The Evolution of the Primate Shoulder: Assessing Constraint and Evolvability

A Dissertation Presented for the
Doctor of Philosophy
Degree
The University of Tennessee, Knoxville

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December 2019

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DEDICATION

For my grandmothers, Thelma Inez Hill and Laura Simonetti-Arroyo de Agosto, who were unable to receive more than an eighth-grade education, and could only dream of the educational opportunities I have had.

For my mom, Deborah Agosto, who instilled a love of learning in me at an early age and continually encourages me to pursue my interests.

For my dad, Daniel Agosto-Simonetti, who taught me the value of hard work and perseverance. You helped make me the person I am today, and I am grateful you were able to see me finish.

You are deeply missed.

ACKNOWLEDGEMENTS

Completing a doctorate degree is not a solo venture, and there are many people I would like thank for their help and guidance along the way. First and foremost, I would like to thank my committee for their advice and assistance throughout this dissertation. Thanks to Brian O'Meara for his help in understanding phylogenetic comparative methods, and guidance for approaching an analysis on the scale I needed for this project. Graciela Cabana has provided valuable feedback on not only this dissertation, but numerous grant applications. Her unique perspective has helped me think about my research in various ways, and improved how I present my work – I will always be grateful for that. Thank you to Charles Roseman, who has provided invaluable insight on quantitative genetics, the esoteric intricacies of the math and theory behind them, and how to best implement these methods to address my research. I appreciate how he would challenge me to think about my research at a level I didn't realize was possible, and offer support throughout this process.

I would especially like to express my deepest gratitude to Ben Auerbach, who has provided unending guidance and support during my time at the University of Tennessee. I will always consider having Ben as my advisor one of the best decisions I made in Tennessee, and I am thankful he was willing to take me on as a student. The journey of this project from 'yeah, I don't see it…' to the finished dissertation has been one of the most challenging and incredibly rewarding experiences, and it would not have been possible without Ben's encouragement and mentorship. I will always be grateful for the opportunities he as provided for my professional development, from allowing me to develop my teaching experience in the human anatomy laboratory, to incorporating me on presentations, research, and into his network of colleagues. Above all, I appreciate his sincere interest and caring in the well-being of his students, for emphasizing a healthy work-life balance, and encouraging us all to take care of ourselves first and foremost over our research. I have no doubt that Ben's mentorship has been a crucial part to my successful completion of this dissertation. Thank you for everything!

None of this would have been possible without the love and support of my family and friends – Mom, Dad, Esther, Jon, Mike, Laura, Ben, & Rachel, Aaron, Autumn, Jackson, & Alexis, Kristen & Nick, Kaleigh & Jessi, Katie, Kaitlyn, Angela, Kate, & Memeow: thank you all from the bottom of my heart. You all have helped keep me (somewhat) sane throughout my many, many years of schooling, and have encouraged me and offered support in ways I never could have imagined. Words cannot adequately express my gratitude in having each and every one of you in my life. Thank you.

I would also like to thank the curators and staff of the institutions I visited during my data collection: Mark Omura of the Museum of Comparative Zoology in Cambridge, MA, Neil Duncan and Marisa Surovy of the American Museum of Natural History in New York, NY, Adam Ferguson and Lauren Smith at the Field Museum of Natural History in Chicago, IL, Yohannes Haileselassie and Lyman Jellema of the Cleveland Museum of Natural History in Cleveland, OH, and Darin Lunde and Megan Krol at the National Museum of Natural History in Washington, D.C, and Dawnie Steadman, Haley, & Marta of the Bass Donated Collection at the University of Tennessee in Knoxville, TN. Thank you all for access to these collections, and for your help and support during the data collection process!

This research has been funded by a National Science Foundation Dissertation Improvement Grant (NSF BCS-1825995), the Thomas Fellowship, the University of Tennessee College of Arts and Sciences Dissertation Fellowship, and a University of Tennessee Chancellor's Fellowship.

ABSTRACT

Observable differences among primate taxa closely align with different demands imposed by the wide range of environments they inhabit. This is reflected in the morphology of the primate shoulder girdle, which is the most variable among placental mammals. Previous research has demonstrated the morphology of the shoulder girdle reflects functional demands of the upper limb. Therefore, researchers hypothesize traits of the scapula are adaptations for specific functions related to locomotion, resource acquisition, or habitat; however, these hypotheses remain untested.

In this dissertation, I use quantitative genetic approaches to assess the role of shared trait covariances on primate shoulder girdle morphology and directly test hypotheses of how this anatomical region evolved using phylogenetic comparative methods. Traits may evolve through shared responses in genetically, developmentally, or functionally covarying traits, via random genetic drift or responses to selection. In primates, the shoulder girdle shares developmental and functional relationships with traits of the basicranium, pelvic girdle, and humerus. Whether these relationships affect the evolution of the shoulder girdle, and ultimately primate morphological diversification, have not been explored. Using a broad sample of extant primate skeletal material, I estimate evolvability and conditioned covariances between the shoulder girdle, basicranium, pelvic girdle, and humerus, compare integration and evolutionary potential of these regions among primates, and directly test factors influencing shoulder girdle morphological variation.

Results indicate the shoulder girdle does not evolve independently, rather its evolution is influenced by traits of the basicranium and pelvic girdle, and vice versa. Further, primate species have different patterns of covariance among these anatomical regions that affect their ability to respond to directional selection, and evolutionary covariance among these anatomical regions is not solely due to size-related variance, but also shape-related functional variance. However, no hypothesized single factor evolutionary model—locomotion, resource acquisition, or habitat—best explains what selection factors motivated evolution across all primates. These findings have

implications for understanding how developmentally and functionally covariant anatomical regions may interact during evolution and their effect on morphological variation in primates and other vertebrates. Models of trait evolution should not be limited to single traits, anatomical regions, or single causes, without extreme caution.

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CHAPTER I

INTRODUCTION, BACKGROUND, AND RESEARCH QUESTIONS

Introduction

Primates inhabit diverse environments, from dense rainforest canopies to savannah and deserts. Researchers have long argued that in conjunction with this breadth of habitats, the limbs have evolved in response to selection allowing for gross motor tasks, such as movement associated with locomotion (Miller 1932; Rose 1974, Roberts 1974; Preuschoft et al 2010), and fine motor tasks, such as manipulation (Szalay and Deslon 1979; Rasmussen 1990; Cartmill 1974, 1992). Differences in mechanical function of the upper limb are therefore anticipated to be reflected in the morphology of the skeleton. A wide range of morphological variation in the shoulder girdle has been shown exist when comparing primates to other mammalian orders, and researchers have related this variation to correspond with locomotor habits (Ashton and Oxnard 1961, 1963, 1964ab; Oxnard 1963; Ashton et al 1965ab; Müller 1967; Roberts 1974; Corruccini and Ciochon 1976; Fleagle 1976; Stern et al 1977; Tuttle and Basmajian 1977, 1978; Kimes et al 1981; Jungers and Stern 1984; Larson and Stern 1986; Shea 1986; Larson et al 1991; Taylor 1997; Krause 2008). Researchers have therefore extensively studied the relationship between form and function of the primate shoulder girdle and patterns of morphological variation across both living and fossil taxa. In turn, researchers often use the morphology of the primate shoulder diagnostically to understand locomotor function in both extant and extinct species (see Oxnard 1967; Lauder 1990; Larson 2013). Due to the associations between aspects of the shoulder girdle - primarily traits of the scapula - and different locomotor functions, differences in trait morphology are often interpreted as adaptations for specific functions (Ashton and Oxnard 1964a). By this logic, differences in shoulder girdle morphology among primates can be explained by selection for traits that would optimize the performance of certain types of locomotion (Witte et al 1991; Preushoft and Witte 1992; Preuschoft 2004). Yet, the underlying hypothesis that form arose in response to direct pressures from natural selection remains untested.

A number of complications exist in drawing direct relationships between morphology, function, and evolutionary forces responsible for shaping the morphology. Fundamentally, without explicit evolutionary models, it is not possible to discern the evolutionary forces that were responsible for trait evolution (Lande 1979, Lande and Arnold 1983, Houle 1991; Arnold 1992; Ackermann and Cheverud 2002; Hansen and Houe 2008; Hallgrímsson et al 2009; Mitteroecker 2009; Rolian et al 2010; Roseman and Auerbach 2015; Savell et al 2016). Not all trait variation is tied to differences in individual fitness. Traits may evolve through neutral processes (e.g., random genetic drift, stabilizing selection, gene flow), through direct responses to selection that result in directional state changes, or from correlational selection in genetically, functionally, or developmentally covarying traits (Lande 1979; Lande and Arnold 1983; Arnold 1992; Falconer and Mackay 1996). The independent evolution of morphological traits is often not possible due to evolutionary covariation among traits (Ackermann and Cheverud 2000; Rolian et al 2010; Grabowski and Roseman 2015; Roseman and Auerbach 2015; Savell et al 2016). Integration through genetic, developmental, or mechanical causes underlies this evolutionary covariance and is often emergent through pleiotropy (Wagner 1996). To assume that all traits represent independent and direct responses to directional selection requires assessment through quantitative genetic or other methods, and cannot be assumed to be the default evolutionary process.

The manner in which shoulder girdle morphology in primates has been investigated thus far, which I review below, has been through the analysis of individual traits or skeletal elements, which inherently assumes their independent evolution. Yet traits of the primate shoulder share both mechanical function (Richmond et al 2001; Diogo and Wood 2012; Zihlman and Underwood 2019) and developmental processes with other anatomical regions, namely the head, neck and pelvis (Matsuoka et al 2005; Huang et al 2006; Valasek et al 2010; Sears et al 2015). Thus, studies of primate shoulder morphological evolution fail to consider the potential influences on trait evolution imposed by other anatomical regions with which it covaries.

In this dissertation, I focus on understanding the effect of trait covariance on the evolution of morphological diversity in the primate shoulder girdle. I examine whether the developmental and mechanical functional covariance with the basicranium, pelvic girdle, and humerus have the potential to influence trait evolution in the shoulder, and test different evolutionary hypotheses of primate shoulder morphological diversity. Towards these general goals, I examine three major questions:

1) Do the traits of the primate shoulder girdle show the ability to respond independently to directional selection, or do these traits exhibit potential to evolve through correlated responses to selection with anatomical regions that share functional and developmental covariance? (Chapter II)
2) Do primates with different shoulder girdle morphologies, which are also associated with both variation in locomotion and in evolutionary history, have similar integration and potential responses to selection among the shoulder girdle, basicranium, pelvic girdle, and distal humerus? (Chapter III)
3) Do hypotheses of primate shoulder girdle morphological diversification argued by other researchers—namely selection in response to habitat, diet, locomotion, or major cladogenesis events—accurately model how this anatomical region evolved, especially in light of the genetic covariance analyzed in the previous two chapters? (Chapter IV)

The three following chapters address these questions, and represent manuscripts that comprise the original research and analysis components of this dissertation. Each chapter provides sufficient background information to supply the context for each question examined. However, to provide a more detailed review of the relevant literature on primate shoulder morphological variation or the theoretical framework for quantitative genetic methods or evolutionary modeling used in this dissertation, I provide a more comprehensive discussion of the relevant literature in this chapter. Below I review primate shoulder morphological variation with respect to its relationship with

locomotor function, the factors hypothesized to affect the evolution of the primate shoulder, the potential covariances between the shoulder and other anatomical regions, and hypotheses proposed in the literature for factors relating to shoulder morphology that affect fitness in primate evolution. The end of this chapter provides a summary of the methods used in this dissertation and defines related concepts.

Establishing Potential Sources of Primate Shoulder Morphological Variation

Primates are argued to have a generally unspecialized morphological structure among mammals, and yet have been able to occupy a wide scope of habitats through behavioral adaptation (Fleagle 2013). Though the primate *bauplan* is not specialized, morphological variation reflecting the diversity of habitats in which they live pervades the skeleton. Primates exhibit the greatest morphological variation in the shoulder girdle among all placental mammals (Preushoft et al 2010), and engage in a type of quadrupedal locomotion that differs from other mammals in terms of gait (Vilensky 1989; Vilensky and Larson 1989), stride length (Alexander and Maloiy 1984; Reynolds 1987), and weight distribution in the fore- and hindlimbs (Kimura et al 1979; Kimura 1985; Demes et al 1990, 1994). As primates are distributed across a wide range of environments—from dense forests, savannahs, deserts, and in every level of the forest canopy (see Silcox et al 2015 and Zihlman and Underwood 2019)—the morphology of the shoulder girdle (both the bony elements of the scapula, clavicle, and proximal humerus, and the associated soft tissue), among other anatomical regions, aligns with the manner in which primates navigate these different environments (Oxnard 1967, 1968; Matsuo et al 2019). Most primates are arboreal, and a majority of primates, including species that are primarily terrestrial, are quadrupedal (Rose 1973) with a broad range of positional behaviors and morphological diversity present in the shoulder girdle (Rose 1973; Fleagle 1977, 1978; Manaster 1979; Rollinson and Martin 1981; Birchette 1982; Ciochon 1986; Schultz 1986; Whitehead 1992; Strasser 1994). The evolutionary success of primates is thought to be due, in part, to their ability to inhabit various environments. Based on the immense variation observed in

shoulder girdle morphology of living primates, it is hypothesized that changes in the shoulder were motivated by and further influenced an adaptive radiation of taxa, especially the diversification of apes and monkeys (Miller 1932; Washburn 1951; Grand 1972).

