen and their precursive mesenchymal structures (as well as simultaneous alterations in the structure and composition of their soft tissue envelopes) that serve as the primary locus for skeletal evolution. These are "translated" into adult structure by conserved response protocols resident in the osteoblast and other connective tissue components. Understanding the evolutionary process, therefore, requires a thorough knowledge of the behavioral repertoire of mammalian and vertebrate osteoblasts and the nature of their systemic response systems.

A number of approaches have been taken to further refine our understanding of osteoblast behavior, including a long and varied history of observing the effects of disease processes, trauma, and clinical intervention, direct experimental manipulation of bones, systemic modeling, and behavioral observation analysis. Recently, individual cell behavior has also become a focus of study. The present contribution is an attempt to add to our knowledge of osteoblast response patterns by means of whole skeletal analysis. We do so by an intensive histological survey of the entire long bone skeletons of a normal mammal and bird, and compare these data with similar data from a sample of modern humans. We reasoned that close examination of the differences and similarities in the distribution of bone type, histological structure, and geometric properties might provide useful information about the complex behavior of bone tissue.

A number of types of adult mammalian bone have been recognized. For the most part it is lamellar, consisting of progressively deposited layers whose included blood channels do little to disturb its general arrangement. However, this type of bone only characterizes animals in which growth rate and size permit it. In mammals, in which growth rates are too rapid, plexiform or laminar bone is deposited instead [11]. In the domestic cat the size and growth rate permit the deployment of "classical" lamellar bone, and as in other species, including humans, much of this bone is later subjected

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to repair and replacement by more “modular” lamellar bone in the form of novel haversian systems. We therefore reasoned that the distribution and pattern of occurrence of these secondary systems might prove informative about the general nature of the behavior of bone tissue and its included cells.

As just noted, often in the development and maintenance of lamellar bone, factors such as repair and/or responses to novel mechanical loading require its form and/or internal composition to be altered, or *remodeled*. Mammalian skeletal remodeling is affected by many primary factors, including the endocrinological environment. Mechanical loading, which may vary from location to location within the skeleton and within each individual history, is an important but largely secondary determinant. For example, in individuals with paralysis or paresis from various spinal birth defects, the femur continues to grow to its normal length and to obtain virtually normal morphology. However, the quantity and quality of its cortical bone suffers. Indeed, as a consequence of differential mechanical loading, different skeletal elements within the same limb, and from side to side in contralateral members of bone pairs. While the phenomenon of skeletal remodeling has been the subject of intense scrutiny for the last several decades, intraindividual variations in the basic parameters of mammalian and vertebrate cortical bone remodeling have not been systematically investigated such that variation can be more readily understood. This research reported here addresses this basic problem.

Haversian remodeling is traditionally presumed, in part, to reflect response to mechanical forces that bone is subjected to during life [11]. Histomorphological variation within and among bones may thus reflect life history, once "background" variation attributable to other causes is understood. The standard paradigm of skeletal remodeling, often based around assumptions of the so-called "Wolff's Law," [12] portrays remodeling of skeletal elements as an adaptive response of bone tissue to the mechanical loads imposed upon it. In recent years, the validity of this assumption as the sole basis of skeletal remodeling has come into question [5, 13, 14]. To test some of these assumptions, we here examine variation within and among skeletal elements and across species, both at the tissue level and the whole bone level. Previous work has demonstrated bilateral symmetry in density of haversian structures (complete and fragmentary osteons per square millimeter in cross section) in cats [15], chickens, and the human forelimb [16]. Remodeling at the microscopic level is also correlated with remodeling and morphology at the macroscopic level [17]. Bilateral asymmetry, either at the whole bone level or at the histological level, may reflect asymmetry of loading history. We here assess bilateral symmetry at the whole bone level by examination of the cross sectional geometric properties of bones (area moments of inertia, polar moments of inertia, and cortical bone cross sectional area). We also examine differences in remodeling in different skeletal elements and between forelimbs and hindlimbs [18-21].

Density of Haversian structures, defined as complete and fragmentary secondary osteons (i.e., haversian systems) per sq. mm. of bone in cross section, are used in numerous ways by anthropologists and other investigators to assess age at death [17, 22, 23], activity levels [11, and references therein], status of health and disease [24, 25]), and populational variation [26]. While multiple locations throughout the skeleton have been examined to assess osseous histomorphology, a systematic overview is generally lacking of the histology of the entire skeleton. Toward this end, we here examine the histomorphology of the midshafts of the major long bones of the human skeleton, and include comparisons to other vertebrates of diverse locomotor styles.

METHODS

Variation in histomorphology can occur both within a single bone and among different skeletal elements. Variation can also occur between species. Here we examine all three levels of variation.

We collected data of a number of types. We examined densities of secondary osteons and osteon fragments per sq. mm. at the midshafts of long bones in a sample of contemporary adult human males and females (n = 39; 23 female, 16 male). We also calculated densities of secondary osteons and osteon fragments in 14 pairs of human ulnae in order to quantify differences between sides in *Homo sapiens*. The right ulnae of these pairs are part of the larger human sample.

To examine intrabone variation, the major long bones of one specimen each of *Gallus gallus* (domestic chicken) and *Felis silvestris catus* (domestic cat) were sectioned at multiple locations along their lengths, including the midshafts. The specimen of *Felis silvestris catus* was a young adult female domestic shorthair. The specimen of *Gallus gallus* was a young adult White Leghorn male. No other information is available regarding these specimens. Additional specimens of other taxa, especially wild specimens, are desirable. These will be the subject of additional studies.

We examined the femur, tibia, humerus, radius, and ulna of all three species. The clavicle in *Homo sapiens* and furculum ("wishbone") in *Gallus gallus* were also examined. *Felis silvestris catus* is functionally aclaviculate (the bone is reduced to a sliver embedded in muscles cranial to the shoulder joint and has lost its connection to the rest of the skeleton [27]. One of the implications of the so-called "Wolff's law" is that bone remodels primarily in response to mechanical loads. We hypothesize that the different loading patterns necessitated by the diverse locomotor patterns of the three species included in this analysis should be apparent if this is the case.

In the specimens of *Felis silvestris catus* and *Gallus gallus*, each bone was transversely sectioned at 9 points at intervals of 10% of the bone’s total length. The human bones were sectioned only at the midshaft, equivalent to the 50% segment in the bones of *Felis silvestris catus* and *Gallus gallus*. Undecalcified thin sections were made at each location. Cross-sectional properties were calculated for each section, including total and cortical area, as well as area moments of inertia and polar moment of inertia [28]. Comparisons of histomorphometric and cross sectional parameters, including complete and fragmentary secondary osteons per square millimeter (i.e., osteon and fragment density) in the section and percent of section composed of haversian bone were made between proximal and distal limb segments, between serially homologous fore and hindlimb bones, and between contra-

lateral members of pairs of bones. Proximodistal variation within bones was also examined by collecting data at each of the 9 sections made at 10 % intervals of the bones' lengths.

For human specimens, data collected include: secondary osteons per sq. mm.; fragments of secondary osteons per sq. mm.; and fraction of section composed of solid bone estimated *via* a grid system. Fraction of the section composed of solid bone gives an estimate of the area of the section that has been resorbed by osteoclastic activity. This was estimated by counting the intersects that overlaid areas of resorbed bone using an eyepiece reticule embedded with a nine-by-nine grid [29]. The percentage of intersects that take place over resorption spaces gives an estimate of the percentage of the section that has been resorbed. Subtracting this figure from 100 gives the estimate of the percent of the field composed of solid bone. Once the portion of the field composed of haversian bone is known, the density of osteons and osteon fragments per square millimeter in that fraction of bone can be calculated. Derived data thus include the number of secondary osteons and osteon fragments per square millimeter normalized by percent of field composed of solid haversian bone. For the 14 pairs of left and right human ulnae, total and cortical area, area moments of inertia, and polar moments of inertia were also calculated for comparison with similar data from *Felis silvestris catus* and *Gallus gallus.*

RESULTS

Comparisons can be made among species, among bones within species, between fore and hindlimbs, between sides, and within individual bones, at both microscopic and macroscopic levels. Both birds and mammals exhibit haversian remodeling within cortical bone [30]. Therefore, remodeling at the microscopic level in both these taxa can be compared directly with that of humans. Since all three species have a dramatically different locomotor style, under the assumptions of the so-called "Wolff's law" we would expect that differential loading of the appendicular skeleton would manifest in histomorphology and/or gross morphology. Presence or absence of these differences can aid in interpreting the role of differential loading in determining macroscopic and microscopic cortical bone morphology.

Intrabone Variation: Comparative Histomorphology

In *Felis silvestris catus*, the amount of haversian (i.e., remodeled) bone varies substantially from one section to another, and from one long bone to another. A definite trend emerges from an examination of the entire feline skeleton with respect to the diaphyseal distribution of secondary haversian systems. There is a clear proximodistal reduction in the number of complete and fragmentary secondary osteons within each individual long bone, with the exception of the humerus, where the trend is less obvious (Table **1**). The limb bones of *Gallus gallus* show a somewhat different pattern, wherein the midshaft regions of the bones show a greater amount of remodeling and osteoblastic activity, while the proximal and distal portions of the bones are generally more quiescent (Table **2**). All bones examined, with the exception of the furculum, were composed of haversian bone. The chicken and cat were both young adult specimens. Some osteon fragments were observed in *Felis silvestris catus*, though they were very infrequent. Additionally, osteons in *Felis silvestris catus* were considerably larger than those in *Gallus gallus.* As a result, the osteons denisities are considerably higher in *Gallus gallus* than in either *Felis silvestris catus* or in *Homo sapiens*. The furculum in the specimen of *Gallus gallus* examined here was quiescent and unremodeled.

Within the skeleton of *Felis silvestris catus*, there are regional differences in the distribution of haversian structures. In the femur, there is a dense concentration of osteons located posterolaterally, in the region of the linea aspera. In the tibia, the same patterns emerge as in the femur, but there are concentrations of osteons associated with the three corners of its essentially triangular cross section. The feline tibia has dense concentrations of osteons and substantial amounts of haversian bone anteriorly, which become progressively less dense in the distal-most few segments, while other regions of the tibia appear more variable. The anterior concentration of osteons and amount of haversian bone in the tibia corresponds to its sharp anterior border. The feline humerus, radius, and ulna also show concentrations of osteons at sharp borders, for example, at the interosseous crests and supracondylar ridges. These are areas of concentrations of Sharpey's fibers which likely influence remodeling rates, because entheses are known to be under specific local control.

In marked distinction to *Felis silvestris catus*, *Gallus gallus* demonstrates a much more general distribution of osteons throughout the cortex, while at the same time showing a much higher concentration of vascular channels. As noted above, the individual haversian systems in Gallus gallus are smaller than those in *Felis silvestris catus* or in *Homo sapiens.* The limb bones of *Gallus gallus*, by contrast to *Felis silvestris catus* or *Homo sapiens*, are generally round to oval in cross section and do not demonstrate sharp interosseous borders. Likewise, they do not demonstrate the localized concentrations of secondary osteons seen in *Felis silvestris catus*. We suggest that sites of muscle attachment, and therefore the distribution of Sharpey's fibers, may be more diffuse and or more periosteal in *Gallus gallus.*

The bones of the antebrachium show greater remodeling activity than the brachium or the bones of the hindlimb, as evinced by densities of complete and fragmentary osteons. In *Felis silvestris catus*, the right antebrachium demonstrates higher numbers of haversian structures per square millimeter than the left (Fig. **1**). In both *Felis silvestris catus* and *Gallus gallus*, the forelimb has a higher density of haversian structures than the hindlimb, and the radius and ulna more than the humerus, but there is no left-right asymmetry in the forelimb of *Gallus gallus*, nor in the hindlimbs of either species (Table **1**). In *Homo sapiens* there is no significant difference in density of haversian structures between forelimb and hindlimb, and, as will be discussed below, no evidence of bilateral asymmetry (see Table **4**).

There are similar patterns of remodeling between *Gallus gallus* and *Felis silvestris catus* (Tables **1** and **2**). While *Gallus gallus* has two to three times the density of channels for blood vessels as a comparable section in *Felis silvestris catus*, both exhibit a very similar pattern; that is, in both taxa and in all bones examined, the highest densities of structures are near midshaft. Further, in both *Gallus gallus* and *Felis silvestris catus*, higher densities are found in the forelimb

Table 1. Densities of Osteons and Fragments, Bilaterally Compared, by Species. (a) Osteons per sq. mm. (b) Osteon Fragments per sq. mm.

(a) Osteons per sq. mm.

SPECIES Felis silvestris catus

Distance from Proximal End of Bone	BONE									
	Left Femur	Left Tibia	Left Humerus	Left Radius	Left Ulna	Right Femur	Right Tibia	Right Humerus	Right Radius	Right Ulna
10%	3.9	5.2	3.8	11.1	6.9	5.6	4.7	3.5	18.1	19.8
20%	9.9	7.6	3.4	11.4	16.9	10.8	7.2	4.7	20.8	29.0
30%	7.1	13.6	6.0	11.8	13.9	6.3	12.3	6.2	18.4	25.8
40%	3.6	11.6	8.4	13.3	11.2	3.4	13.3	10.1	18.3	24.6
50%	8.0	12.6	6.6	14.5	11.4	4.3	16.9	14.1	16.8	15.5
60%	10.6	7.9	5.0	8.6	13.9	10.2	12.7	8.0	13.3	13.0
70%	6.3	11.8	2.9	6.2	11.2	7.8	13.2	6.5	10.1	7.8
80%	3.8	6.3	4.0	4.5	3.8	5.7	6.6	4.3	5.2	5.9
90%	1.7	4.4	4.6	3.8	2.6	3.7	2.8	7.8	4.5	1.9

SPECIES Gallus gallus

Distance from Proximal End of Bone	BONE									
	Left Femur	Left Tibia	Left Humerus	Left Radius	Left Ulna	Right Femur	Right Tibia	Right Humerus	Right Radius	Right Ulna
10%	.0	1.6	1.7	.3	7.9	.0	.0	7.2	1.0	6.6
20%	4.3	8.5	8.5	2.1	31.2	2.3	6.2	15.4	5.6	21.7
30%	5.6	7.0	28.2	27.0	67.1	12.9	6.5	20.8	39.5	44.0
40%	25.2	12.2	36.1	97.7	68.4	30.7	20.9	40.1	96.0	54.3
50%	18.9	29.0	62.2	83.3	75.4	17.0	27.0	81.2	66.2	80.0
60%	22.9	37.2	58.6	55.2	84.9	26.0	37.8	40.4	65.9	91.0
70%	20.5	55.7	12.9	43.0	29.7	23.6	37.3	13.8	47.5	63.5
80%	16.4	14.9	13.5	17.9	5.9	8.6	11.4	18.9	42.4	14.6
90%	.0	7.3	16.2	.4	.0	1.2	2.2	13.5	.6	.1

(b) Osteon Fragments per sq. mm.

SPECIES Felis silvestris catus

Distance from Proximal End of Bone	BONE									
	Left Femur	Left Tibia	Left Humerus	Left Radius	Left Ulna	Right Femur	Right Tibia	Right Humerus	Right Radius	Right Ulna
10%	.3	2.6	1.7	1.1	1.1	.4	1.5	.9	3.5	1.3
20%	2.4	2.3	.4	1.6	2.8	2.1	2.1	1.4	1.6	2.5
30%	1.0	3.6	.7	2.3	4.3	.7	2.3	1.0	3.1	1.6
40%	.2	2.0	.8	1.9	3.7	.8	2.5	1.0	4.1	3.9
50%	1.0	2.5	1.1	.9	2.0	1.5	2.3	1.6	1.8	2.3
60%	1.1	1.4	.7	1.0	2.0	1.6	1.7	1.2	2.4	1.4
70%	.4	1.4	.6	.8	1.3	.9	1.4	.7	1.7	1.4
80%	.6	.5	.6	.5	.5	.4	.7	.6	1.3	.6
90%	1.5	.9	.5	.6	.5	.3	.9	.6	1.8	.5

SPECIES *Gallus gallus*; All values 0.

