

Turley, K.,
White, F.J.,
& Frost, S.R.

*Department of Anthropology,
University of Oregon,
Eugene, Oregon 97403-1218, USA.
E-mail: kturley@uoregon.edu*

DOI: 10.14673/HE2015121002

Phenotypic Plasticity: The Impact of Habitat and Behavior (Substrate Use) on Adult Talo-Crural Articular Joint Shape Both Between and Within Closely Related Hominoid Species.

The hominin fossil record is punctuated by variation and rapid change in talo-crural articular joint shape. Prior studies in a diverse Catarrhine sample using Singular Warp analysis has revealed that similar shape is observed across superfamilies due to substrate use, but genera can differ in shape in response to the same behavioral stimulus. Ontogenetic data show these changes arise in the adult. Phenotypic plasticity, the response of the joint to an epigenetic behavioral factor, substrate use, is explored in three comparably sized closely related extant hominoid species.

Matched talo-crural articular surfaces were laser surface scanned, landmarked and analyzed in 114 adult specimens of *Pan paniscus*, *Pan troglodytes* (three subspecies) and *Homo sapiens* (5 global locations). Articular shape was compared to previously described flexible (arboreal), and stable (terrestrial) morphologies, and the effect of habitat evaluated.

Pan paniscus had a flexible talo-crural joint shape profile consistent with its highly arboreal substrate use. Differences within the *Pan troglodytes* and *Homo sapiens* subsets reflected differing substrate use due to habitat, and, in the case of the latter, technology (footwear). The three *Pan troglodytes* subspecies clustered with a more stable joint surface profile, with the exception of a series of *Pan troglodytes troglodytes* from southern Cameroon. A more flexible profile was manifest in this group associated with a human ground presence (Baka) for an extended period. *Homo sapiens*, a single species with a diverse global habitat, showed a continuum of grades from stable, in heavily shod populations in hard surface habitats, to flexible, in unshod populations in soft surface habitats.

Overall, *Pan paniscus* showed uniformity of talo-crural shape, *Pan troglodytes* an environmental effect, and *Homo sapiens* provided insights into the mechanism of rapid shape change, phenotypic plasticity, due to the behavioral factor, substrate use, observed in the fossil record.

KEY WORDS: *phenotypic plasticity, effect of use on Hominoid ankle shape, effect of habitat on behavior.*

The appositional articular morphology of the talo-crural joint is an interface between substrate and organism that can provide insights into the mechanism of evolutionary changes in post-cranial morphology. Closely related taxa provide an ideal cohort for investigating the effects of behavior, in the form of substrate use, and phenotypic plasticity on morphology.

In catarrhines, the shapes of both the proximal talus and distal tibia reflect substrate preference (Turley et al., 2011; Turley & Frost, 2013). Singular warp analysis allows examination of the shape of the appositional articular surfaces of both elements as a unit, and more clearly shows that appositional articular morphology reflects substrate use in catarrhines than when a single element is studied (Turley & Frost, 2014a). Interestingly, talo-crural appositional articular morphology appears convergent among distantly related taxa, such that terrestrial and arboreal hominoids differ from each other in the same ways as terrestrial and arboreal cercopithecoids, which may suggest shape is responding to similar functional pressures (Turley & Frost, 2014a). At the same time, there is often differentiation among species within genera such as *Pan* and *Macaca*, implying that these differences can appear quite rapidly over evolutionary time (Turley & Frost, 2014a).

Furthermore, examination of the ontogeny of appositional articular shape revealed a behavioral, epigenetic, response to substrate use (Turley & Frost, 2014b). Juveniles of *Pan paniscus*, *Pan troglodytes*, and *Homo sapiens* with their second molars in occlusion, but with their third molars not yet fully erupted, were similar in the appositional articular morphology of their talo-crural joints. However, the talo-crural appositional articular morphology of adults of these three species sorted by substrate use with *Pan paniscus* the most flexible profile, *Pan troglodytes* with a more stable profile, and *Homo sapiens* with the most stable profile, possibly implying that their ankle morphology was remodeled during their ontogeny based on their substrate use (Turley & Frost, 2014b). This divergent morphology of the talo-crural appositional articular joint shape in the adult sample of these three closely related taxa is the subject of this analysis. These three closely related species are a natural experiment that can provide insights into the possible role of phenotypic plasticity on the variation in shape both between such taxa and among individuals within species. It may allow further assessment of the relationship of habitat to the behavioral response, substrate use, and its impact on joint shape.

Molecular genetic studies suggest divergence dates for *Homo* and *Pan* at ~6 MYA and the two species of *Pan*, *Pan paniscus* and *Pan troglodytes*, at ~1.8 MYA (Prado-Martinez et al., 2013). The age for the divergence between *Homo* and *Pan* is consistent with the available paleontological evidence (Haile-Selassie, 2001; Senut et al., 2001; Brunet et al., 2002). *Pan paniscus* constitutes a single species with a comparatively homogeneous habitat, the high precipitation Guinea-Congolese rainforest, isolated by the Congo River. *Pan troglodytes* has been divided into four subspecies western (*Pan troglodytes verus*), Gulf of Guinea (*Pan troglodytes ellioti*), central (*Pan troglodytes troglodytes*), and eastern (*Pan troglodytes schweinfurthii*), and although the classification has

been challenged, the greatest genetic diversity is observed in the central group (Groves, 2001; Groves, 2005; Fisher et al., 2004; Fisher et al., 2006; Oates et al., 2009; Gonder et al., 2011; Bowden et al., 2012). These subgroups inhabit a broad expanse of western and central Africa with diverse habitats and regions of potential ecological isolation. Finally, *Homo sapiens* constitutes a single species with a highly diverse habitat, and the technology to alter the interface between substrate and organism.

Using this cohort, the effect of substrate use on talo-crural appositional articular joint shape among these closely related taxa may be examined, and the effect of habitat, both in the substrates available and physical isolation assessed, as well as the effect of substrate modification (footwear). These findings yield insights into mechanisms of speciation, changes in post-cranial morphology in response to alterations in habitat, and the origin of the mosaic of ankle shape exhibited in the Plio-Pleistocene. (Harcourt-Smith & Aiello, 2004; Turley & Frost, 2014b)

Materials and Methods

Sample

The study group consisted of 114 specimens of matched left or right distal tibial and proximal talar articular facets from single individuals. All specimens were adults with the third molar fully erupted, and all were without evidence of pathology. All 64 non-human specimens had provenience documented, and all were wild-shot. There were 10 *Pan paniscus*, 5 males and 5 females from Zaire; 5 *Pan troglodytes verus*, 2 males and 3 females from Guinea (2), Sierra Leone (1), Liberia (1) and Cote d'Ivoire (1); 9 *Pan troglodytes schweinfurthii*, 8 males and 1 female from Zaire (8) and Uganda (1); and 40 *Pan troglodytes troglodytes*, 16 males and 23 females and one unknown from Cameroon (38) and Gabon (2). Figure 1 identifies the collection sites. The 50 human specimens were from five habitats, California Paleoamerican from the environs of San Francisco Bay (Shell Midden Cultures ~300 to 2500 B.P.) (n=13), Southwestern Paleo-Amerindian (New Mexico Canyon de Chelly Cliff Dwellers ~1000 B.P.) (n=6), Alaskan Paleo-Eskimo (Point Hope, ~300 and 1500 B.P.) (n=9), Egyptian/Nubian (El Hesa ~1350-1600 B.P.) (n=7), early 20th Century New Yorkers (n=15) with dates, habitat and technology documented (Table 1). See Acknowledgements for institutional sources.