The earliest studies of the primate shoulder girdle focused on characterizing the morphological differences in the scapula and clavicle among taxa, which were believed to be of value only to systematics, with no relation to function (Graves 1921; Frey 1923, 1924; Schultz 1930). Miller (1932) was one of the first researchers to note functional significance of the muscular and bony features of the shoulder. The shoulder girdle was observed as functioning differently among broadly defined locomotor groups of primates and described in terms that related the forelimb to typified forces during locomotion (Ashton and Oxnard 1961, 1963; Napier 1963; Oxnard 1963): quadrupeds subject the shoulder to compression forces during locomotion, whereas the shoulder in brachiators experience tensile forces, and semi-brachiators intermittently subject their shoulders to both kinds of forces. Adaptations for brachiators (Hominoidea) were defined as cranially oriented and elongated acromia, more caudally positioned inferior angles, and cranially oriented glenoids compared to quadrupeds (Cercopithecoidae and Cebidae) (Ashton and Oxnard 1961, 1963, 1964a; Oxnard 1963; Ashton et al 1965ab), whereas these authors argued that semi-brachiators (Atelidae and Colobinae) express an intermediate morphology (Ashton and Oxnard 1964a; Oxnard 1967).

However, considerable variation is present in the scapula, even within broad locomotor groups, with more variation observed among arboreal species than terrestrial ones (Young 2006). Long, narrow scapulae are observed among both arboreal and terrestrial quadrupeds (Figure I.1ab; all Figures are located in Appendix I). Species that more often engage in climbing activities have comparatively broad scapulae, with the scapular spine inclined towards the cranial border as opposed to perpendicular to the blade (Figure I.1c). The scapulae of suspensory species differ markedly from those of quadrupeds, with enlargement of both the supraspinous and infraspinous fossae (Figure I.1d). Brachiating species display the most unique morphology (Figure I.1e), the blade is medio-laterally narrower, cranially to caudally elongated, and the oblique orientation of the

spine provides similar sized supraspinatus and infraspinatus fossae. Several researchers have worked to place this variation within a morphometric framework (Miller 1932; Inman et al 1944; Davis 1949; Smith and Savage 1956; Ashton and Oxnard 1963, 1964ab, Erikson 1963; Oxnard 1963), and despite increasing evidence that locomotor function has been a strong influence on morphology of the scapula, taxonomic explanations for this variation persisted through the 1960s. This was not changed until Ashton, Oxnard, and their colleagues (Ashton and Oxnard 1964ab; Oxnard 1967; Ashton et al 1965a, 1971) demonstrated that multivariate discriminant statistics separate the morphology of the scapula into broad groups that reflect locomotor function; a body of work that has since been continued (Müller 1967; Roberts 1974; Corruccini and Ciochon 1976; Fleagle 1976; Kimes et al 1981; Shea 1986; Taylor 1997; Krause 2008). While these studies demonstrated that the morphology of the scapula matches well-established locomotor groups (quadrupedalism, brachiation, and semi-brachiation), corresponding this information to function of the shoulder was not possible due to the limited knowledge of shoulder mechanics and motion among species within these broad groups (Schmidt and Krause 2011).

In addition to variation in scapular skeletal morphology, differences in the configuration of shoulder muscles were also observed among primates engaging in different locomotor functions (Inman et al 1944; Ashton and Oxnard 1961, 1963; Oxnard 1963). Inman and colleagues (1944) noted that differences in scapular shape seemed to be influenced by changing proportions of two rotator cuff muscles, supraspinatus and infraspinatus; primarily how size differences in these muscles affected the scapular index (ratio of scapular length to scapular breadth). However, the influence of the rotator cuff muscles on scapular shape was considered minimal compared to those muscles associated with arm raising (trapezius, deltoid, and caudal serratus anterior). These muscles were noted as larger in brachiators compared to quadrupedal primates, and therefore thought to be more influential on human evolution (Ashton and Oxnard 1961; Oxnard 1963). A series of studies using electromyographic (EMG) data have since been performed to assess which muscle fibers are active during particular movements, such as arm raising, and confirmed differences

between forelimb postures and broad locomotor groups (Stern et al 1977; Tuttle and Basmajian 1977, 1978; Jungers and Stern 1984; Larson and Stern 1986; Larson et al 1991; Larson 1993, 1998; Whitehead and Larson 1994). Roberts (1974) reestablished the influence of the rotator cuff muscles by determining the functional importance of this muscle group for the stabilization of the shoulder joint during abduction of the arm (such as arm raising). He further demonstrated that increases in size of both the supraspinous and infraspinous scapular fossae occurred in primates that more often engaged the forelimb in overheard postures and locomotion (Roberts 1974). These studies were paramount in establishing the influence of function over phylogeny on scapular morphology (see Figure I.2). The broad functional groupings of taxa, while somewhat arbitrary, have still shown to be useful in studies exploring locomotor differences on a more detailed level (e.g. Corrunccini and Ciochon 1976; Fleagle 1977; Fleagle and Meldrum 1988; Larson 1993; Fleagle and McGraw 2002).

In more recent decades, researchers have reported on studies of shoulder girdle function that have provided a well-established understanding of the correspondence of muscle activity with shoulder movement (Stern et al 1977; Tuttle and Basmajian 1977, 1978; Jungers and Stern 1984; Larson and Stern 1986; Larson et al 1991; Larson 1993, 1998; Larson 1993, 1998, 2013, 2015; Whitehead and Larson 1994). This research demonstrates high variation in which muscle fibers activate during the same functional behavior, which provides redundant pathways to perform the same behavior. In more recent years, researchers have suggested that this functional redundancy provides a means to avoid fatigue of particular muscle fibers (Preuschoft et al 2010). While muscle activity patterns were established in these studies, the mechanical stresses affecting the shape of the scapula are only recently being established.

Preuschoft and colleagues (2010) performed the most comprehensive biomechanical analysis of the shoulder in quadrupedal primates to date. They identified the major biomechanical factors influencing the shoulder complex and compared those with the skeletal morphology. In accordance with expectations of the principles of bone functional adaptation (Ruff et al 2006), Preuschoft and colleagues (2010) concluded that the morphology of the scapula aligns with the flow of stresses

imposed by muscle activation during different locomotor functions (e.g., suspension vs. quadrupedal movements). Their results were the first to demonstrate that scapular morphology closely relates to the internal forces associated with muscle activity, though whether muscle function determines skeletal form was beyond the scope of their analyses. Nevertheless, one outcome of their study was a reinforcement of the important ways in which the size, shape, and orientation of muscles attaching to the scapula may be a source of variation in the bone's morphology across taxa. This is further reinforced by interspecific shape variance being present in infants and unchanged during ontogeny, thus, indicating scapular morphology is not solely the reflection of plastic responses to biomechanical demands encountered over the lifetime of an individual (see Young 2006).

An additional take-away from these many studies is that researchers have thoroughly examined the morphology of both the hard and soft tissues of the primate shoulder, but they have examined these largely in isolation from other parts of the body. No published research has examined the shoulder (especially the scapula) in conjunction with the basicranium or axial postcranial skeleton, despite the direct connections of shoulder muscles with these skeletal elements. The body of research encompassing morphological variation of the primate shoulder girdle instead emphasizes either shared ancestry or the effects of muscular loading and load transmission as determinants of scapular shape (Roberts 1974; Larson 1993). These are important factors. It is clear that the scapula provides a scaffold for the muscles of the glenohumeral joint, stabilizers of scapular motion, and transmission of body weight to the forelimbs, while it is further complicated by the geometric constraint the clavicle and thorax impose on its motion (Jenkins et al 1978; Larson 1993; Preuschoft et al 2003; Chan 2007). The vast improvements in scapular biomechanics established since the 1960s have emphasized the importance of mechanical function on form in the shoulder joint, and this is an area of ongoing research. Nevertheless, the difficulty remains in explaining the *sources* of the variation that has been established among primates, as well as the evolutionary processes by which scapular shape has diversified. Rather, the hypotheses for explaining the evolution of the

primate shoulder girdle are closely tied to the major factors that are hypothesized to have motivated primate evolution as a whole.

Hypothesized Factors Influencing Primate Shoulder Evolution

In pursuit of a better understanding of how humans evolved, with non-human primate groups providing context for interpreting the morphological changes observed in fossil hominins, researchers have extensively studied primate species phylogeny and posited evolutionary processes responsible for diversification. Several factors have been presented as drivers of primate diversification. As I argued above, the evolution of the primate shoulder has been associated with many of these factors. Of these, researchers have identified four major influences that are hypothesized to have driven the evolution of the primate shoulder: evolutionary relationships, diet, habitat, and locomotion.

Primate Phylogeny and Biogeography

The earliest arguments for the observable diversity among primates are based on evolutionary relationships (see Keith 1927; Osborn 1927, 1930; Gregory 1928; Miller 1929; Schultz 1930, 1936), constructed from the logic that species that are more closely related tend to be more similar due to their shared history. By this argument, morphological variation among primates reflects, and has been restricted by, the more similar, shared genetic covariance among traits found in closely related species. The greater similarities in trait morphologies between closer relations is the reason why phylogenetic relationships among taxa can bias the outcome of comparative studies (see Felsenstein 1985, McKitrick 1993); thus, evolutionary relationships among taxa are an important factor in understanding the structure of their morphological variation.

In recent decades, phylogenetic relatedness has been used an alternative hypothesis to functional or ecological factors affecting morphology (e.g., Young 2006; Young and Badyaev 2006; Schmidt and Krause 2011), which creates a model under which trait evolution reflects

macroevolutionary events instead of responses to factors that impose selection on traits. Thus, researchers may think of this population structure model as a type of baseline against which to compare evolutionary models that incorporate fitness.

In light of this model, an overview of the phylogenetic relationships among primates is necessary to understand the broader analyses used in this dissertation. I base the species relationships used in this dissertation on the molecular phylogeny presented by Perelman and colleagues (2011), along with the approximate geographical locations of these divergences. A molecular phylogeny is preferred over those constructed using other sources of information, such as biogeographical, adaptive, morphological, reproductive, and behavioral traits, as those can provide contradictory or tautological results (see Goodman et al 1998; Groves 2001; Wilson and Reeder 2005). A visual representation of the full primate phylogeny can be found in Figure I.3.

Broadly, the origin of the Primate Order from Mammals occurred approximately 80 to 90 million years ago (MYA) (Goodman et al 1998; Wilson and Reeder 2005). The earliest mammalian lineages associated with primates (Plesiadapiformes) are found in North America (Fox 1991), with the presence of additional primitive primate lineages in Asia (Fu et al 2002). The Plesiadapiformes are a sister taxonomic group to the order Dermoptera (including extant colugos, also known as flying lemurs), and both of these taxonomic groups are closely related to Scandentia (treeshrews). Euprimates (taxa that display a complex of traits associated with modern primates; see Silcox et al 2015) appear suddenly, on a geological scale, in North America, which suggests a different origin for this group. The current context of fossil evidence supports Euprimate origins in Asia, Europe, Africa, or North America (Silcox 2001, 2008; Bloch et al 2007), whereas molecular data places this origin in Asia (Springer et al 2012). Regardless of the location of their origin, Euprimates represent a large order of species that began to diversify during the Paleogene.

The major extant primate lineages (Strepsirrhini, Tarsiiformes, and Simiiformes) formed during an Eocene expansion. Tarsiiformes were broadly distributed throughout the northern continents of the world (i.e., the Holarctic) during the Eocene, but presently inhabit the islands of Borneo,

Sumatra, Sulawesi, and the Philippines (Kay et al 1997). Tarsiiformes are an ancient lineage that split with suborder Haplorrhini around 87 MYA, and are a sister lineage to Simiiformes (Perelman et al 2011). Strepsirrhines split from suborder Haplorrhini (comprised of Infraorders Tarsiiformes and Simiiformes) around 87 MYA (Perelman et al 2011). Strepsirrhines experienced a major split into the progenitors of Lemurformes/Chiromyiformes and Lorisiformes. Lemurformes and Chiromyiformes colonized the island of Madagascar and underwent extensive adaptive evolution (Mittermeier et al 2008). The evolution of Lorisiformes includes the radiation of Lorisdae and Galagidae (Perelman et al 2011). Lorisidae consists of extant genera in both Africa and Asia, while Galagidae are only found in Africa.

Simiiformes are comprised of Platyrrhines (New World Monkeys) and Catarrhines. The Catarrhines are composed of Cercopithecoidea (Old World Monkeys – OWM) and Hominoidea (gibbons, great apes, and humans). Around 43.5 MYA during the Eocene, Platyrrhines diverged from a common ancestor with Catarrhines (Perelman et al 2011). New World Monkeys (NWM) are found in the tropical regions of Central and South America, and Mexico. Three families of NWM diverged from a common ancestor 24.8 MYA. Pitheciidae are found in the neotropical Amazonian basin, and Atelidae are widely distributed from Mexico to Argentina. The Cebidae radiation began around 20 MYA with two sister taxa, Cebinae and Saimirinae (Opazo et al 2006; Osterholz et al 2009), that are found throughout tropical and subtropical Central and South America. A subsequent lineage arose and split into *Aotus* (night monkeys) and Callitrichinae (tamarins and marmosets) (Perelman et al 2011).

