Statement of the aims and objectives of the project

I am seeking sabbatical leave for academic year 2015-2016 to conduct research into the evolution of the human upper limb. This is my first sabbatical application. My proposed research will involve analysis of the *humerus* (arm bone) of apes and humans to test hypotheses regarding *species identification* and *upper limb function* in our early ancestors. The three major goals of this research are noted below. Although presented separately, these goals are interrelated and are not meant to be addressed in isolation from one another.

1) *To assess the extent to which fossil species can be recognized based on humeral anatomy*. Subsequent to human origins about 5-7 Mya (million years ago), it was typical for multiple species of hominins[1] to coexist in Africa at any given time (until about 1 Mya). The existence of multiple contemporary species presents a challenge for identification of postcranial[2] material, especially as fossil species are invariably defined on the basis of skull anatomy. Many fossil limb bones are not associated with cranial material and are consequently left unidentified (other than being recognized as hominin). In general, these potentially informative specimens receive little attention, especially if incomplete.

2) *To test hypotheses regarding upper limb use in fossil hominins*. Previous studies of hominin postcranial evolution tend to focus on *lower limb* function. Meanwhile, we still know relatively little about the evolution of the human *upper limb* (especially the shoulder and elbow joints). Various aspects of hand anatomy have been linked to early hominin activities such as habitual tree-climbing and the ability to manufacture stone tools. To what extent these tasks (and other potential uses of the upper limb) are reflected in the design of the humerus is unknown, despite the fact that the humerus is one of the most abundant postcranial elements in the hominin fossil record.

3) *To establish a comparative context for interpreting a new fossil upper limb*. During a recent field season at the site of Ileret (Kenya), a team of international researchers (Ileret Research Team) recovered the fossilized remains of a hominin right upper limb (designated KNM-ER 47000). The individual to which this upper limb belonged died about 1.5 Mya along the shore of an ancient stream. This specimen has not yet been identified to species nor described in publication. Owing to my established expertise in primate postcranial anatomy and my previous research record, I was asked by expedition leader Dr. Brian Richmond (*Curator of Anthropology, American Museum of Natural History*, NY) to lead all research pertaining to the KNM-ER 47000 partial humerus. Substantial progress related to the first two goals is necessary to provide sufficient context for the interpretation of ER 47000.

Background work already accomplished

My entire research career has been geared toward fostering a greater understanding of the evolution of the hominin postcranial skeleton. Much of my previous research has addressed the effects of body mass on skeletal shape among primates, and several papers deal specifically with humeri (see CV). Most recently, I published a paper in the *Journal of Human Evolution* (October, 2014) that explores whether or not specimen size should be taken into account when comparing elbow shape between fossil and modern humans. My research has been funded by major grants, published in the top peer-reviewed journals of my field, and presented at professional meetings.

Thanks to previous NSF funding, my colleagues and I have collected 3D laser scans of over one thousand modern primate bones and fossil hominin postcranial specimens. This vast collection of skeletal specimens from around the world took years to complete and provides me with a "virtual museum" for collecting data now and well into the future. When dealing with fossils, it is also extremely useful to observe and manipulate physical (as opposed to only virtual) representations. During my time at Stockton, I have purchased several research-quality casts of fossil humeri from museums in both South Africa and Kenya. In addition, the recent acquisition of a 3D printer at Stockton gives me the opportunity to print high-resolution replicas of any specimen for which I have a scan. In short, given my expertise in

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[1] The term "hominin" applies to modern humans and all extinct species more closely related to modern humans than to chimpanzees.

[2] The term "postcranial" refers to any bone within the skeleton that is not part of the skull (which is "cranial").

anatomy and evolution, my previous research record, and my unprecedented instant access to hundreds of skeletal specimens, I am uniquely qualified to undertake the research project described herein.

Statement of the procedures/methodology

The majority of my sabbatical time will involve data collection, multivariate statistical analysis, and preparation and submission of manuscripts for publication (see *Outcome* section). Extant taxa to be studied include modern humans and nonhuman hominoids (chimpanzees, gorillas, orangutans, gibbons). These taxa will provide a comparative context for analyzing almost three dozen fossil specimens from across Africa, representing over three million years of human evolution. Although this research will require months of computer-based data collection, virtually all of the specimens are already available to me in the form of 3D surface scans. Hence, no travel to museums is required, other than to collect additional scans of small-bodied humans available at The Natural History Museum in London.

Three-dimensional coordinate landmarks will be quantified on the scans using freely available software (*Landmark Editor*) designed for accurately placing landmark points on complex surfaces. This software can also be used to collect traditional linear measurements (e.g., bone length) as needed. I intend to collect data in stages from three different functionally relevant regions of the humerus. The initial stage (#1) will cover aspects of elbow joint anatomy not considered in my most recent publication (Lague, 2014). Additional stages of data collection (#2, #3) will target cross-sectional shape of the humeral shaft in two different regions.[3] For each set of data, raw coordinates will be exported to additional software (*PAST*, *tpsRelw*) for landmark-based statistical shape analysis. Analyses will include techniques for visualization of shape variation (e.g., geometric morphometrics, principal components analysis), as well as algorithms for statistically testing hypotheses regarding group membership (e.g., Mantel matrix correlation tests).