Global location and local substrate factors, including the geography, topography, aquatic and local ground conditions which might impact substrate use, were documented from museum records (Acknowledgements) and the literature (Strahler & Strahler, 1992). Climatic regions were identified using Koppen codes as modified by Geiger (Strahler & Strahler, 1992; Peel et al., 2007), Takhajan's phytchorium numbering system was used for the worldwide distribution of specimen sites with the addition of White's detailed description for African phytchoria (White, 1983; Strahler & Strahler, 1992).

Archeological collections of human artifacts from the studied populations were examined and their technology (footwear) impacting substrate use was documented

(American Museum of Natural History Collections; P. A. Hearst Museum Collections; Kankaien, 1995; Newton, 2002; Dumond, 2011; Dumond, 2014; Francigny et al., 2014; Irish, 2014).

Data collection

Each specimen was laser surface scanned and digitally reconstructed using either a Konica Minolta Vivid 910 Noncontact 3-D Digitizer and Geomagic Studio 8 software, or a NextEngine Desktop 3-D Scanner and ScanStudio HD software. Twenty-seven landmarks were placed by a single observer (KT): 12 on the distal tibial facets, and 15 on the proximal talar facets, using Landmark Editor software (Wiley, 2006). These landmarks were illustrated in prior publications examining the shape of the tibia and talus (Turley & Frost, 2014b; Figure 1).

Observational error was previously assessed in both the tibial and talar subsets using single specimens of *Homo sapiens* landmarked 10 times (Turley et al., 2011; Turley & Frost, 2013). Principal component analysis demonstrated tight clustering of the repeated measures compared to variation within and among the taxa studied, and have been found to reliably distinguish talar and tibial morphology among taxa (Turley et al., 2011; Turley & Frost, 2013).

Generalized Procrustes Analysis

Generalized Procrustes Analysis (GPA) was performed using Morpheus (Slice, 1998). GPA superimposes landmark configurations and removes variance due to position and rotation, and scales each to unit centroid size (Rohlf & Slice, 1990). Centroid size is the square root of the sum of the squared distances of each landmark to the centroid (Rohlf & Slice, 1990), and is stored as a separate variable during GPA. Centroid size was transformed to its natural logarithm for subsequent analysis. GPA was done with reflection allowed, since our data set included both the right and left specimens. Separate GPAs were performed for the tibial and talar landmark subsets for each data set studied, the total, *Pan* spp., *Pan paniscus*, *Pan troglodytes*, and *Homo sapiens*. All subsequent statistical analyses were performed using SAS 9.1 (SAS Institute, Cary NC). As GPA aligned coordinates have a very high correspondence with their Euclidean tangent space projections, un-projected aligned coordinates were used. Shape differences among landmark configurations were measured by Procrustes chord distance; the Pythagorean distance between the two Procrustes superimposed landmark configurations (Bookstein, 1991; Slice, 2001; Turley et al., 2011).

Singular Warp Analysis

Singular Warp analysis of the cross-covariance matrix of the appositional articular shape was used in this study to explore the relation of the matched surfaces of the distal tibial facets and proximal talar facets. This is the application of Partial Least Squares within morphometrics that computes two unit vectors such that their covariance is maxi-

Table 1. *Homo sapiens* Populations, Specimen Date, Habitat, and Technology.

POPULATION	DATES	M	F	HABITAT/CODE	TECHNOLOGY/FOOTWEAR
New Yorkers	20 th C.	8	7	New York 20 th C. Cfa, Cwa, 3,30.	Heavy Leather Shoes/Boots
Paleo-Pueblo	~1000 BP	4	2	Cliff Dwelling BWh, 3,61.	Heavy Double Yucca Sandal
Egyptian/Nubian	~1600 BP	4	3	Nile Island/Maritime BWh/BSh, 7, 48.	Thin Leather Shoes
Paleo-Eskimo	~500-1500 BP	4	5	Arctic/Maritime ET, 1.	Seal Skin Boots
Native American	~500-2500BP	8	5	Delta/Mudflat Cs, 9, 62.	Unshod

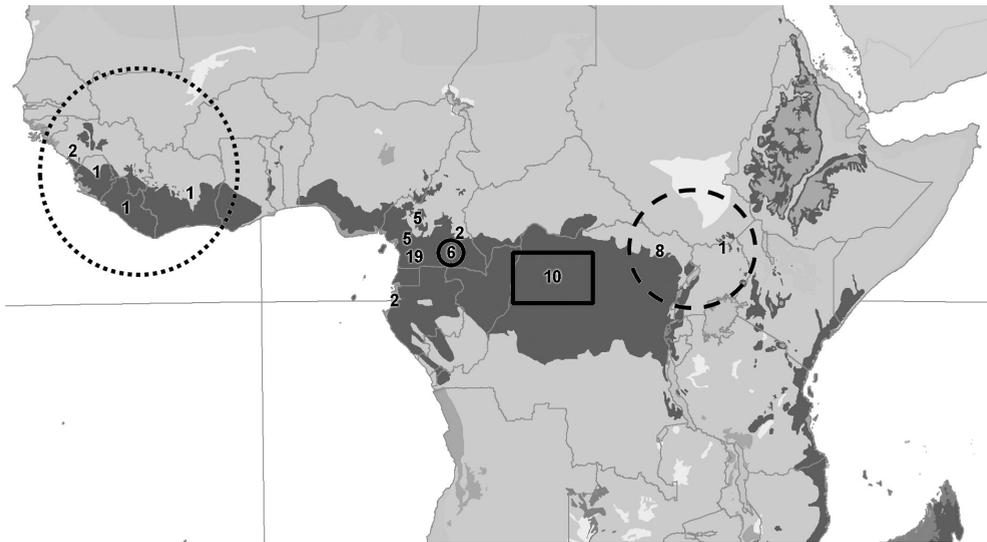


Figure 1. Map of the procurement sites and their biomes, Af-equatorial rainforest (*Pan paniscus*) with no dry season (solid rectangle) in the Congo and all *Pan troglodytes*, Am-rainforest-monsoon cycle in dark, and in light, Aw-rainforest with winter dry season. The western (dotted circle), eastern (dashed circle) and the central (*Pan. troglodytes*) populations are shown with the southern central Cameroon component of the central (*Pan. troglodytes troglodytes*) with a solid circle, as well as, *Pan paniscus* (solid rectangle) south of the Congo River in Zaire. Modified from Population, Landscape and Climate Estimates, v3 (PLACE III): Biomes Africa. Center for International Earth Science Information Network.

mized. It describes how two sets of variables covary with each other (McNulty, 2009). In this case, shape coordinates from the tibia form one submatrix and shape coordinates from the talus form the other, which have the greatest mutual linear predictive power (Rohlf & Corti, 2000; Bookstein et al., 2003; Frost et al., 2003; Harcourt-Smith et al., 2008). The correlation “ r ”, a measure of integration, was computed for each (Bookstein et al., 2003; Bastir & Rosas, 2005). Matched surfaces of each data set studied were separately analyzed, the total data set, as well as the *Pan* spp., *Pan paniscus*, *Pan troglodytes*, and *Homo sapiens* data sets.

Visualization

Visualization of shape differences was accomplished by comparing landmark configurations directly in Morphueus and by warping an exemplar surface to fit those landmark configurations using Landmark Editor. Mean landmark configurations were computed for each subgroup. The exemplar appositional articular surfaces from the Singular Warp analysis were visualized using Landmark Editor. The singular vectors were shown as surface-morphs (Gunz & Harvati, 2007).