Speciation patterns among Cercopithecidae are unclear due to hybridization among taxa, and symplesiomorphic (shared, ancestral) morphological traits (see Groves 2001, Tosi et al 2003; Xing et al 2007). Hybridization between two taxa will cause molecular phylogenies to indicate temporally shallower divergences than the “actual” speciation event, though it is debatable whether hybridization between taxa constitutes grounds for those taxa to not be designated as species, but rather as semispecies (Shanker et al 2017). Nevertheless, phylogenetic relationships at the genus

level are considered as generally well-resolved among most primates. Two subfamilies, Colobinae and Cercopithecinae, diverged 18 MYA (Perelman et al 2011). Colobinae are comprised of African and Asian tribes that are adapted to an arboreal habitat (Ting et al 2008). The remaining OWM, tribes Papionini and Cercopithecini, emerged roughly 11.5 MYA from a common ancestor. Cercopithecini lineages are characterized by a transition from an arboreal to a terrestrial lifestyle (Perelman et al 2011). In contrast, tribe Papionini is characterized by a complex taxonomy among its members—macaques, baboons, mandrills, drills, mangabey, and geladas—in which hybridization among species is common, leading to some uncertainty in the phylogenetic trees (Groves 2001). *Macaca* is represented by African and Asian lineages (Ziegler et al 2007) that diverged 5.1 MYA. *Papio, Lophocebus,* and *Theropithecus* form distinct clades. Collectively, the Papionini represent a breadth of adaptations to a range of habitats and locomotion, including arboreal, terrestrial, and semi-arboreal (see *Locomotion* below).

Apes diverged from other Catarrhines during the early Miocene and exhibit an adaptive evolutionary expansion in the fossil record; extant apes represent a vestige of this adaptive radiation. Hominoidea is a monophyletic group that diverged from Cercopithecoidea 20.4 MYA and is comprised of two families of apes: Hylobatidae and Hominidae. Hylobatidae, gibbons and siamangs, are native to Asia and experienced rapid divergence 8.9 MYA (Perelman et al 2011). The great apes (Hominidae) are comprised of *Pongo, Gorilla, Pan,* and *Homo*. *Pongo*. *Pongo* diverged from the other apes roughly 17 MYA to form a sister lineage to Homininae (Perelman et al 2011). During the Pleistocene, the ancestor sister taxa of *Pongo*, as well as orangutans, were widespread across Southeast Asia, but orangutans are presently restricted to the islands of Borneo and Sumatra. *Pongo* is the only arboreal great ape. Rapid speciation occurred early in Homininae evolution, with *Gorilla* diverging 8.3 MYA and the *Homo-Pan* split roughly 6.6 MYA. *Gorilla* are distributed discontinuously across high mountains and lowland forests of Central Sub-Saharan Africa (Zihlman and Underwood 2019). *Pan* inhabits forested regions of Central and West Africa (Stumpf 2011). Modern humans originated in Africa and dispersed globally (Reyes-Centeno et al 2015; Hunley et al

2016). Debate continues about the morphology of the common ancestor of the Homininae, especially concerning the form of locomotion that this common ancestor practiced; some researchers suggest that a (facultative) biped is the ancestral condition for gorillas, chimpanzees, and hominins (Jablonski and Chaplin 1993; Wrangham and Pilbeam 2001; Richmond et al 2001). Regardless, humans and their recent ancestors represent the only habitual bipedal primates.

Diet

As I have noted previously, the origin of primates and their subsequent diversification has been hypothesized to be related to several ecological factors, such as diet, terrain, and climate. Researchers have consistently focused on five major scenarios to explain the origin and diversification of the Primate order: transition to arboreality (Le Gros Clark 1959), adoption of grasp-leaping (Szalay and Delson, 1979; Szalay and Dagosto 1980, 1988; Szalay et al 1987; Dagosto1988), visual predation (Cartmill 1972, 1974, 1992, 2012), terminal branch feeding associated with angiosperm diversification (Sussman 1991; Sussman and Raven 1978; Sussman et al 2013), and a combination of terminal branch feeding with subsequent visual predation (Rasmussen 1990). Of these, the angiosperm diversification hypothesis is most consistent with the morphological and fossil evidence (Sussman et al 2013; see also Silcox et al 2015). This hypothesis posits that as angiosperms (plants that produce flowers, fruit, and seeds) developed, opportunities for non-insect pollen and seed dispersal systems through flowers and fruit also appeared. Ancestral Euprimates developed features that supported terminal branch locomotion to exploit these resources (Sussman and Raven 1978). This hypothesis predicts two stages of primate evolution. The first, a shift in dentition reflecting greater use of plant-based resources associated with mixed arboreal feeding zones, followed by grasping and dental features associated with terminal branch foraging (Silcox et al 2015).

As a continuation of this hypothesis, researchers have also thought of diet as a major selection factor that the diversification of primate genera (see Scott 2019). Diet-driven hypotheses of primate

diversification have primarily focused on cranial traits (Rosenberger 1992; Fish and Lockwood 2003; Allen and Kay 2012), with noted differences observed in the dentition (see Gebo 2014), eye placement (Cartmill 1972, 1974, 1992, 2012), and jaw morphology (Daegling 1992; Ravosa 1996). Changes in the postcranial skeleton arise subsequently and even concurrently with cranial changes (Cartmill 1974, 1992; Sussman and Raven 1978; Bloch and Boyer 2002; Kirk et al 2003; Sussman et al 2013; see also Silcox et al 2015). Postcranial changes are indirectly associated with diet, as they are employed in resource acquisition and manipulation, but not consumption. The observed changes relate to increased grasping behaviors (Cartmill 1972, 1974, 1992, 2012; Rasmussen 1990; Kirk et al 2003; see also Nyakatura 2019), as well as increased mobility of the shoulder (as seen in brachiating primates), which together allow for a greater scope of feeding strategies and shorter reach distances when accessing resources on terminal branches (Grand 1972). Postcranial hypotheses of diet-driven diversification among primates, especially of proximal elements like those associated with the shoulder, are therefore difficult to tease apart from those of locomotor function (see Rosenberger 1992), as the ability to access food sources on terminal branches is related to how the organism navigates this substrate.

Locomotion

Changes in shoulder girdle morphology are hypothesized to be a major driver, or consistent result, of selection pressures occurring throughout primate evolution, especially in the diversification of monkeys and apes (see Miller 1932; Washburn 1951; Grand 1972). This hypothesis is in part reinforced by the immense variation observed in the shoulder girdle of living primates. Due to the correspondence of this variation with differences in locomotor function, it is further hypothesized variation in the shoulder girdle reflects adaptations for specific locomotor repertoires. As previously discussed, morphological variation in the primate shoulder girdle most closely reflects differences in functional demands of the upper limb and shoulder during locomotor function. The role of function associated with movement in shaping primate shoulder girdle morphology over other influences,

such as diet, also gains support by the amount of stress sustained by the skeleton during locomotion over other behaviors (Preuschoft et al 2011). The forces transmitted across the shoulder are much higher during locomotion than they are during feeding and fine manipulation behaviors (like social grooming). Muscle forces must be reduced during such movements, otherwise they would move the whole body (Preuschoft et al 2011).

Specific morphologies have been hypothesized has having particular advantages for different types of locomotion. These are classified into broad categories, including scansorial (climbing and scurrying), saltatorial (leaping), arboreal quadrupedalism, terrestrial quadrupedalism, arboreal/terrestrial quadrupedalism, brachiation/suspension, and bipedalism. These categories provide generalized descriptions of how primates navigate different environments, and provide more nuance to the different types of locomotion observed in arboreal environments. Morphological differences in the scapula among these different modes of locomotion have focused on the shape of the scapular fossae, the shape of the angles of the scapular blade, the orientation and morphology of the scapular spine, and the shape and orientation of the glenoid fossa relative to the scapular body, among other traits (Young 2004, 2006, 2008).

As an example, we can focus on hominoid scapular traits. The morphology of the hominoid scapula is thought to relate to climbing or brachiating, and is hypothesized to be an adaptation for arm raising due to the increases in mechanical advantage the skeletal morphology provides to facilitate the action of the trapezius and caudal serratus anterior muscles (see Selby and Lovejoy 2017). The angle of the scapular spine in hominoids places the muscle fibers for the superior portion of the trapezius in a more cranially oriented position, whereas these fibers, and thus the less angled scapular spine, are more laterally oriented in quadrupedal species (Ashton and Oxnard 1961; Oxnard 1963). In contrast, the lever arm for the caudal serratus anterior fibers are elongated by the caudal orientation of the inferior angle of the scapula in hominoids. Both morphologies are associated with reductions in the power needed to produce enough force to raise the arm. It has further been hypothesized that the cranial orientation of the glenoid in hominoids reduces the need

for scapular rotation during arm-raising (Ashton et al 1965a; Ashton and Oxnard 1964b; Oxnard 1967; Andrews and Groves 1976; Tuttle and Basmajian 1977; Hunt 1991). Alternatively, EMG studies suggest these features may be related to stabilizing and turning the head (Jungers and Stern 1984; Larson et al 1991) and controlling the rate of descent of the trunk relative to the scapula during suspensory locomotion (Jungers and Stern 1984; Larson et al 1991; Stern et al 1977), respectively. Highly suspensory primates (i.e., orangutans, gibbons, spider monkeys) are also noted to have a narrower (mediolaterally) and elongated (craniocaudally) scapula relative to terrestrial quadrupeds; such scapular morphology is thought to permit greater mobility of the shoulder girdle (Mivart 1867; Schultz 1930; Jolly 1967; Larson 1993). An elongated vertebral border is hypothesized as providing greater mechanical advantage for the rhomboids and serratus anterior (Miller 1932; Clark 1959; Ashton and Oxnard 1964a), as well as providing adequate room for the rotator cuff muscles to promote joint stabilization during suspension (Roberts 1974). Other researchers hypothesize that the orientation of the scapular spine is related to the line of action of the infraspinatus muscle and is an adaptation for joint stabilization during suspension (Green and Alemseged 2012; Larson and Stern 2013).

In general, there is no question that the morphology of the scapula, just as all other aspects of the shoulder girdle, reinforce the function of the multiple joints in the shoulder under mechanical loads. Whether these arose evolutionarily from differences in fitness associated with locomotion, or the ability to exploit new substrates, remains unresolved within a quantitative genetic or comparative method framework. Thus, researchers find form and function correlations, but whether function was a selection factor on skeletal form, or if evolutionary modifications to skeletal form permitted the functionality, is unknown. It is also possible that by focusing on specific aspects of niches—diet or locomotion—researchers are not capturing the many variables that together impose a multi-factor selection on skeletal form among primates. The environment, or habitat, of primates may therefore better encompass these multiple, overlapping factors.

Habitat

Primates inhabit a wide variety of environments, and the postcranial morphology of primates aligns with the way species navigate the challenges presented by their environment. However, linking specific aspects of morphology to particular behaviors associated with different ecological niches is difficult due to the wide array of observable behaviors. Currently, for example, there are 32 primate positional modes that are divided into 52 postural sub-modes and 74 possible locomotor sub-modes (see Hunt et al 1996) that are used to describe how primates interact with their environment. While more specific and standardized methods are necessary to understand the intricacies of primate locomotor behaviors within a given ecological context, such studies have not been completed for all taxa. Thus, more generalized habitat groups, such as arboreal, semi-terrestrial, and terrestrial, are used to frame these hypotheses in this dissertation.

As I suggest above, 'habitat' is a multi-factorial classification that overlaps with both diet and locomotion, among other factors that are difficult to quantify. Thus, habitat-based hypotheses of primate morphological diversity are often framed in terms of one of these factors. For example, as I discussed previously, early primate evolution is often linked to the ability to successfully exploit resources on terminal branches in arboreal habitats (Jones 1916; Le Gros Clark 1959). In such scenarios, grasping behaviors are often linked to the need to securely anchor to a landing point after rapid jumping between branches (Le Gros Clark 1959; Szalay and Delson 1979; Szalay and Dagosto 1988). These changes have also been hypothesized to be linked to visual predation in primates (Cartmill 1974). Cartmill (1970; 1972; 1974) further hypothesized that all the complex of morphological features associated with modern primates could be explained by living in an arboreal habitat. Despite the rigor in using comparative morphology, behavioral observation, and quantification of skeletal morphology, the breadth of studies that have made such linkages correlate broad patterns without considering population history or the genetic covariance of traits, among many important evolutionary variables.

