Anatomical Network Analysis: Introducing to the AAA and the anatomical community a powerful new method to quantify musculoskeletal modularity, integration, complexity and evolvability*

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1. PROPOSAL ABSTRACT
Defining the mechanisms of development, function, and evolution in a comprehensive, body-wide sense has been a persistent challenge for anatomists. For instance, how do various anatomical parts (modules) of the vertebrate body develop and evolve cohesively (integration) without risking the individual's survival? This question is vital not only for basic science but also for contemporary cross-disciplinary work that weaves together anatomical insights from biological anthropology, human evolution, developmental biology, and medical applications. Answering this question will require overcoming technical obstacles to measuring and integrating vast amounts of anatomical data from different body parts, tissue types, and taxa. We need a novel powerful, quantitative, accessible approach to investigate and compare anatomical integration and modularity. Anatomical Network Analysis (AnNA) offers a full conceptual framework and methodology to explore broad, ambitious questions about anatomical modularity, integration, complexity and evolvability towards clarifying the macroevolutionary, developmental and medical implications of anatomical variation and birth defects. AnNA is uniquely suited to meet this challenge because it codes connectivity patterns (e.g. bone-bone, bone-muscle, muscle-muscle contacts) as the nodes and links of network models by using tools and statistics borrowed from network theory, which, surprisingly, has not been explored in the field of anatomy. AnNA is powerful because, unlike other methods used to study integration/modularity, it enables direct comparisons between different tissue types and body parts with vastly different architectures (e.g. head/limbs), and between and among both closely and distantly related animal groups. This project will generate exceptional new insights by teaching AAA members and the anatomical community in general how to apply AnNA to their research. By promoting the use - by anatomists and scientists in general - of an innovative technique with a high potential impact for biological and biomedical research, AAA will reinforce its place as the main source for information about the field of anatomy. Through AnNA, anatomy is cross-linked with other fields (e.g. theoretical biology, mathematics, bioinformatics, biomedicine) to open fresh avenues of investigation that will have a high impact on research within these fields and areas such as evolutionary and developmental biology and medicine.

2. SPECIFIC AIMS
1. Develop and host a user-friendly website for AAA members that provides all the necessary resources to intuitively learn and appropriately apply AnNA.
   • Aim 1.A. Develop website
   • Aim 1.B. Host website

2. Perform a case study on primate head and limbs to showcase the value of AnNA and demonstrate the method using real data, including some preliminary data already obtained.
   • Aim 2.A. Pilot study in members of each major primate group
   • Aim 2.B. Pilot study in key human fossil taxa through detailed muscle reconstructions
   • Aim 2.C. Pilot study in normal vs. abnormal (e.g. trisomy 13, 18 and 21) development in humans

3. Disseminate AnNA via a symposium and a workshop at the AAA 2017 meeting (EB 2017), and via webinars for AAA members.
   • Aim 3.A. AAA Symposium
   • Aim 3.B. AAA Workshop
   • Aim 3.C. Webinar for AAA members

4. Disseminate the project's results to specialists and to the media and broader public.
   • Aim 4.A. Dissemination to specialists
   • Aim 4.B. Dissemination to media and broader public

5. Assessment of success, including tracking traffic of flow of website and of use/impact of AnNA for AAA members.
   • Aim 5.A. Tracking the traffic flow of the website
   • Aim 5.B. Tracking use and impact of AnNA within AAA members
3. SIGNIFICANCE
A long-standing challenge to anatomists has been to define the mechanisms by which anatomy develops, functions and evolves in a comprehensive, body-wide sense. For instance, how do various anatomical parts (modules) of the vertebrate body evolve into distinct integrated forms (integration) without risking the individual’s survival? Specifically, what transformations occurred in primate evolution to allow the head and limb morphology of modern humans to carry out complex functions such as breathing, speaking, chewing, swallowing, walking, running, and using tools, while also remaining evolvable (i.e. able to adapt/change to respond to selective pressures) (Lieberman 2011)? These questions are vital not only to basic science but also crucial for contemporary cross-disciplinary work that weaves together anatomical insights from biological anthropology, human evolution, developmental biology, and medical applications.

To address these questions, two concepts are paramount: modularity and integration (e.g. Marroig & Cheverud 2001, 2005; Goswami 2007; Marroig et al. 2009; Porto et al. 2009, 2013; Santana & Lofgren 2013). Ever since Bateson’s (1894) and Olson & Miller’s (1958) seminal works on these concepts, the idea of an animal’s body as a set of nested parts within parts (modularity) that maintain a level of autonomy to change while still growing and adapting in coordinated ways (integration) continues to gain support as a central mechanism of evolution (e.g. Muller 2007; Wagner & Zhang 2011). These concepts are tightly linked to questions about complexity and evolvability: modularity enables flexibility because the direction and magnitude of evolutionary change among and within parts can vary without sacrificing function (e.g. Moss & Salentijn 1969; Atchley & Hall 1991; Raff 1996; Monteiro et al. 2005; Rasskin-Gutman 2005; Wagner et al. 2001; Zelditch et al. 2008; Corneet et al. 2013). These concepts are particularly crucial to our understanding of the evolution and modern anatomy of humans (e.g. Hallgrimsson et al. 2002, 2007, 2009; Young & Hallgrimsson 2005; Lieberman et al. 2008; Rolian 2009; Young et al. 2010; Lewton 2012). For instance, the evolution of the human (Hominini) lineage is notable among primates for the magnitude of morphological shifts in the musculoskeletal system, in particular the pervasive changes in the limbs, trunk and skull associated with the evolution of bipedalism, but also more specific changes in the skull in contexts such as the reduction of facial prognathism in Homo or the evolution of the ‘robust’ skulls of Paranthropus robustus and P. boisei (e.g. Lieberman 2011).