Results

The scatter plot of the scores from the first singular warp of the appositional articular shape of the talo-crural joints in the total sample was highly significant ($p > 0.0001$) ($r = 0.86$) and revealed sorting by species, as previously observed in catarrhine adults (Turley & Frost, 2014a). The positive pole of the vector corresponded to the most flexible shape profile, *Pan paniscus*, and the negative to the most stable shape profile, *Homo sapiens*. The stable and flexible shape profiles reflected in the first singular warp found in this analysis are essentially the same as those found previously and are described as:

Stable: “A narrow more trapezoid trochlear shape with flat plane, square medial crest angle, and medial malleolar-trochlear angle.” There was distal displacement of both the medial and lateral crests with less concave curvature, as well as flatter central groove, distal extension of the medial crest, medial malleolar apex, and medial facet apex (Turley & Frost, 2014b).

Flexible: “An oval trochlea with angular plane and deeper central groove, and a tibial trochlear facet with obtuse medial malleolar-trochlear angle.” There was a concave medial facet with central apex and corresponding medial malleolar apex, as well as an obtuse medial crest angle with symmetrically curved crests and deeper central groove consistent with decreased joint angular excursion. These shape configurations provide flexibility of joint movement, but stability on unsteady, compliant curvilinear surfaces (Turley & Frost, 2014b).

The scatter plot of the scores from the first singular warp of the *Pan* spp. data set is presented in Figure 2. The scores correlation was highly significant ($p > 0.0001$) ($r = 0.67$)

with the separation of *Pan paniscus* and the subspecies of *Pan troglodytes* evident. *Pan paniscus* sorted at the positive (flexible shape) pole and *Pan troglodytes* at the negative (stable shape) pole.

Pan paniscus, a single species with a comparatively isolated Congolese habitat, is placed at the positive pole of the Singular warp vector and showed no significant differences ($p < 0.4$) ($r = 0.30$) among the sample population. The shape of the appositional articular morphology at the positive pole of the singular warp vector evidenced in the total and *Pan* spp. data sets are illustrated in Figure 3.

The subspecies of *Pan troglodytes*, *Pan troglodytes troglodytes*, *Pan troglodytes verus* and *Pan troglodytes schweinfurthii*, with diverse African habitats ranging from Guinea in the west to Uganda in the east, all clustered together on the first singular warp excepting a series of *Pan troglodytes troglodytes* individuals from the south central Cameroon ($p < 0.0001$) ($r = 0.69$) (Figure 2). Twenty-one of the *Pan troglodytes troglodytes* clustered together with the other subspecies. These included 2 specimens from Gabon, 14 from known locations in Cameroon (5 from Daoula, 3 from Metet, 6 from Ebolowa) and 5 from Cameroon with the procurement site unknown (Figure 1). Nineteen specimens, all 6 collected from Djaposten, Cameroon and 13 of 19 from Ebolowa, Cameroon, separated from the other *Pan troglodytes troglodytes* and the other subspecies (Figure 1). The difference in shape between the two subgroups is illustrated in Figure 3. The first singular warp scores of the *Pan* spp. demonstrated that these 19 specimens of *Pan troglodytes troglodytes* separated from the other *Pan troglodytes* in the sample, with their singular warp scores approaching those of *Pan paniscus* (Figure 2).

The human cohort, a single species with a diverse global habitat, showed a continuum of grades from the negative to positive singular warp poles ($p, 0.001$) ($r = 0.65$) (Figure 4). These sorted into three clusters illustrated by the mean scores, Early 20th Century New Yorkers, and Cliff Dwellers from Canyon de Chelly were similar to each other (Group 1) and separated from Paleo-Eskimos from Point Hope and Byzantine Period Egyptians/Nubians (Group 2) but with overlap, while Native Americans from the environs of San Francisco Bay (Group 3) formed a third distinct cluster (Figure 4). Differences in footwear employed by each group to cope with substrate demands are described in Table 1. The greatest difference in shape is between the Group 1 hard surface shod individuals and the soft surface unshod Group 3 individuals, with the differences in shape at the poles of the vector illustrated in Figure 3. No difference in shape was observed between males and females in any subgroup except those of the Paleo-Eskimo sample where females have a more stable talo-crural shape profile compared to the more flexible shape profile among males. In fact two Paleo-Eskimo males approach the Native American (Group 3) cluster (Figure 4). A single female from El Hesa was also distinctive with singular warp scores within the ranges of Group 3 (Figure 4).

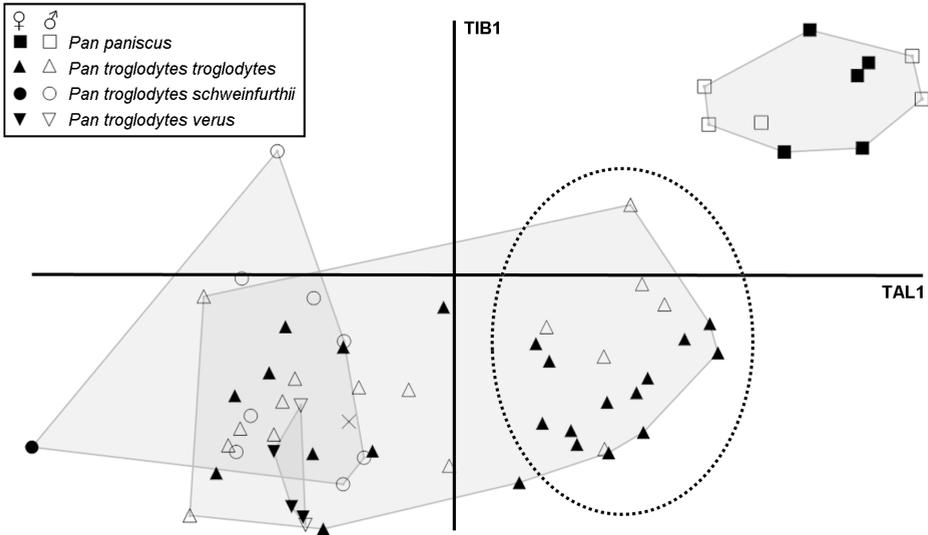


Figure 2. *Pan* spp. first singular warp scores with *Pan troglodytes* subspecies at the negative, stable shape, pole, with the exception of a component of *Pan troglodytes troglodytes* from the south central Cameroon (circled), and *Pan paniscus* at the positive, flexible shape, pole.

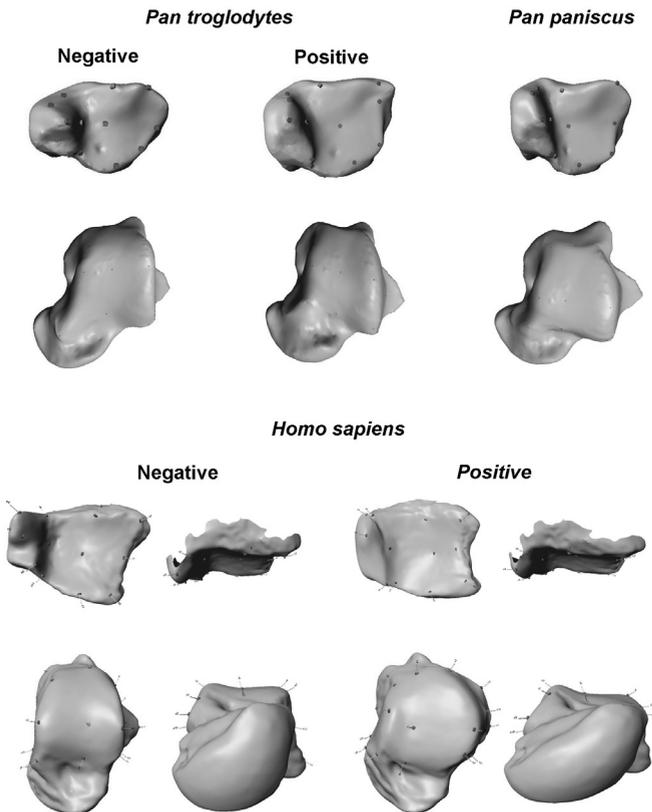


Figure 3 Visualization of the appositional articular shape differences among the *Pan* spp. (upper) and *Homo sapiens* (lower). Note the talar and tibial facet shapes, plane and medial facet crest angle, and medial malleolar shape and apical location. The stable profile is observed at the negative pole and flexible profile at the positive pole, with *Homo sapiens* shod at the negative and unshod at the positive poles.