Within skeletal elements, for example, we could anticipate differences in genetic covariances in traits, and thus morphological integration (see below), that relate to habitats. Primates that engage in arboreal quadrupedalism tend to display more morphological variation in scapular morphology than terrestrial quadrupeds (Young 2006; Schmidt and Krause 2011). Arboreal habitats are more complex than terrestrial ones, as they are comprised of a variety of different supports; they can be broad or narrow, rigid or flexible, rough or smooth, and variably oriented (horizontal, oblique, or vertical) (Nyakatura 2019). Additionally, substrates vary based on the size of branch (e.g., round shaped in smaller twigs and branches, and flatter in larger trunks), and the way the primate interacts will be affected by its size (Nyakatura 2019). Therefore, navigating arboreal habitats are connected to diverse functional demands. It would be reasonable therefore to hypothesize that the range of variation in the shoulder girdle is related to the necessity to meet these demands. The functional demands encountered by terrestrial quadrupeds is less varied, in contrast, and so we would likewise expect the shoulder morphology in these species to also be less varied. This has been demonstrated in studies by Young (2006). Young further hypothesized that, overall, given the differences in morphology, selection would favor more morphological integration in concert with greater locomotor efficiency in committed terrestrial quadrupeds, whereas in arboreal species greater fitness would be associated with evolutionary flexibility (more trait independence) as well as various limb postures to navigate the complexities of life in the trees (Young 2006). Thus, the degree of evolutionary covariance among traits within and between skeletal elements, which arise from development and from shared function, should reflect these hypotheses about the evolutionary forces that shaped the evolution of the shoulder.

Functional and Developmental Covariances Between the Shoulder Girdle and Other Anatomical Regions

A fundamental concept postulated in this dissertation is that underlying covariances between the shoulder girdle and other anatomical regions may have influenced the evolution of diversity among

primates. How traits respond to selection can be influenced by the genetic covariances they have with other traits (Lande and Arnold 1983; Arnold 1992; Cheverud 1996; Rolian 2009; Rolian et al 2010). As noted in the previous section, the magnitude of the genetic covariance between traits may explain differences that have been observed in trait variation among species with different mechanical functions, as differences in the genetic covariance structure among taxa may result in different responses to the same pressure of directional selection. Two non-exclusive potential sources of covariance that can be identified from phenotypic data are those due to shared function and those due to development (meaning both the cellular and tissue layer interactions that produce structures, and the growth of those structures once they are established). Functional and developmental covariance can arise from function-induced growth that may result in a match between functional and developmental integration, where functional integration is built into the developmental system (Zelditch et al 2009). How these translate to evolutionary covariance among traits is presented in detail in the next section (see Evolutionary Quantitative Genetic Methods below*)*. This section provides an overview of the developmentally and functionally related traits from adjacent anatomical regions, namely the basicranium and the shoulder girdle, that may influence how traits of the shoulder girdle can evolve, which can ultimately affect the morphological variation observed in extant taxa.

Developmental Covariances

The mature shoulder girdle is a combination of the scapula, clavicle, and proximal humerus, in addition to the soft tissues that further connect these elements to ribs, the sternum, vertebrae, the ilium, and, in some primates, the basicranium. Development across these anatomical structures is beyond the scope of this dissertation. As most of the studies of the shoulder girdle focus on the scapula, this overview of development will emphasize the general origins and growth of the tissues that comprise the scapula and the similarities it has with other anatomical regions during development: the clavicle, humerus, basicranium, and pelvis.

The scapula itself has a complex developmental program, and throughout ontogeny it shares molecular pathways, cell lineages and correlated growth with multiple skeletal elements, namely the basicranium, pelvic girdle, and humerus. Due to myriad non-linear, overlapping processes that contribute to adult morphology, it is not possible to ascertain individual sources of covariance from definitive (mature) anatomy (Young 2004; Hallgrímsson et al 2009, Young and Capellini 2016). Rather, variation within a phenotype is structured by development (Raff and Kaufman 1983; Arthur 2004), and so the phenotypes upon which evolutionary forces act can be biased by developmental processes. Growth and developmental processes ultimately produce phenotypes that are visible to natural selection, and so it is important to understand these processes (Hallgrímsson et al 2009).

Development of the shoulder girdle relies on the precise timing of gene expression across several tissue types and gestational time points to coordinate the patterning of specific functional compartments of the scapula by different cell populations (Sears et al 2015). Additionally, these different cell populations need to come together to form an integrated composite skeletal element through highly coordinated gene regulation and control of cell behavior (Sears et al 2015). Morphogenesis of the scapula not only is dependent its direct cellular progenitors, it must also receive signaling cues from the surrounding tissues to help coordinate scapular development (Sears et al 2015).

There are three distinct cell progenitor populations that contribute to the scapula. The somatopleure, a layer of tissue that comprises the ectoderm and outer layer of the lateral plate mesoderm, contributes to the head (glenoid and surrounding area), blade, and portions of the spine of the scapula (Huang et al 2000; Huang et al 2006; Sears et al 2015). The dermomyotome, which comprises a portion of each somite, exclusively forms the vertebral or medial border of the scapula (Huang et al 2000; Huang et al 2006; Durland et al 2008). In mammals, migrating post-otic neural crest cells, which originate from the neural ridge distal to the developing ear (see below for more detail about this cell layer), contribute to the spine, acromion, and coracoid of the scapula (Matsuoka et al 2005).

The coordination and condensation of these progenitor tissue layers and cells occurs through several genetic pathways. The formation of the scapula is primarily regulated by hierarchical actions of interacting *Pbx* genes (*Pbx1-3*) (Capellini et al 2011; Sears et al 2015). The initial condensation of the body of the scapula is controlled by *Pbx1* transcription factors *Emx2* and *Tbx5*, with the subsequent condensation and patterning of the blade being impacted by signaling molecules from *Wnt*, *Fgf*, and *BMP* families (Sears et al 2015). *Fgf* signaling is important for the initial formation of the scapula due to its role in limb formation; formation of the scapula is reliant on the initial patterning of the limbs, but does not require limb outgrowth (Boulet et al 2004; Min et al 1998). *Wnt* and *BMP* signaling regulate early blade formation through their impact on progenitor cell differentiation into mesenchyme, as well as cell migration of the dermomyotome into the scapular field to form scapular blade condensations and cartilages through the expression of *Pax1*. The expression of *Tbx5* and *Emx2* in the somatopleure also play critical roles in early formation of the scapular blade through their expression of *Fgf10* and *Sox9*, respectively (Bi et al 2001; Pellegrini et al 2001).

Additional genes and their interactions in the mesodermal cells of the somatopleure have been demonstrated to influence the later development of the scapular blade: *Gli3, Alx3, Alxl,* and *Tbx15* (Kuijper et al 2005). The patterning pathways of the blade that involve these genes are also hierarchically regulated by *Pbx* genes (Selleri et al 2001; Capellini et al 2010). The mesodermal somatopleure also gives rise to the glenoid, coracoid process, acromion, and components of the head, neck, and spine of the scapula (Ehehalt et al 2004; Durland et al 2008). Their development is regulated by *Hoxa5* (Aubin et al 1998), *Hoxc6* (Oliver et al 1990), *Pax1*, retinoic acid receptors, *Emx2,* and *Pbx* (Oliver et al 1990; Vargesson et al 1997; Aubin et al 1998; Capellini et al 2010).

The scapula also shares several developmental similarities with the clavicle and humerus. Like the scapula, the clavicle also has progenitor cells from the lateral plate mesoderm (Nagshima et al 2016) and post-otic neural crest (Matsuoka et al 2005). Both skeletal elements also both serve as attachment points for the deltoid muscle, which is important in arm abduction (raising). Given their

shared development and function, there is likely genetic covariance between the scapula and clavicle. The development of the scapula is also reliant on the initial patterning of the limb buds, which is manifest in the lateral plate mesoderm, but the persistence of the scapula is not reliant on the outgrowth of those limb buds (Boulet et al 2004; Min et al 1998). Thus, there may be some developmental independence of the humerus and scapula. However, the humerus and the scapula physically interact at the shoulder joint and both serve as attachments for the muscles surrounding the glenohumeral joint, namely the rotator cuff muscles (supraspinatus, infraspinatus, teres minor, and subscapularis), as well as the deltoid and teres major muscles. Due to their close anatomical proximity and shared musculature, the scapula, clavicle, and humerus would be expected to exhibit correlated growth during ontogeny to maintain body proportions and optimal functionality of the shoulder. Therefore, the scapula may not be evolutionarily independent of the humerus and clavicle.

The scapula may also have underlying covariances with the basicranium that lead to their correlated evolution. The spine of the scapula, acromion, and coracoid process are all partially derived from post-otic neural crest cells (PONC). PONC originate in the neural ridge alongside the developing cranium and migrate caudally to form the muscle attachment sites for the branchial muscles (trapezius and sternocleidomastoid) on the basicranium, scapula, vertebral spines, and clavicle (Matsuoka et al 2005). Additionally, PONC regulates the mechanisms for muscle organization and connectivity between the head, neck, and shoulder (Matsuoka et al 2005). The physical muscular connections between the scapula, basicranium, and clavicle require the correlated growth of the regions during ontogeny. Furthermore, changes in one of these regions, such as the basicranium, may affect the morphology of the corresponding muscle attachment sites, such as the scapular spine. (See my discussion of the relationship of muscle morphology with scapular spine morphology above.) Such changes have the potential to affect the orientation or shape of these muscles, therefore, affecting locomotor function in shoulder girdle. These relationships are a major potential source of covariance for these regions, and in this dissertation, hypothesized to be primary factor contributing towards the evolutionary non-independence of these anatomical regions.

Once thought to be serially homologous, the shoulder and pelvic appendages first appear in the fossil record at different times, with the shoulder girdle predating the pelvic girdle by roughly 20 million years (Boisvert 2005; Clack 2009, 2012). The limb girdles have been shown to have different developmental pathways (see Sears et al 2015). Where the shoulder girdle has three separate cell progenitor populations, the pelvic girdle is derived solely from mesodermal cells of the somatopleure (Malashichev et al 2005; Pomikal and Streicher 2010). However, some of the aspects of the networks regulating patterning of the limb girdles are similar, such as *Pbx* function (Sears et al 2015). This further suggests the derived co-option of similar developmental programs from the shoulder region during pelvic girdle and hindlimb evolution (Diogo et al 2013). While the developmental programs of the shoulder and pelvic girdles differ, as limb girdles, they share analogous features and serve similar anatomical functions. The blades of the scapula and the ilium have the most similarities in the gene networks affecting development, mainly through the hierarchical expressions of *Pbx* genes and the regulation of *Sox9* by *Emx2* (Sears et al 2015). Despite the differences in developmental pathways, as parts of limb girdles, the scapula and the ilium serve critical roles in integrating the appendicular and axial system by serving as the point of attachment for the axio-appendicular muscles. As such, they share analogous characteristics in function as well as development. The shared roles of the shoulder and pelvic girdles in in support and attachment of the appendicular skeleton, especially among quadrupedal primates where stability of the joints is necessary during locomotion, may be a source of covariation among them that could lead to their evolutionary non-independence.

Functional Covariances

Locomotion is dependent on a suite of interconnected traits that work to perform a similar function, like raising the arm. Morphological traits that are associated with mechanical function belong to a suite of related traits that directly influence the performance of a mechanical function (Arnold 1983; Calow 1987). Through their influence on performance, functional traits indirectly affect

organismal fitness (Arnold 1983). Therefore, trait mechanical relationships, such as the connection of skeletal elements by muscles, can have evolutionary consequences (Arnold 1983; Wainwright 2007). Functionally related traits can respond to selection with varying independence as a result of the underlying genetic association among them (Arnold 1992), and so these traits can often exhibit correlated responses to selective pressures. The functional relationships among traits can be emergent through pleiotropic effects at the loci affecting them (Wagner 1996), but can also arise through developmental processes (Young 2004) with no underlying genetic covariance among them (Boughner 2016). Therefore, mechanically related morphological traits will covary functionally, but may or may not covary genetically.

The primate shoulder girdle shares musculature with the head, neck, back, thorax, and upper limb (see Diogo and Wood 2012; Zihlman and Underwood 2019). Mechanical function links these regions through muscle fibers and layers of connective. Among the muscles that link these regions are the trapezius, levator scapulae, rhomboid, deltopectoral, latissimus dorsi, supraspinatus, infraspinatus, subscapularis, teres major and minor, and major muscles of the arm; these muscular relationships are fairly conserved among primates (Richmond et al 2001; Diogo and Wood 2012; Zihlman and Underwood 2019). Due to their shared functions, the shoulder girdle may display evolutionary non-independence with those skeletal elements with which it is physically linked.

A logical extension, then, would be to examine trait variation among the bones in which all shoulder girdle muscles attach, such as the basicranium, and not only the scapula. Yet, most studies have examined the scapula in isolation, arguing that the strength of the relationship between organismal locomotion and scapular morphology is strong enough to result in evolutionary convergences that override taxonomic differentiation (Ashton and Oxanard 1964a; Oxanrd 1967; Young 2008; Selby and Lovejoy 2017). As a consequence of this approach, the morphology of the scapula is attributed as reflecting adaptations to particular locomotor functions, a presumption that affects interpretations of the fossil record, as these traits are presumed to be the direct, individual result of natural selection.