Despite increasing interest in modularity and integration in the human musculoskeletal system from scientists - anatomists in particular - and the broader public in general, questions about the patterns and mechanisms of human evolution remain mainly unanswered. These questions have been the subject of numerous papers and books, but various researchers have differing views about how to answer them (see e.g. Ross 2013 review of Lieberman 2011). In fact, as stressed by Ross (2013), most comparative anatomical works refer to concepts such as “module” and “integration” without defining them or clearly explaining how to quantitatively study them. One of the major reasons why our knowledge of morphological modularity, integration, complexity and evolvability in the human musculoskeletal system remains limited is the difficulty of studying the myriad interactions among the body’s hard and soft-tissues. In reality, in no small part due to the challenge of managing and making sense of complex datasets, most studies on human/primate modularity and integration focus on the head, and specifically on its hard tissues (cranial bones and teeth; e.g. Cheverud 1982; Marroig & Cheverud 2001; Ackermann 2002, 2005; Bastir & Rosas 2005; Mitteroecker & Bookstein 2008). Only a few studies have investigated modularity and integration of the limbs, and they have exclusively focused on the skeleton (e.g. Young et al. 2010; Rolian et al. 2010) and are mainly concerned with quantitative skeletal traits (e.g. bone length, skull width). However, functional and morphological changes in human evolution also involved the reorganization and evolution of traits that are not amenable to these types of measurements (e.g. presence/absence of muscles, bones and articulations; Lieberman 2011).

For all of these reasons, there is currently a huge gap in our understanding of the evolution and function of the human musculoskeletal system as a whole. New studies, methods and techniques are thus needed to identify and compare patterns of organization, integration, modularity, evolvability and complexity of the muscles and skeleton of the head and limbs to gain a more comprehensive and integrative view of the evolutionary history of the human body. We need to overcome persistent technical obstacles to measure and make sense of vast amounts of anatomical data from not only different body parts but also dissimilar tissue types such as muscle and bone in diverse taxa. We can now offer to the AAA members and to the greater anatomical community a novel powerful, quantitative, accessible network approach to investigate and compare anatomical integration and modularity.

4. INNOVATIONS
Anatomical Network Analysis (AnNA) offers a full conceptual framework and operative methodology to explore broader and more ambitious questions about anatomical modularity, integration, complexity and evolvability (Rasskin-Gutman & Esteve-Altava 2014) and drill further down into the macroevolutionary, developmental and medical implications of anatomical evolution, variation and birth defects (Esteve-Altava et al. 2015a, 2015b). AnNA is primed to succeed here because of its level of abstraction and its focus on structural relations among body parts; it codes connectivity patterns (e.g. bone-bone, bone-muscle contacts) as the nodes and links of a network models and uses algorithms adapted from network theory to analyze morphological organization. AnNA is a powerful innovative tool because, unlike other methods used to study integration/modularity, its level of abstraction enables direct comparisons between different tissues and body parts with vastly different architectures (e.g. head/limbs),
between and among both closely and distantly related animal groups. Quantifying and comparing very different structures and taxa makes possible a deeper understanding of their anatomical, developmental and evolutionary changes (more details are given below).

4.1. Pilot data obtained for this project, to be included in AAA Website

We recently incorporated muscle data from the human head into AnNA to obtain preliminary data to test whether our network methodology can be successfully expanded and used by us and by others to study musculoskeletal connectivity. This preliminary data will be included in the AAA website that will result from this project, together with the data we will obtain from the case study described below. Our results confirmed that AnNA is particularly effective at unveiling muscle and musculoskeletal modules that were not previously described in the anatomical literature (Esteve-Altava et al. 2015b). For instance, AnNA revealed that the human head muscle network comprises 136 skeletal muscles sparsely connected at 78 contact points (fiber fusions and well-defined tendons) and includes 21 smaller blocks of two to four muscles each and three major modules: a single ocular/upper face module plus left and right orofacial modules (Fig. 1). It is remarkable that the three largest muscle modules are composed exclusively of facial expression muscles, because these muscles have undergone more evolutionary change (e.g. in shape, number and attachments) than any other muscles in human evolution (Diogo & Wood 2012), likely because they are crucial to our particular abilities for verbal and visual communication as noted above. Within the context of the results obtained for our AnNA preliminary data, we specifically tested the hypothesis that these three muscle modules are developmental complexes that integrate muscles with similar ontogenetic origins. Our results contradicted this hypothesis: each module is instead a functional complex integrating muscles with different phylogenetic and developmental origins. Importantly, our results bring new insight to help resolve the debate on the symmetry/asymmetry of facial expression in humans. Functional, anatomical and medical studies have shown that asymmetrical use (contraction) of facial muscles in humans is crucial to make complex facial expressions, but is less prominent in the upper face than in the mid-face and lower face (e.g. Schmidt et al. 2006; Ahn et al. 2013). The discovery of a single ocular/upper face module and of left and right orofacial (mid/ lower face) modules by AnNA thus places these functional, medical and anatomical observations in a novel quantitative context and contributes to the understanding of our ability to asymmetrically contract or relax the facial muscles of the mid/ lower face in particular (i.e. left and right sides are not as interconnected in orofacial region as they are in upper face), and thus to produce more complex facial expressions.

To test the utility of AnNA for researchers working on non-human animals and thus for a broader fraction of the anatomical community as a whole, we also included cranial data from various non-human primates into our AnNA. Specifically, we tested whether the skeletal differences that exist between extant primates can be successfully recovered using AnNA and whether the data obtained by using our approach can be effectively used to address topics such as the evolution of the human face. Our results showed that AnNA is a particularly powerful tool to study primate and human morphological evolution (Esteve-Altava et al. 2015a). For instance, we specifically tested a) the hypothesis that the neurocranial region is, in general, more complex than the facial region in primates; and b) the burden-rank hypothesis that more complex networks (i.e. with higher connectivity between the individual structures forming them) are evolutionary more conserved (i.e. less evolvable) than less complex ones (supposedly due to the amount of developmental and/or functional co-dependences at stake). Our results supported both hypotheses: in primates there is a “neurocranial connectivity module” that is highly conserved and complex, while facial bones group more variably into less complex facial connectivity modules (Fig. 2); and modularity and complexity showed a significant inverse correlation. AnNA can thus be used to successfully analyze primate/human modularity, integration, complexity and evolvability and rigorously quantify the specific correlations between all these parameters, providing data that cannot be obtained by other methods.