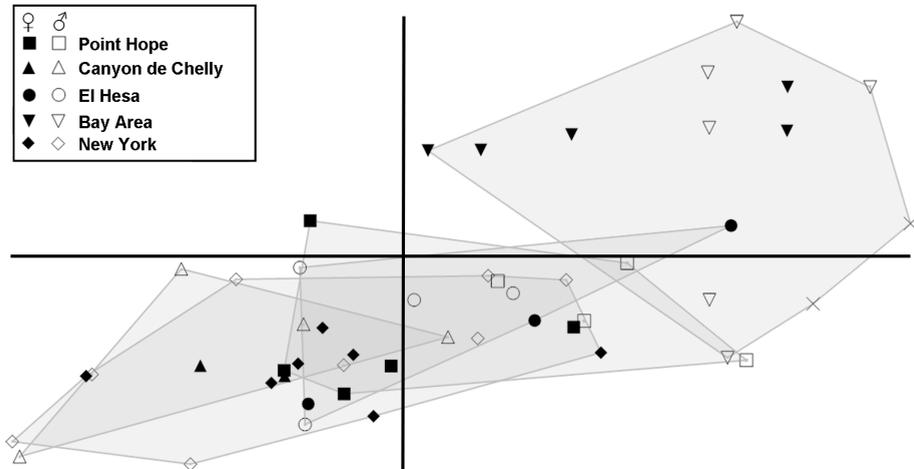


Figure 4. *Homo sapiens* first singular warp scores with 20th Century New Yorkers and 10th Century Paleo-Pueblo peoples clustering at the negative, stable shape, pole (shod-hard surfaces), Paleo-Eskimos and 5th Century Egyptian-Nubiens central, and San Francisco Bay Shell Midden peoples at the positive, flexible shape, pole (unshod-soft surfaces).

Discussion

The influence of substrate use on the appositional particular morphology of the talo-crural joint has been suggested in a previous examination of a diverse sample of Catarrhine taxa (Turley & Frost, 2014a). Three closely related species, *Pan paniscus*, *Pan troglodytes*, and *Homo sapiens*, formed the experimental cohort of the current study group. They were of particular interest for this study because they differed dramatically in talo-crural shape as adults despite being more comparable in shape as juveniles (Turley & Frost, 2014b). Furthermore, their adult talo-crural morphology differed based on substrate use: *Pan paniscus* had a flexible profile, *Pan troglodytes* a more stable profile comparable to terrestrial cercopithecoids, and *Homo sapiens* the greatest expression of a stable profile among catarrhines (Turley & Frost, 2014b).

These differences may reflect the strain forces manifest in adult ankles due to use, a behavioral response, or the genetic expression of ankle articular morphology resulting from natural selection or genetically controlled behavioral change. Shape change due to use is the physical manifestation of gravity, mass, positional repertoires and behavioral differences in activity, while the genetic expression is the result of development of the joint surfaces and programmed changes in activity altering shape. A behavioral genetic effect constitutes a shape change due to a genetically mediated alteration in activity (i.e.

Homo sapiens bipedal gait). These behavioral effects may have been selected for in response to environmental pressures and are uniform in expression across a species. They differ from behavioral differences expressed by individuals within a species in response to such pressures, or a “cultural,” extra genetic, tradition expressed by groups of individuals within a species to comparable pressures. Each may be manifest in specific alterations in the first singular warp profile of the talo-crural joint consistent with the strain forces applied. Thus, examination of the potential etiology of the shape profiles is critical for understanding the relationship of use to the differences and similarities observed.

A naturally occurring experimental design was provided by the three closely related taxa in which gene sequences and prior genetic studies are available (The Chimpanzee Sequencing and Analysis Consortium, 2005). These studies provide insights into the shape component of the study group, as well as the genetic relation of the subgroups. Likewise, the profound differences in the sample taxa habitat, with its potential to influence behavior and use, provided the potential to explore the environmental influence on these processes.

Habitat, the natural conditions and environment in which an organism lives, provides the milieu in which taxa develop, one of the stimuli for change, and the greatest challenges for survival if alterations in the eco-system occur. Biomes, their abiotic and biotic constituents characterize habitats, and these are intimately related to and are controlled by climate. Coding of these help to define their nature, however, topography, ground conditions, aquatic conditions, flora (canopy type, primary/secondary growth, height and distribution, and food availability and type), fauna (competition and predation pressure), and in the case of other taxa, human presence, all impact the nature of the habitat and the organisms behavioral response to its challenges.

An important additional component of habitat, which is critical to the study of speciation, is isolation. Allopatric speciation requires separation of populations. This may be dichopatric, due to new geographic barriers between two contiguous components of a parent population, or peripatric, involving a founder population beyond the range of the parental gene population. Both are “exceptionally vulnerable to extinction” and “exposed to the increased selective pressure of an entirely new biotic and abiotic environment” (Mayr, 2001). Isolation effects all three factors in the study, genetics by both mechanisms, habitat due to the environmental differences in flora and fauna altering access to nutrients and changes in predation, and behavior resulting in a unique response to change. All have been proposed as important factors in speciation events (Mayr, 2001).

These components, likewise, provide the context within which the genetic effects on joint morphology, behavioral genetic influences on shape, and the results of individual behavior (substrate use) can be examined.

Pan paniscus experienced a speciation event from Proto-pan (Prado-Martinez et al., 2013). Geological and genetic data suggest isolation from other Proto-pan by the Congo River in central Africa at ~3.5 MYA, and with divergence from *Pan troglodytes* at ~1.8 MYA (Myers Thompson, 2003; Prado-Martinez et al., 2013). The topography

of the river system provided a botanic center of endemism for the southern population, the Marungu Mountains, with The Lukuga Gorge and Lualaba River separating it from northern populations, while providing a refuge forest during times of forest contracture (Beadle, 1981; Myers Thompson, 2003). The Congo River, with its position on the equator and a constant flow from its headwaters in Lake Tanganyika, provided a reproductive barrier between the populations. With multiple tributaries of the Congo, periodic inundations and both high temperatures year round and high rainfall, it provides conditions for an extensive primary growth continuous canopy, which characterizes this portion of the Guineo-Congolian regional center of endemism (Figure 1). Critically, White (1992) has observed a 95% arboreal substrate preference among extant *Pan paniscus* in non-provisioned sites reflecting these conditions, consistent with the differences in shape observed in this study. Within these rainforests, fruits with high sugar content and a relatively continuous canopy provide access to food sources without the constraints of terrestrial foraging with its risks of predation (White, 1983). The population also differs in its behavior from *Pan troglodytes* with higher social status derived from the maternal status and decreased ground patrolling and hunting in the troop (White, 1996; Stumpf, 2007). The *Pan paniscus* population speciated within reproductive isolation but the current study suggests that a specific behavior, substrate use, may impact first singular warp oppositional articular shape with a flexible ankle profile in adults reflecting habitat use.