Furthermore, the relationship between the morphology of the scapula and locomotion has been used by paleoanthropologists to not only infer the functional demands of the shoulder and forelimb in fossil organisms, but to facilitate the reconstruction of the latest common ancestor of humans and other apes (Larson 2013; Young et al. 2015; Green et al. 2016). These authors state their awareness that the scapula is part of a suite of functionally related traits, but due to the fragmentary state of the fossil record, researchers will isolate traits within the complex in order to make more direct comparisons with incomplete remains (Oxnard 1967). As a result, isolated features, such as the orientation of the glenoid cavity, are used to build evolutionary models of function (Ashton and Oxnard 1964b; MacLatchy et al. 2000; Larson et al. 2007; Feuerriegel et al. 2017). This is a problematic approach to studying the evolution of any trait. Evaluating a skeletal element, let alone a single trait or fragment, in isolation implicitly ignores the effects of developmental and functional covariance on the formation of morphology, and assumes that the element has undergone independent evolution where its evolutionary trajectory has not been affected by other traits. This oversimplifies the form-function relationship among functionally related skeletal elements. Such oversimplifications may be addressed, however, through the application of evolutionary quantitative genetic methods.

Evolutionary Quantitative Genetic Methods

Evolutionary quantitative genetics is concerned with the inheritance of continuous traits that are affected by multiple genes (Falconer and Mackay 1996). The theory and methods of study in quantitative genetics are founded in Mendelian principles but are concerned with inheritance on a population level as opposed to that of individuals. The basis of this extension of Mendelian genetics was established by the work of Fisher (1918), Wright (1921), and Haldane (1932) and has since been developed by an array of researchers (e.g. Lande 1979; Lande and Arnold 1983; Hansen and Houle 2008). Quantitative genetic methods allow for the estimation of the genetic properties of a population and the prediction of the outcomes of specified breeding plans, therefore forming a

foundation for the understanding of evolutionary change across generations. This goal is accomplished by assessing the influence of evolutionary processes, namely natural selection, genetic drift, mutation, and gene flow, on the evolution of organismal form, behavior, and function, and development (Falconer and Mackay 1996; Hansen et al 2011).

Natural selection refers to differential survival and reproduction of individuals within a population (Falconer and Mackay 1996); changes in the genotype can occur through the effect of natural selection on the phenotype. Natural selection can reduce variation within a population by maintaining phenotypes that increase organismal fitness (Lande and Arnold 1983; Arnold 1983; Cheverud 1984; Whitlock 1999; Lewontin 2000; Hallgrímsson et al 2009; Hansen and Houle 2008; Hansen et al 2011). There are three primary forms of natural selection that differ based on their effect on the mean phenotype in a population. Directional selection occurs when changes in genotype frequency over many generations causes the mean phenotype of a population to shift in a new direction (Falconer and Mackay 1996). During disruptive selection, extreme forms of a phenotype are favored over intermediate ones (Falconer and Mackay 1996). Stabilizing selection results in no change in the mean of a phenotype, and instead maintains an intermediate population phenotype at an optimum through the reduction in phenotypic variation (Falconer and Mackay 1996).

Other than selection there are three additional primary evolutionary mechanisms: genetic drift, mutation, and gene flow. Genetic drift is the change in allele frequencies in a population due to random sampling (Falconer and Mackay 1996; Lewontin 2000), and therefore could result in stochastic shifts in the phenotypic mean within a population between generations. Like natural selection, genetic drift reduces variation in a population, but does so in a random manner until a genetic variant is either fixed (frequency = 1) or lost (frequency = 0). The chance that a genetic variant will reach fixation is equal to its frequency in the current population, and since this probability is not reliant on any historical factors, it is not possible to predict what the frequency will do from one generation to the next (Futuyma 2013). The effect of genetic drift is strongest in small populations, as the likelihood of genetic variants being identical by descent has the potential to be higher than in

a large population (Lynch 2007). In small populations, genetic drift can be just as powerful, if not more so, than natural selection in its effect on gene frequencies.

Both gene flow and mutation add genetic variation to a population. The process of gene flow involves the transfer of genetic variation between two populations that are not randomly mating, where the majority of the breeding occurs within each respective population (Falconer and Mackay 1996). Mutation increases genetic variance through a random and permanent change in the sequence of nucleotides in the coding portion of a gene or in the regulatory sequences that control the expression of a gene (Falconer and Mackay 1996). If a population were left solely under the forces of genetic drift and selection, genetic variation would be lost as variants were either fixed or lost, and the population would be unable to adapt to a changing environment, which may lead to extinction (Futuyma 2013); mutation and gene flow both prevent this.

Both phenotypic and genotypic variation must be present for evolutionary processes to act in a population (Lande and Arnold 1983; Arnold 1983; Cheverud 1984; Whitlock 1999; Lewontin 2000; Hallgrímsson et al 2009; Hansen and Houle 2008; Hansen et al 2011). This is especially true for natural selection; strong directional selection on a trait will have no effect on a population if there is no variation in that trait, as the population will be unable to respond. Variance within a population is an important aspect to quantitative genetic methods, as these approaches assess the apportionment of variance within a population and the effect this structure has on the ability of evolutionary forces to act upon a population. Below, I review the quantitative genetic methods used throughout this dissertation to evaluate the structure of variance and covariance among anatomical regions and their effect on the observable morphological variation among primates.

Morphological Integration

As I reviewed in the previous section, development maintains the functional associations among the anatomical structures and individual traits within an organism, and therefore structures the expression of phenotypic variation that is visible to natural selection (Alberch 1982; Hall 1999). This

process can occur through the morphological integration of traits or anatomical regions (Cheverud 1996; Wagner 1996), and so is an important factor in how traits can respond to the force of directional selection. Morphological integration is the synchronized variation among morphological traits that arises through the interaction between functional, developmental, and evolutionary processes that create covariation (Hallgrímsson et al 2009). The foundations of this concept were formalized by Olsen and Miller (1958), who used statistical correlations among traits as a way to quantify integration. Their approach ascribed functional and developmental explanations for high correlations among traits but was based on phenotypic patterns, which may not accurately reflect the interactions of the underlying determinants of the observed variation, such as function or development (see Mitteroecker 2009).

The study of integration was put into a theoretic framework of quantitative genetics (Lande 1979, 1980), which provides a set of processes the evolution of coordinate phenotypic variation, by Cheverud (1995; 1996), Wagner (1984; 1990; 1996) and colleagues (1996), and Hallgrímsson and colleagues (2002). Cheverud (1996) identified four types of integration that are hierarchically organized among individuals and populations. He proposed that integration is driven by functional and developmental factors within individuals, whereas integration on a population level is driven by genetic and evolutionary factors. Developmental integration occurs when morphological traits have a shared developmental program or interact during organismal development (Cheverud 1996; Rolian 2009). Functional integration occurs when morphological traits participate in a common function, and their interactions affect the performance of that function. Developmental and functional integration are related, as functional relationships among traits are emergent through developmental processes (Cheverud 1996); thus, the functional relationship among traits may incur better fitness when those traits are coordinated, which will reinforce the developmental processes underlying them, which will ultimately strengthen both types of integration.

Morphological traits can become integrated at the genetic level within populations. Genetic integration occurs through the biased inheritance of sets of phenotypic traits to the exclusion of

others (Cheverud 1996). Cheverud (1996) proposed that this process is due to either pleiotropy among traits, where a single gene affects the phenotype of multiple traits, or linkage disequilibrium, where two genes affecting the same trait are inherited together (Falconer 1989). The independent inheritance morphological traits can either be an indication of the absences of pleiotropy between them or the balance between positive and negative pleiotropy cancelling the effects of both (Cheverud 1984, 1996; Mitteroecker 2009). Finally, genetic integration can lead to evolutionary integration, when morphological traits evolve due to shared responses to selection (Cheverud 1996; Rolian 2009).

Pleiotropy is a primary mechanism underlying these four types of integration (Cheverud 1996; Wagner 1996; Wagner and Altenberg 1996). The hierarchy of integration proposed by Cheverud (1996) implies that as traits become increasingly integrated on the population level, their ability to independently respond to selection becomes reduced due to their increasingly coordinated responses to selection (Rolian 2009). This process, however, is not reversible, otherwise traits would lose their ability to respond to selection altogether (Rolian 2009). Selection can act against integration among traits. This process can be achieved through the reduction of pleiotropy among traits (Wagner and Altenberg 1996; Hansen 2003). For example, reduction in pleiotropy could lead to the dissociation of traits when those traits, which were once associated by common function or development, are selected to be functionally specialized (Hallgrímsson et al 2002); this should result in the increased ability of these traits to evolve independently (Rolian 2009).

Morphological integration is a useful tool to identify which traits are more likely to experience correlated responses to selection. However, these methods are unable to characterize how these traits will respond to that force in the context of other, correlated traits. This relationship can be ascertained, however, through Hansen and Houle's (2008) measures of evolvability, which are employed for a majority of the analyses in this dissertation.

Evolvability and Evolvability Indices

Estimates of evolvability provide a means to characterize the *potential* ability of a trait, or traits, to respond to a selective challenge (Hansen 2003; Hansen and Houle 2008). The methodological approach for two of the research directives in this dissertation relies on this definition, as well as its related calculations of indices (Hansen and Houle 2008; Rolian 2009; Marroig et al 2009).

To measure the potential evolutionary consequences of trait integration at a population level, researchers depend on estimates of trait covariance within the context of the multivariate breeder's equation (Lande 1979; Hansen and Houle 2008; Rolian 2014),

$$R = h^2 S, \quad (1)$$

where R is the predicted change in the mean phenotype after selection, h^2 is the proportion of a trait's variance due to additive genetic factors (heritability), and S is the phenotypic difference between selected individuals and the trait population mean prior to selection (Falconer and Mackay 1996; Rolian 2014). Lande (1979) adapted this equation into a multivariate framework to allow for the estimation of the response to directional selection across correlated traits. Lande's equation is given by

$$\Delta\bar{z} = G\beta, \quad (2)$$

in which $\Delta\bar{z}$ is the observed change in population mean of a trait after selection has taken place, *G* is the genetic variance-covariance matrix, and β is the selection gradient, which is a vector of partial regression coefficients of relative fitness on each trait in a multivariate system (Lande 1979). The selection gradient essentially characterizes the direction and magnitude of selection on phenotypic traits. In this equation, *G* often is substituted with the proportional phenotypic variance-covariance matrix (P) (see Cheverud 1988; Roff 1995, 1996; Roseman 2012; Sodini et al 2018).

Hansen and Houle (2008) adapted this equation to estimate the capacity of a multivariate (i.e., multi-trait) population mean to respond to the directional selection. This measure, evolvability, provides an estimate of the potential for traits to evolve in phenotypic space, given their covariances with other traits and thus the potential constraints on patterns of variation characterized by the

population's VCV matrix (Rolian 2009). Evolvability can be understood in two ways. The first, as a relationship between the selection gradient (β) and the genotypic variance-covariance matrix (G):

$$e(\beta) \equiv \beta' G \beta \quad (4)$$

The second, as the length of the projection of evolutionary response vector ($\Delta\bar{z}$) on the selection gradient (β):

$$E(\beta) = |\Delta z(\beta)| cos\theta / |\beta| \quad (3)$$

where cos θ is the angle between the response vector and the selection gradient, and the other variables are the same as in Equation 2. This measure of multivariate evolvability is unique to each direction of selection in multivariate phenotypic space (Rolian 2009), therefore, evolvability is different for each β.

By subjecting the VCV matrix of a population to a number of random selection gradients, and calculating the average evolvability across all selection gradients, the evolutionary potential of a population can be estimated (Rolian 2009). The average evolvability is equivalent to the average character variance if the selection gradients are symmetrically distributed in p-dimensional space, with a mean gradient length of 1 (Hansen and Houle 2008). Thus, the average evolvability in p-dimensional space strongly correlates with the total variance in a population, which prevents the comparison of average evolvability across taxa with unequal variances (Rolian 2009, p. 105). However, this does not mean interspecific comparisons cannot be performed. A similar measure of evolvability, evolutionary flexibility, captures how closely the evolutionary response vector follows the selection gradient in phenotypic space (Marroig et al 2009; Rolian 2009), and is measured as the cosine between these two vectors

$$\text{Evolutionary flexibility} = \cos\theta = |\beta| \cdot |\Delta z(\beta)| \quad (4)$$

This is the portion of Hansen and Houle's evolvability that measures the direction of the response of the population mean to the selection gradient, regardless of the magnitude of evolutionary response (Rolian 2009). Essentially, evolutionary flexibility captures the orientation of evolutionary response in phenotypic space (Marroig et al 2009); it provides a measure of whether or not evolutionary

response is aligned with the direction of selection. This is a standardized measure and can be used to compare evolutionary responses across taxa. The relationship among these three equations is visually represented in Figure I.4.

One additional measure of evolvability is also used in this dissertation, this is a variant of conditional evolvability, the conditioned covariance. Conditioned covariance provides an estimate of the potential constraint a set of traits under stabilizing selection (x) imposes on a set of traits (y) to respond to directional selection. This provides an estimate of the conditioned genetic covariance of y given x (Hansen and Houle 2008) and can be thought of as a general measure of the genetic constraint among traits, or suites of traits. Conditioned covariance is calculated as

$$c(y|x) \equiv P_y - P_{yx}P_x^{-1}P_{xy} \quad (5)$$

in which P_y is the phenotypic variance in y, P_x is the phenotypic variance in x, and P_{xy} and P_{yx} are the column and row vectors of covariances between y and the traits in x (Hansen 2003; Hansen et al 2003; Hansen and Houle 2008).