4.2. Using data obtained from previous work and from case study in website as showcase of innovation potential

Taking into account these preliminary data and the insights and fascinating questions they raise, in the proposed project we will use our successful methods to undertake a case-study where we will use in-depth AnNA of the structures of the head (including the hyoid bone and laryngeal cartilages) and limbs of the extant primate taxa studied in Esteve-Altava (2015a), and incorporate skull data from fossil Hominini. The pilot data and the new data
from this case study will be uploaded onto the AnNA website, allowing us and other AAA members and other researchers to address crucial anatomical issues with implications for basic science - including understanding our own evolution - and medicine. The combined pilot data, and the subsequent use of AnNA by AAA members and other researchers will lead to a more comprehensive knowledge about the human body and its musculoskeletal modularity and integration and thus about the global functioning of its various structures. Therefore, this project will lead to exceptional new insights by teaching AAA members and the anatomical community in general how to apply AnNA to their research, including cross-linking anatomy with other fields (e.g. theoretical biology, mathematics, bioinformatics, biomedicine) to open fresh avenues of investigation that will have a high impact on research within these fields and areas such as evolutionary and developmental biology.

5. APPROACH

5.1. Website. We will work closely together with professional Web Developers, and IT specialist, consultants, a member of the AAA administration, and a project manager (see Section 8.2 for more details).

5.1.1. Develop website. The website will consist of: A) Textual and visual information, including videos, interactive multimedia and a wiki explaining AnNA step-by-step; B) Downloads containing scripts in the free programming environment R plus sample datasets; C) Applications containing case studies - the most detailed one being our proposed study on primate head and limbs (see below); and D) A forum for discussions, including addressing questions, solving problems, and informing AAA members of updated and synergetic AnNA projects and tools, which will be complemented by a Twitter account (hash tag #AnNA). We will host our website - which will be directly linked to the AAA website - through an online web-hosting service (Bluehost). This will also allow us to have 24/7 service and security for the site. The database will be set-up through Bluehost and all downloadable documents for the website will be stored on multiple PCs at the Diogo lab and at the Boughner lab. The FTP site, Cyberduck, will allow quick editing and upload of new material on a regular basis for the site. Maintenance will be conducted regularly to ensure material is constantly updated and all features of the website are fully functional. All papers on AnNA published in open-access journals will also be available to download from our website.

5.1.2. Host website. The website will be hosted through Bluehost; the cost of hosting and maintenance for 4 years (3-year project + one additional year) is included in the budget section. All AAA members will have full access to our website, and the website and the AAA website will have direct links to each other. Integration between our AnNA website and the AAA website will be achieved through consulting with the AAA staff and web developers to make our AnNA site easily accessible through the AAA homepage, and we will provide updated content for the AnNA site to social media outlets for the AAA to bring in new interest to our site and to AAA. On the one hand, following AAA’s strategic goal of having AAA the premier source for information about anatomy for anatomists, the general public will have access to some components of the website, such as the wiki and videos explaining AnNA, downloadable papers on AnNA, one script and one sample dataset. That is, the AnNA website will be a separate website in the sense that users can login and access these components without having to login into the AAA website. However, on the other hand, following AAA’s strategic plan of attracting scientists to AAA and maximize member engagement, only AAA members will enjoy the full breadth of the resources we have to offer (e.g. interactive media, all datasets/scripts, all case studies, and the discussion forum), using a special login link on our AnNA website homepage for members to login with their AAA username and password to access these special components. This way, non-AAA members will be “given a taste” of AnNA, and will know they can only fully explore the website by becoming AAA members. Furthermore, as all users (i.e., AAA members and non-AAA members) will need to provide their contact information when they create an account in the AnNA website before they can login to access its general components, the contact information of all non-AAA members that signed up to the website will be shared with AAA for potential recruitment of non-AAA members. A member of AAA’s administration will be invited to join the monthly 2h-skype meeting of AnNA website’s team (see Section 5.6) as a consultant to ensure that all pieces of information/components that are planned to be included by the team in the AnNA website after each meeting fit within AAA’s liability rules/strategic goals. An explicit mention that the AnNA website was created through AAA funds - and thus that AAA has to be acknowledged in any papers/other outcomes that will be derived from using the AnNA website or the materials provided in the AAA workshops and webinars organized by us - will be displayed in AnNA's homepage and in all introductory guidelines provided to users in the website, workshops and webinars.

5.2. Brief description of AnNA methods

In order to explain the originality, power, and diverse applications of AnNA to AAA members and to anatomists and other researchers in general, and thus to allow a better understanding of the content of our AnNA website, we will provide here a brief description of the AnNA methods. Due to lack of space, and because these methods are described in detail by Esteve et al. (2015), we will only briefly summarize their major points by using the case study that will be done for this project as a practical example. AnNA is the study of the connectivity patterns that define the morphological organization of anatomy using tools and statistics borrowed from network theory. For this specific case study, we will code the absence (0) or presence (1) of contact among anatomical elements (bones and muscles) using adjacency matrices in Excel. One matrix will be completed for each of the three body regions (head and fore- and hindlimb) of each primate taxon included in Esteve-Altava (2015a). With the data compiled in the matrices we will build three types of anatomical network models: 1) skeletal, with bones and their contacts; 2)
muscular, with muscles and their contacts; 3) musculoskeletal, with bones, muscles and their contacts. Network modeling and modularity/phylogenetic analyses will be done using the R packages igraph and ape respectively.