Table 2. Normalized Anteroposterior Area Moment of Inertia (NI_{ap}), Normalized Mediolateral Area Moment of Inertia (NI_{ml}), Normalized Polar Moment of Inertia (NJ), and Normalized Cortical Area (NCA), by Side and by Species. (a) NI_{ap}, in *Felis silvestris catus*. (b) NI_{ap}, in *Gallus gallus*. (c) NI_{ml}, in *Felis silvestris catus*. (d) NI_{ml}, in *Gallus gallus*. (e) NJ in *Felis silvestris catus*. (f) NJ in *Gallus gallus*. (g) NCA in *Felis silvestris catus*. (h) NCA in *Gallus gallus*

(a) NI_{ap}, in *Felis silvestris catus*

Distance from Proximal End of Bone	BONE									
	Left Femur	Left Tibia	Left Humerus	Left Radius	Left Ulna	Right Femur	Right Tibia	Right Humerus	Right Radius	Right Ulna
10%	4.37	5.11	5.64	.23	.88	3.85	5.60	4.31	.16	1.99
20%	1.82	3.28	3.05	.09	1.28	1.26	2.52	3.58	.07	1.30
30%	1.13	1.56	2.52	.12	.60	.95	1.37	2.63	.06	.56
40%	1.05	1.31	1.80	.09	.38	1.17	1.06	1.58	.08	.39
50%	.95	1.18	1.41	.09	.29	.86	.91	1.17	.07	.22
60%	.97	.97	.96	.11	.12	.97	.69	.90	.08	.16
70%	1.05	.72	.95	.13	.14	.88	.67	.81	.09	.17
80%	1.81	.74	1.26	.12	.12	1.08	.67	1.10	.10	.10
90%	3.53	.96	2.19	.20	.16	2.24	1.18	1.75	.24	.15

(b) NI_{ap}, in *Gallus gallus*

Distance from Proximal End of Bone	BONE									
	Left Femur	Left Tibia	Left Humerus	Left Radius	Left Ulna	Right Femur	Right Tibia	Right Humerus	Right Radius	Right Ulna
10%	6.60	3.37	3.17	.28	1.46	6.51	5.14	2.01	.31	2.02
20%	3.06	2.56	4.11	.19	.92	5.33	4.10	4.74	.31	2.18
30%	4.61	3.36	1.84	.09	.69	2.61	3.23	2.14	.17	2.02
40%	2.20	3.14	1.24	.07	.69	2.26	1.72	1.21	.15	1.21
50%	2.82	2.47	1.24	.08	.84	2.77	2.15	1.12	.10	.51
60%	3.73	2.22	.87	.09	.78	3.64	1.71	1.81	.11	.49
70%	3.85	1.91	1.32	.15	.84	4.18	2.24	1.51	.11	.37
80%	3.51	2.64	1.62	.12	1.19	3.82	2.16	1.86	.14	.80
90%	4.49	2.68	.81	.22	1.84	3.97	3.81	.61	.26	.86

(c) NI_{ml}, in *Felis silvestris catus*

Distance from Proximal End of Bone	BONE									
	Left Femur	Left Tibia	Left Humerus	Left Radius	Left Ulna	Right Femur	Right Tibia	Right Humerus	Right Radius	Right Ulna
10%	2.95	3.45	2.70	.28	.29	2.11	2.98	2.37	.24	.23
20%	1.87	2.04	2.52	.20	.23	1.35	1.67	2.12	.14	.27
30%	1.15	1.08	1.54	.35	.09	1.12	.90	2.02	.16	.06
40%	1.14	.80	1.18	.26	.17	1.26	.78	1.07	.22	.15
50%	1.03	.69	.83	.24	.17	1.15	.56	.87	.23	.12
60%	1.20	.92	.68	.27	.03	1.27	.85	.76	.24	.11
70%	1.31	.56	.97	.31	.15	1.24	.61	.89	.19	.16
80%	2.31	1.15	3.33	.28	.19	1.28	.86	2.33	.22	.16
90%	4.55	1.54	10.77	.56	.09	3.25	1.39	.97	.55	.07

(Table 2) contd….

(d) NI_{ml}, in *Gallus gallus*

Distance from Proximal End of Bone	BONE									
	Left Femur	**Left Tibia**	**Left Humerus**	**Left Radius**	**Left Ulna**	**Right Femur**	**Right Tibia**	**Right humerus**	**Right Radius**	**Right Ulna**
10%	11.82	6.40	11.87	.50	3.14	14.98	2.93	11.57	.39	1.83
20%	1.83	3.22	11.68	.28	2.02	3.11	2.86	11.27	.30	1.70
30%	2.95	2.60	3.72	.14	1.12	2.42	3.13	3.38	.17	1.81
40%	3.41	1.86	2.34	.09	1.37	2.24	1.99	1.94	.12	1.53
50%	3.33	1.42	1.66	.11	.52	2.41	2.25	1.79	.10	1.04
60%	4.21	2.32	1.19	.12	.52	4.09	2.50	2.00	.11	.78
70%	4.45	2.81	2.06	.20	.60	5.04	3.54	1.89	.13	.54
80%	4.20	3.74	4.27	.24	.69	6.67	4.13	3.90	.11	1.04
90%	7.57	4.14	3.91	.43	1.54	5.43	7.22	3.58	.20	1.24

(e) NJ in *Felis silvestris catus*

Distance from Proximal End of Bone	BONE									
	Left Femur	**Left Tibia**	**Left Humerus**	**Left Radius**	**Left Ulna**	**Right Femur**	**Right Tibia**	**Right Humerus**	**Right Radius**	**Right Ulna**
10%	7.32	8.57	8.34	.50	1.17	5.96	8.59	6.68	.40	2.22
20%	3.69	5.32	5.58	.29	1.50	2.61	4.19	5.70	.21	1.57
30%	2.28	2.63	4.05	.46	.69	2.06	2.27	4.65	.22	.62
40%	2.19	2.11	2.97	.35	.55	2.42	1.84	2.65	.30	.54
50%	1.98	1.87	2.24	.33	.46	2.01	1.47	2.03	.30	.34
60%	2.16	1.89	1.64	.38	.15	2.23	1.54	1.66	.32	.28
70%	2.36	1.27	1.92	.43	.29	2.12	1.27	1.70	.28	.32
80%	4.12	1.88	4.59	.40	.31	2.36	1.53	3.42	.31	.26
90%	8.07	2.51	12.96	.76	.25	5.50	2.58	2.72	.80	.22

(f) NJ in *Gallus gallus*

Distance from Proximal End of Bone	BONE									
	Left Femur	**Left Tibia**	**Left Humerus**	**Left Radius**	**Left Ulna**	**Right Femur**	**Right Tibia**	**Right Humerus**	**Right Radius**	**Right Ulna**
10%	18.42	9.76	15.04	.78	4.61	21.49	8.07	13.58	.71	3.85
20%	4.89	5.78	15.79	.47	2.94	8.44	6.96	16.01	.61	3.88
30%	7.56	5.96	5.56	.23	1.81	5.03	6.37	5.52	.34	3.83
40%	5.61	5.00	3.57	.16	2.06	4.49	3.71	3.15	.28	2.74
50%	6.16	3.88	2.90	.19	1.36	5.18	4.40	2.91	.20	1.54
60%	7.93	4.54	2.06	.22	1.29	7.73	4.22	3.81	.22	1.27
70%	8.30	4.72	3.38	.35	1.44	9.21	5.78	3.40	.24	.91
80%	7.70	6.38	5.89	.36	1.88	10.48	6.29	5.76	.25	1.84
90%	12.06	6.82	4.72	.65	3.38	9.40	11.02	4.19	.46	2.10

(Table 2) contd….

(g) NCA in *Felis silvestris catus*

Distance from Proximal End of Bone	BONE									
	Left Femur	**Left Tibia**	**Left Humerus**	**Left Radius**	**Left Ulna**	**Right Femur**	**Right Tibia**	**Right Humerus**	**Right Radius**	**Right Ulna**
10%	4.25	3.56	3.38	1.74	1.54	2.44	2.69	2.80	1.26	1.06
20%	2.79	3.19	3.34	1.36	1.95	2.12	2.46	2.70	1.13	2.01
30%	2.37	2.31	3.42	1.50	1.39	2.07	1.96	3.03	1.08	1.21
40%	2.47	2.24	3.11	1.37	1.35	2.24	2.10	2.65	1.21	1.26
50%	2.17	2.35	3.13	1.37	1.30	2.09	2.05	2.42	1.18	1.06
60%	2.29	2.46	2.54	1.44	.78	2.05	2.13	2.27	1.22	.95
70%	2.52	1.93	3.15	1.50	1.05	2.16	1.77	2.37	1.25	1.06
80%	3.53	2.20	4.05	1.44	1.11	2.05	1.92	3.41	1.19	.95
90%	1.27	2.24	4.54	1.48	.66	1.63	1.77	2.84	1.29	.72

(h) NCA in *Gallus gallus*

Distance from Proximal End of Bone	BONE									
	Left Femur	**Left Tibia**	**Left Humerus**	**Left Radius**	**Left Ulna**	**Right Femur**	**Right Tibia**	**Right Humerus**	**Right Radius**	**Right Ulna**
10%	7.14	1.68	6.74	2.91	4.20	6.96	1.61	5.50	2.29	4.22
20%	3.30	2.24	10.01	2.35	4.09	4.64	3.94	8.88	2.29	4.43
30%	5.80	3.98	5.50	1.58	3.23	3.93	4.32	5.65	2.28	5.27
40%	4.86	3.74	5.19	1.45	3.77	4.11	2.93	4.28	1.68	4.78
50%	6.33	3.50	5.00	1.69	3.41	5.16	4.24	4.82	1.70	3.53
60%	7.18	4.18	4.01	1.90	3.02	6.35	3.91	5.65	1.76	3.05
70%	6.00	3.53	3.95	2.29	3.02	5.56	4.01	4.51	1.70	2.14
80%	5.04	3.00	6.09	2.21	3.22	6.10	3.16	5.53	1.71	2.99
90%	7.43	2.57	3.99	2.11	2.97	3.53	3.83	3.18	1.44	2.88

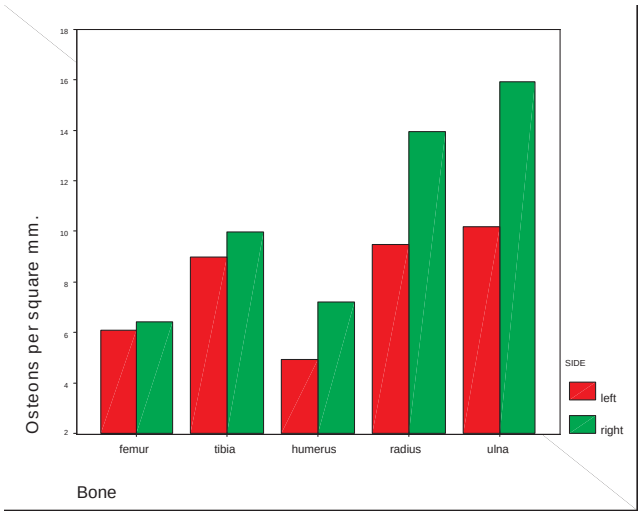

Fig. (1). Bilateral distribution of osteons per sq. mm. in *Felis silvestris catus.*

than in the hindlimb. In both species the radius and ulna exhibit higher densities of secondary osteons and fragments than do other limb bones. The major difference between the two species is that the midshaft humerus is relatively more remodeled in *Gallus gallus* than in *Felis silvestris catus*. There is also a proximodistal gradient in densities of haversian structures in *Felis silvestris catus*, with higher densities in the more proximal sections of the bones, while in *Gallus gallus*, greatest concentrations are at midshaft with a definite reduction in density toward the proximal and distal extremities (Tables **1** and **2**).

Interbone Variation: Bilateral Comparisons

A complete or partial secondary osteon (haversian system) is an indication of a bone remodeling event. In *Felis silvestris catus* the right radius and ulna demonstrate the highest remodeling activity based on this observation, particularly at their proximal extremities (Table **1**). This implies asymmetric remodeling of the antebrachium in *Felis silvestris catus*. The humerus, both in terms of overall size and

remodeling activity, resembles more closely the tibia and femur in contradistinction to the other forelimb bones. Moreover, haversian remodeling in left and right humeri in *Felis silvestris catus* is symmetrical. Both fore and hindlimb bones in *Gallus gallus* are also symmetrical in their remodeling (Fig. **2**). The asymmetry noted in the *Felis silvestris catus* forelimb is not present in *Gallus gallus*; nor is it present in *Homo sapiens*, as will be discussed below.

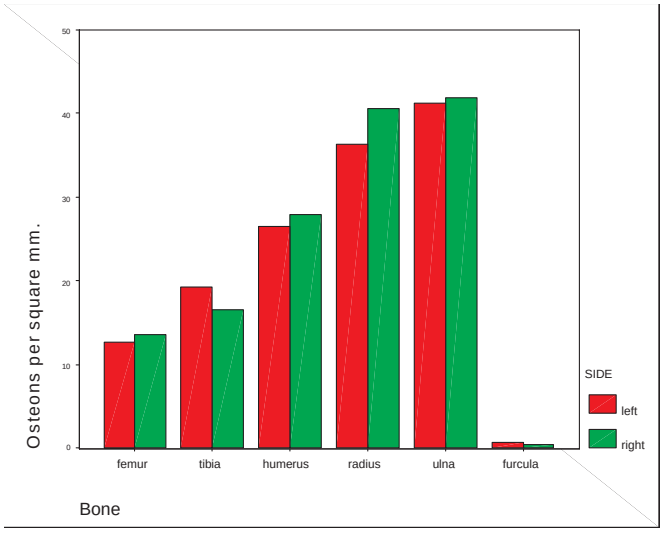

Fig. (2). Bilateral distribution of osteons per sq. mm. in *Gallus gallus.*

The above results suggest an hypothesis: that forelimb remodeling is asymmetric due to differential limb use from side to side. Some evidence suggests that cats, like many mammals, have a tendency to use one forelimb preferentially in manipulating their environments [31-33]. There is some evidence that forelimb preference has a genetic basis in mammals [34, for example]. This could possibly explain the forelimb asymmetry noted in *Felis silvestris catus* if haversian remodeling is, in fact, solely a reflection of imposed mechanical loads on bones. If this were indeed the case, then corroborative evidence should be available from the bones of *Homo sapiens* (It should be noted, however, that the total number of haversian structures is low in all the bones of *Felis silvestris catus* examined here. The bones are not highly remodeled and the side to side differences between the left and right radii and ulnae may well be due to sampling error.) The bones of *Gallus gallus* were also examined for evidence of forelimb remodeling asymmetry, as were the forelimbs of *Homo sapiens* (Fig. **3**). It was hypothesized that the chicken would show no asymmetry in its forelimbs, since it was highly unlikely that there could be a preference for greater use of one wing over the other. Humans obviously demonstrate handedness, and in the case of elite athletes such as tennis players, the dominant arm has been demonstrated to show higher bone mineral density and greater bone width than the nondominant arm [35]. (The same group of researchers, however, found no side-to-side differences in upper limb bones following an asymmetric weight training program among non-elite athletes). This suggests, along with evidence from the cat skeleton, that the bones of the human antebrachium should demonstrate asymmetry in remodeling. This would accord with the assumptions of the standard paradigm of skeletal remodeling.