The second species, *Pan troglodytes*, isolated from the (Proto-) *Pan paniscus* by the Congo River, inhabit areas across west, central and eastern central Africa with a number of subpopulations suggested by genetic studies (Figure 1). Isolation of these groups is afforded by the dry Dahomey Gap (present for ~5000 Yrs but a recurring feature) which separates the Western from related Nigeria-Cameroon; the Sanaga River separating Nigeria-Cameroon from Central Cameroon with a south-central group possibly isolated by the Dja River, and Eastern inhabiting central and east Africa north of the Congo River (Gonder et al., 2006; Oates et al., 2009; Bowden et al., 2012). Genetic studies show population divergence times along the Sanaga River, a boundary between the Cross-Sanaga-Bioko coastal forests and the Atlantic Equatorial costal forest, at 0.9 MYA, with split times at 0.5 MYA of the Western and Nigeria-Cameroon and Central and Eastern subgroups (Gonder et al., 2011; Prado-Martinez et al., 2013). The subgroup population divergence times for both were 0.7 MYA with divergence times of 0.3 and 0.2 MYA respectively. Finally, Central and Eastern subgroups diverged from a south central group at 0.11 MYA. Their habitats lie mainly coastal within an Am climate (high temperatures year round and high rainfall, a rainforest climate with a dry season in a monsoon type cycle) or inland, with an Aw climate (high temperatures year round and high rainfall, with a dry season in the winter of the respective hemisphere) with savanna populations (Stumpf, 2007). The regions are included in the Guineo-Congolian regional center of endemism, Region I in White's Phytochoria classification and Region 10 Sub-region 65 Upper Guinean Forest and 66 Nigerian-Cameroon, in Takhtajan. Topography varied dramatically among the northern populations, and their sub-populations, with an

isolated wet, humid, tropical rainforest with continuous canopy and arboreal nutrient sources less frequent, but transitional zones with savanna conditions common (Jabbour, 2008; Strumpf, 2007). This is reflected in the ground conditions that also vary across regions and make terrestrial foraging, patrolling and hunting frequent (Strumpf, 2007). The phytochoria reflect a commonality of available nutrient sources, as does the faunal assemblage of small cercopithecoids (White, 1983; Strumpf, 2007). The interface of *Pan troglodytes* with terrestrial and arboreal predators is well documented in the literature, and although potentially vulnerable, these large bodied hominoids behavioral systems are effective in thwarting non-hominin predation (Campbell et al. 2007; Suzuki, 1969; Kano, 1971; McGraw et al., 1979; Zuberbuller & Jenney, 2002).

The sources and dates of acquisition of the osteological sample used in this investigation are given in Table 2. A component of the sample was acquired from Western and Eastern subgroups, as well as the northern Cameroon, Gabon, and six specimens from Ebolowa in the south of Cameroon collected by F.H. Hope in a 1929-30 expedition. The first singular warp appositional articular shape of these specimens reflect a stable profile. However, a component of the sample, all six collected from Djaposten (a former German administrative outpost situated on the north shore of the Dja River), two by W.S. Lehman in 1930 and four by unknown hunters in 1939, and 13 of 19 from Ebolowa (a town situated between the coastal and Dja regions) by H.F. Hope collected in 1929-1930, demonstrate differences in shape with a more flexible profile. Differences in talo-crural shape due to curation, preparation, and conservation techniques from this era were excluded by re-examination of the individual specimens. Furthermore, a sample of 42 *Gorilla gorilla* specimens from the same expeditions has uniform distribution of first singular warp scores (Turley & Frost, 2014a). Of note, all the specimens with a more flexible profile were collected prior to 1940 with only four procured subsequent to 1932 by unknown hunters. The French administration of Cameroon established the Dja Reserve in 1950, however, prior to this time in 1932 hunting was restricted in these areas. No specimens of this sample were collected during the Second World War, and there was displacement of the few farmers within the Dja river boundaries from the future reserve lands in 1946. Strict enforcement of regulations in the post-war period is possibly reflected in the F.H. Hope contributions in that year sorting with the more stable profile.

The Reserve was established in 1950 (UNESCO, 2013). The topography of the south central region reflects a Pre-Cambrian subsurface with a low plateau (544-851 meters) and fault system to the south. The Dja River almost completely encircles the 2030 square mile Reserve with 60-meter cliffs along the river to the south along a fault line and mountainous terrain to the southeast. The ground conditions include rivulets and swampy open areas of inundation called “rochers,” rocky outcropping with natural springs. The primary canopy is 30-40 meters, with regions 60 meters in height common, and almost pure stands of *Gilbertiodendron dewevrei* rich in lianes, that probably reflect the conditions of the south central area prior to the Reserves inception and commercial logging and agriculture in this relatively remote location (UNESCO, 2013). The climate

Table 2. Sources, locations and dates of acquisition of the *Pan troglodytes* sample.

<i>Pan troglodytes</i>	Collector	Year	Location
- <i>verus</i> (Western)	J. Sabater (2) Unknown (1) D.A. Schitter (1) J.W. Leduc (1)	1956 1932 1971 1969	2 Guinea 1 Sierra Leone 1 Liberia 1 Cote d'Ivoire
- <i>schweinfurthii</i> (Eastern)	H. Lang/J.P. Chapman (8) H.C. Craven (1)	1909 - 1914 1920	8 Zaire 1 Uganda
- <i>troglodytes</i> (Central)	K.A. Haberer (4) - C. Newbolt (1) F.H. Hope (6) M.C. Grisset (3) C.R. Aschemeier (2) F.H. Hope (4) – Unknown (1)	1912 - 1932 1929 & 1930 1923 & 1924 1917 & 1918 1946	5 Daoula 6 Ebolowa 3 Metet 2 Gabon 5 Cameroon
- <i>troglodytes</i> (Southern)	W.S. Lehman (2) – Unknown (4) F.H. Hope (13)	1930 - 1939 1929 & 1930	6 Djaposten 13 Ebolowa

is coded Am with extremes of both rainfall and humidity (Strahler & Strahler, 1992; White, 1983). Predation is limited to leopard (*Panthera pardus*), which studies have suggested hunt primates on the ground in daylight (Zuberbiller & Jenney, 2002). Decreased ground nesting is noted in the south central region in the Dja Reserve, with a total absence of ground nesting among the chimpanzees, despite the absence of intrusive human activities such as logging (Dupain et al., 2004; Last & Muh, 2013; Tagg et al., 2013). However, the Baka, Pygmy hunter-gatherers indigenous to this region of south central Cameroon remain in the Reserve practicing their traditional lifestyle. DNA studies of Western African human populations demonstrate a divergence of ancestral pygmies from non-pygmy groups at ~ 54,000 YBP, and divergence among pygmy populations at ~2800 YBP (Hewlett, 1996; Verdu et al., 2009). Genetic data for selection of HIV host susceptibility genes in the Baka from the Democratic Republic of the Congo suggest a ~20000 YBP presence in the West African region with the highest frequency of protective alleles among such sub-Sahara Africans (Keele et al., 2006; Zhao et al., 2012). These protective alleles among Pygmy populations, including the Baka, suggest a high copy number of CCL3L1 and ancestral CCR5 alleles providing resistance to immunodeficiency viruses (Zhao et al., 2012). It is proposed immunodeficiency viruses may have shaped the genomes of this population with a coalescence date for SIV strains in chimpanzees greater than 20,000 YBP and an extended human hunter-gatherer chimpanzee interface in at least the past 2800 years. The SIVcpz genome, the DNA of the chimpanzee virus source of HIV-1 group M, the main form of AIDS virus infecting humans, appears to be a recombinant of SIVrcm from red-capped mangabey (*Cercopithecus torquatus*) and SIVgsn from greater spot-nosed monkeys (*Cercopithecus nictans*) (Sharp & Hahn, 2010). Closely related viruses to SIVgsn, have hosts in the mustached guenon (*Cercopithecus cephus*), SIVmus, and the mona monkey (*Cercopithecus mona*), SIVmon, and

may have been involved in the recombinant event generating SIVc_{zp}. All species overlap their inhabited ranges with *Pan troglodytes* and are prey species. The genetic data suggests a close association of the hunter-gatherers and the south-central chimpanzees, and evidence for repeated body fluid contact suggesting predation by both humans on chimpanzees and chimpanzee populations on monkey viral reservoirs for thousands of years (Joiris, 1996; Sharp & Hahn, 2010). Thus, the potential for a human ground presence, for an extended period, documented by the location and genetic interaction of the species impacting chimpanzee behavior and influencing substrate use, can be proposed.