To assess modularity using AnNA, we define a connectivity module as a group of anatomical elements with more connections among them than to any other elements. We will identify the number and composition of connectivity modules using a hierarchical cluster analysis of the pair-wise bone similarity, which is quantified as the topological overlap (TO) between each pair of elements. Regarding the assessment of integration within modules, a system with modules is free to change in many directions, so (structural) intra-module integration is measured using the network modularity Q-value: a quality index that quantifies how well a potential partition groups the nodes of the network compared to other possible partitions; if the number of connections among nodes in the same module is not higher than expected at random then Q = 0, otherwise Q > 0: the higher the Q, the better the partition. We will quantify the strength of modularity (S) in skull networks as the product of the number of modules and Q. We will then quantify the network complexity of an anatomical structure or system (e.g. entire head, or limb module) using three network parameters - density (D), clustering (C), and heterogeneity of connections (H) - that capture diverse qualities of complex morphological structures. D measures the compactness of the structure/system as the number of existing node-node connections with respect to the total maximum possible: D = 2KN(N−1), where K and N are the number of links and nodes respectively. C measures the redundancy of interactions among anatomical parts as the average of triangular loops among the network nodes: C = 1/N · Σ(τ(τ, k−1)). H measures the disparity or diversity of the number of connections among anatomical parts as the ratio between the variance and the mean of connectivity: H = σ/μ, where σ is the variance of the number of connections of all network nodes and μ is the mean of the number of connections. Finally, morphological evolvability refers to the capacity of the phenotype to vary in evolution, for instance through its modular organization; thus, the strength of the modular organization of an anatomical system determines its capacity for further evolutionary change. AnNA posits a straightforward measure of the strength of modularity using the parameter S: the product of the number of modules and the partition quality. The higher the S of an anatomical system, the higher its evolvability. This measure facilitates a quantitative comparison of evolvability between different structures, body regions, and tissues. The use of specific network parameters to quantify complexity and evolvability in AnNA allows us to make precise predictions and test hypotheses concerning human evolution and the function, modularity and integration of the human head within a rigorous phylogenetic and quantitative comparative context.

5.3. Case study

The case study is crucial to enhance the educational value of the project, showcase the value of AnNA and increase interest in the method, and demonstrate the method to AAA members and other researchers using real data. After publication of the results, we will post our raw data in the website to show to AAA members how AnNA is applied to real datasets, step by step. Because many of the required data have already been collected, the case study will consume a relatively small proportion of the time and budget. Specifically, we will include and complete the data obtained in our pilot studies (see Section 4) to perform the first quantitative, comprehensive analysis of the links between integration, modularity, complexity and evolvability in primate evolution by using AnNA to compare network connectivity patterns for both the skeleton and muscles of the head and upper and lower limbs. By also including data on human abnormal development, we will be able to investigate the value of AnNA in understanding congenital malformations from a broader anatomical and evolutionary perspective, and to illustrate the medical implications and applications of AnNA. Esteve-Altava and students under supervision of Diogo will drive the AnNA for this case study, and the case study will include:

5.3.1. Members of each major primate group. As explained in Section 4, we have already used AnNA to study the integration/modularity of the musculoskeletal structures of the human head (Esteve-Altava et al. 2015b), and of the skull of key primate taxa representing all the major extant primate groups (Esteve-Altava et al. 2015a). We will now use our proven methods, experience, and know-how in the proposed project to expand our AnNA to human limb musculature data and head and limb muscle data for all the other primate taxa included in Esteve-Altava’s 2015a study to further investigate these and other crucial anatomical and evolutionary questions. For instance, is the division into left and right orofacial muscle modules unique to humans (thus being potentially related to the more complex/greater number of human facial expressions), or does it have a deeper evolutionary origin?

Table 1. Fossil skulls that will be studied. BW, B. Wood (GWU, DC); JC, J. Clark (NMNH, DC); BV, B. Villmoare (UNLV).

<table>
<thead>
<tr>
<th>Species</th>
<th>Specimens</th>
<th>Materials</th>
<th>Permits</th>
</tr>
</thead>
<tbody>
<tr>
<td>Au. afarensis</td>
<td>AL 444-2, AL 822-1</td>
<td>CT scans, casts, photos, 3D images</td>
<td>BW, BV, JC</td>
</tr>
<tr>
<td>Au. africanaus</td>
<td>S6s 5, 52, 71</td>
<td>CT scans, casts, photos, 3D images</td>
<td>JC, BV</td>
</tr>
<tr>
<td>Au. sediba</td>
<td>MH1</td>
<td>CT scans, casts, photos, 3D images</td>
<td>JC, BV</td>
</tr>
<tr>
<td>H. erectus</td>
<td>D2282, 3444, 2700, KNM-ER 3733, Sangiran 17</td>
<td>CT scans, casts, photos, 3D images</td>
<td>JC, BV</td>
</tr>
<tr>
<td>H. floresiensis</td>
<td>KNM-ER 1470, KNM-ER 1813</td>
<td>CT scans, casts, photos, 3D images</td>
<td>BW, BV, JC</td>
</tr>
<tr>
<td>H. neanderthalensis</td>
<td>Gibraltar 1, Spy 1</td>
<td>CT scans, casts, photos, 3D images</td>
<td>JC, BV</td>
</tr>
<tr>
<td>H. floresiensis</td>
<td>LB1</td>
<td>Casts, photos, 3D images</td>
<td>JC</td>
</tr>
<tr>
<td>P. boisei</td>
<td>KNM-ER 406, KNM-ER 732, OH-5</td>
<td>CT scans, casts, photos, 3D images</td>
<td>BW, JC, BV</td>
</tr>
<tr>
<td>P. robustus</td>
<td>KMN-WT 17000</td>
<td>CT scans, casts, photos, 3D images</td>
<td>JC, BV</td>
</tr>
</tbody>
</table>
During this project, Diogo will complete the matrix sections for the limb muscles of humans and for the head and limb muscles of all 20 taxa included in Esteve-Altava (2015a) using the data previously compiled by him and his colleagues (based on dissection of hundreds of specimens and an extensive literature review); so the total sample sizes per taxon are sufficient to determine the normal muscle phenotype for each taxon (see Biosketch). That is, this project does not require further muscle dissections. Regarding the absence/presence of bones and bone-bone connections, our pilot analyses have already provided data for the cranium of the 20 taxa, using our direct observations of actual skulls and literature review. We will use the same approach to fill the limb skeletal matrices, using the literature and postcranial skeletal materials - Boughner and Molnar will collect data for the limb skeleton of all 20 taxa, including at the AMNH (support letter already obtained; see also Budget).

5.3.2. Key human fossil taxa through detailed muscle reconstructions. The general procedure to undertake AnNA of fossils is the same used for extant taxa: in our pilot studies AnNa was successfully applied to extinct tetrapod species using high-resolution images of fossil materials and literature descriptions (e.g. Esteve-Altava et al. 2013). Using this proven methodology we will undertake AnNA of the skulls of the Homini taxon shown in Table 1. Esteve-Altava will populate the matrices for these taxa under Diogo’s supervision using data that will be collected by Molnar from direct observations of high-quality NMNH/GWU skull casts, UNLV CT data, and online/literature data (Table 1).