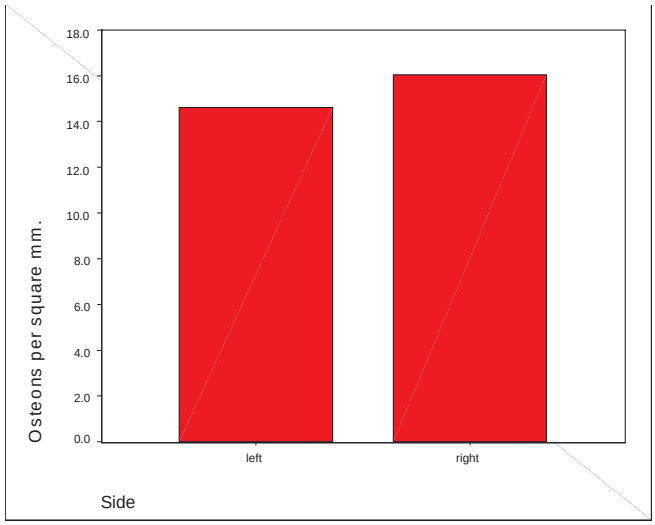

Fig. (3). Bilateral distribution of osteons per sq. mm. in the left and right ulnae of *Homo sapiens.*

As hypothesized, the chicken skeleton did not show evidence of bilateral asymmetry (Fig. **2**). There is no statistically significant difference from side to side. To examine asymmetry in haversian remodeling in humans, undecalcified thin sections were made of the midshafts of 14 pairs of human left and right ulnae. Osteons and fragments per square mm. were examined in four fields located anteriorly, posteriorly, medially and laterally around the perimeter of the midshaft. Cross sectional geometrical properties were also calculated for these midshafts, including cortical area, endosteal area, anteroposterior area moment of inertia, mediolateral area moment of inertia, and polar moment of inertia. Cross sectional geometric properties were size normalized by ulnar length. Wilcoxon signed rank tests demonstrate no significant differences between left and right sides in either haversian structures or cross sectional properties at an experiment wise alpha (Bonferroni corrected) of .05 (Table **3**). The standard paradigm would suggest that there should be asymmetry in these properties, given the distinct handedness expressed in human beings. However, no such asymmetry is in evidence. Alternatively, if skeletal anlagen are "translated" from early development to adult structure by conserved response protocols resident in the osteoblast and other connective tissue components, then we would expect there to be no significant difference between sides, and indeed we should see similar responses across vertebrate taxa. Results here collectively support the latter view, and since there was an absence of asymmetry within the human specimens, the most likely explanation of any differences seen in the cat specimen was simply sampling error.

Interbone Variation: Geometric Properties

Geometric properties of long bone cross sections putatively reflect the results of skeletal growth and remodeling at the macroscopic level, just as histomorphology is believed to reflect these processes at the microscopic level. As with histomorphometric properties, substantial variations in geometric properties were present from one bone to another in our sample (Table **3**). Cross sectional geometric properties observed include normalized anteroposterior area moment of

Table 3. Wilcoxon Signed Rank Tests for Human Ulnae. Expirement Wise Bonferroni Corrected Alpha = .05 (.0071 for Individual Comparisons)

	Osteon Fragments	Complete Osteons	Normalized Cortical Area	Normalized Endosteal Area	Normalized A-P Area Moment of Inertia	Normalized M-L Area Moment of Inertia	Normalized Polar Area Moment of Inertia
Z	-1.538	-1.978	-1.350	-1.664	-1.099	-.157	-.031
Asymp. Sig. (2-tailed)	.124	.048	.177	.096	.272	.875	.975

inertia (I_{ap}) (Figs. **4-6**), normalized mediolateral area moment of inertia (I_{ml}) (Figs. **7-9**) and normalized polar moment of inertia (J) (Figs. **10-12**). I_{ap} is a measure of the relative resistance to bending along the anteroposterior axis of the bone, I_{ml} of the relative resistance to bending along the mediolateral axis, and J a measure of the relative resistance to torsional deformation [36]. Additionally, cross sectional cortical area (Figs. **13-15**) and endosteal area were calculated for each section. If there are bilateral differences in mechanical loading of bones, and if bone responds primarily to adapt to these differential loadings, we would expect to see asymmetry in these various parameters. However, in general, contralateral members of pairs of bones resemble each other substantially in their cross sectional geometric properties (Figs. **4-15**). In Figs. (**4-15**), the graphs present averages for

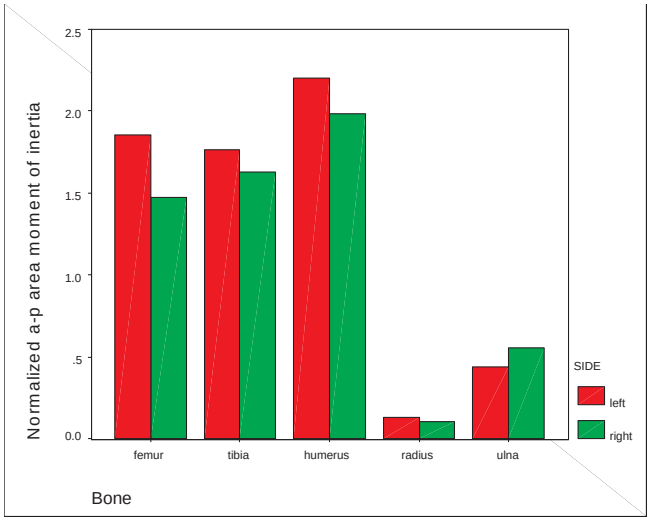

Fig. (4). Normalized anteroposterior area moment of inertia (NI_{ap}) by bone and side in *Felis silvestris catus.*

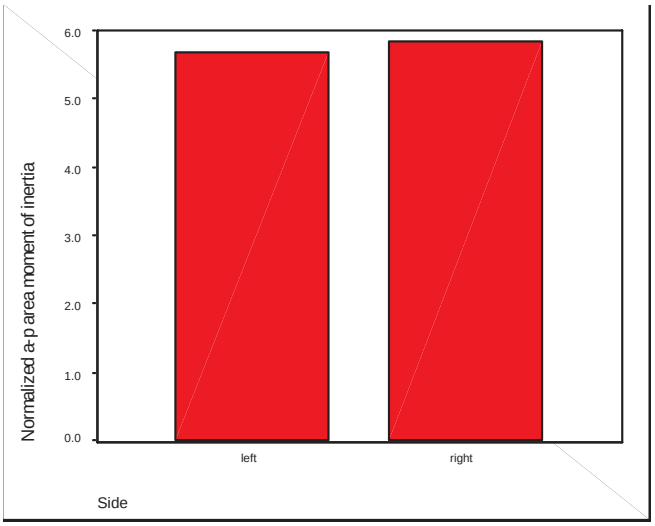

Fig. (6). Normalized anteroposterior area moment of inertia (NI_{ap}) in left and right ulnae of *Homo sapiens*.

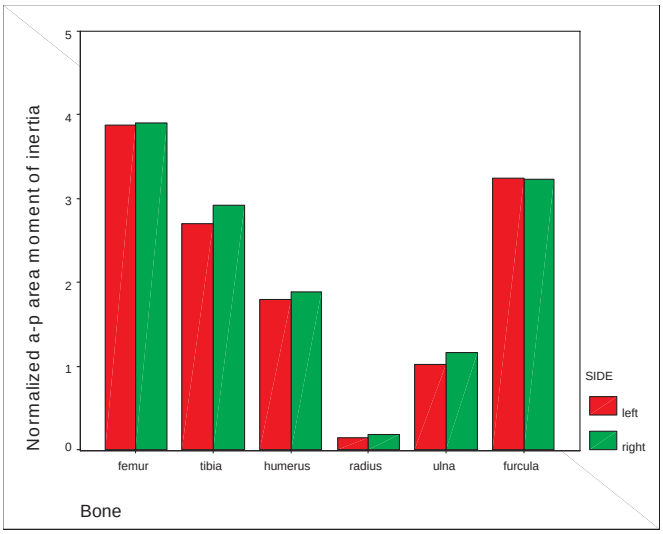

Fig. (5). Normalized anteroposterior area moment of inertia (NI_{ap}) by bone and side in *Gallus gallus.*

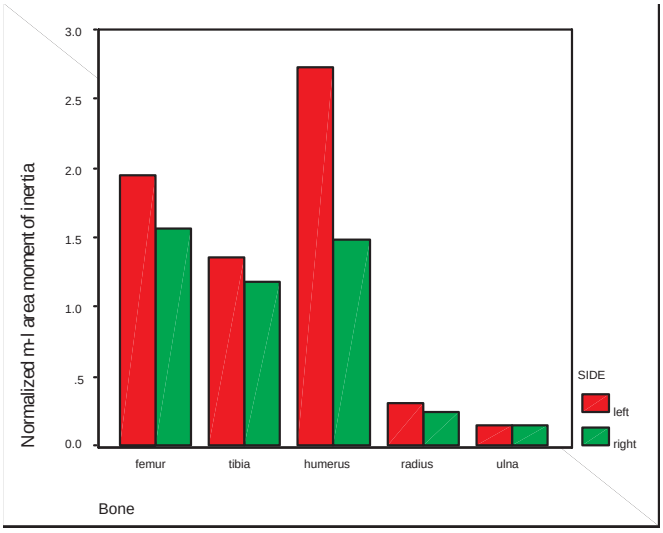

Fig. (7). Normalized mediolateral area moment of inertia (NI_{ml}) by bone and side in *Felis silvestris catus*.

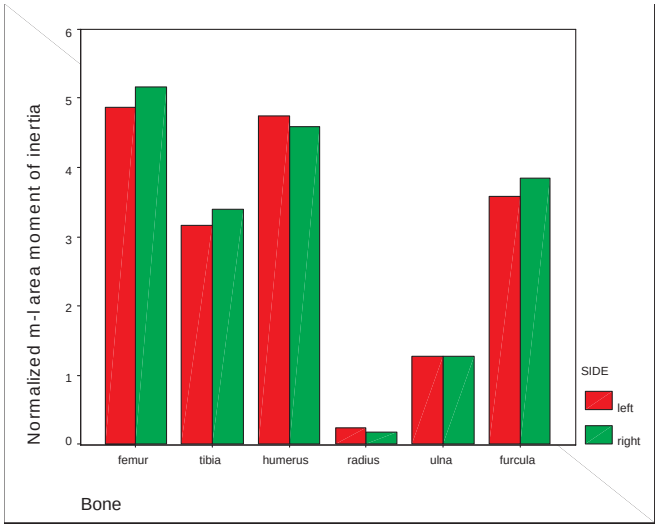

Fig. (8). Normalized mediolateral area moment of inertia (NI_{ml}) by bone and side in *Gallus gallus*.

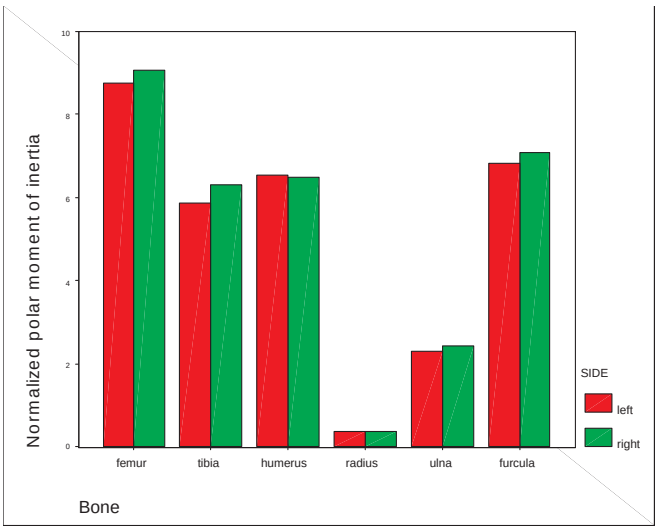

Fig. (11). Normalized polar moment of inertia (NJ) by bone and side in *Gallus gallus*.

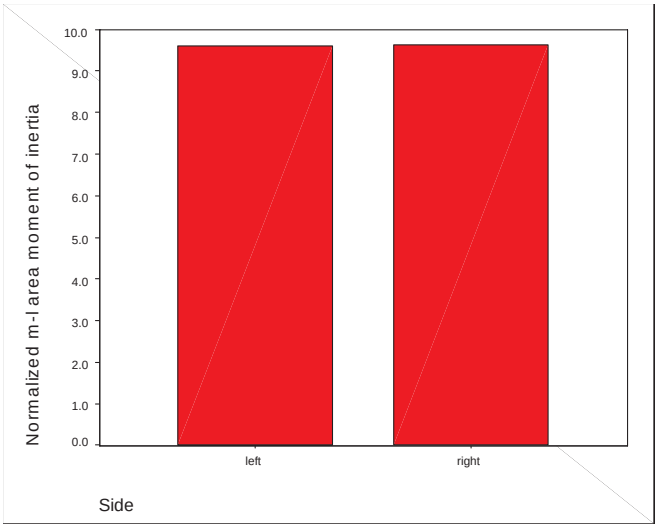

Fig. (9). Normalized mediolateral area moment of inertia (NI_{ml}) in left and right ulnae of *Homo sapiens*.

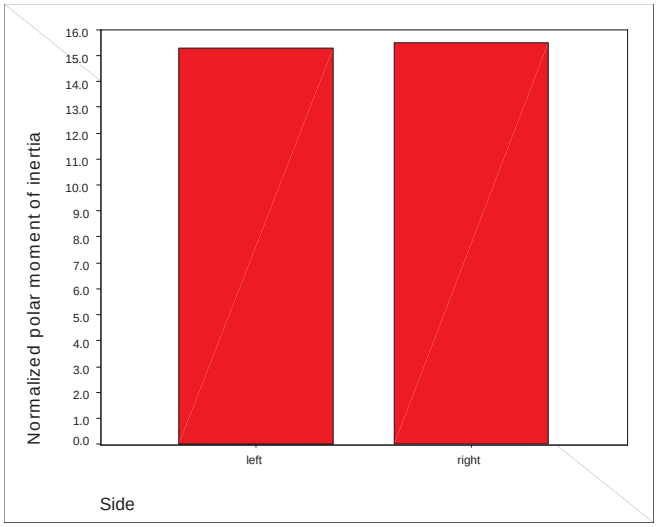

Fig. (12). Normalized polar moment of inertia (NJ) in left and right ulnae of *Homo sapiens*.

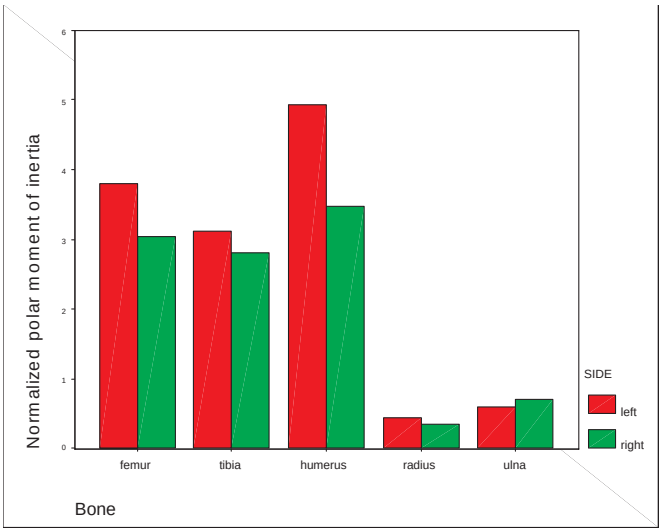

Fig. (10). Normalized polar moment of inertia (NJ) by bone and side in *Felis silvestris catus*.

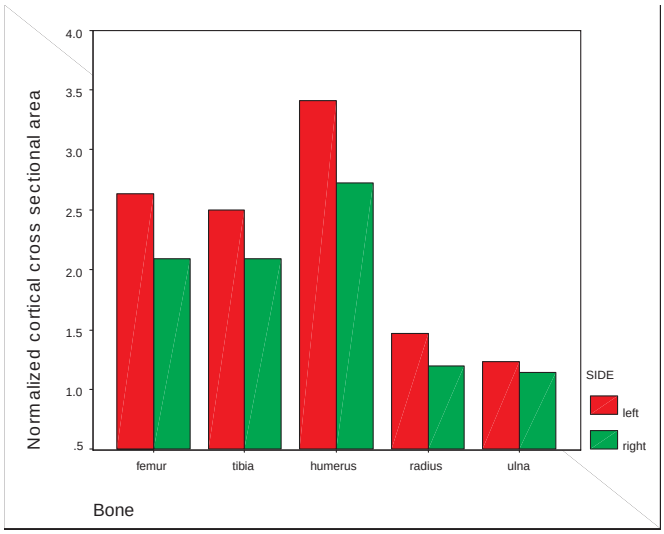

Fig. (13). Normalized cortical area (NCA) by bone and side in *Felis silvestris catus*.