Taken together, evolvability, and the indices that characterize different aspects of it, provide a robust approach to assessing how correlated traits may react when presented with a selective challenge. Measures of integration can present researchers with the strength of the covariances underlying correlated characters, and evolvability provides a depiction of how that covariance is structured. However, estimates of evolvability and integration only provide a framework for the evolutionary *potential* of traits, but are unable to assess through what processes traits ultimately *did* evolve and the effect this had on morphological variation. In this dissertation, these questions are assessed using phylogenetic comparative methods (PCM).

Phylogenetic Comparative Analysis: Testing Hypotheses of Adaptive Evolution

Phylogenetic comparative methods are routinely employed to assess the adaptive significance of organismal character states. These methods comprise an array of avenues by which to make inferences about organismal evolution, such as the evolutionary history of a character state across a

phylogeny. One of the challenges faced when doing interspecific comparative analyses, is that species are not independent; the shared, common evolutionary history among them can bias the perceived relationships among taxa (Butler and King 2004). Species can appear more similar when they share a selective regime, or selective factor, that drives them towards a common optimal trait value. Lineages comprising selective regimes may, in fact, be closely related, but may also inhabit similar environments.

While numerous methods have been proposed to address this problem (see Harvey and Pagel 1991), most of these methods employ a purely random model of evolution, Brownian motion, to assess against the evolutionary dynamics of traits presumed to evolve in response to directional selection (Harvey and Purvis 1991; Harvey and Rambaut 2000; Martins et al 2002). This practice is especially problematic for situations where the same selective regime is acting on different lineages, and when evolutionary changes on successive branches are correlated due to the persistence of selection (Felsenstein 1985). To address this issue, Hansen (1997) proposed using Ornstein-Uhlenbeck processes with multiple optima to model evolution. This has proven useful to test adaptive hypothesis of trait evolution (see Butler and King 2004; Uyeda and Harmon 2014), and is the approach taken in this dissertation.

Under Brownian motion (BM), trait evolution is modeled as a stochastic process motivated by neutral evolutionary forces. In contrast, an OU process models both drift and stabilizing selection (neutral processes) while allowing for multiple trait optima (Hansen 1997; Butler and King 2004; Uyeda and Harmon 2014). Essentially, changes in quantitative characters are decomposed into stochastic and deterministic parts. As such, an OU model has two terms:

$$d\bar{z} = \alpha(\theta - \bar{z}) + \sigma dW \quad (6)$$

Equation 6 expresses the change in a quantitative character, $d\bar{z}$, with respect to the intensity of random fluctuations in the evolutionary process (σ), the strength of selection (α), and the optimum trait value (θ). The term dW is a continuous-time Wiener process (think of it as "white noise"), and $\bar{z}$ is the trait mean (Uyeda and Harmon 2014). If $\alpha = 0$, the process reduces to a BM process. Refer to

Figures I.5 and I.6 (reproduced from Butler and King 2004) to see the effect of σ on the BM process and α on the OU process, respectively.

The OU process is associated with a variety of interpretations, one of which is pertinent to how the results of these models are interpreted in this dissertation. Hansen (1997) proposed that a variety of conflicting selective demands (e.g. environmental) are placed upon phenotypic traits, so that their current state is reflective of a compromise of those demands. Essentially, this interpretation views the OU process as a qualitative model that captures changes of adaptive peaks in an adaptive landscape and how populations respond to them (see Butler and King 2004). The evolution of a single lineage can, therefore, be described using an OU process, and this can be applied across a phylogenetic tree to infer evolutionary differentiation among taxa.

An advantage of this method is the ability to test adaptive hypotheses of phenotypic evolution across a phylogeny. However, this approach to model fitting is dependent on the quality of the hypotheses tested, as *a priori* may not adequately capture the dynamic nature of character evolution (Uyeda and Harmon 2014). To address this, Uyeda and Harmon (2014) developed a Bayesian approach to modeling OU processes on phylogenetic data that draws from the data itself to locate adaptive shifts along the phylogeny, without the need of *a priori* hypotheses. This method has the advantage of being able to identify unanticipated trends in organismal evolution.

In this dissertation I employ both traditional phylogenetic comparative methods to test the effect of factors such as selection-driven lineage divergence, habitat, diet, and locomotion on primate morphological diversification, and the unrestrained Bayesian approach to evaluate the ability of these hypotheses to accurately characterize primate evolution.

Materials Overview

Prior to discussing the three research questions addressed in this dissertation, it is useful to review the data used throughout this project. Methods are all based on the quantitative genetics

approaches discussed above, and additional data sources, such as the primate phylogenetic tree (Chapter IV) are reviewed in more detail for each study.

To examine the influence of trait covariance on primate shoulder girdle morphological variation, phenotypic data representing a broad sample of different primate taxa is necessary. I collected data from 1046 skeletonized specimens, representing 85 different primate species and three species of tree shrew (*Tupaia*). Specimens were housed in the following North American institutions: The University of Tennessee in Knoxville, TN, Museum of Comparative Zoology in Cambridge, MA, Field Museum of Natural History in Chicago, IL, Cleveland Museum of Natural History in Cleveland, OH, American Museum of Natural History in New York City, NY, and the National Museum of Natural History in Washington, D.C. The collective sample broadly represents species of prosimians, New World monkeys, Old World monkeys, and apes, that inhabit a range of environments and utilize different locomotor functions.

Three-dimensional coordinate data were captured from the left side of each specimen (if unavailable, the right side was measured) using an Immersion G2X MiscroScribe digitizer across five skeletal elements: basicranium, scapula, clavicle, humerus, and os coxa. Linear dimensions were calculated for traits with functional relevance, such as attachment sites for muscles spanning the shoulder girdle and basicranium. Linear dimensions for the five smallest genera (*Callithrix, Galago, Saguinus, Tarsius,* and *Tupaia*) were collected using Mitutoyo Absolute IP 67 sliding digital calipers, as the accurate placement of the microscribe was error-prone in these small taxa. All traits were measured in millimeters. Intra-observer error, assessed by a repeated measures ANOVA through three independent trials on all specimens, is less than three percent across all elements and taxa; a majority of measurements have less than one percent error.

More details about species sampled, sample sizes, and analytical methods are described in each of the ensuing chapters.

Research Questions and Dissertation Organization

This dissertation is comprised of three interrelated research projects. These projects broadly ask questions about the three topics introduced at the beginning of this chapter, and each is addressed in the following three chapters. Here are those questions, and their predicted outcomes based on the overview provided in this chapter:

1. *Is the evolvability of the shoulder girdle with the basicranium smaller than estimated evolvabilities of the shoulder or basicranium with the pelvis? Is the shoulder less evolvable when the basicranium or pelvis is under stabilizing selection?* (Chapter II)

   I predict that the developmental and mechanical covariances among the traits of the basicranium and shoulder girdle will constrain the ability of these regions to independently respond to directional selection.

2. *Are the evolutionary relationships between the shoulder girdle, basicranium, and pelvic girdle identified by Agosto and Auerbach (in review) present and consistent among primate taxa? Is there evidence for the genetic covariances observed to have affected trait evolution among primates?* (Chapter III)

   I predict that anatomical regions with clear functional and/or developmental relationships, such as the basicranium and shoulder girdle, will have greater magnitudes of integration and lower flexibility than functionally unrelated traits with each taxon. I anticipate that these patterns of covariance will be similar across taxa, while the measures of integration and flexibility themselves will differ across taxa, with potentially more independence among apes than monkeys. Further, traits associated with shared muscle attachments or functional relationships will have greater covariance and will be highest between pairs of anatomical regions exhibiting the lowest flexibility.

3. *Researchers hypothesize that responses to selection motivated by habitat, by diet, or by locomotion, best explain diversification in morphology; is there support for these models among traits of the shoulder girdle, basicranium, pelvic girdle, and humerus? Has the evolution of morphological diversity among primates been motivated by size, or size-related shape differences in traits? Do anatomical regions evolve in response to selection?* (Chapter IV)

   I predict that traits that exhibit more evolutionary covariance, as identified in the first two research directives, will follow similar evolutionary trajectories.

Following the investigations of these questions, I provide a synthesis of the results in a final Conclusions chapter (Chapter V). This chapter will examine the key points from each research directive in detail, their broader implications for our understanding of the evolution of primate morphological variation, as well as a discussion of the study limitations and avenues for future research.

Significance of Research

Overall, the significance of the research presented in this dissertation is to better understand the evolution of the morphology of an anatomical region within the context of its development, function, and surrounding tissues, as explored through the analysis of genetic covariances in a quantitative genetic framework. Evolutionary studies of primate shoulder skeletal morphology often examine skeletal traits in isolation, thus implicitly assuming they evolve independent of other anatomical regions. This dissertation research provides a model of primate shoulder girdle morphological evolution that considers the developmental and functional covariances it shares with the basicranium, pelvic girdle, and to a lesser degree, the humerus. Together, the whole of this research elucidates how the functional and developmental covariances among these anatomical regions may have shaped the morphological variation in the primate shoulder girdle. It adds to the understanding

of shoulder girdle morphological variation among primates by examining how the evolution of trait variation is explained in the context of evolutionary relationships among taxa versus hypothesized selection factors. A goal of this dissertation is to illustrate the need to include evolutionary covariant traits in models of evolution for a particular element or region, and the potentially misleading understanding of evolution that results from examining traits in isolation. This work furthers the field by improving our understanding of how anatomical regions interact during morphological evolution through a process-based approach. Overall, the results of my dissertation promote the application of a multivariate approach to modeling trait evolution, and advocates for a "whole-organism" approach to studying the evolution of trait complexes, especially those of the primate shoulder girdle.

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Appendix I

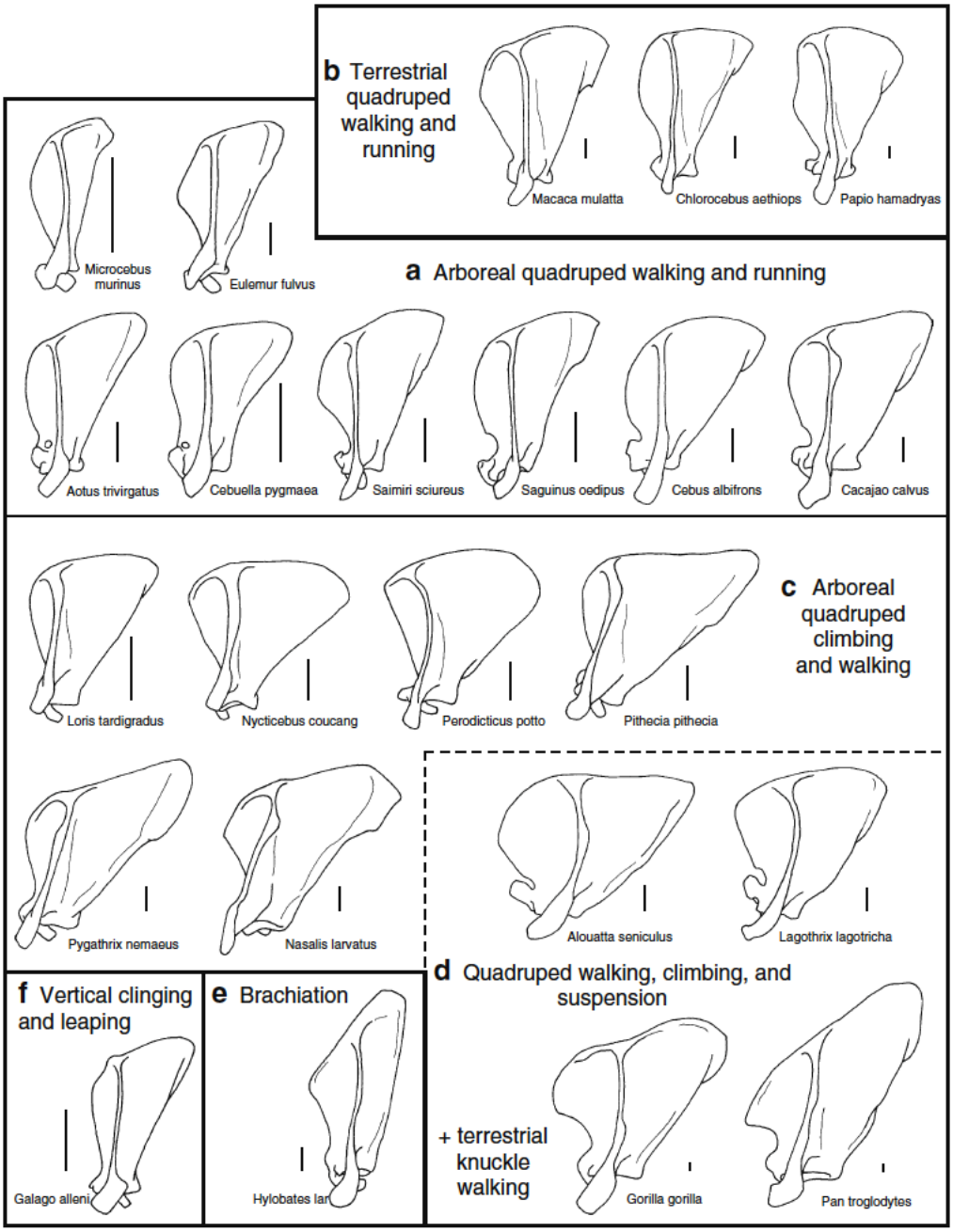


Figure I.1. Morphological variation and associated locomotor modes among select primates. Scale bar in each illustration corresponds to 1cm. (**a**) Arboreal quadruped walking and running. (**b**) Terrestrial quadruped walking and running. (**c**) Arboreal quadruped climbing and walking. (**d**) Quadruped walking, climbing, and suspension. (**e**) Brachiation. (**f**) Vertical climbing and leaping. Figure reproduced from Schmidt and Krause (2011: p. 98).