5.3.3. Normal vs. abnormal (e.g. trisomy 13, 18 and 21) development in humans. The general procedure to undertake AnNA of karyotypically abnormal human individuals is the same used for karyotypically normal individuals. Diogo will complete the matrix sections for the limb and head muscles of fetuses and neonates with trisomy 13, 18 and 21 using the data previously compiled by him, Smith and colleagues. These data are based on dissection of dozens of fetuses and neonates and an extensive literature review, and were already published by Smith et al. (2015), so this project does not require further muscle dissections of human individuals. Using AnNA to study the musculoskeletal modularity and integration of the head and limbs of trisomic human fetuses and neonates and compare them with those of normal newborns and adults will allow us a glimpse into the morphological integration patterns resulting from a perturbed genetic condition causing severe phenotypic malformations. In particular, the present case study will provide new data to discuss broader developmental and evolutionary hypotheses and to better understand the links between normal and abnormal development, morphological diversity and anatomical variations and defects, and modularity, integration and evolvability.

5.4. Engaging the AAA community

5.4.1. AAA Symposium. In the morning symposium - chaired by Diogo, Boughner and Esteve-Altava - we will demonstrate AnNA’s broad reach by introducing its theoretical foundation and practical applications by presenting the latest AnNA research on vertebrate, primate and human anatomy, the modular network organization of the human body, and their medical implications. We plan to include 9 talks (30 min + questions); most speakers have been already contacted and agreed to participate: 1) D. Rasskin-Gutman: From Geoffroy Saint-Hilaire to AnNa: connectivity as the missing link in vertebrate morphology; 2) R. Diogo: AnNA of the head/limbs of model non-tetrapod organisms: implications for macroevolution and medicine; 3) V. Abdala: AnNA as a tool to explore the vertebrate musculoskeletal system as a tensegrity structure; 4) B. Esteve-Altava: AnNA of the limbs/fins of early tetrapod fossil and close relatives: implications for limb evolution and water-land transition; 5) J.C. Boughner: AnNA of the head in wild type vs. mutants of mouse models: implications for developmental biology; 6) B. Villmoare: AnNA of primate head: implications for human evolution and biological anthropology; 7) C. Rolian: AnNA of primate limbs: implications for human evolution and biological anthropology; 8) C. Smith: AnNA of head/limbs in normal vs. abnormal human development: implications for medicine; 9) M. Gondre-Lewis: AnNA of brain in normal vs. abnormal human development: implications for developmental biology and medicine.

5.4.2. AAA Workshop. In the afternoon workshop Diogo and Esteve-Altava will train participants in AnNA, including teaching them about free resources, including our website, to perform AnNA. The workshop will consist of an introductory lecture (30m), a hands-on computer session (2h), and a roundtable discussion to collect feedback from the participants and greater AAA community (1h). The introduction will also emphasize the applications of AnNA in diverse areas, including comparative anatomy, biological anthropology and human evolution, evo-devo, and medicine, by providing selected examples from our own recently published and preliminary data. In the hands-on computer sessions the participants will learn how to build and analyze their own morphological network models. A real-time workflow display will help any attendee without personal computer to follow the hands-on computer sessions. The general discussion and round table will consist of analysis/discussion of the data obtained in the workshop, future directions and applications of the data, and feedback and suggestions from participants about how AnNa can provide new venues of research and in teaching within anatomical and related fields.

5.4.3. Webinars for AAA members. Using standard software such as Go To Meeting, we will produce and lead six interactive webinars to teach the theory and practice of AnNA to AAA members across the globe. Each 120m webinar will 1) be visual (i.e. slides) and auditory (i.e. instructors/participants will be able to listen and speak) and will begin with a talk by Diogo, Boughner and Esteve-Altava with scheduled breaks to solicit feedback and questions, concluding with a period of questions and discussion; 2) be recorded and hosted on our AnNA website - which will be linked to the AAA website, see above - so that AAA members can freely watch and download the lesson podcasts. We will include a transcript of the lesson for members who are hearing impaired, and a translation in Spanish to reach a broad audience in the Latino community in the US and abroad (i.e. Spain and Latin America).
5.5. Disseminate the project's results to AAA, to specialists, and to the media and broader public

5.5.1. Dissemination to specialists. The results will be disseminated through our website and publications (including AAA's Anatomical Records and Anatomical Sciences Education), thereby helping to advance AAA's reputation as a premier source of innovative anatomical research and communication. We will produce one or more technical publications explaining our methods and the results of our case study to scientists who wish to use AnNA on their datasets. In the interests of reproducibility and education, we will provide open access under CC-BY license to all data and protocols using the web and other public repositories when needed (e.g. via Figshare). Green/Gold open access publications, for which we will use additional external funds where necessary, will be sought to increase the accessibility and overall impact of the research. All publications will include high-quality explanatory diagrams and illustrations to reinforce the concepts behind AnNA, appeal to the media, and broaden the publication's audience. Smith and Molnar are professional medical illustrators with experience in depicting AnNA results.

5.5.2. Dissemination to media and broader public. The topic of this proposal appeals broadly to the anatomical, scientific and medical community and the lay public, so we will also use Twitter (hashtag #AnNA) and a Facebook page for the broader public focusing mainly on topics directly related to human evolution and medicine. We will produce one or more short, non-technical articles or blog posts explaining the idea behind AnNA in a way that will be accessible to interested laypersons. The article(s) and Facebook page will include additional explanatory illustrations and photographs. We will capitalize on this project's broad appeal for public engagement and outreach activities by using various media (e.g. Howard Univ.'s and Saskatchewan's TV and radio stations, AAA interviews, and the web, including blogs of each of the personnel involved in this project).