Finally, populations of *Homo sapiens* are found throughout the world's eco-systems. Our species provides a unique experimental platform to explore the effect of vastly different substrates and substrate modification in the form of footwear. Individuals from five habitats were included in the study group (Table 1). These sorted into three subgroups although from markedly different biomes (Strahler & Strahler, 1992). 20th Century New Yorkers first singular warp scores (from a humid subtropical Cfa or Cwa climate, with a Takhtajan 3 North American Region, 30 Atlantic and Gulf Coastal Plain phytocorium) clustered with the scores of 10th Century Paleo-Pueblo peoples from New Mexico (BWh dry arid hot climate, with a 3 Colorado Plateau 61 phytocorium). Paleo-Eskimos from Point Hope Alaska (ET tundra climate, phytocorium 1 Circumboreal Arctic) scores clustered with the scores of Byzantine Period inhabitants from the Nile River island of El Hesa (BWh/BSH with a dry arid climate moderated by the river, phytocorium 7 Sahara-Arabian Region, Egypt 48) (Figure 4). Finally, Shell Midden Native Americans (Cs Mediterranean climate with hot summers moderated by the Sacramento Delta and San Francisco Bay, phytocorium 9 Madrean Californian 62) separated from all other subgroups (Figure 4).

Differences in the population lifestyles, modes of subsistence and the substrates use may explain the sorting observed, as well as substrate interface modification in the form of footwear (Table 1). The Shell Midden people of the Sacramento Delta and environs of San Francisco Bay are California native peoples with a deep history and archaeological record (Breschini, 1983). Post-contact and the archaeological record suggests a hunter-gather lifestyle with dependence on aquatic resources of the coastal and delta environs. The sample included 13 well-documented specimens from Marin, Contra Costa, Santa Clara, San Francisco and San Joaquin. Dates of habitation differed from 2500 to 500 YBP. Likewise, the topography and ground conditions differed from inland, bay and sea-shore. All clustered at the most flexible pole of the first singular warp vector. However, within the group two specimens from the Early to Middle Period (2500 YBP) from San Joaquin were most flexible and the three from the Late Period (500 YBP), including two associated with "late" projectile points and post contact fragments were the most stable. The Shell Midden people were unshod (post-contact reports and archaeological record) allowing maximal flexibility in ankle function in their environment.

The Paleo-Eskimo specimens in the current study are from Point Hope, Alaska, and were excavated by Larsen and Rainey from 1939 to 1941 (Newton, 2002). Two compo-

nents of the burial site have been identified, with skeletal remains from the “Ipiutak”, now suggested to be the Norton culture, dated as early as 1500 YBP with 105 burial sites and 70 houses excavated, and “Tigara”, with more than 300 burial sites, and a long history of occupation post-dating 700 YBP (Dumond, 2014). The habitat of the former coincided with the Dark Ages Cold Period (1700-1200 YBP) and the latter the Little Ice Age (700-200YBP) on a snowy and permafrost peninsula jutting into the Arctic Ocean at 63°20’N. Post contact reports document subsistence on marine mammals, which archaeological evidence from the study periods confirms (Dumond, 2011; Dumond, 2014). Of the subgroups examined, the Point Hope sample was the only one where the sexes differed in shape. All males had a flexible profile while four of five females had a stable profile consistent with a cultural division of labor. This was observed in post-contact communities with women working in the permafrost terrestrial camp environs and male maritime hunting with a requirement of flexibility of movement even in cold conditions. The footwear used by both, sealskin boots, provided a common modality to alter the interface between ankle and substrate in this demanding environment.

El Hesa was an island in the Nile River near Aswan (24°5’), with soft powdery sand, fluvial fields from the yearly Nile inundation, and a maritime existence on an island community in the Nile. It has been submerged by the construction of the Aswan Dam; however, the specimens retrieved in 1907-1908 are dated to the Byzantine Period (1350-1600 YBP) (Schillaci et al., 2009; Francigny et al., 2014; Irish, 2014). Unshod, sandals or soft leather boots would represent the footwear for the challenges of the stability and flexibility requirements of the fishing, farming and commerce on the Nile. The El Hesa subset had one outlier, a female; with the first singular warp scores of the remainder clustering within a central region of the study group.

The most stable profiles were observed in the 20th Century New York and 10th Century Paleo-Pueblo specimens. Both sort to the negative pole of the first singular warp vector. Both inhabit environs dramatically impacted by their presence. The topography and ground conditions of the former are the asphalt and steel infrastructure of an industrial urban setting. The sample may, however, have reflected the diversity of such a population, with agrarian, maritime and urban backgrounds and the impact for migration. Change of the substrate interface was most likely achieved with footwear such as leather shoes or boots (AMNH Collection). The Paleo-Pueblo peoples of Canyon de Chelly constructed elaborate Cliff Dwellings in the deep canyons with entry ladders for security and defensive structures on the high mesas of the Four Corners region of the current United States (Plog, 1997). The topography and ground conditions reflected both the location and effect of human modification. Likewise, the substrate was modified by footwear, double layer woven yucca sandals unique to the region and the demands of its inhabitants (Kankainen, 1995).

The current study provides insights on the epigenetic influence of substrate use among and within closely related species. Recent studies suggest interaction-driven evolutionary divergence, as previously proposed in mutually negative interactions among

closely related species, may profoundly impact natural selection in isolated settings in observable time scales (Brown & Wilson, 1956; Pfennig & Pfennig, 2012; Stuart et al. 2014). These findings may relate to our findings, as well as the fossil record of the Plio-Pleistocene, which has been described as a mosaic of ankle morphology (Harcourt-Smith & Aiello, 2004). Phenotypic plasticity in shape resulting from substrate use may provide an explanation, within the context of interaction-driven evolutionary divergence, of the rapid variations observed in this fossil assemblage within a limited timeframe but one in which competitive cogeners were present and rapid variations in habitat occurred. Further examination of the Plio-Pleistocene fossil assemblage using this technique is warranted. Likewise, this method may provide a vehicle by which to dissect phenotypic plasticity, the epigenetic influence of substrate use derived by behavior observed in this study, from genetics differences, and provide insights into the influence of shape change due to use on Natural Selection.

ACKNOWLEDGEMENTS — Grant Sponsorship: NSF (BCS-0452538), (IIS-513660) and University of Oregon . We are grateful to Will Harcourt-Smith and Eric Delson of the Department of Vertebrate Paleontology, AMNH, for their assistance and for providing scans from the AMNH, as well as, Eileen Westwig and Gisselle Garcia, AMNH, Yohannes Haile-Selassie and Lyman Jellema, CMNH, Linda K. Gordon and Darrin P. Lunde, NMNH, Emmanuel Gilissen, RMCA, and Natasha Johnson and Paolo Pellegatti of the P.A. Hearst Museum, UC Berkeley, for access to their collections and documentation of provenience, and Tim White and Mike Black.