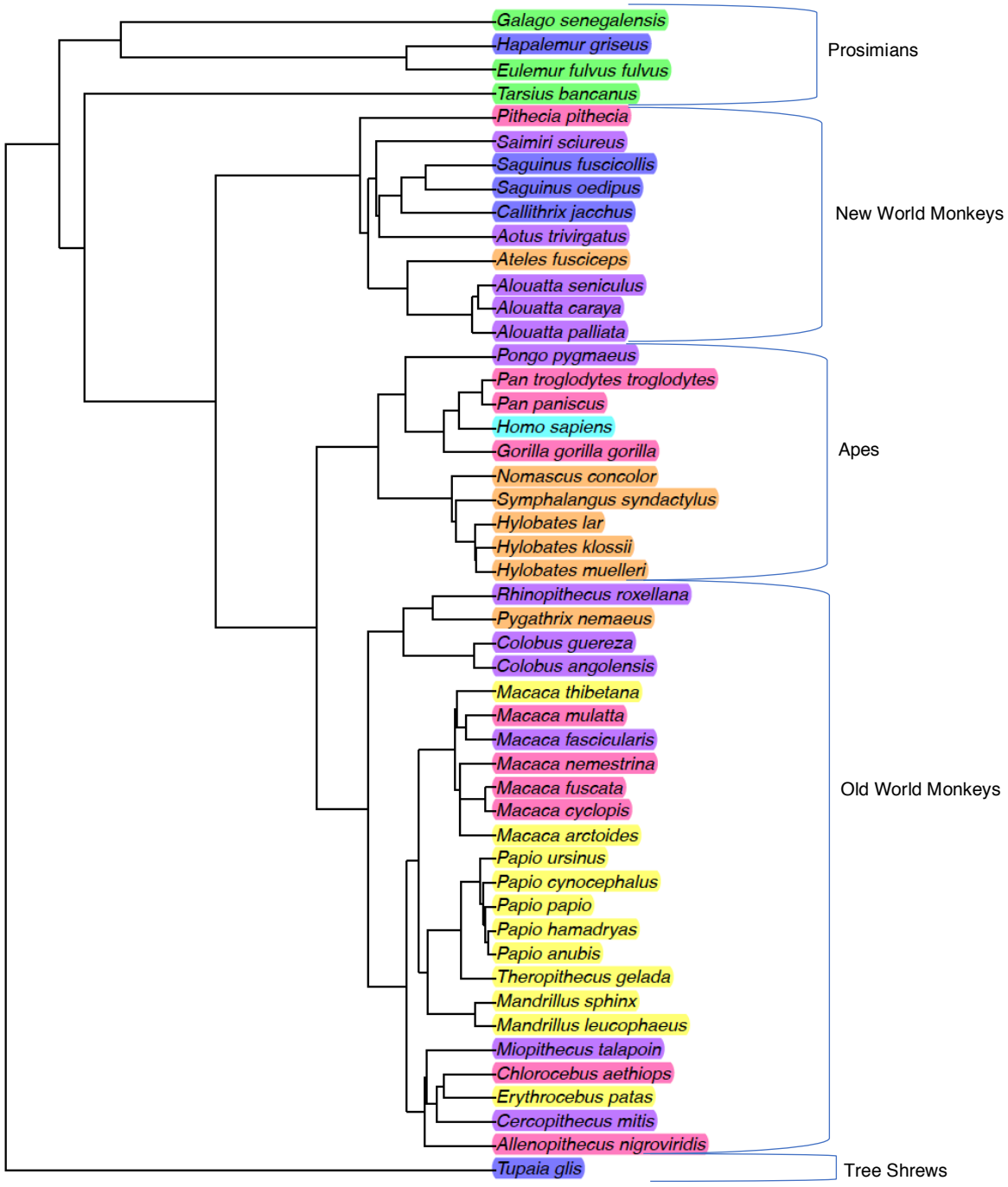


Figure I.2. Primate phylogeny use throughout this dissertation. Brackets indicate major groups of primates (New World monkeys, Old World monkeys, Apes, and Prosimians) and the outgroup (tree shrews), whereas species names are highlighted according to locomotor behavior. The following locomotor behaviors are mapped: saltatorial (green), scansorial (blue), semiterrestrial quadruped (pink), arboreal quadruped (purple), brachiation/suspension (orange), bipedalism (light blue), terrestrial quadruped (yellow).

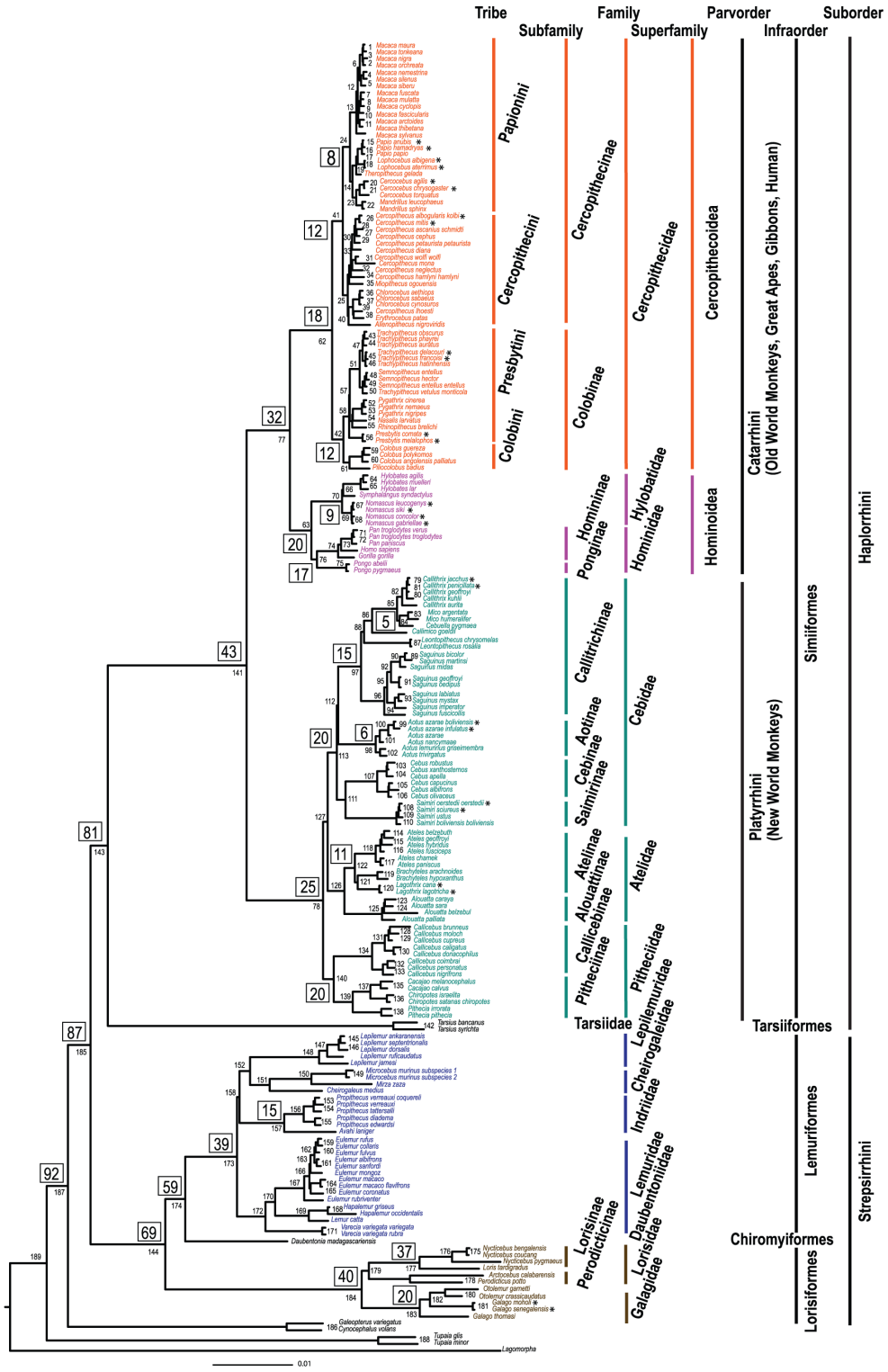


Figure I.3. Molecular phylogeny of 186 primates and two outgroup orders of Scandentia, Dermoptera, and rooted by Lagomorphia. Numbers in boxes represent estimate divergence times for major nodes. Image reproduced from Perelman and colleagues (2011: p. 11).

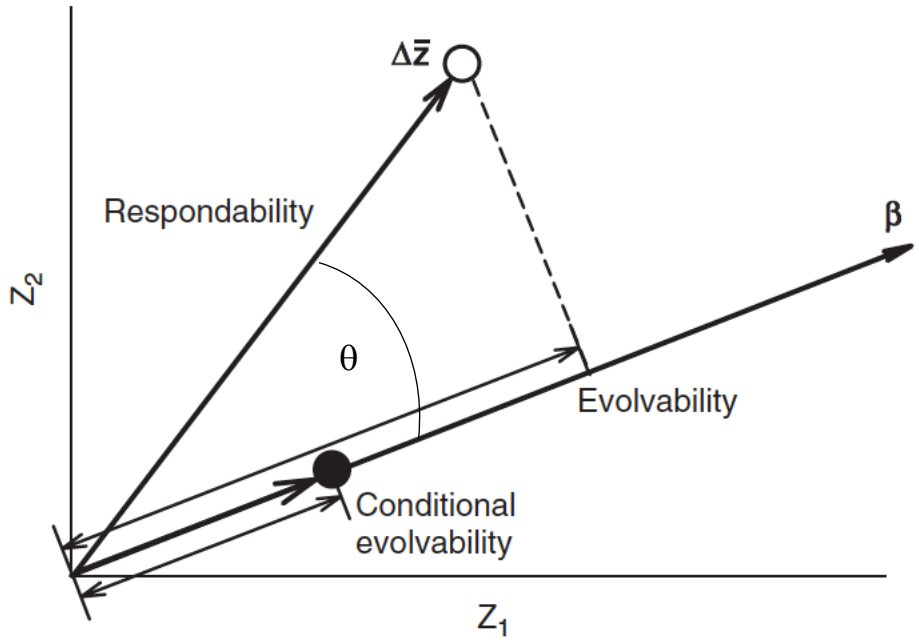


Figure I.4. Measures of selection response. Circles demonstrate the response to selection in two traits, z_1 and z_2, in response to two scenarios. The open circle is the response to the selection gradient (β). Respondability is the predicted response to selection. Evolvability is the length of response in the direction of β. The closed circle shows selection response under a scenario of stabilizing selection around the direction of β; the length of the constrained response is conditional evolvability. The angle between the response vector and β, is denoted by θ. Image adapted from Hansen and Houle (2008: p. 1204).

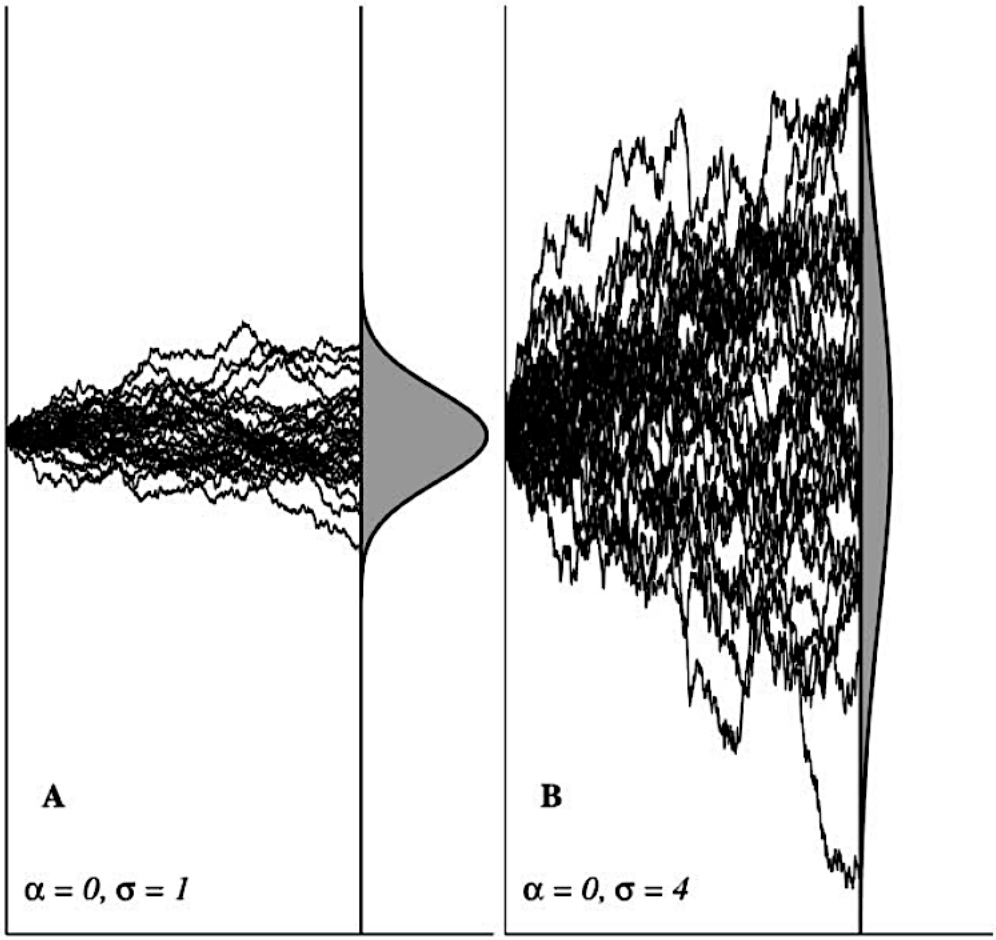


Figure I.5. Effect of varying σ in a Brownian motion (BM) process. Image reproduced from Butler and King (2004: p. 685).