5.6. Assessment of success

In order to prevent/resolve potential problems, Diogo, Molnar, Smith and Esteve-Altava (all at Diogo's lab) will be involved in all phases of the project and will meet weekly to carefully evaluate results and contemplate the next steps. In addition, they will all meet regularly online by Skype (a 2h meeting, each month) during the 3-year project with Boughner to discuss the project's results and progress. All five members of the team will meet physically at least once in each of the three years of the project at AAA meetings. They will have an intensive 3-day meeting after the last day of each AAA meeting, in which each team member will share his/her results, comments and questions with the other five members. Diogo will produce a detailed report to assess the team's successful progress with the proposed schedule (Section 6), and will use it as the basis for his report to the AAA. Because the team members will be presenting, from year 1, the results of their pilot studies and new analyses for this project in the AAA meetings, and likely in other meetings such as those of the AAPA (Am. Assoc. Phys. Anthropol.) and SICB (Soc. Integr. & Comp. Biol.) societies, and submitting their results to peer-reviewed journals, they will also receive direct feedback from their peers. Thus, this type of peer review will also be used to gauge the impact of AnNA and its applications to the proposed project specifically, but also for the research field generally. By the end of year 1, in April 2016 - when we will disseminate the first results by participating and conduct the workshop and symposium at AAA 2016, and when the website will already be partly functional - evaluation by our peers will begin in a fully dynamic way. Therefore, at all phases of the project there will be a careful, ongoing and informed evaluation of the project components and progress. Furthermore, we will assess success by: 1) number of individuals who use our dataset, methods and/or results using the detailed metrics available for each website hosted by Bluehost (number of views per specific page, of downloads, etc.), as one of the project's major goals is to provide students and researchers with a meaningful and useful dataset and tools that can be applied to research questions within the field of Anatomy as well as across other disciplines; and 2) level of dissemination to and feedback from the scientific community and general public measured, for example, by the number of times our data are accessed online, used and cited, and the number of solicitations we receive to present our results and their broader implications in scientific institutions, publications and meetings as well as in the media/press. As a quantifiable, precisely measure of assessment, we will:

5.6.1. Track the traffic flow of the website. As explained above, we will use the detailed metrics available for each website hosted by Bluehost (number of views per specific page, of downloads, etc.) to monitorize the number of times our data are accessed in, and downloaded from, our AnNA website. We will also analyze the reach of the website around the anatomical and scientific community around the globe by mining the specific number and locations of users via website hits and downloads, available at Bluehost.

5.6.2. Track use and impact of AnNA within AAA members and the scientific community. We will track and quantify interest, application and impact of AnNA by mining the number of citations of and media references about our proposed case study using traditional (e.g. citations, h-index, PubMed, Google Scholar) and non-traditional metrics (e.g. altmetrics). We will also conduct a qualitative survey, ideally using AAA survey templates but otherwise a tool such as Survey Monkey, to parse out what anatomists and AAA members value most about AnNA, and how they have applied AnNA to research as well as education, and what improvements and future directions they would suggest. Maintaining a user e-mail list and an active AAA/AnNA forum will also help us to engage and converse with AnNA adopters, including requesting these AAA members to post summaries of their publications/other outcomes in the website's forum. While we can envision how AnNA is applicable to an array of anatomical research questions and animal model systems, we are most excited by how the AAA community will newly interpret and use AnNA to address scientific questions and instructional challenges. These insights will be valuable to help identify and serve the interests and needs of AAA members.
6. OVERALL SCHEDULE

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<tr>
<th>Deliverables</th>
<th>2016</th>
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<th>2018</th>
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<td>Analysis &amp; Sharing</td>
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<tr>
<td>Monitoring success</td>
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<td>AAA Reports</td>
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7. REFERENCES CITED


8. BUDGET AND BUDGET JUSTIFICATION

8.1. Budget summary. Funds to build and maintain the website during the 3-year project and for one additional year (total of 4 years) ($37,000), computer equipment for hosting the website ($4,500), travel for research for case study ($7,000), and organization/logistics for the symposium, workshop, and webinars ($1,500).

8.2. Budget Justification.
- Creation of the AAA-AnNA website: Total $37,000. This cost includes:
  1) A one-time start-up fee for creating the website and interactive media hosted on the website ($25,000), which will include $5,000 for an IT specialist that will work on server procurement, database infrastructure, and bandwidth; as the plan is to integrate the AnNA website with the new AAA website, web designers/informaticians that had previous experience with AAA’s website development will be solicited for developing the AnNA website.
2) Maintenance of changes to the server and website ($1,500/year for 3-year project + 1 additional year, so $6,000 total).

3) In addition, a project manager ($2,000/year for 3-year project, so $6,000 for three years) will supervise the AnNA website (e.g., mailing, work on repositories, and so on) and its integration with the AAA website by working closely, with the member of AAA’s administration that will be invited to be a consultant to ensure that all pieces of information/components that are planned to be included by the team in the AnNA website after each meeting they fit within AAA’s liability rules and strategic goals (see Section 5.1).

- **Purchase of computer, monitor and three 1 TB external hard drives** to develop the AnNA website, and to store all materials included in it as well as the data obtained during the research project (e.g. images, network matrices) and to undertake the network analyses for this project and prepare the AAA workshop and symposium: **Total: 4,500.**

- **Travel for Research:** During year 1, Molnar and Boughner will travel for three weeks to the American Museum of Natural History (AMNH) to directly observe cranial and limb bones of some of the 21 extant taxa included in the project, in order to complete the network matrices for the limbs skeleton of the non-primate taxa, and for the head/limb skeleton of the key human fossil taxa, included in the project. *Per diem* expenses including lodging of c. $160, so for total of 21 days, total will be c. $3360, plus c. $240 for plane tickets DC-NY-DC, the total cost will be c. $3500 for each person). **Total = 2X$3,500 = $7,000.**

- **Organization and logistics of workshop, symposium and webinars: $1,500.** If the proposal for an AAA 2017 seminar and workshop is accepted and/or the awarding of this AAA innovation proposal is coordinated with AAA 2017 organizers so the symposium/workshop are hosted at AAA, then no additional costs (other than the usual AAA funds for symposia organizers) would be needed to cover the trips of the organizers to AAA. Funds are thus only being requested here to cover the organization of materials to be used/displayed at the symposium and workshop (e.g. software, paper copies, handouts, multimedia). Funds are also requested to then organize and cover the necessary logistics for the six webinars for AAA members, during the remaining period of the three-year project (November 2016, 2017, 2018; March 2017, 2018, 2019).