It is worth noting that previous researchers have largely ignored fossil specimens lacking joint surfaces, resulting in the exclusion of a large number of more fragmentary specimens. Modern technology now facilitates the analysis of aspects of limb anatomy that were previously difficult to measure. Analysis of cross-sectional morphology, in particular, will allow me to incorporate far more fossil hominin postcranial specimens than are typically analyzed in a single research project.

Based on my recent familiarity with all of the methodology described above, it is not possible to collect all of the data, analyze it, and submit resulting papers to journals in the short time provided by a one-semester sabbatical. A single semester will not provide adequate time to fully address my broader goals, or interpret the ER 47000 humerus within the timeframe required by the Ileret Research Team. (Our plan is to submit an initial announcement paper for ER 47000 by next spring, followed by several more detailed analyses to be presented in a special issue of the *Journal of Human Evolution*). The proposed sabbatical will "jump-start" many years of future research by allowing me to focus all of my professional time on a labor-intensive project that would otherwise require multiple years to complete. The momentum gained by completing the proposed project in a shorter time span will facilitate subsequent related research. My projected timeline is as follows:

SUMMER 2015. Collect scans at NMH (London). Collect and analyze data set #1. Submit Paper #1.
FALL 2015. Collect and analyze data set #2. Submit Paper #2. Present select results at annual meeting of *Mid-Atlantic Bioanthropology Interest Group;* date TBA).
SPRING 2016. Collect and analyze data set #3. Contribute to ER 47000 announcement paper. Present select results at annual meeting of *American Association of Physical Anthropologists* (Atlanta, GA; April 11-16, 2016).
SUMMER 2016. Submit Paper #3. Prepare and submit paper on ER 47000 humerus for special issue of the *Journal of Human Evolution.*

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[3] Stage #2: a horizontal section through an anatomical feature called the *olecranon fossa* that will be useful for assessing elbow function; Stage #3: a horizontal section just proximal to the olecranon fossa that will be useful for assessing how force is distributed through the humeral shaft.

Importance or value

This study will facilitate taxonomic identification of isolated skeletal remains, and will foster a greater understanding of habitual forelimb use in extinct hominins. The existence of many unidentified postcranial specimens confounds our attempts to gain a full understanding of human prehistory. This project represents an initial step in solving the postcranial puzzle that has long vexed biological anthropologists. The ER 47000 specimen, for example, holds the promise of serving as a "Rosetta Stone" of early hominin upper limb morphology, as it represents a rare case in which multiple fossil limb elements are known from a single individual. Functional analysis of the upper limb in apes and humans has the potential to reveal information regarding the behavior of our ancestors (e.g., propensity for climbing trees, manufacture and use of tools). The humerus, in particular, is often the only preserved aspect of upper limb anatomy available for reconstructing forelimb function in a given fossil individual.

This project will promote my research through presentations and publications, including co-authored papers with international colleagues. It will bolster professional ties with current colleagues, and potentially open up new opportunities for collaboration with other biological anthropologists, benefitting both me and my future undergraduate research students. This research will also enhance my teaching in courses such as introductory biology (BIOL 1400) and *Human Evolution* (BIOL 3240), where I use my own research to illustrate key concepts.

Further research or study

The morphometric data collected for this project will be useful for years to come, both in my own professional research and that involving undergraduates. The results will undoubtedly generate new questions and hypotheses for future testing. I will eventually incorporate forearm bones (radius, ulna) to more fully investigate the elbow joint as a functional complex. I will also incorporate data from various monkey species to provide a broader functional context for interpreting upper limb function. Little to no funding is necessary for the additional bones/species noted above, since I already have scans of these specimens. Eventually, however, I hope to parlay the successful completion of this work into future external funding (e.g., NSF, Leakey Foundation) that will support the collection of scans of fossil ape specimens housed in Africa and Europe.

Outcome

This research will generate tangible outcomes related to my previous NSF grant (for collecting bone scans). I intend to submit a series of related papers to peer-reviewed scientific journals (e.g., *Journal of Human Evolution, American Journal of Physical Anthropology*) based on the results for the different regions of humeral anatomy described above. One of these papers will be co-authored by John Rowan, a former Stockton undergraduate (and current ASU graduate student) who helped initiate a pilot project related to data set #2 when he was my research student. I will also present the results of the sabbatical project at annual professional meetings (e.g., *American Association of Physical Anthropology, Mid-Atlantic Bioanthropology Interest Group*) for the next several years.

The broader research presented in the above papers and presentations will provide a context for interpreting the new ER 47000 upper limb from Ileret, Kenya. I will collaborate with international colleagues on the Ileret Research Team to prepare and submit an initial announcement paper about the ER 47000 upper limb to the journal *Science*. Subsequently, I will contribute (as lead author) a paper that focuses specifically on the ER 47000 humerus; this paper will be part of an upcoming special issue of the *Journal of Human Evolution* devoted entirely to the research taking place at Ileret. (Our proposal for a special issue has already been accepted by *JHE* editor Mark Teaford).

Over the course of my sabbatical, I will also be printing replicas of many fossil specimens that will subsequently be available for both research and teaching. Given the hundreds of fossil scans in my possession and the recent availability of a 3D printer, I hope to provide Stockton with one of the most prolific collections of fossil hominin postcranial specimens outside of a major museum.