References

- Bastir, M., & Rosas, A. (2005). Hierarchical Nature of Morphological Integration and Modularity in the Human Posterior Face. *Amer. J. Phys. Anthropol.*, 128:26-34.
- Beadle, L.C. (1981). *The Inland Waters of Tropical Africa*. London: Longman.
- Bookstein, F.L. (1991). *Morphometric Tools for Landmark Data*. Cambridge: Cambridge University Press.
- Bookstein, F.L., Gunz, P., Mitteroecker, P., Prossinger, H., Schaefer, K., & Horst, S. (2003). Cranial Integration in *Homo*: Singular Warps Analysis of the Midsagittal Plane in Ontogeny and Evolution. *J. Hum. Evol.*, 44:167-187.
- Bowden, R., MacFie, T.S., Myers, S., Hellenthal, G., Nerrienet, G., Bontrop, R.E., Freeman, C., Donnelly, P., & Mundy, N.I. (2012). Genomic Tools for Evolution and Conservation in the Chimpanzee: *Pan troglodytes ellioti* is a Genetically Distinct Population. *PLoS Genetics*, 8:1-10, e1002504.
- Breschini, G.S. (1983). *Models of Population Movements in Central California Prehistory*. Ph.D. Dissertation, University of Washington, <http://www.californiaprehistory.com/reports01/rep0025>.
- Brown, W.L., & Wilson, E.O. (1956). Character Displacement. *Syst. Zool.*, 5:49-64.
- Brunet, M., Guy, F., Pilbeam, D., Mackaye, H.T., Likius, A., Ahounta, D., Beauvilain, A., Blondel, C., Bocherens, H., Boisserie, J-R., De Bonis, L., Coppens, Y., Dejax, J., Denys, C., Doring, P., Eisenmann, V., Fanone, G., Fronty, P., Geraads, D., Lehmann, T., Lihoreau, F., Louchart, A., Mahamat, A., Merceron, G., Mouchelin, G., Otero, O., Campomanes, P.P., Ponce de Leon, M., Rage, J-C., Sapanet, M., Schuster, M., Sudre, J., Tassy, P., Valentin, X., Vignaud, P., Viriot, L., Zazzo, A., & Zollikofer, C. (2002.) A New Hominid from the Upper Miocene of Chad, Central Africa. *Nature*, 418:145-152.

- Dumond, D.E. (2011). *Archaeology on the Alaskan Peninsula: The Northern Section, Fifty Years Onward*. University of Oregon Anthropological Papers 70. Eugene.
- Dumond, D.E. (2014). Personal Communication.
- Dupain, J., Guislain, P., Nguenang, G.M., De Vleeschouwer, K., & Van Elsacker, L. (2004). High Chimpanzee and Gorilla Densities in a Non-Protected Area on the Northern Periphery of the Dja Faunal Reserve, Cameroon. *Oryx*, 38:209-216.
- Fischer, A., Wiebe, V., Paabo, S., & Przeworski, M. (2004). Evidence for a Complex Demographic History of Chimpanzees. *Mol. Biol. Evol.*, 21:799-808.
- Fischer, A., Pollack, J., Thalmann, O., Nickel, B., & Paabo, S. (2006). Demographic History and Genetic Differentiation in Apes. *Curr. Biol.*, 16:1133-1138.
- Francigny, V., de Voogt, A., Kahn, J., & Harcourt-Smith, W.E.H. (2014). At the Border Between Egypt and Nubia: Skeletal Material from El Hesa Cemetery 2. *J. Ancient Egypt Interconnections*, 6: 5-10.
- Frost, S.R., Marcus, L.F., Bookstein, F.L., Reddy, D.P., & Delson, E. (2003). Cranial Allometry, Phylogeography, and Systematics of Large-Bodied Papionins (Primates: *Cercopithecinae*) Inferred from Morphometric Analysis of Landmark Data. *Anat. Rec. Part A*, 275A:1048-1072.
- Goldberg, T.L. & Ruvolo, M. (1997). The Geographic Apportionment of Mitochondrial Genetic Diversity in East African Chimpanzees, *Pan troglodytes schweinfurthii*. *Moll. Biol. Evol.*, 14:976-984.
- Gonder, M.K., Disotell, T.R., & Oates, J.F. (2006). New Genetic Evidence on the Evolution of Chimpanzee Populations and Implications for Taxonomy. *Int. J. Primatol.*, 27:1103-1127.
- Gonder, M.K., Locatelli, S., Ghobrial, L., Mitchell, M.W., Kujawski, J.T., Lankester, F.J., Stewart, C., & Tishkoff S.A. (2011). Evidence from Cameroon Reveals Differences in the Genetic Structure and Histories of Chimpanzee Populations. *PNAS*, 108: 4766-4771.
- Groves, C.P. (2001). *Primate Taxonomy*. Washington, DC: Smithsonian Institution. Vol. VIII. 350 p.
- Groves, C.P. (2005). Geographic Variation Within Eastern Chimpanzees. *Australas. Primatol.*, 17:19-46.
- Gunz, P., & Harvati, K. (2007). The Neanderthal “Chignon”: Variation, Integration and Homology. *J. Hum. Evol.*, 52:262-274.
- Harcourt-Smith, W.E.H., & Aiello, L.C. (2004). Fossils, Feet and the Evolution of Human Bipedal Locomotion. *J. Anat.*, 204: 403-416.
- Harcourt-Smith, W.E.H., Tallman, M., Frost, S.R., Wiley, D.F., Roklf, F.J., & Delson, E. (2008). Analysis of Selected Hominoid Joint Surfaces Using Laser Scanning and Geometric Morphometrics: A Preliminary Report. In E.J. Sargis and M. Dagosto (Eds.), *Mammalian Evolutionary Morphology: A Tribute to Fredrick S. Szalay* (pp. 373-383). Dordrecht: Springer.
- Haile-Selassie, Y. (2001). Late Miocene Hominids from the Middle Awash, Ethiopia. *Nature*, 412:178-181.
- Hewlett, B. (1996). Cultural Diversity Among African Pygmies. In S. Kent (Ed.), *Cultural Diversity Among Twentieth Century Foragers* (pp. 215-244). Cambridge: Cambridge University Press.
- Irish, J.D. (2014). Personal Communication.
- Jabbour, R.S. (2008). *Geographic Variation in the Forelimb and Hindlimb Skeletons of African Apes*. Ph.D. Thesis, The City University of New York. UMI, ProQuest LLC, Ann Arbor, MI.
- Joiris, D.V. (1996). A Comparative Approach to Hunting Rituals Among Baka Pygmies (Southeastern Cameroon). In S. Kent (Ed.), *Cultural Diversity Among Twentieth Century Foragers* (pp. 245-275). Cambridge: Cambridge University Press.
- Kankainen, K. (1995). *Treading in the Past: Sandals of the Anasazi*. Salt Lake City: University of Utah Press.
- Kano, T. (1971). Chimpanzees of Filabanga, Western Tanzania. *Primates*, 12:229-246.