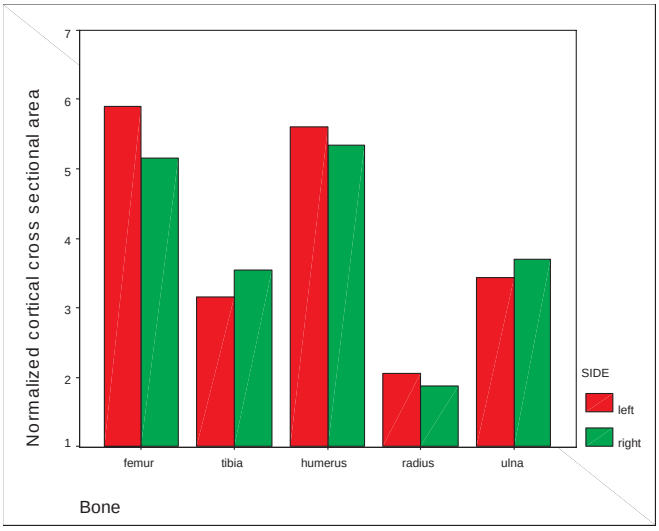

Fig. (14). Normalized cortical area (NCA) by bone and side in *Gallus gallus.*

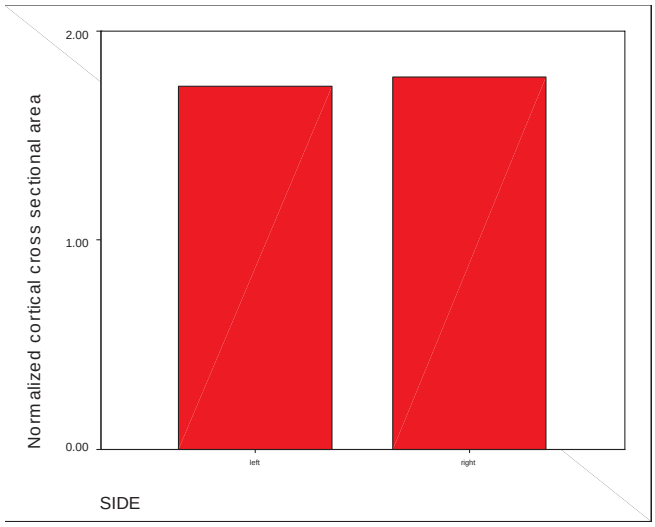

Fig. (15). Normalized cortical area (NCA) in left and right ulnae of *Homo sapiens.*

all 9 sections in each bone in *Felis silvestris catus* and *Gallus gallus*. The data for *Homo sapiens* represents the midshaft of the bone. Side to side comparisons in *Felis silvestris catus* and *Gallus gallus* of normalized cortical area, normalized I_{ap}, normalized I_{ml} and normalized J demonstrate the general similarity of size and shape for all these geometric properties in both species examined along the length of the bone shaft. Despite apparent differences in microstructure from side to side in the forelimb of the cat, there is no disparity at the macroscopic level. The same appears to be true of humans (Table **2**). Differences between left and right midshaft human ulnae are nonsignificant at an experiment-wide alpha level of .05.

Interbone Variation: *Homo Sapiens*

Data from *Felis silvestris catus* and *Gallus gallus*, and data from the human ulna sample, support the hypothesis that bilateral symmetry in bone macro- and micromorphology is due to underlying genetic and developmental control, and is largely unaffected by differential use from side to side under ordinary circumstances and normal ranges of loading. A further question arises in how histomorphology varies from bone to bone within the skeleton. To explore this question, the midshafts of the right femur, tibia, fibula, humerus, radius, ulna and clavicle were examined in a sample of human skeletons (n = 39; 23 female, 16 male). The ulnae in this sample include the right side members of the 14 pairs of ulnae observed for side to side differences. Histomorphometric data were normalized to account for bone resorption by recomputing osteon and fragment densities per sq. mm. on only that percent of the field of view which has not been resorbed. The resulting normalized densities of osteons and fragments per square millimeter are therefore densities of just the unresorbed bone that remains in the section. Therefore, these can be directly compared to data from midshaft sections of the same bones in *Felis silvestris catus* and *Gallus gallus.*

The most prominent difference in the human sample occurs between the sexes. Females show considerably greater numbers of fragments per sq. mm. than do males. Osteons and osteon fragments are relics of the remodeling process and serve as proxies for remodeling events. It is well established that human females, particularly following menopause, demonstrate greater rates of bone resorption and remodeling of remaining bone [17, 37]. In this sample, females show greater numbers of osteon fragments for all bones examined (Table **4**). Females also show greater amounts of resorption in all bones, except the clavicle and fibula (Fig. **16**).

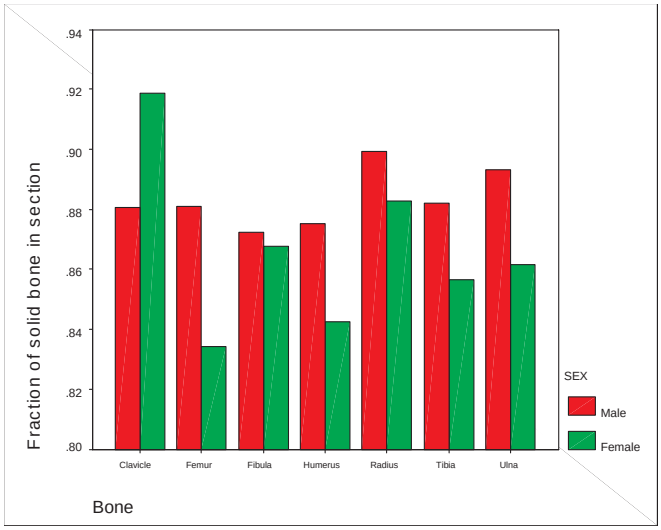

Fig. (16). Percent of field composed of solid bone in males and females, *Homo sapiens* only.

There are significant differences in mean complete and fragmentary osteon densities among bones (Table **4**). The proximal bones of both upper and lower limb show lower osteon and fragment densities than do the more distal elements. This echoes our findings for *Gallus gallus* and *Felis silvestris catus* as noted earlier. In *Homo sapiens*, a two way ANOVA with sex and bone types as main effects demonstrates that sex is *not* a significant factor affecting osteon density, whereas osteon densities are significantly different *among bones* (Table **5**). By contrast, a similar analysis

Table 4. Complete Osteons and Osteon Fragments Per Square mm. by Bone in *Homo sapiens*. (a) Osteons per sq. mm. (b) Osteon Fragments per sq. mm.

(a) Osteons per sq. mm.

		SEX					
		Male			Female		
		Mean	Std Deviation	Valid N	Mean	Std Deviation	Valid N
Bone	Femur	58.14	11.61	N=29	57.42	14.40	N=38
	Tibia	60.24	12.48	N=29	59.74	14.60	N=35
	Fibula	53.06	7.57	N=17	53.29	13.71	N=17
	Humerus	62.26	13.88	N=19	59.95	11.32	N=19
	Radius	50.38	8.30	N=13	57.15	14.43	N=20
	Ulna	52.58	10.88	N=12	52.95	14.13	N=20
	Clavicle	53.11	11.83	N=9	55.60	11.61	N=10

(b) Osteon Fragments per sq. mm.

		SEX					
		Male			Female		
		Mean	Std Deviation	Valid N	Mean	Std Deviation	Valid N
Bone	Femur	19.28	7.40	N=29	23.42	8.52	N=38
	Tibia	21.45	9.87	N=29	24.31	10.49	N=35
	Fibula	23.41	9.32	N=17	27.76	15.49	N=17
	Humerus	20.37	7.48	N=19	21.68	10.54	N=19
	Radius	24.00	7.16	N=13	24.90	10.41	N=20
	Ulna	20.92	10.72	N=12	27.85	11.80	N=20
	Clavicle	20.11	7.24	N=9	29.80	12.28	N=10

Table 5. ANOVA: Osteons per sq. mm. by Sex and Bone in *Homo sapiens*

			Sum of Squares	df	Mean Square	F	Sig.
Osteons per sq. mm.	Main Effects	(Combined)	2758.579	7	394.083	2.393	.022
		Sex	48.900	1	48.900	.297	.586
		Bone	2744.371	6	457.395	2.777	.012
	2-Way Interactions	Sex * Bone	443.530	6	73.922	.449	.846
	Model		3088.404	13	237.570	1.442	.140
	Residual		44964.592	273	164.705		
	Total		48052.997	286	168.017		

demonstrates that element type within the skeleton is not a significant factor affecting the density of osteon fragments. However, there is a significant difference in mean osteon fragment density between males and females (Table **6**).

Fore Limb - Hind Limb Comparisons in *Homo sapiens*

The forelimb and the hindlimb are loaded in different manners during locomotion. This is obviously true in *Homo sapiens*. Under the standard paradigm of bone remodeling, it would be expected that the human lower limb should show much greater levels of haversian remodeling than would the upper limb. However, results of analysis of variance show that the differences in osteon and fragment densities are non-signficant between upper and lower limbs in *Homo sapiens.* When upper limb is compared to lower limb, only the percentage of section composed of solid bone approaches significance between limbs (Table **7**). This parameter is a measure of the amount of resorption of bone, and likely reflects the differential effect of osteoporosis on the upper and lower limb. Interestingly, in *Felis silvestris catus,* the forelimb has significantly higher osteon and fragment densities than does the hindlimb.

Principal Components Analyses

Principal components analysis (PCA) provides a means with which to examine variation within a data set by summarizing them as a series of orthogonal axes. These axes, or principal components, are so arranged that variance away from each axis is minimized. Each component thus accounts for a percentage of the variance in the sample. The first component explains the largest percentage of variance, the second the second highest percentage of variance and so forth [38]. The principal components derived are not correlated with one another, but the variables which describe the sample can be correlated with them to one degree or another. By this means, the variance in a sample defined by a number of variables can be reduced to a number of principal components. The correlation of variables with these components can then be used to describe how well the components explain variance within the sample.

For the human data, PCA was performed using fraction of the field of view composed of solid bone, normalized osteons per sq. mm. and normalized osteon fragments per sq. mm. as the variables in the analysis (Table **8**). The first two principal components extracted account for over 74 % of the variance in the sample. For the first principal component, normalized osteon density loads highly positively, while fraction of solid bone in the section loads highly negatively. Thus, it appears that this component represents variation in haversian remodeling from bone to bone as measured by osteon density, and accounts for about 40% of the variation in the sample. For the second principal component, the fraction of the field composed of solid bone and the normalized density of osteons per square millimeter load negatively, while normalized osteon fragments load highly positively. This factor appears to represent the secondary remodeling of already existing haversian bone, and accounts for an almost equal portion of the variation in the sample (about 35%). For the third principal component, all three variables load positively, osteon density and fraction of solid bone in the section especially so. This factor accounts for 25.6% of the variation in the sample. Both osteon density and fragment density load positively on the first principal component, though osteon density loads higher than fragment density. Fragment density, however, loads extremely positively on the second component while both osteon density and percent of field composed of solid bone load negatively. Osteon fragment density stands out distinctly on the second principal component.

A second PCA was conducted on data available for *Homo sapiens, Felis silvestris catus* and *Gallus gallus.* Variables included in the analysis included three histological variables: osteons per square mm., osteon fragments per square mm., and percent of the field composed of haversian bone. They also include two measures of bone mass or robusticity: normalized cortical area and normalized endosteal area; and three measures of bone cross sectional geometry: normalized I_{ap}, normalized I_{ml}, and normalized J. While principal components analysis extracted 7 principal components, the first four of these account for over 90 % of the variance in the sample (Table **9**). The first principal component accounts for 45.5 % of the variance in the sample. The three measures of bone geometry load very highly positively on this component, and the two measures of bone mass load moderately high on this component. Two of the three histomorphological variables load negatively on this component. While all the measures of bone strength and mass have been

Table 6. ANOVA: Osteon Fragments per sq. mm. by Sex and Bone in *Homo sapiens*

			Sum of Squares	df	Mean Square	F	Sig.
Osteon fragments per sq. mm.	Main Effects	(Combined)	1948.143	7	278.306	2.785	.008
		Sex	1114.944	1	1114.944	11.157	.001
		Bone	750.689	6	125.115	1.252	.280
	2-Way Interactions	Sex * Bone	381.180	6	63.530	.636	.702
	Model		2211.397	13	170.107	1.702	.060
	Residual		27281.230	273	99.931		
	Total		29492.627	286	103.121		

Table 7. ANOVA: Osteons, Fragments, Solid Bone in Section by Limb and Bone in *Homo sapiens*. (a) Osteons per sq. mm. by Limb and Sex. (b) Osteon Fragments per sq. mm. by Limb and Sex. (c) Fraction of Section Composed of Solid Bone by Limb and Sex

(a) Osteons per sq. mm. by Limb and Sex in *Homo sapiens*

			Unique Method				
			Sum of Squares	**df**	**Mean Square**	**F**	**Sig.**
Osteons per sq. mm.	Main Effects	(Combined)	188.411	2	94.205	.557	.574
		Limb	184.124	1	184.124	1.089	.298
		Sex	6.627	1	6.627	.039	.843
	2-Way Interactions	Limb*Sex	22.091	1	22.091	.131	.718
	Model		196.778	3	65.593	.388	.762
	Residual		47856.219	283	169.103		
	Total		48052.997	286	168.017		

(b) Osteon Fragments per sq. mm. by Limb and Sex in *Homo sapiens*

			Unique Method				
			Sum of Squares	**df**	**Mean Square**	**F**	**Sig.**
Osteon fragments per sq. mm.	Main Effects	(Combined)	1088.461	2	544.231	5.423	.005
		Limb	28.216	1	28.216	.281	.596
		Sex	1045.939	1	1045.939	10.422	.001
	2-Way Interactions	Limb*Sex	8.587	1	8.587	.086	.770
	Model		1090.353	3	363.451	3.621	.014
	Residual		28402.274	283	100.361		
	Total		29492.627	286	103.121		

(c) Fraction of Section Composed of Solid Bone by Limb and Sex in *Homo sapiens*

			Unique Method				
			Sum of Squares	**df**	**Mean Square**	**F**	**Sig.**
Fraction of solid bone in section	Main Effects	(Combined)	5.163E-02	2	2.582E-02	5.566	.004
		Limb	1.762E-02	1	1.762E-02	3.798	.052
		Sex	3.582E-02	1	3.582E-02	7.722	.006
	2-Way Interactions	Limb*Sex	5.141E-03	1	5.141E-03	1.108	.293
	Model		6.523E-02	3	2.174E-02	4.688	.003
	Residual		1.313	283	4.638E-03		
	Total		1.378	286	4.817E-03		

Table 8. Principal Components Analysis, *Homo sapiens* Only: Eigenvalues and Factor Score Coefficient Matrix. (Factor Scores for Individual Specimens are Presented in Appendix A2)

Eigenvalues

Component		Variance Explained	Cumulative Variance Explained
1	1.193	39.758	39.758
2	1.038	34.594	74.352
3	.769	25.648	100.000

Extraction Method: Principal Component Analysis.