**Total budget: $37,000 + $4,500 + $7,000 + $1,500 = $50,000.**

9. **BIOSKETCH OF PI**

**Expertise as related to the proposed research.** I will bring to this project my 17 years of expertise in vertebrate muscle developmental, comparative and evolutionary anatomy. I have studied the gross anatomy, development and/or regeneration of the skeletal muscles of hundreds of specimens from each major vertebrate clade. Of particular importance for this project, I have dissected several individuals of each major primate extant clade, and studied in detail (and published several papers, monographs, and photographic and descriptive atlases about) the comparative anatomy, evolution and homologies of the skeletal and muscular elements of the head and limbs of primates. In addition, I have published several papers and books focused on the broader evolutionary questions that will be addressed in the present project, e.g. about morphological evolution, modularity, integration, and the spatial and developmental correlations between hard and soft tissues, as well as about macroevolution and human evolution. Also of particular importance for this project, I have also ample experience in leading and/or managing major projects - including several grant projects - with numerous collaborators and postdoctoral researchers and PhD, Master, Medical, Dental and undergraduate students, as in disseminating the results obtained in these projects, trough websites, interviews for TV shows and TV news channels, for newspapers and blogs and other media, articles in National Geographic, entries in Wikipedia, covers of major scientific journals (e.g. Biol. Rev., J. Exp. Zool., Belg. J. Zool.), talks as plenary/invited speaker in numerous international meetings, and the publication of several books, book chapters, and papers in the most renowned journals (e.g. Nature, PLOS Biol, Biol Rev.), among others.

**(a) Professional Preparation**

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<thead>
<tr>
<th>Degree</th>
<th>Institution</th>
<th>Years</th>
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<tbody>
<tr>
<td>B.A.</td>
<td>Univ. Aveiro, Portugal (Biology)</td>
<td>1993-1998</td>
</tr>
<tr>
<td>Ph.D.</td>
<td>Univ. Liege, Belgium (Evolutionary Biology)</td>
<td>1998-2003</td>
</tr>
<tr>
<td>Post-doctoral research</td>
<td>National Mus. Nat. Sciences, Spain (Comparative anatomy)</td>
<td>2003-2006</td>
</tr>
<tr>
<td>Post-doctoral research</td>
<td>King’s College, UK (Developmental Biology)</td>
<td>2005-2006</td>
</tr>
<tr>
<td>M.A.</td>
<td>George Washington Univ., US (Hominid Paleobiology)</td>
<td>2006-2010</td>
</tr>
</tbody>
</table>

**(b) Appointments**

2015 to present, **Associate Professor**, Howard Univ. College of Medicine, Dep. Anatomy

2011 to 2015, **Assistant Professor**, Howard Univ. College of Medicine, Dep. Anatomy
2009 to 2011, **Professional Lecturer, Biological Anthropology**, GWU, Dep. Anthropology
2008 to 2009, **Graduate-Teaching-Assistant, Biological Anthropology**, GWU, Dep. Anthropology
2007 to 2008, **Graduate-Teaching-Assistant, Gross Anatomy**, GWU, Dep. Anatomy
2007, **Internship**, National Geographic, Washington DC

(c) **Products - Publications most closely related to project**


**ii. Other significant publications (selected from 25 book chapters, 12 books and 125 papers)**


(d) **Synergistic activities**

1) 2010 to present: **Divulgation of Science** in numerous TV shows (e.g. Spanish “Castilla y Leon 7”) and newspapers and in *National Geographic* (Science divulgation reports/articles)

2) 2010 to present: Consortium Member of "**Timetree Project"** - website + book (www.timetree.org).

3) 2010 to present: Member of "**American Association of Anatomists**" and "**Pan-American Society for Evolutionary Developmental Biology**".


5) 2011 to present: **Co-administrator of Morphobank.org’s project P705**, titled "Soft-tissue anatomy of the primates: phylogenetic analyses based on the muscles of the head, neck, pectoral region and upper limb, with notes on the evolution of these muscles": http://www.morphobank.org

(e) **Grants**

**Current grants**

- 1 August 2015-31 July 2016: "A multidisciplinary network analysis of musculoskeletal complexity, integration, modularity and evolvability of the primate head and limbs (Federal Award ID number 1516557)". **NSF (BIO ANTH). DIOGO'S ROLE: PI** (B. Villmoare Co-PI; C. Rolian, J. Boughner, D. Rasskin-Gutman collaborators). Total Amount **$80,159**

- 15 September 2014-31 August 2017: "Collaborative research: Skeletal muscle constraint on relative brain size (Federal Award ID number 1440624)". **NSF (BIO ANTH). ROLE: PI**. Collaborative/multi PI research grant in collaboration with M. Muchlinks and A. Hartstone-Rose. Total Amount **$243,936** (Howard Amount: $18,724).
- 1 September 2013-31 August 2016: "Development of large-scale dense scene capture and tracking instrument (Federal Award number 1337722)'. NSF - MRI (Major Research Instrumentation Proposal). ROLE: COLLABORATOR (PI: J. Hahn, GWU). Total Amount: $714,000 ($500,000 from NSF + $214,000 from GWU).
- "MARIE SKŁODOWSKA-CURIE EUROPEAN COMMUNITY" Postdoctoral Grant for Borja Esteve-Altava to do a postdoc at Diogo's lab (Howard Univ. -2 years) and at Hutchinson's lab (Royal Veterinary College, UK - 1 year). ROLE: CO-PI (John Hutchinson PI) (Summer 2015-Summer 2018). Network Analysis of Musculoskeletal Evolution and Modularity During the Fin to Limb Transition. $285,530 (251,857 euros); $181,109 (160,130 euros) for HU.
- "PNPD/CAPES 2015 MINISTRY OF EDUCATION BRAZIL" Postdoctoral Grant for Gaelle Bello to do a postdoc at Tiana's Kohlshdorf's lab (Sao Paulo Univ. - 20 months) and at Diogo's lab (Howard Univ. - 2 months). ROLE: CO-PI (Tiana Kohlshdorf PI) (Summer 2015-Summer 2017). An Integrative Analysis of the Evolutionary Changes of the Number of Digits in Tetrapod Vertebrates: Mechanisms and Consequences of hard and Soft Tissue Alterations. $150,000.
- "09-05-2014 PU" grant from the Pontifical Xavierian University (Bogota, Colombia) to support Julio Hoyos' (PI) and Javier Maldonado-Ocampo's (Colombian co-PI) and Rui Diogo's (International co-PI) study on the phylogeny and evolution of the Sternoptygidae family of electric fishes (Gymnotiformes) based on both hard and soft tissues (October 2014-September 2017). $20000.