- Keele, B.F., Van Heuverswyn, F., Li, Y., Bailes, E., Takehisa, J., Santiago, M.L., Bibollet-Ruche, F., Chen, Y., Wain, L.V., Liegeois, F., Loul, S., Ngole, E.M., Bienvenue, Y., Delaporte, E., Brookfield, J.F.Y., Sharp, P.M., Shaw, G.W., Peeters, M., & Hahn, B.H. (2006). Chimpanzee Reservoirs of Pandemic and Nonpandemic HIV-1. *Science*, 313:523-526.
- Last, C., & Muh, B. (2013). Effects of Human Presence on Chimpanzee Nest Location in the Lebialem-Mone Forest Landscape, Southwest Region, Cameroon. *Folia Primatol.*, 84:51-63.
- Mann, M.E., Zhang, Z., Hughes, M.K., Bradley, R.S., Miller, S.K., Rutherford, S., & Ni, F. (2008). Proxy-Based Reconstructions of Hemispheric and Global Surface Temperature Variations Over the Past Two Millennia. *PNAS*, 105: 13252-13257.
- Mayr, E. (2001). *What Evolution Is*. New York: Basic Books.
- McGrew, W., Baldwin, P.J., & Titin, C.E.G. (1979). Chimpanzees, Tools, and Termites: Cross-Cultural Comparisons of Senegal, Tanzania, and Rio Muni. *Man*, 14:185-214.
- McNulty, K.P. (2009). Computing Singular Warps from Procrustes Aligned Coordinates. *J. Hum. Evol.*, 57:191-194.
- Myers Thompson, J.A. (2003). A Model of the Biogeographical Journey from *Proto-Pan* to *Pan paniscus*. *Primates*, 44:191-197.
- Newton, J.I.M. (2002). *About Time: Chronological Variation as Seen in the Burial Features at Ipiutak, Point Hope*. Thesis, University of Alaska Fairbanks.
- Oates, J.F., Groves, C.P., & Jenkins, P.D. (2009). The Type Locality of *PAN troglodytes vellerosus* (Gray, 1862), and Implications for the Nomenclature of West African Chimpanzees. *Primates*, 50:78-80.
- Peel, M.C., Finlayson, B.L., & McMahon, T.A. (2007). Updated World Map of the Köppen-Geiger Climate Classification. *Hydrol. Earth Syst. Sci.*, 11: 1633-1644.
- Pfennig, D.W., & Pfennig, K.S. (2012). *Evolution's Wedge: Competition and the Origins of Diversity*. Berkeley and Los Angeles, California: University of California Press.
- Plog, S. (1997). *Ancient Peoples of the American Southwest*. London: Thames and Hudson Ltd.
- Prado-Martinez, J., Sudmant, P.H., Kidd, J.M., Li, H., Kelley, J.L., Lorente-Galdos, B., Veeramah, K.R., Woerner, A.E., O'Connor, T.D., Satpere, G., Cagan, A., Theunert, C., Casals, F., Laayouni, H., Munch, K., Hobolth, A., Halager, A.E., Malg, M., Hernandez-Rodriguez, J., Hernando-Herraez, I., Prufer, K., Pybus, M., Johnstone, L., Lachmann, M., & Alkan, C. (2013). Great Ape Genetic Diversity and Population History. *Nature*, 499:471-475.
- Rohlf, F.J., & Corti, M. (2000). Use of Two-Block Partial Least-Squares to Study Covariation of Shape. *Sys. Biol.*, 49(4):740-753.
- Rohlf, F.J., & Slice, D. (1990). Extensions of the Procrustes Method for the Optimal Superposition of Landmarks. *Sys. Zool.*, 39:40-59.
- SAS. (2006). SAS 9.1. Cary, NC: SAS Institute.
- Schillaci, M.A., Irish, J.D., & Wood, C.C.E. (2009). Further Analysis of the Population History of Ancient Egyptians. *Amer. J. Phys. Anthropol.*, 139:235-243.
- Senut, B., Pickford, M., Gommery, D., Mein, P., Cheboi, K., Coppens, Y. 2001. First Hominid from the Miocene (Lukeino Formation, Kenya). *C. R. Acad. Sci. Paris, Ser. Ila* 332:137-144.
- Sharp, P.M., & Hahn, B.H. (2014). The Evolution of HIV-1 and the Origin of AIDS. *Phil. Trans. R. Soc. B*, 365:2487-2494.
- Slice, D.E. (1998). *Morpheus et al. Ecology and Evolution*. Stony Brook: State University of New York.
- Slice, D.E. (2001). Landmark Coordinates Aligned by Procrustes Analysis Do Not Lie In Kendall's Shape Space. *Syst. Zool.*, 50: 141-149.
- Strahler, A.H., & Strahler, A.N. (1992). *Modern Physical Geography*. New York: John Wiley & Sons, Inc.

- Strumpf, R. (2007). Chimpanzees and Bonobos. In C.J. Campbell, A. Fuentes, K.C. Mackinnon, M. Panger and S.K. Bearder (Eds.), *Primates in Perspective*. Oxford, UK: Oxford University Press.
- Stuart, Y.E., Campbell, T.S., Hohenlohe, P.A., Reynolds, R.G., Revell, L.J., & Losos, J.B. (2014). Rapid Evolution of a Native Species Following Invasion by a Congener. *Science*, 346(6208):463-466.
- Suzuki, A. (1969). An Ecological Study of Chimpanzees in a Savanna Woodland. *Primates*, 10:103-148.
- Tagg, N., Willie, J., Petre, C., & Haggis, O. (2013). Ground Night Nesting in Chimpanzees: New Insights from Central Chimpanzees (*Pan troglodytes troglodytes*) in South-East Cameroon. *Folio Primatol.*, 84:362-383.
- The Chimpanzee Sequencing and Analysis Consortium. (2005). Initial Sequence of the Chimpanzee Genome and Comparison with the Human Genome. *Nature*, 437:69-87.
- Turley, K., Henderson, E.H., & Frost, S.R. (2011). Geometric Morphometric Analysis of Tibial Shape and Presentation among Catarrhine Taxa. *Anat. Rec.*, 294: 217-230.
- Turley, K., & Frost, S.R. (2013). Shape and Presentation of the Talus: A Geometric Morphometric Analysis. *Anat. Rec.*, 296: 877-890.
- Turley, K., & Frost, S.R. (2014a). The Appositional Morphology of the Talo-Crural Joint: The Influence of Substrate Use on Joint Shape. *Anat. Rec.*, 297: 618-629.
- Turley, K., & Frost, S.R. (2014b). The Ontogeny of Talo-Crural Appositional; Articular Shape Among Catarrhine Taxa: Adult Shape Reflects Substrate Use. *Amer. J. Phys. Anthropol.*, 154:447-458.
- UNESCO (2013). Dja Faunal Reserve Cameroon. <http://whc.unesco.org/list/407>.
- Verdu, P., Austerlitz, F., Estoup, A., Vitalis, R., Georges, M., Thery, S., Froment, A., Le Bomin, S., Gessain, A., Hombert, J., Van der Veen, L., Quintana-Murci, L., Bahuchet, S., & Heyer E. (2009). Origins and Genetic Diversity of Pygmy Hunter-Gatherers of Western Central Africa. *Current Biology*, 19:312-318.
- White, F. (1983). *The Vegetation of Africa*. Paris: UNESCO.
- White, F.J. (1992). Pygmy Chimpanzee Social Organization: Variation in Party Size and Between Study Sites. *Amer. J. Primatol.*, 26:203-214.
- White, F.J. (1996). Comparative Socio-Ecology of *Pan paniscus*. In W.C. McGrew, L.F. Marchant, & T. Nishida (Eds.), *Great Apes Societies*. Cambridge: Cambridge University Press.
- Wiley, D.F. (2006). Landmark Editor. University of California, Davis. wiley@ucdavis.edu.
- Zhao, K., Ishida, Y., Oleksyk, T.K., Winkler, C.A., & Roca, A.L. (2012). Evidence for Selection A HIV Host Susceptibility Genes in a Human West Central African Human Population. *Evol. Biol.*, 12:237, <http://www.biomedcentral.com/1471-2148/12/237>.
- Zuberbuller, K., & Jenny D. (2002). Leopard Predation and Primate Evolution. *J. Hum. Evol.*, 43: 873-886.