Factor Score Coefficient Matrix

	Component		
	1	2	3
Normalized osteons per sq. mm.	.699	-.470	.539
Normalized fragments per sq. mm.	.256	.895	.364
Fraction of solid bone in section	-.799	-.124	.588

Table 9. Principal Components Analysis, *Felis silvestris catus, Gallus gallus and Homo sapiens*: Eigenvalues and Factor Score Coefficient Matrix. (Factor Scores for Individual Specimens are Presented in Appendix A3)

Eigenvalues

Component		Variance Explained	Cumulative Variance Explained
1	3.632	45.405	45.405
2	1.917	23.960	69.365
3	1.101	13.768	83.133
4	.581	7.262	90.395
5	.485	6.064	96.458
6	.182	2.276	98.734
7	.101	1.266	100.000

Factor Score Coefficient Matrix

	Component						
	1	2	3	4	5	6	7
osteons per square mm.	-.316	.350	.757	-.318	.322	.001	-.011
osteon fragments per square mm.	.412	.653	-.204	.420	.429	.026	-.023
percent haversian bone: mean of four fields	-.327	.598	.485	.380	-.395	-.002	.009
normalized endosteal cross sectional area	.567	-.632	.353	.249	.092	-.290	.020
normalized cortical cross sectional area	.615	-.606	.351	.182	.033	.311	.013
normalized anteroposterior area moment of inertia	.931	.194	.054	-.132	-.133	-.019	-.240
normalized mediolateral area moment of inertia	.900	.346	-.003	-.154	-.070	-.009	.204
normalized polar moment of inertia	.938	.295	.020	-.150	-.097	-.013	.032

normalized by bone length, this component is still clearly a "size" component, reflecting relative robusticity. It is not surprising that measures of size and robusticity should account for almost half the variance in a sample made up of three taxa as diverse as the three analyzed here. The second principal component explains 24 % of the variance in the sample. This component appears to represent variation in haversian remodeling. Osteon fragments per square millimeter and percent of field composed of haversian bone load strongly positively on this component, while cortical and endosteal area load strongly negatively. The third principal component explains 13.8 % of the variance in the sample. Number of osteons per square millimeter loads highly positively on this component, and so this component likely rep-

resents variation in numbers of secondary osteons. The first three principal components together explain over 83 % of the variance in the sample.

DISCUSSION

Given the diversity of locomotor patterns of the three species examined here, and the resulting environmental differences in the loading of their appendicular skeletons, the histomorphological patterns observed suggest that remodeling is subject to modulation by intrinsic developmental factors, in addition to any effects of mechanical loading [41]. The cohesion within the patterns of remodeling in the three species examined suggests an underlying genetic basis to their similarity. Numerous workers, notably initiated by Bertram and Swartz [13], have questioned the real explanatory power of the so called "Wolff's law" in the remodeling of bone. Results of this study accord with the notion that factors other than simple mechanical loading may be the primary determinants of skeletal remodeling. Additional vertebrate taxa need to be examined in order to resolve this issue more fully. Neither histomorphology nor cross sectional properties differ by side in our sample of human ulnas. The lack of such asymmetry in haversian structures suggests that habitual asymmetric loading under normal circumstances is too subtle to permit detection. This conclusion is opposite that of the traditional anthropological model of cortical bone haversian remodeling.

This work is a pilot study. In the future we hope to accumulate further data on the taxa already examined here, as well as to expand the sample and include wild specimens. Such work is already ongoing in our laboratory. One of the purposes of the principal components analyses presented here are to assess variation in cortical bone properties across species. As noted above, principal components derived are not correlated with one another, but the variables which describe the sample can be correlated with them to one degree or another. The correlation of variables with these components can then be used to describe how the components explain variance within the sample. When data from all three species are included in a principal components analysis, the first component, responsible for almost half the variance in the sample, is, not surprisingly, a size component. The measures of the geometric properties of the sections, which serve as proxies for size, correlate highly on that component. Osteon fragment density has a very high positive correlation with the second component while both osteon density and percent of field composed of solid bone correlate negatively. Osteon fragment density stands with a distinctively high correlation with the second principal component. Percent of the field composed of haversian bone correlates only slightly less highly. This component explains a quarter of the variance in the sample, and suggests that modeling and remodeling of haversian bone is a greater source of variation than the density of complete osteons in cross-species comparisons. This may be related to the wide size range of the species examined, or to differences in developmental ages of the specimens. In future research we plan to examine additional taxa of a greater size range and at additional developmental stages. In the other principal components analysis presented, only human specimens were included. In this analysis we examined variation within a single species (*Homo sapiens)* among three histomorphological variables: density of complete osteons, density of fragmentary osteons, and percentage of field composed of haversian bone. We found that osteon density is highly correlated with the first principal component, while fragment density is only poorly correlated with this component. Percent of field composed of haversian bone is highly negatively correlated with the first component. Osteon fragment density is highly positively correlated with the second component. These results suggest that within species, certainly among *Homo sapiens*, densities of complete osteons are independent of densities of fragmentary osteons. Future research will include examination of the effects of body size, developmental phase and rates of development on histomorphometric and geometric properties of cortical bone.

If, indeed, variation in histomorphological and cross sectional properties of cortical bone, particularly human cortical bone, owe more to underlying genetic regulatory mechanisms and less to environmental factors, then this throws into question assumptions made about activity levels or activity patterns deduced from cross sectional geometry and histomorphology of human cortical bone. Major studies which have shown bone hypertrophy in response to noninvasive loading [39, 40, 42] have been carried out on subadults. Similar effects on human adults have not been demonstrated. As has been shown here, there appears to be no significant effect in adults of asymmetric loading of the forelimb. Persistent scars of union of fractured bones in human adults are a further indication of the lack of response of bone tissue to mechanical loading in adults [5]. Further, it has been shown that when long bone length, age and sex are fully considered, perceived populational differences in femoral cortical thickness are nonsignificant [43]. All of these factors throw into question how much conjecture is permissible about human activities solely from evidence of skeletal remodeling. Indeed, in this study the most important determinant of variation in histomorphometry is that due to sex, which is clearly caused by differences in genetics and endocrine environments in males and females.

Within the diaphysis of a long bone, the primary site of ossification is approximately at midshaft (or more accurately located by the site at which the nutrient artery first penetrates the endosteum) and the diaphysis subsequently ossifies towards the two ends of the bone. Therefore, the midshaft has the oldest "ossification-age," with proximal and distal ends of the diaphysis having a younger "ossification-age." Since remodeling should in part reflect age, the evidence presented for a greater amount of remodeling at midshaft may at least partly be explained by the greater 'ossification-age' of the midshaft. Indeed, this supports the case for genetically controlled processes rather than Wolffian ones. Additionally, as has long been known, among mammals one end of a particular bone may grow much faster than the other. Humans demonstrate the typical mammalian pattern. In *Homo sapiens*, the more rapidly growing end (which is also that at which epiphyseal union is most delayed) in each of the major long bones is as follows: femur - distal; tibia - proximal; humerus - proximal; radius - distal; ulna - distal [44]. The bone in the "growing end" of the bone is therefore developmentally younger than the bone at the midshaft. The similar growth behavior of the knee epiphyses is largely a consequence of their origin within the same HOX territory and accounts for the marked stability of the crural index (femur/tibia) in the

hindlimb but a much more varied brachial index in the forelimb, where the primary growth plates do not share a territory [45]. In our study this same pattern is revealed by the higher densities of haversian structures at midshaft. Additionally, the distal ends of the bones, which are developmentally younger than the midshaft and proximal ends, show gradually lower osteon densities from the midshaft to the distal end. This is especially apparent in the radius and ulna of *Felis silvestris catus*, and is clearly the result of genetically programmed growth, rather than as a result of mechanical loading.

CONCLUSIONS

Obviously the locomotor anatomy of *Felis silvestris catus* and *Gallus gallus* vary significantly from each other and from that of *Homo sapiens*, and loading environments for the human fore and hindlimb are substantially different from that of a cursorial quadruped or bird. However, it can be expected that the *types* of variation present in the appendicular skeletons of *Felis silvestris catus* and *Gallus gallus* will also evince themselves in other vertebrate species, including humans. There are many claims about the sensitivity of bone as a "dynamic tissue" with intricate responses to loading, yet the external morphology of left and right bones from an individual can match nearly perfectly and yet have nonidentical loading histories (forelimbs in humans for example). Data thus far collected suggest that this differential loading may be relatively unimportant as an influence on rates and patterns of skeletal remodeling in adult humans. We suggest that the underlying conservatism of regulatory genes affecting the skeletal system among vertebrates may be a much greater influence on skeletal morphology, both at the macroscopic and microscopic levels.

In summary, bone remodeling is not uniform throughout the skeleton. There is no universal, tissue-wide response of bone to age. Independent bones behave as independent organs, demonstrating substantial variation in remodeling, both among different skeletal elements, and within different regions of a single bone. Evidence presented here suggests that bone morphology, at both the microscopic and macroscopic level, is largely the result of genetically controlled processes.

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Appendix A1. Raw data for the human ulna cross section specimens. AGE = chronological age in years. SEX: 1 = male, 2 = female. Osteons = complete osteons per square millimeter. Fragments = fragmentary osteons per square millimeter. NIap = normalized area moment of inertia along the anteroposterior axis. NIml = normalized area moment of inertia along the mediolateral axis. NJ = polar moment of inertia.

SPECIMEN		SIDE	
		LEFT	RIGHT
9711	AGE	75	75
	SEX	1	1
	osteons	13.1	13.4
	fragments	6.9	7.1
	NIap	6.4	4.99
	NIml	9.41	7.15
	NJ	15.81	12.14
9712	AGE	84	84
	SEX	2	2
	osteons	5.4	5.9
	fragments	6.4	8.4
	NIap	2.73	2.26
	NIml	3.95	3.67
	NJ	6.69	5.93
9713	AGE	76	76
	SEX	2	2
	osteons	15.9	17.2
	fragments	12.7	15.6
	NIap	4.69	5.62
	NIml	7.63	12.75
	NJ	12.33	18.37

(Appendix A1) contd….

SPECIMEN		SIDE	
		LEFT	**RIGHT**
9714	AGE	71	71
	SEX	2	2
	osteons	16	17.9
	fragments	7.5	8
	NIap	2.38	3.14
	NIml	4.3	5.83
	NJ	6.68	8.96
9715	AGE	74	74
	SEX	1	1
	osteons	13.4	9.5
	fragments	5.8	4.7
	NIap	14.19	13.47
	NIml	16.57	17.53
	NJ	30.76	31
9716	AGE	66	66
	SEX	1	1
	osteons	24.1	21.8
	fragments	18.1	15.6
	NIap	8.62	8.95
	NIml	20.5	17.51
	NJ	29.12	26.45
9717	AGE	83	83
	SEX	1	1
	osteons	15.9	19.1
	fragments	7.7	11.8
	NIap	6.09	5.85
	NIml	10.34	11.64
	NJ	16.43	17.49
9718	AGE	94	94
	SEX	2	2
	osteons	13.3	17.5
	fragments	14.1	13.9
	NIap	5.99	6.04
	NIml	9.35	8.81
	NJ	15.34	14.86
9719	AGE	53	53
	SEX	2	2
	osteons	17.2	19.9
	fragments	9.4	10.5
	NIap	3.47	3.96
	NIml	8.01	6.7
	NJ	11.48	10.66

(Appendix A1) contd….

SPECIMEN		SIDE	
		LEFT	**RIGHT**
9720	AGE	87	87
	SEX	2	2
	osteons	15.8	17.5
	fragments	9.2	15.2
	NIap	3.52	4.53
	NIml	4.35	4.66
	NJ	7.87	9.19
9721	AGE	72	72
	SEX	1	1
	osteons	13.7	15.8
	fragments	8	6.5
	NIap	5.2	6.09
	NIml	8.89	10.49
	NJ	14.09	16.58
9722	AGE	100	100
	SEX	2	2
	osteons	12.1	14.1
	fragments	14.2	21.2
	NIap	3.86	3.28
	NIml	6.84	6.1
	NJ	10.7	9.38
9723	AGE	77	77
	SEX	1	1
	osteons	13.7	18
	fragments	10.7	9
	NIap	5.75	6.77
	NIml	13.2	11.99
	NJ	18.94	18.76
9801	AGE	65	65
	SEX	1	1
	osteons	14.8	16.6
	fragments	10.3	16.1
	NIap	6.26	6.81
	NIml	11.23	9.95
	NJ	17.49	16.76

Appendix A2. Factor scores for individual specimens of *Homo sapiens* included in the principal components analysis presented in Table 8. SPECIMEN = individual cadaver. BONENUMB: 1 = femur, 2 = tibia, 3 = humerus, 4 = radius, 5 = ulna. AGE = chronological age in years. SEX: 1 = male, 2 = female. FAC1 – FAC3 indicate the factor scores for the individual section on the three derived principal components.

SPECIMEN	BONENUMB	SEX	AGE	FAC1	FAC2	FAC3
82-14	1.00	2.00	75.00	-1.21936	-0.00116	-0.56710

(Appendix A2) contd….

SPECIMEN	BONENUMB	SEX	AGE	FAC1	FAC2	FAC3
82-14	1.00	2.00	75.00	-0.06606	0.30429	-1.95960
82-14	1.00	2.00	75.00	-0.05102	-0.82282	0.24124
82-14	2.00	2.00	75.00	-1.49216	-0.04055	-1.24823
82-14	3.00	2.00	75.00	0.45274	1.83251	-0.62975
82-14	4.00	2.00	75.00	-0.66191	-1.82723	-0.80064
82-14	5.00	2.00	75.00	0.41719	0.76995	-0.90258
82-14	6.00	2.00	75.00	0.08226	1.02913	1.72063
82-14	6.00	2.00	75.00	-0.05490	1.74910	-0.12745
82-14A	1.00	2.00	75.00	0.44403	0.02120	-1.32670
82-14A	2.00	2.00	75.00	0.15657	-0.84622	0.21589
82-14A	2.00	2.00	75.00	-0.82339	0.97258	0.47876
82-14A	3.00	2.00	75.00	-0.84695	0.91715	-0.16961
82-14A	3.00	2.00	75.00	-0.52012	0.81857	-0.04892
82-14A	4.00	2.00	75.00	1.65462	-0.21172	-2.45286
82-14A	5.00	2.00	75.00	-1.26065	0.07188	-0.91007
82-14A	5.00	2.00	75.00	0.20538	0.61292	0.59055
82-14A	6.00	2.00	75.00	0.62710	1.25442	-2.63143
82-14A	6.00	2.00	75.00	-0.94607	-0.57556	-3.03832
82-19	1.00	2.00	78.00	0.25126	1.83218	-1.81041
82-19	1.00	2.00	78.00	1.73340	-1.54464	1.30270
82-19	1.00	2.00	78.00	2.33851	0.46650	-0.77610
82-19	2.00	2.00	78.00	0.91289	-0.68136	1.58017
82-19	3.00	2.00	78.00	0.75625	-1.51959	-0.01902
82-19	4.00	2.00	78.00	-0.70767	-0.15588	0.39742
82-19	5.00	2.00	78.00	2.10718	-1.54978	1.20457
82-19	6.00	2.00	78.00	0.57056	1.02950	1.17453
82-21	1.00	1.00	78.00	0.29111	-0.28987	-0.69314
82-21	1.00	1.00	78.00	0.03039	0.39527	-0.60008
82-21	2.00	1.00	78.00	1.17368	-0.91724	-1.44112
82-21	3.00	1.00	78.00	1.50936	-0.50924	-2.10834
82-21	3.00	1.00	78.00	0.36099	0.60658	0.19588
82-21	4.00	1.00	78.00	0.18370	-0.70882	0.58410
82-21	4.00	1.00	78.00	2.90275	-1.39469	1.41079
82-21	5.00	1.00	78.00	-0.19546	0.31741	-0.62092
82-21	6.00	1.00	78.00	-0.73994	-0.45346	-0.91860
82-21	7.00	1.00	78.00	-0.07428	0.32988	0.15094
82-23	1.00	1.00	54.00	-1.23984	-0.30411	0.24805

(Appendix A2) contd….