Past grants
- "CPF/MF: 777.562.661-53" grant from the Federal Republic of Brazil (CNPq - Conselho Nacional de Desenvolvimento Científico e Tecnológico) to support Tiana Kohlshdorf's (PI) and Rui Diogo's and Virginia Abdala's (co-PIs) study of the evolutionary changes (both of hard and soft tissues) associated with limb reduction in lizards (September-December 2011). $ 2421 (= R$4000 in Brazil).

(f) Collaborations & Other Affiliations
Collaborators and Co-Editors: Alexandre Perez-Perez, Univ. Barcelona (Spain); Anne Burrows, Duquesne University (US); Ashraf Aziz, Howard University (US); Bernard Wood, George Washington University (US); Brian Richmond, George Washington University (US); Bridget Waller, Univ. Portsmouth (UK); Christopher Bonar, Dallas World Aquarium (US); Claudia Munoz, Univ. Barcelona (Spain); Elly Tanaka, Max Planck Institute (Germany). Eric Parmentier, Univ. Liege (Belgium); Eva Ferrero, Universidad de Valladolid (Spain); Felix de la Paz, Universidad de Valladolid (Spain); Francisco Pastor, Universidad de Valladolid (Spain); Gaele Bello-Hellegouarch, Univ. Barcelona (Spain); Henry Evard, Max Planck Institute for Biological Cybernetics (Germany); Ignacio Doadrio, Museo de Ciencias Naturales (Spain); Karen Sears, Univ. Illinois (US); Katja Liebal, Max Planc (Germany); Jaye Sedlmayr, Louisiana State University (US); Josh Snodgrass, Univ. Oregon (US); Lisa Nevell, Univ. Utah (US); Luke Matthews, Harvard University; Luis Boto, Museo Nacional de Ciencias Naturales (Spain); Josep Potau, Univ. Barcelona (Spain); Juan Daza, Fundacion Miguel Lillo of Tucuman (Argentina). Julia Arias-Martorell, Univ. Barcelona (Spain); Magdalena Muchlinski, Univ. Kentucky (US); Mercedes Barbosa, Universidad de Valladolid (Spain); Michael Kern, George Washington University (US); Michel Chardon, Univ. Liege (Belgium); Miguel Monzo, Univ. Barcelona (Spain); Miriam Ashley-Ross, Northern Arizona University; Nadia Francys, Howard University (US); Nicole Theodosiou, Union College (US); Peter Johnston, Univ. Auckland (New Zealand). Pierre Lemelin, Univ. Alberta (Canada); Pierre Vandewalle, Univ. Liege (Belgium); Rebecca Fisher, The Univ. Arizona (US); Sharlene Santana, UCLA (US); Shunping Peng, Chinese Academy of Sciences (China). Simon Hughes, King's College (UK); Tales Aversi-Ferreira, Univ. Toyama (Japan); Tiana Kohlshdorf, Universidade de Sao Paulo (Brazil); Virginia Fundacion Miguel Lillo of Tucuman (Argentina).

Thesis Advisor (5) and Undergraduate (12) and Postgraduate-Scholar (8 masters, 9 postdocs) Sponsor: 1999-2000 Claudia Oliveira, Univ. Liege (Master); 2000-2001 Benjamín Michel, Univ. Liege (Master); 2011 Eva Ferrero, Howard Univ. (Post-Doc); 2011 Gaelle Bello, Univ. Barcelona (PhD); 2011 Michael Kern, GWU (Master); 2011 Nadia Francis, Howard Univ. (Master); 2012-2013 Naina Bathia, Howard Univ. (Post-Doc); 2012-2014 Janine Ziermann, Howard Univ. (Post-Doc); 2012-2013 Behrouz Beheshtin, Howard Univ. (Undergraduate); 2012-2013 Juliette Augustin, Howard Univ. (Undergraduate); 2012-present Mayowa Abegboyega, Howard Univ. (Undergraduate); 2012-present Sean Walsh, Howard Univ. (Undergraduate); 2013_Valerie Fair, Howard Univ.
(Undergraduate); 2013 Lucia Gratao, Univ. Tocains (PhD); 2013 Tales Aversi-Ferreira, Univ. Tocains (Post-Doc); 2013 Guillerme Nascimento, Univ. Tocains (Post-Doc); 2013 Raqueline Aversi-Ferreira, Univ. Tocains (PhD research); 2013 Eddie Bauer, Howard Univ. (Master); 2013-present Bianca Wilson, Howard Univ. (Master); 2013-present Christopher Smith, Johns Hopkins Univ. (Master); 2013 Melaina Glanton, Howard Univ. (Undergraduate); 2013-present Janelle Eradiri, Howard Univ. (Undergraduate); 2013-present Edidioangabasi Okon, Howard Univ. (Undergraduate); 2013-present Lorraine Kabert, Howard Univ. (Undergraduate); 2013-present Kristie Grimes-Mallard, Howard Univ. (Undergraduate); 2013-present Taffal Nour-Eddin, Howard Univ. (Undergraduate); 2013-present De Aris Emerson-Greenidge, Howard Univ. (Undergraduate); 2013-present Veronica Amajoyi, Howard Univ. (Undergraduate); 2013-present Taina de Abreu, Univ. Tocains (Undergraduate); 2013-present Ediana Vasconcelos da Silva, Univ. Tocains (Undergraduate); 2013-present Angela Vinhal Ferreira, Univ. Tocains (Undergraduate); 2014-2015 Malak Alghamdi, Howard Univ. (Master); 2014-2015 Aamina Malik, Howard Univ. (Master); 2015-present Malak Alghamdi, Howard Univ. (PhD); 2014-present Christopher Smith, Howard Univ. (PhD); 2014-present Jeffrey Robinson, Howard Univ. (Post-Doc); 2015-present Borja Esteve-Altava, Howard Univ. (Post-Doc); 2015-present Julia Molnar, Howard Univ. (Post-Doc).