SPECIMEN	BONENUMB	SEX	AGE	FAC1	FAC2	FAC3
82-23	2.00	1.00	54.00	0.05778	2.12390	0.70944
82-23	3.00	1.00	54.00	-1.81223	1.58868	0.77772
82-23	3.00	1.00	54.00	-1.13772	0.40975	-0.97405
82-23	4.00	1.00	54.00	-2.09845	0.85770	-0.37012
82-23	5.00	1.00	54.00	-0.85811	1.42546	1.13198
82-23	6.00	1.00	54.00	-1.79119	2.32985	0.05595
82-24	1.00	2.00	79.00	-0.05598	-0.58911	-2.13472
82-24	1.00	2.00	79.00	0.72851	0.05896	-1.23471
82-24	3.00	2.00	79.00	0.51417	0.64619	-0.49470
82-24	4.00	2.00	72.00	2.82167	0.23498	-3.79683
82-24	4.00	2.00	72.00	1.93796	-0.43047	-2.11429
82-24	4.00	2.00	79.00	-0.46255	0.03091	-0.43953
82-24	5.00	2.00	72.00	-0.71666	0.62245	-0.05494
82-24	5.00	2.00	79.00	0.76262	1.38214	-0.90875
82-24	6.00	2.00	72.00	-1.03493	2.15428	0.13890
82-31	1.00	1.00	65.00	-0.92607	-1.44813	-0.77693
82-31	1.00	1.00	65.00	0.81936	-1.47316	-1.43513
82-31	2.00	1.00	65.00	-0.74992	-1.05039	0.75566
82-31	2.00	1.00	65.00	-0.61406	-0.28355	-1.31640
82-31	2.00	1.00	65.00	-0.87197	-0.61640	-0.52769
82-31	4.00	1.00	65.00	-0.49771	-1.16678	-0.43807
82-31	5.00	1.00	65.00	-1.02642	-0.23814	0.24949
82-31	6.00	1.00	65.00	-0.89403	-0.27039	-0.78685
83-05	1.00	2.00	73.00	-1.36850	0.25220	-1.01842
83-05	1.00	2.00	73.00	0.92061	0.02056	0.52970
83-05	2.00	2.00	73.00	0.41317	-0.04979	0.12803
83-05	2.00	2.00	73.00	-1.68761	0.40151	-1.42023
83-05	3.00	2.00	73.00	-0.86563	2.16965	-1.13959
83-05	3.00	2.00	73.00	0.70558	0.37279	-0.89721
83-05	4.00	2.00	73.00	-0.45164	-0.35858	0.09763
83-05	5.00	2.00	73.00	-0.94183	-1.82235	0.33189
83-05	6.00	2.00	73.00	1.09209	0.93008	0.95479
83-05	7.00	2.00	73.00	-0.66733	0.00204	-0.11907
83-11	1.00	2.00	69.00	1.59208	0.35182	-2.41868
83-11	1.00	2.00	69.00	1.59208	0.35182	-2.41868
83-11	1.00	2.00	69.00	2.01797	0.57049	-2.09642
83-11	2.00	2.00	69.00	1.98690	0.37795	0.23932

(Appendix A2) contd….

SPECIMEN	BONENUMB	SEX	AGE	FAC1	FAC2	FAC3
83-11	2.00	2.00	75.00	-0.41196	-0.33689	-1.05322
83-11	2.00	2.00	69.00	1.27993	-0.84944	-1.88716
83-11	3.00	2.00	69.00	-0.93961	0.78923	-1.53179
83-11	4.00	2.00	69.00	-0.43496	-0.41509	1.01533
83-11	5.00	2.00	69.00	0.58819	1.62927	-1.09341
83-11	6.00	2.00	69.00	-0.59325	-0.30580	-0.38586
83-11	6.00	2.00	69.00	0.08898	0.36934	-1.43297
83-21	1.00	1.00	71.00	0.04480	0.85069	-0.18193
83-21	2.00	1.00	71.00	1.23873	-0.49273	0.55091
83-21	2.00	1.00	71.00	-0.28309	2.13063	-0.35671
83-21	3.00	1.00	71.00	-0.52985	-0.05476	0.35795
83-21	4.00	1.00	71.00	-1.08176	0.75429	-0.22057
83-21	4.00	1.00	71.00	-0.04788	1.12760	-0.24927
83-21	5.00	1.00	71.00	-0.60701	0.04980	0.57760
83-21	6.00	1.00	71.00	1.97599	0.33293	0.51731
83-21	7.00	1.00	71.00	-1.17724	-0.03367	-0.51678
83-23	1.00	1.00	76.00	0.06990	0.30637	0.94644
83-23	1.00	1.00	76.00	0.90788	-0.04488	-2.82704
83-23	2.00	1.00	76.00	-0.79813	0.73799	-0.44350
83-23	2.00	1.00	76.00	0.15430	-0.64489	0.25536
83-23	3.00	1.00	76.00	-1.09429	0.33166	-0.62924
83-23	4.00	1.00	76.00	-0.14126	0.48138	0.09200
83-23	4.00	1.00	76.00	0.15203	-0.44356	0.29482
83-23	5.00	1.00	76.00	-0.71142	0.40770	-1.30253
83-25	1.00	2.00	79.00	-0.48664	0.33473	0.80129
83-25	1.00	2.00	79.00	-0.49699	1.15517	-0.24870
83-25	2.00	2.00	79.00	-0.24874	1.87927	-1.27017
83-25	2.00	2.00	79.00	-0.51202	1.24090	0.35367
83-25	2.00	2.00	79.00	0.93348	1.64742	1.79797
83-25	4.00	2.00	79.00	-0.15263	0.48970	-0.52634
83-25	5.00	2.00	79.00	-1.58197	0.41701	-1.27350
83-25	6.00	2.00	79.00	0.54610	1.35502	-2.11552
9001	1.00	1.00	14.00	-0.93956	-0.03844	-0.79966
9001	1.00	1.00	14.00	-1.22154	0.19201	-0.52924
9201	1.00	2.00	70.00	-0.14152	-1.20098	1.24774
9201	1.00	2.00	70.00	-0.55286	-0.76571	-0.12587
9205	1.00	1.00	84.00	0.49748	-1.08630	1.83744

(Appendix A2) contd….

SPECIMEN	BONENUMB	SEX	AGE	FAC1	FAC2	FAC3
9205	1.00	1.00	84.00	0.28935	-0.98100	-0.23693
9207	1.00	2.00	69.00	1.42481	-0.63638	0.77325
9207	1.00	2.00	69.00	0.35056	0.55854	0.47390
9208	1.00	2.00	64.00	-0.74952	-0.93835	-0.12710
9208	1.00	2.00	64.00	0.94783	-1.52199	0.84531
9208	2.00	2.00	64.00	-0.24258	-0.13176	0.42947
9208	2.00	2.00	64.00	0.94783	-1.79741	0.48478
9208	3.00	2.00	64.00	-0.55220	-0.14069	-0.29522
9208	4.00	2.00	64.00	-0.39790	-1.37062	-0.04327
9208	5.00	2.00	64.00	0.25118	-1.51800	0.20241
9208	6.00	2.00	64.00	0.26518	-0.83029	0.36676
9208	7.00	2.00	64.00	-0.54543	-1.39228	0.96110
9210	1.00	1.00	83.00	0.84934	-0.72083	-0.02612
9210	1.00	1.00	83.00	-0.98117	-0.64597	0.22476
9210	1.00	1.00	83.00	0.26382	0.42308	0.32746
9210	2.00	1.00	83.00	-0.09646	0.04659	0.66560
9210	2.00	1.00	83.00	0.53934	0.67425	0.45239
9210	2.00	1.00	83.00	-1.09084	-1.06323	0.28997
9210	3.00	1.00	83.00	-0.38353	-0.07199	0.55303
9210	4.00	1.00	83.00	0.37502	-0.63642	-0.04777
9210	6.00	1.00	83.00	-0.12380	-0.07782	0.29986
9210	7.00	1.00	83.00	-0.82159	-1.01260	0.06166
9211	1.00	2.00	95.00	-0.48615	-0.29008	-0.23709
9211	2.00	2.00	95.00	1.13091	-0.14513	1.38493
9211	5.00	2.00	95.00	-0.24022	-1.16876	-0.08881
9216	1.00	1.00	71.00	-0.43496	-0.41509	1.01533
9216	1.00	1.00	71.00	0.40656	-0.72867	-0.32676
9216	2.00	1.00	71.00	0.30945	1.03152	0.82035
9216	2.00	1.00	71.00	1.67915	0.56210	0.16263
9216	3.00	1.00	71.00	0.46763	0.51302	-0.88839
9216	4.00	1.00	71.00	0.45948	-0.42972	1.01760
9216	5.00	1.00	71.00	-0.64850	0.49555	0.91779
9216	6.00	1.00	71.00	-0.53929	-0.47481	0.55869
9216	7.00	1.00	71.00	-0.12210	-1.03976	0.70353
9219	1.00	1.00	73.00	-1.29672	-0.48260	-1.07623
9219	2.00	1.00	73.00	-1.72100	0.76165	-1.69179
9219	2.00	1.00	73.00	-1.05553	-0.35966	-0.11805

(Appendix A2) contd….

SPECIMEN	BONENUMB	SEX	AGE	FAC1	FAC2	FAC3
9219	3.00	1.00	73.00	1.49274	1.20421	0.34751
9219	3.00	1.00	73.00	-0.13672	0.07872	0.01307
9219	4.00	1.00	73.00	-0.38353	0.12270	-0.01049
9219	5.00	1.00	73.00	-1.33533	0.70655	-0.27270
9219	6.00	1.00	73.00	-0.69420	0.50806	-0.04862
9220	1.00	1.00	72.00	-0.50884	-1.34852	0.41540
9220	1.00	1.00	72.00	0.21319	-1.42040	0.47376
9220	2.00	1.00	72.00	-0.07998	-1.07228	0.75386
9220	2.00	1.00	72.00	0.15493	-1.60331	0.65832
9220	3.00	1.00	72.00	-0.27411	-0.64868	-0.93191
9220	4.00	1.00	72.00	2.51425	-1.93568	-0.13814
9220	4.00	1.00	72.00	-0.20466	-1.61685	0.16711
9220	5.00	1.00	72.00	-0.39091	-0.11430	0.23172
9220	6.00	1.00	72.00	-0.63877	-1.50256	-0.09594
9220	7.00	1.00	72.00	-0.12078	-0.69699	-0.43156
9221	2.00	2.00	67.00	2.35010	-2.03029	1.13059
9221	2.00	2.00	67.00	-0.06926	-1.97128	0.88075
9221	3.00	2.00	67.00	-0.88070	-1.25036	-0.06886
9221	4.00	2.00	67.00	0.25346	-1.71933	0.16294
9221	5.00	2.00	67.00	-0.14420	-0.57770	-0.43814
9221	6.00	2.00	67.00	0.62637	-1.39466	-0.47132
9221	7.00	2.00	67.00	0.22253	-0.34267	-0.79742
9222	1.00	1.00	73.00	0.05096	-0.47330	-1.66269
9222	1.00	1.00	73.00	-1.09709	-0.32758	-0.16771
9222	2.00	1.00	73.00	-0.12590	-1.09533	0.38429
9222	2.00	1.00	73.00	-0.66828	-1.35364	0.50011
9222	3.00	1.00	73.00	-0.43838	-0.72057	-0.26320
9222	3.00	1.00	73.00	-0.35259	-0.70523	-0.36112
9222	4.00	1.00	73.00	-0.37067	-0.03288	0.27642
9222	4.00	1.00	73.00	0.50501	-0.66167	1.03041
9222	5.00	1.00	73.00	-0.47410	-0.24419	0.09131
9222	6.00	1.00	73.00	-0.40674	-0.58736	0.11026
9401	1.00	2.00	90.00	-0.70058	-0.08469	-0.78722
9401	1.00	2.00	90.00	-0.75208	0.66875	0.81372
9401	2.00	2.00	90.00	-0.19989	-0.16473	0.48049
9401	2.00	2.00	90.00	-0.53005	0.96366	0.27059
9401	2.00	2.00	90.00	-0.96447	-0.38943	-0.30301

(Appendix A2) contd….

SPECIMEN	BONENUMB	SEX	AGE	FAC1	FAC2	FAC3
9401	3.00	2.00	90.00	-1.18779	1.08650	1.21728
9401	4.00	2.00	90.00	0.13612	0.96575	0.57107
9401	5.00	2.00	90.00	-1.34389	-0.67633	0.63273
9401	6.00	2.00	90.00	-1.02043	0.18004	0.04368
9401	6.00	2.00	90.00	-1.08421	0.12782	0.55068
9401	7.00	2.00	90.00	-0.91331	-0.18606	0.11178
9402	1.00	1.00	71.00	0.60028	0.18807	1.64171
9402	1.00	1.00	71.00	-0.18636	-0.89440	0.64697
9402	2.00	1.00	71.00	0.77922	-0.74311	0.47861
9402	2.00	1.00	71.00	-0.35048	-1.15067	0.36994
9402	3.00	1.00	71.00	0.59371	-0.12931	-0.85292
9402	4.00	1.00	71.00	0.01801	-0.72117	0.65881
9402	4.00	1.00	71.00	-0.62982	-0.86798	-0.55433
9402	5.00	1.00	71.00	-0.02935	-0.14317	-2.30665
9402	6.00	1.00	71.00	-0.54032	-0.67674	-0.99702
9402	7.00	1.00	71.00	-1.78946	-0.19835	-0.17368
9403	1.00	2.00	83.00	3.77620	2.05571	1.20988
9403	1.00	2.00	83.00	0.80015	-0.64561	1.73695
9403	2.00	2.00	83.00	0.56589	0.44654	-1.67597
9403	2.00	2.00	83.00	1.10632	-0.33119	0.70756
9403	3.00	2.00	83.00	-0.26075	-1.25132	-0.13413
9403	4.00	2.00	83.00	0.86376	0.06112	1.06571
9403	5.00	2.00	83.00	-0.08601	-0.55916	-0.05287
9403	6.00	2.00	83.00	-0.22455	0.14548	0.51256
9403	7.00	2.00	83.00	0.13741	1.10071	2.11298
9405	1.00	2.00	84.00	0.77024	2.03620	1.05380
9405	1.00	2.00	84.00	1.84207	0.59066	-0.51707
9405	2.00	2.00	84.00	2.94190	-0.46527	-2.57223
9405	2.00	2.00	84.00	-0.20519	-0.80457	-0.87125
9405	3.00	2.00	84.00	0.04712	-0.01296	0.54568
9405	4.00	2.00	84.00	1.82006	-0.29316	-0.12909
9405	5.00	2.00	84.00	2.07313	1.45352	1.49072
9405	7.00	2.00	84.00	-0.59186	0.94387	1.39178
9501	1.00	2.00	101.00	3.81662	-0.76309	-0.54027
9501	2.00	2.00	101.00	0.05041	-0.22187	-0.09866
9501	2.00	2.00	101.00	0.56565	-0.46353	0.85232
9501	4.00	2.00	101.00	-0.09356	-0.54498	1.75384

(Appendix A2) contd….

SPECIMEN	BONENUMB	SEX	AGE	FAC1	FAC2	FAC3
9501	5.00	2.00	101.00	-0.30851	0.72512	1.73034
9501	6.00	2.00	101.00	-0.62456	-0.22005	0.49673
9501	7.00	2.00	101.00	-0.19109	1.52356	1.45390
9502	1.00	2.00	98.00	-0.81168	-0.91070	0.70131
9502	1.00	2.00	98.00	-0.41865	-0.00299	-0.38707
9502	2.00	2.00	98.00	0.27860	-1.31057	0.88814
9502	2.00	2.00	98.00	-1.00485	-0.34801	0.25556
9502	3.00	2.00	98.00	0.02942	-1.14721	-0.02040
9502	4.00	2.00	98.00	-1.62873	-0.81036	0.82224
9502	5.00	2.00	98.00	-0.54006	-0.34542	1.49197
9502	6.00	2.00	98.00	-0.83019	-0.25023	0.21110
9502	7.00	2.00	98.00	-0.98423	-0.04446	-0.55927
9601	1.00	2.00	88.00	0.94725	1.98051	-0.83389
9601	1.00	2.00	88.00	-0.54145	0.09897	0.07236
9601	2.00	2.00	88.00	1.03659	2.24129	1.45886
9601	2.00	2.00	88.00	0.48949	1.12346	0.47963
9601	3.00	2.00	88.00	1.44275	-0.02321	1.53186
9601	4.00	2.00	88.00	0.41351	1.45012	1.05014
9601	5.00	2.00	88.00	0.20939	1.07217	1.29772
9601	6.00	2.00	88.00	2.22845	1.70407	2.35926
9601	7.00	2.00	88.00	-1.95406	1.40903	0.24481
9603	1.00	2.00	107.00	0.68767	-0.96348	0.26236
9603	1.00	2.00	107.00	2.46303	0.63168	1.24188
9603	2.00	2.00	107.00	1.76115	-0.10972	-1.37963
9603	2.00	2.00	107.00	-0.21499	-0.45123	1.60874
9603	2.00	2.00	107.00	0.99170	1.88775	0.41619
9603	3.00	2.00	107.00	-0.00116	4.72868	1.78454
9603	4.00	2.00	107.00	1.17640	-0.22830	1.12680
9603	5.00	2.00	107.00	-0.90972	1.11934	-0.51444
9603	6.00	2.00	107.00	0.50684	1.29594	-0.36734
9603	7.00	2.00	107.00	-0.31488	1.64414	0.40429
9605	1.00	1.00	69.00	-0.81379	-0.79299	-0.18366
9605	1.00	1.00	69.00	-0.21038	-0.01098	0.19641
9605	2.00	1.00	69.00	-0.67028	0.66344	1.52835
9605	2.00	1.00	69.00	1.24533	-0.38419	1.18746
9605	2.00	1.00	69.00	0.20970	-0.64850	0.02751
9605	2.00	1.00	69.00	-0.46747	-0.83164	-0.02384

(Appendix A2) contd….

SPECIMEN	BONENUMB	SEX	AGE	FAC1	FAC2	FAC3
9605	3.00	1.00	69.00	-1.19727	-0.52100	0.26002
9605	3.00	1.00	69.00	-0.83891	1.50265	1.17436
9605	4.00	1.00	69.00	0.39232	0.53261	-0.07953
9605	5.00	1.00	69.00	-1.54447	0.02309	-0.09651
9605	6.00	1.00	69.00	-1.20984	0.59285	0.47836
9605	7.00	1.00	69.00	1.70548	2.91099	-2.02615
9605	7.00	1.00	69.00	-1.79454	-0.59747	0.03740
9606	1.00	1.00	67.00	-0.99970	0.88243	-0.08205
9606	1.00	2.00	95.00	-0.23299	-0.23895	1.02450
9606	1.00	2.00	95.00	0.31582	0.64145	0.14191
9606	2.00	2.00	95.00	0.23631	0.33298	0.87573
9606	2.00	1.00	67.00	-0.08539	0.58884	-0.71640
9606	2.00	1.00	67.00	0.50549	-0.91602	0.67498
9606	2.00	2.00	95.00	-0.16435	0.59899	0.08550
9606	3.00	2.00	95.00	0.41850	0.40487	0.53369
9606	4.00	2.00	95.00	0.69755	1.10036	1.05963
9606	5.00	1.00	67.00	-0.41664	0.07744	-0.97200
9606	5.00	2.00	95.00	-1.26552	0.75965	0.74031
9606	6.00	2.00	95.00	-0.38393	1.14201	0.50672
9704	1.00	1.00	64.00	-0.00223	-0.80259	0.61411
9704	1.00	1.00	64.00	-0.13300	-0.07392	0.89285
9704	2.00	1.00	64.00	-0.33958	-2.11651	0.18062
9704	3.00	1.00	64.00	0.13576	-0.92994	0.16993
9704	4.00	1.00	64.00	-0.31645	-1.96938	0.54545
9704	5.00	1.00	64.00	-0.62671	-0.02946	0.53409
9704	6.00	1.00	64.00	-0.92953	-1.00561	-1.29276
9704	7.00	1.00	64.00	0.77595	-0.34694	-0.04676

Appendix A3. Factor scores for individual specimens included in the principal components analysis presented in Table 9. KEY TO THE SPECIMEN NUMBERS: In the specimen number, Cat indicates that this is a section from *Felis silvestris catus.* Chk or Ch indicates that this is a section from *Gallus gallus.* LF, RF = left and right femur. LT, RT = left and right tibia. LH, RH = left and right humerus. LR, RR = left and right radius. LU, RU = left and right ulna. LFUR, RFUR = left and right furcula. Numerals 1 through 9 indicate that the section is taken at 10% through 90% of the bone's length from it's proximal end. All human specimens are taken at the 50% section of the left and right ulnae. The specimen numbers of the human sections indicate cadaver number and whether the section is taken from the left or right ulna. FAC1 – FAC7 indicate the factor scores for the individual section on the seven derived principal components.

SPECIMEN	FAC1	FAC2	FAC3	FAC4	FAC5	FAC6	FAC7
LF 1 Cat	0.22126	-0.02795	-0.50988	-0.43255	-1.06059	-0.19360	-1.78937
LF 2 Cat	-0.18144	-0.05558	-0.52305	0.13460	0.15994	0.03734	-0.37493

(Appendix A3) contd….

SPECIMEN	FAC1	FAC2	FAC3	FAC4	FAC5	FAC6	FAC7
LF 3 Cat	-0.56335	0.34162	0.34146	1.44755	-1.82026	0.01171	0.10837
LF 4 Cat	-0.50342	-0.03854	-0.13125	0.83542	-1.38904	-0.00353	0.15977
LF 5 Cat	-0.48799	-0.06994	-0.19533	0.61339	-0.70789	0.03687	0.07511
LF 6 Cat	-0.46454	-0.06969	-0.17169	0.44558	-0.49338	0.03802	0.11804
LF 7 Cat	-0.36784	-0.42035	-0.65601	-0.13461	-0.13925	0.01375	0.09598
LF 8 Cat	-0.15162	-0.30190	-0.72302	-0.19768	-0.36603	-0.03802	-0.01793
LF 9 Cat	0.40478	-0.21332	-1.11409	-0.87584	-0.00655	-0.15668	-0.38681
LT 1 Cat	0.46368	0.17181	-0.69795	-0.38124	-0.35761	-0.15548	-2.32739
LT 2 Cat	0.03985	0.02253	-0.56037	-0.00204	-0.16179	-0.04240	-1.50829
LT 3 Cat	-0.32264	0.16782	-0.23833	0.68947	0.23099	0.10701	-0.62103
LT 4 Cat	-0.45355	0.09133	-0.07883	0.75040	-0.44380	0.06431	-0.42266
LT 5 Cat	-0.53639	0.35681	0.24778	1.31826	-0.85632	0.08532	-0.33979
LT 6 Cat	-0.53971	0.16418	0.05976	1.13358	-1.12562	0.05032	0.03227
LT 7 Cat	-0.52648	-0.20236	-0.30846	0.33040	-0.02344	0.08023	-0.06650
LT 8 Cat	-0.40224	-0.50392	-0.76718	-0.19136	0.13000	0.04176	0.24261
LT 9 Cat	-0.27852	-0.56438	-1.01150	-0.38120	0.40468	0.03840	0.21457
LH 1 Cat	0.49508	-0.12862	-0.95963	-0.89209	-0.14817	-0.19603	-3.17194
LH 2 Cat	0.07568	-0.37774	-0.90324	-0.70144	-0.23144	-0.11130	-0.98221
LH 3 Cat	-0.12143	-0.34654	-0.72416	-0.38676	-0.15611	-0.05187	-1.05622
LH 4 Cat	-0.28217	-0.31071	-0.56108	-0.16021	-0.10779	-0.00487	-0.63599
LH 5 Cat	-0.34817	-0.34880	-0.66235	0.02897	0.00997	0.03712	-0.50411
LH 6 Cat	-0.46555	-0.31063	-0.52943	0.33468	-0.40461	0.04172	-0.14031
LH 7 Cat	-0.52422	-0.00329	-0.14794	1.00918	-1.34503	0.02208	0.13301
LH 8 Cat	-0.14796	-0.19716	-0.62101	-0.09918	-0.54551	-0.03676	1.01551
LH 9 Cat	0.74905	0.21346	-0.76598	-1.29833	-0.76113	-0.25170	4.13550
LR 1 Cat	-0.60235	-0.36544	-0.44512	0.21030	0.18618	0.10298	0.19541
LR 2 Cat	-0.68384	-0.08252	-0.12067	0.84180	-0.28468	0.12383	0.31244
LR 3 Cat	-0.59122	-0.19769	-0.41153	0.54358	0.37521	0.15135	0.26317
LR 4 Cat	-0.61894	-0.22769	-0.34853	0.43625	0.35857	0.14113	0.24999
LR 5 Cat	-0.63209	-0.40351	-0.38215	0.01311	0.39025	0.10556	0.27051
LR 6 Cat	-0.61486	-0.38339	-0.50719	0.32259	0.05608	0.10518	0.31446
LR 7 Cat	-0.57191	-0.53141	-0.73794	0.11211	0.21339	0.09917	0.31073
LR 8 Cat	-0.55704	-0.64866	-0.88127	-0.04493	0.26339	0.08964	0.30699
LR 9 Cat	-0.50023	-0.66723	-0.97046	-0.13704	0.35170	0.08382	0.37108
LU 1 Cat	-0.46163	-0.47193	-0.73642	0.02258	0.24484	0.07274	-0.35998
LU 2 Cat	-0.52342	0.19487	0.10812	0.85997	-0.11451	0.10733	-0.76670
LU 3 Cat	-0.61798	0.43027	0.15165	1.70602	-0.19693	0.19637	-0.29431

(Appendix A3) contd….

SPECIMEN	FAC1	FAC2	FAC3	FAC4	FAC5	FAC6	FAC7
LU 4 Cat	-0.58978	0.13274	-0.19828	1.24367	0.10009	0.18527	-0.07175
LU 5 Cat	-0.59922	-0.20889	-0.37553	0.53731	0.21556	0.13359	0.05265
LU 6 Cat	-0.66767	-0.12652	-0.18635	0.66391	0.14856	0.14405	0.12755
LU 7 Cat	-0.62290	-0.34627	-0.44385	0.30226	0.23832	0.11821	0.19144
LU 8 Cat	-0.56063	-0.65937	-0.91335	-0.01224	0.26818	0.09356	0.25783
LU 9 Cat	-0.52409	-0.80421	-1.13410	-0.24261	0.55422	0.09590	0.14703
RF 1 Cat	0.06223	-0.08904	-0.46117	-0.30558	-0.87938	-0.15160	-1.81237
RF 2 Cat	-0.30988	-0.18641	-0.54704	0.08175	0.33208	0.06568	-0.18328
RF 3 Cat	-0.39490	-0.39318	-0.65490	-0.00549	-0.06435	0.03550	0.06228
RF 4 Cat	-0.33323	-0.40565	-0.77252	0.01996	-0.16294	0.02275	-0.04133
RF 5 Cat	-0.32862	-0.50001	-0.97667	-0.11720	0.43767	0.07092	0.07885
RF 6 Cat	-0.44827	0.01652	-0.16778	0.63232	-0.46771	0.05614	0.13324
RF 7 Cat	-0.39194	-0.36394	-0.62003	-0.02374	0.03473	0.04326	0.16458
RF 8 Cat	-0.33100	-0.54727	-0.84326	-0.37241	0.14698	0.01506	0.02709
RF 9 Cat	0.06866	-0.49688	-1.06905	-0.93781	0.13234	-0.09217	0.06061
RT 1 Cat	0.44315	0.10383	-0.60310	-0.51043	-0.75538	-0.21441	-2.91642
RT 2 Cat	-0.24353	0.40016	0.09021	1.09261	-1.34844	-0.02272	-0.89592
RT 3 Cat	-0.45476	0.20898	0.05017	0.92056	-0.58115	0.06424	-0.41559
RT 4 Cat	-0.46364	0.06551	-0.14174	0.68418	-0.06712	0.09714	-0.28200
RT 5 Cat	-0.52867	0.06173	-0.00198	0.59166	0.03645	0.10321	-0.28115
RT 6 Cat	-0.46275	-0.24998	-0.44752	0.12231	0.36903	0.09373	0.05708
RT 7 Cat	-0.55844	-0.08835	-0.13447	0.50356	-0.19190	0.08178	0.01617
RT 8 Cat	-0.42070	-0.56147	-0.84131	-0.24084	0.34827	0.05962	0.12294
RT 9 Cat	-0.24601	-0.60952	-1.11341	-0.41862	0.42806	0.03049	-0.05210
RH 1 Cat	0.25864	-0.29952	-0.95502	-0.82105	-0.15567	-0.15179	-2.16811
RH 2 Cat	0.12545	-0.25555	-0.86898	-0.54301	-0.04571	-0.09462	-1.69484
RH 3 Cat	-0.24456	0.40836	0.22807	1.04191	-1.88611	-0.07941	-0.71260
RH 4 Cat	-0.49892	0.30365	0.33382	1.13173	-1.54745	-0.00537	-0.34911
RH 5 Cat	-0.57146	0.35207	0.42533	1.19502	-1.17747	0.04430	-0.17268
RH 6 Cat	-0.55140	0.06190	-0.02514	0.96850	-0.96983	0.05060	0.00159
RH 7 Cat	-0.58582	0.09971	0.07538	1.11087	-1.37595	0.03058	0.20565
RH 8 Cat	-0.42650	0.28322	0.15102	1.17925	-1.85689	-0.02164	0.77750
RH 9 Cat	-0.43154	0.07334	0.01424	0.73475	-1.23459	-0.01760	-0.57305
RR 1 Cat	-0.72397	0.42723	0.41186	1.57011	-0.35207	0.18023	0.21085
RR 2 Cat	-0.77382	0.12512	0.39547	0.85068	-0.31465	0.12135	0.28915
RR 3 Cat	-0.72943	0.29041	0.30202	1.31305	-0.16178	0.17660	0.24119
RR 4 Cat	-0.69382	0.38958	0.26225	1.50922	0.03626	0.21059	0.20374

(Appendix A3) contd….

SPECIMEN	FAC1	FAC2	FAC3	FAC4	FAC5	FAC6	FAC7
RR 5 Cat	-0.71622	0.03004	0.12544	0.82284	-0.19058	0.12923	0.31972
RR 6 Cat	-0.76948	0.35998	0.40933	1.67504	-0.97497	0.13944	0.39140
RR 7 Cat	-0.78500	0.28648	0.35922	1.68204	-1.29779	0.11300	0.41451
RR 8 Cat	-0.80444	0.33002	0.37015	1.99999	-1.85849	0.09386	0.50716
RR 9 Cat	-0.72905	0.36834	0.29700	1.99450	-1.76003	0.09403	0.53482
RU 1 Cat	-0.55237	0.36621	0.63001	0.89751	-1.06894	0.00505	-1.21944
RU 2 Cat	-0.68870	0.67921	1.09055	1.28589	-0.77615	0.08673	-0.69724
RU 3 Cat	-0.78121	0.35795	0.80123	0.99605	-0.60601	0.09621	-0.15237
RU 4 Cat	-0.68821	0.44391	0.48531	1.26315	0.20217	0.19367	-0.13034
RU 5 Cat	-0.77443	0.37555	0.49400	1.59683	-0.93295	0.13256	0.20344
RU 6 Cat	-0.77965	0.20023	0.35509	1.36164	-1.04380	0.10348	0.29011
RU 7 Cat	-0.76946	0.20965	0.25456	1.61937	-1.38283	0.09835	0.35793
RU 8 Cat	-0.82282	0.22669	0.37232	1.76120	-1.89402	0.06927	0.50081
RU 9 Cat	-0.65423	-0.37209	-0.52799	0.70197	-0.64044	0.08005	0.28715
LF 1 chk	1.40270	0.64994	-0.53000	-1.52032	-2.19833	-0.53957	1.08097
LF 2 chk	-0.13610	-0.00457	-0.21669	0.20697	-1.41449	-0.13670	-1.20311
LF 3 chk	0.19318	0.12753	-0.20689	-0.23964	-1.52295	-0.22967	-1.94078
LF 4 chk	-0.22683	0.36753	0.67788	-0.17338	-1.01706	-0.12140	0.29157
LF 5 chk	-0.19232	0.58836	0.81563	0.45004	-1.95342	-0.15519	-0.17173
LF 6 chk	0.08982	0.42252	0.53236	-0.52774	-1.16802	-0.20825	-0.58420
LF 7 chk	0.23295	0.10719	0.00659	-1.16461	-0.45516	-0.21642	-0.64767
LF 8 chk	0.12836	0.20743	0.10410	-0.60944	-0.99251	-0.20465	-0.40974
LF 9 chk	0.72296	0.14704	-0.71613	-1.01784	-1.40150	-0.32266	0.58167
LT 1 chk	0.50528	-0.18244	-0.96133	-1.21321	-0.60722	-0.25680	0.83927
LT 2 chk	0.02607	-0.29262	-0.62744	-0.81051	-0.27735	-0.12760	-0.17967
LT 3 chk	-0.05286	0.16145	-0.01894	0.16059	-1.59736	-0.15927	-1.04012
LT 4 chk	-0.21864	0.28681	0.35408	0.40818	-1.70578	-0.13452	-1.23430
LT 5 chk	-0.40992	0.30773	0.83792	-0.07161	-0.84538	-0.08407	-1.00944
LT 6 chk	-0.49329	0.78164	1.62117	0.37528	-1.51029	-0.10055	-0.25890
LT 7 chk	-0.49967	0.72953	1.93004	-0.65611	-0.25041	-0.08706	0.09288
LT 8 chk	0.01889	-0.05105	-0.20177	-0.75300	-0.47928	-0.14248	0.03749
LT 9 chk	0.12683	-0.19461	-0.60747	-0.80109	-0.49974	-0.15598	0.22232
LH 1 chk	0.82638	0.83268	-0.01590	-0.36527	-2.65842	-0.38025	4.10975
LH 2 chk	0.90504	0.94179	0.24049	-0.65379	-2.54355	-0.40678	3.17359
LH 3 chk	-0.15059	0.02326	0.25363	-1.02153	0.07836	-0.09698	0.62759
LH 4 chk	-0.45574	0.14668	0.76515	-0.65390	0.05191	-0.03558	0.41840
LH 5 chk	-0.50738	-0.10980	1.04047	-2.27252	2.17096	0.00167	-0.21972

(Appendix A3) contd….

SPECIMEN	FAC1	FAC2	FAC3	FAC4	FAC5	FAC6	FAC7
LH 6 chk	-0.71820	0.25406	1.54013	-1.13120	0.95096	0.01372	-0.00117
LH 7 chk	-0.36884	-0.08095	-0.04621	0.02192	-0.73730	-0.04464	0.32278
LH 8 chk	-0.14039	0.18140	0.11734	-0.06822	-1.13500	-0.10807	1.27486
LH 9 chk	-0.21315	-0.15889	-0.21879	-0.61734	-0.15239	-0.05456	1.66565
LR 1 chk	-0.44218	-0.93992	-1.32711	-0.54694	0.57776	0.06480	0.26974
LR 2 chk	-0.58124	-0.60792	-0.79518	0.14114	-0.21144	0.06361	0.32470
LR 3 chk	-0.70406	-0.44416	0.00332	-0.64456	0.79773	0.07839	0.18060
LR 4 chk	-1.26091	1.02113	3.63181	-0.92070	1.09231	0.06991	0.03753
LR 5 chk	-1.16576	0.79386	2.99222	-0.72112	0.85004	0.06936	0.09211
LR 6 chk	-1.02018	0.47266	1.91944	-0.06439	0.05268	0.06456	0.21738
LR 7 chk	-0.97842	0.46298	1.62679	0.46445	-0.62406	0.05431	0.30965
LR 8 chk	-0.61890	-0.62659	-0.46471	-0.62689	0.75630	0.07736	0.23025
LR 9 chk	-0.50050	-0.80115	-1.11844	-0.22867	0.21389	0.06233	0.33458
LU 1 chk	-0.14586	-0.30466	-0.57765	-0.50653	-0.32299	-0.07259	0.73039
LU 2 chk	-0.45623	-0.11898	0.33364	-0.82315	0.41925	-0.01143	0.49029
LU 3 chk	-0.89309	0.68292	2.35143	-0.57551	0.31821	0.01102	0.18223
LU 4 chk	-0.78855	0.41586	1.97963	-1.25698	1.11617	0.01716	0.22186
LU 5 chk	-0.97054	0.73716	2.65476	-0.75210	0.60012	0.02162	-0.31429
LU 6 chk	-1.02636	0.83779	3.00922	-0.97417	0.88696	0.02505	-0.30390
LU 7 chk	-0.64770	-0.07069	0.50147	-0.28656	0.04895	0.02026	-0.13270
LU 8 chk	-0.35792	-0.70764	-0.94972	-0.59977	0.34328	0.00911	-0.38779
LU 9 chk	-0.12590	-0.78130	-1.30026	-0.83466	0.29408	-0.05075	-0.49177
RF 1 chk	1.83424	0.39611	-1.17038	-2.79286	-1.19571	-0.59549	2.69733
RF 2 chk	0.49241	-0.44164	-1.14032	-1.49515	-0.19349	-0.25856	-2.62052
RF 3 chk	-0.11341	-0.13628	-0.23947	-0.50537	-0.51956	-0.11447	-0.61636
RF 4 chk	-0.29126	0.10937	0.53760	-0.70576	-0.15095	-0.08980	-0.47839
RF 5 chk	-0.17697	0.13957	0.23001	-0.16507	-0.99243	-0.12246	-0.70886
RF 6 chk	0.04035	0.48274	0.70243	-0.49964	-1.15883	-0.20540	-0.58187
RF 7 chk	0.39479	-0.05839	-0.23428	-1.87913	0.22506	-0.24091	-0.70038
RF 8 chk	0.57390	-0.11520	-0.76924	-1.58956	-0.33053	-0.26214	0.55068
RF 9 chk	0.53164	-0.34627	-1.14971	-1.45066	-0.29656	-0.25932	-0.21897
RT 1 chk	0.45949	-0.48791	-1.22648	-1.38605	-0.23508	-0.25844	-2.54028
RT 2 chk	0.26186	-0.42372	-0.93241	-1.27949	-0.06834	-0.18267	-1.71549
RT 3 chk	0.14618	-0.37341	-0.82437	-1.03541	-0.17583	-0.14604	-0.81510
RT 4 chk	-0.28580	-0.23501	-0.11043	-0.77076	0.13715	-0.04905	-0.16585
RT 5 chk	-0.23683	-0.10782	0.15150	-0.96693	0.20143	-0.07155	-0.41599
RT 6 chk	-0.35700	0.11389	0.70834	-0.97045	0.27282	-0.05827	0.07033

(Appendix A3) contd….

SPECIMEN	FAC1	FAC2	FAC3	FAC4	FAC5	FAC6	FAC7
RT 7 chk	-0.22185	0.35323	0.90476	-0.82615	-0.25718	-0.11480	0.22292
RT 8 chk	0.01108	-0.09743	-0.34843	-0.65987	-0.52974	-0.12675	0.66611
RT 9 chk	0.62773	-0.04370	-0.86299	-1.27011	-0.82806	-0.27906	0.91096
RH 1 chk	0.81294	0.10652	-0.81644	-1.78655	-0.50470	-0.29194	4.69356
RH 2 chk	0.98798	0.77958	0.16154	-1.37982	-1.74763	-0.42559	2.31520
RH 3 chk	-0.02750	-0.33660	-0.40478	-1.41991	0.55934	-0.09573	0.15596
RH 4 chk	-0.41869	-0.18256	0.42773	-1.43241	1.10115	-0.01589	0.10849
RH 5 chk	-0.78767	0.73692	2.64830	-1.40456	1.08206	-0.01390	0.04599
RH 6 chk	-0.44154	0.23650	0.98097	-0.73418	0.04854	-0.05553	-0.25105
RH 7 chk	-0.30794	-0.26572	-0.28430	-0.41646	-0.21554	-0.04066	0.01154
RH 8 chk	0.01411	-0.40785	-0.57581	-1.53238	0.68283	-0.09237	0.65443
RH 9 chk	-0.19510	-0.44340	-0.63648	-0.95661	0.39192	-0.03246	1.60473
RR 1 chk	-0.45180	-0.93836	-1.30116	-0.55999	0.60546	0.06374	0.18809
RR 2 chk	-0.49841	-0.84373	-1.05961	-0.55527	0.61368	0.06584	0.13707
RR 3 chk	-0.78145	-0.19930	0.61709	-0.75453	0.89529	0.07424	0.10340
RR 4 chk	-1.20682	0.90362	3.42034	-1.11474	1.30465	0.06765	-0.03831
RR 5 chk	-0.96969	0.22618	1.81414	-1.09875	1.33146	0.07830	0.04041
RR 6 chk	-0.91488	0.04621	1.55412	-1.46908	1.78795	0.08351	-0.02038
RR 7 chk	-0.80432	-0.21508	0.77664	-1.14161	1.39346	0.08140	0.06255
RR 8 chk	-0.82050	-0.11956	0.79891	-0.70190	0.84611	0.07431	0.09790
RR 9 chk	-0.47658	-0.95852	-1.31757	-0.52146	0.61107	0.06861	0.13163
RU 1 chk	-0.10414	-0.68145	-1.05527	-1.05686	0.45421	-0.05805	-0.52246
RU 2 chk	-0.19025	-0.44510	-0.38650	-1.29211	0.71229	-0.06153	-0.77933
RU 3 chk	-0.35831	-0.03858	0.67620	-1.48761	0.95897	-0.05334	-0.63964
RU 4 chk	-0.62275	0.27024	1.41665	-1.06213	0.70581	-0.01233	-0.08025
RU 5 chk	-0.95421	0.68586	2.65668	-1.11586	1.04577	0.03130	0.19060
RU 6 chk	-0.99789	0.65792	2.88548	-1.63713	1.73717	0.04310	-0.02442
RU 7 chk	-0.85544	0.16800	1.61750	-1.26194	1.37791	0.05325	0.03677
RU 8 chk	-0.43428	-0.55694	-0.55356	-0.68305	0.48242	0.01876	0.09620
RU 9 chk	-0.29322	-0.84364	-1.29871	-0.65599	0.40716	0.01157	0.18027
LFUR 1 ch	6.77964	-3.53070	4.23863	0.79096	-1.25117	2.19784	-0.73913
LFUR 2 ch	0.53304	-2.10427	0.00832	0.54476	0.65999	4.95369	-0.23257
LFUR 3 ch	0.17944	-1.86126	-0.34828	0.38740	0.75310	3.07766	0.26871
LFUR 4 ch	0.16908	-1.87220	-0.34528	0.43520	0.80504	2.10477	0.50128
LFUR 5 ch	0.18579	-1.91944	-0.30214	0.53121	0.87602	0.80587	0.70182
LFUR 6 ch	0.14965	-1.86054	-0.36440	0.43798	0.81603	1.56961	0.30893
LFUR 7 ch	0.11631	-1.92168	-0.14893	0.54059	1.13714	-1.33624	0.67980

(Appendix A3) contd….

SPECIMEN	FAC1	FAC2	FAC3	FAC4	FAC5	FAC6	FAC7
LFUR 8 ch	0.27034	-2.32668	0.03852	1.19008	1.27474	-4.65493	0.99601
LFUR 9 ch	1.89589	-3.27929	1.60114	1.95263	1.11166	-4.72989	-0.02881
RFUR 1 ch	6.77964	-3.53070	4.23863	0.79096	-1.25117	2.19784	-0.73913
RFUR 2 ch	0.78547	-2.25981	0.25401	0.67034	0.66560	5.87926	1.13631
RFUR 3 ch	0.30503	-1.97292	-0.20172	0.50706	0.78588	2.95070	0.70500
RFUR 4 ch	0.19175	-1.89898	-0.31390	0.47474	0.82731	1.78473	0.64916
RFUR 5 ch	0.32655	-2.02356	-0.15428	0.60739	0.85276	1.50245	0.69063
RFUR 6 ch	0.16726	-1.94009	-0.28858	0.60401	0.92067	-0.26148	0.63114
RFUR 7 ch	0.16934	-2.03094	-0.10327	0.71554	1.15695	-2.21399	0.70527
RFUR 8 ch	0.67009	-2.60656	0.44619	1.42973	1.24798	-4.18536	0.99131
RFUR 9 ch	1.66618	-3.39782	1.52597	2.24716	1.31942	-7.14545	-0.28651
9711 left	1.26559	1.28854	-0.33934	-0.17651	-0.11433	-0.19807	-0.49882
9712 left	0.33305	0.29419	-1.08228	0.35437	1.10368	0.09547	-0.30760
9713 left	1.03436	1.56552	-0.63460	1.14753	1.81055	0.14776	-0.37240
9714 left	0.21443	0.80893	-0.32612	0.93565	0.92457	0.13989	0.14497
9715 left	2.98507	2.17480	-0.05577	-2.04063	-1.93842	-0.78922	-3.21393
9716 left	2.95297	3.25288	-0.46425	0.19607	1.92926	-0.13483	2.77595
9717 left	1.31468	1.47138	-0.22597	-0.07162	0.04080	-0.17260	0.20655
9718 left	1.41070	1.93997	-0.65283	1.31552	1.56077	0.09371	-0.60556
9719 left	0.78705	1.27915	-0.38318	0.69432	1.09315	0.07600	1.06465
9720 left	0.43023	1.01856	-0.41338	1.08873	1.19949	0.14640	-0.89713
9721 left	1.05168	1.38981	-0.25113	0.43920	0.08465	-0.08762	0.20218
9722 left	0.89899	1.58408	-0.82940	1.77325	2.13640	0.26101	-0.15276
9723 left	1.64456	1.90867	-0.42672	0.35075	0.48310	-0.11069	1.84947
9801 left	1.51816	1.73106	-0.43554	0.27219	0.62192	-0.10419	0.37565
9711 right	0.86823	1.03126	-0.43128	0.17435	0.38459	-0.06778	-0.53169
9712 right	0.30559	0.40907	-1.20506	0.76379	1.72890	0.20095	-0.18783
9713 right	1.69912	2.39838	-0.47310	1.36377	1.65795	0.08946	1.42597
9714 right	0.41255	1.23411	0.03745	1.17591	0.34762	0.07989	0.33750
9715 right	3.05459	1.75366	-0.58278	-2.79129	-1.49815	-0.80671	-2.10003
9716 right	2.62325	2.87792	-0.34974	0.15557	1.28182	-0.17910	1.08621
9717 right	1.53739	1.87904	-0.40693	0.38618	1.22432	-0.03365	0.81889
9718 right	1.35078	1.89098	-0.54825	1.12957	1.78241	0.09777	-0.95556
9719 right	0.72367	1.42163	-0.22838	1.06080	1.26543	0.12055	-0.10247
9720 right	0.77021	1.65800	-0.62610	2.03249	2.50789	0.31466	-1.95346
9721 right	1.26272	1.48011	-0.01822	-0.08787	-0.53467	-0.22524	0.39027
9722 right	0.94851	2.14913	-1.11640	3.20563	3.96942	0.56897	-0.48304

(Appendix A3) contd….

SPECIMEN	FAC1	FAC2	FAC3	FAC4	FAC5	FAC6	FAC7
9723 right	1.61019	1.72144	-0.25225	-0.21614	0.31932	-0.19438	0.40706
9801 right	1.61313	2.28684	-0.55273	1.53700	1.87497	0.11291	-1.10403

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