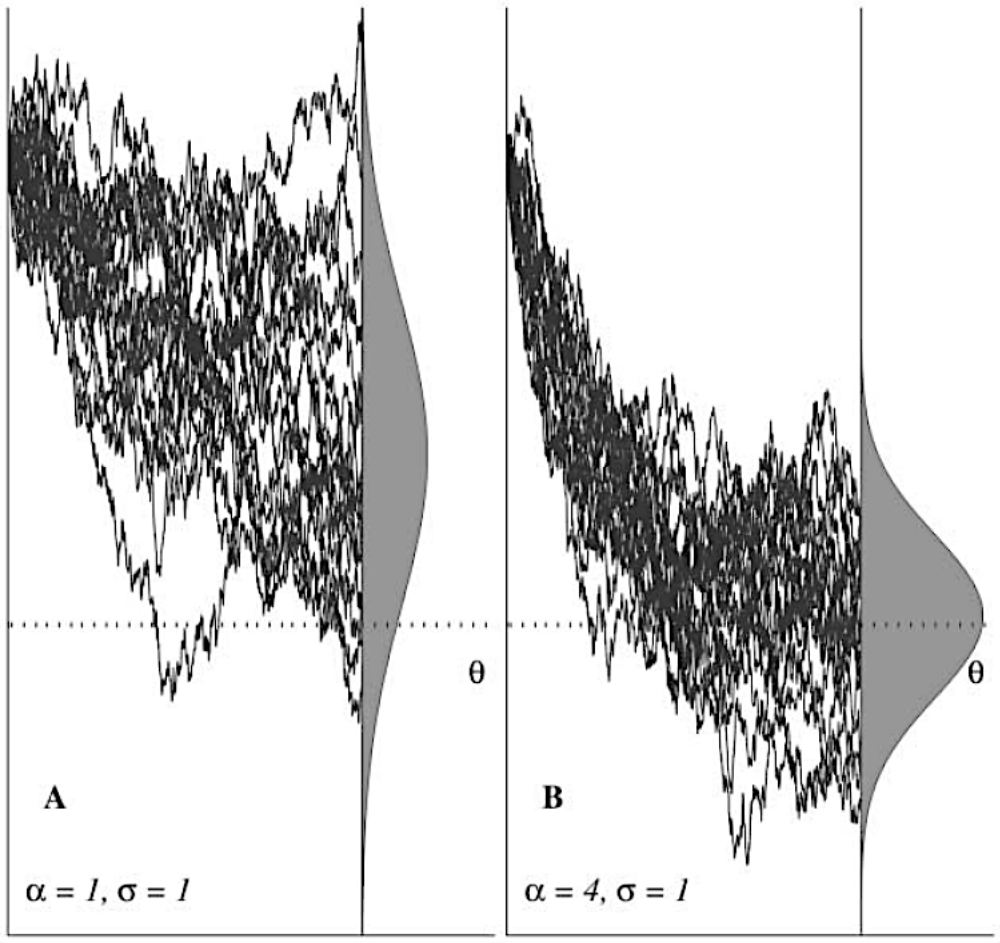


Figure 1.6. Influence of the strength of selection (α) and optimum trait value (θ) on a trait evolving under an Ornstein-Uhlenbeck (OU) process. Large values of α imply stronger selection and therefore, more rapid approach to the optimum (dotted line). Image reproduced from Butler and King (2004: p. 685).

Transition from Chapter I to Chapter II

In Chapter I, I argue that the morphological variation in the primate shoulder girdle, especially the scapula, can be attributed to the functional demands of the upper limb, and is not an artifact of the phylogenetic relationships among taxa. Patterns of morphological variation are often attributed to the selective pressures associated with locomotor function and behavior, resource acquisition (diet), and habitat. These pattern-based studies are often conducted on individual skeletal elements (the scapula), individual traits, or fragmentary remains. This practice implicitly assumes the scapula, and its traits, evolve only in response to their own, direct selective pressures. However, the scapula shares functional and developmental relationships with other anatomical regions, such as the basicranium, pelvis, and humerus, that may affect how it may respond to selective pressures.

In Chapter II, I, with B. Auerbach as coauthor, address this dissertation's first research question by evaluating the potential for traits of the shoulder girdle, basicranium, and pelvic girdle to constrain each other during evolution using a sample of colobus monkeys, tamarins, and rhesus macaques. We use quantitative genetic methods to assess whether there are differences in the potential constraint among pairs of anatomical regions, such as the shoulder girdle and basicranium versus the shoulder girdle and pelvic girdle, when these groups are subjected to directional selection. Through further exploration we assess whether one anatomical region within a paired group exerts greater potential constraint on the other by estimating the ability of the traits in one anatomical region to respond to directional selection when the traits in the other anatomical region are under stabilizing selection.

CHAPTER II

EVOLVABILITY AND CONSTRAINT IN THE PRIMATE BASICRANIUM, SHOULDER, AND HIP AND THE IMPORTANCE OF MULTI-TRAIT EVOLUTION

A version of this chapter has been prepared for publication by Elizabeth R. Agosto and Benjamin M. Auerbach as:

Agosto ER, Auerbach BM (2019) Evolvability and constraint in the primate basicranium, shoulder, and hip and the importance of multi-trait evolution. *In review*.

This chapter is a research chapter. The text of this chapter regularly uses the pronouns "we" and "our" to reference the contributions of my coauthor, Dr. Benjamin M. Auerbach. It should be noted, however, that in addition to conducting a majority of the research and performing the analyses, I am the author in the ordinary sense.

Abstract

The scapula shares developmental and functional relationships with traits of the basicranium, vertebral column, humerus, and clavicle. As part of a limb girdle, it also shares analogous characteristics with the pelvis. Despite these relationships, analyses of primate shoulder girdle evolution often focus on traits of the scapula in isolation. Such analyses may lead to spurious conclusions, as they implicitly model the scapula as evolving in isolation of other skeletal elements, and thus, the shoulder girdle in isolation of other anatomical regions. Traits of the shoulder girdle share genetic covariances with each other, as well as potential covariances with the dimensions of other skeletal elements. To create accurate models of shoulder girdle evolution, it is imperative to account for the constraints imposed by these sources of covariance. Here, we use evolutionary quantitative methods to test a model in which shoulder girdle morphological evolution is influenced by its developmental and functional covariances with the basicranium in the genus *Colobus*. This evolutionary relationship is also assessed with the morphology of the pelvis to provide context to the evolutionary covariance among traits of the basicranium and shoulder girdle. Our results show that the ability of the shoulder girdle to respond to directional selection is affected by both the basicranium and pelvis, and vice versa. We further propose that the shoulder girdle and basicranium may be examples of developmental, mechanical, and genetic covariances among traits that manifest

an evolutionary suite of mutually constrained morphologies, i.e., a functional trait complex. We demonstrate novel evolutionary relationships among the shoulder girdle and basicranium that affect not only primate shoulder girdle evolution but have broader implications for modeling trait evolution across the skeleton.

Introduction

Traits within an organism often cannot evolve independent of other traits due to evolutionary integration (Ackermann and Cheverud 2000; Rolian et al 2010; Grabowski and Roseman 2015; Roseman and Auerbach 2015; Savell et al 2016). This evolutionary covariation among traits arises from integration in response to genetic, developmental, or mechanical causes, among others (Felsenstein 1988; Cheverud 1996). Such relationships among traits can be emergent through pleiotropy (Wagner 1996), but can also arise through developmental processes among adjacent or related tissues and cells (Young 2004; Boughner 2016). Despite the prevalence of evolutionary covariance, researchers often evaluate traits with the implicit assumption of independent evolution. One example of this tendency is the study of primate shoulder girdle evolution, where researchers often focus on the morphology of the scapula, or even its individual traits, (Schultz 1930, 1950; Ashton and Oxnard 1964ab; Ashton et al 1965; Oxnard 1963, 1967, 1969; Roberts 1974; MacLatchy et al 2000; Larson et al 2007; Feuerriegel et al 2017; Selby and Lovejoy 2017).

The scapula shares both developmental and functional relationships with the clavicle, humerus, basicranium, and vertebrae. Similar tissue contributions during ontogeny shape these skeletal elements (Matsuoka et al 2005; Huang et al 2006; Durland et al 2008; Valasek et al 2010), such as post-otic neural crest (PONC), which migrates caudally from the cranium to form muscle attachments and regulate the mechanisms for muscle organization and connectivity between the head and shoulder (Matsuoka et al 2005). Ultimately, these elements serve as attachment points for, and are therefore linked by, muscles responsible for movement at the shoulder, neck, and upper limb (Diogo and Wood 2012). In addition to the shared development and function of these

anatomical regions, the scapula is also analogous to the pelvis, as both are limb girdles (Sears et al 2015). Genetic covariances underlie all of these relationships, and these covariances among traits potentially result in non-independent evolution of morphologies.

Thus, traits exist within integrated groups, and so individual trait responses to selection are a combination of relationships with fitness independent of any other characteristic, and the correlated responses that trait has with other, genetically covarying traits (Rolian et al 2010). These genetic correlations among traits can mask the strength and direction of natural selection that shaped the observable variation among morphological traits; as a result, it would be potentially inaccurate to interpret directional selection from the mean trait differences among populations alone (Lande and Arnold 1983; Houle 1991; Arnold 1992; Hansen and Houle 2008). This has been demonstrated in humans for the bones of the cranium (Katz et al 2016), pelvis (Grabowski and Roseman 2015), hands and feet (Rolian et al 2010), and body shape and size (Roseman and Auerbach 2015; Savell et al 2016). As we note above, the scapula itself has developmental and mechanical processes that shape its morphology that are also associated with traits within other anatomical regions.

Developmental covariance is often difficult to ascertain from adult morphology in the absence of experimental research designs (Hallgrímsson et al 2009), which can be problematic for 'evo-devo' based models of trait evolution. This issue can be addressed through the examination of traits with shared mechanical function. The emergent functional covariance of traits arises through developmental processes (Cheverud 1988), as developmental units are replaced by functional units through ontogeny (Huseynov et al 2017). Thus, adult morphology reflects both the mechanical and developmental relationships among traits, as the structure of integration cannot be decomposed into its constituent parts (Zelditch et al 2009). Traits that are linked through shared mechanics can impact organismal fitness by directly affecting the performance of a function, which may, therefore, have evolutionary consequences for these traits (Arnold 1983; Wainwright 1988). The basicranium and the shoulder girdle are linked through mechanical function by the layers of connective and muscle

tissue that physically link these regions; these muscular relationships are fairly conserved among primates (Diogo and Wood 2012; Richmond et al 2001).

Developmental and functional sources of covariation are therefore important in shaping morphological evolution. The shoulder girdle has both with adjacent anatomical regions, yet the evolutionary consequences of these relationships has not been explored in primates. To create accurate models of shoulder girdle evolution, it is essential to account for the constraints imposed by these sources of covariance. To address this, we test a model in which the morphological evolution of the shoulder girdle is influenced by its functional and developmental covariances with the basicranium. Specifically, we assess whether the ability of the shoulder girdle to respond to the force of directional selection would be constrained by its covariances with traits of the basicranium. We hypothesize that the developmental and mechanical covariances among the traits in these regions thus manifest an evolutionary and functional suite of mutually constrained morphologies, which we propose below as a potentially testable model of specific modularity, the *functional trait complex*.

To examine our model of non-independent shoulder girdle evolution, we examine whether the functional and developmental relationships between the scapula, clavicle, and basicranium are reflected in genetic covariances among their morphological traits that in turn, may constrain the ability of these traits to respond to directional selection. Two questions are asked: (i) Is the evolvability (Hansen and Houle 2008) of the shoulder girdle with the basicranium smaller than estimated evolvabilities of the shoulder girdle or basicranium with the pelvis? (ii) Is the shoulder girdle less evolvable when the basicranium or pelvis is under stabilizing selection? To assess these questions, we obtained associated cranial and postcranial linear dimensions from a sample of 69 adults from the *Colobus* genus. Additional analyses on the same traits were performed on macaques and tamarins. We also include pelvic dimensions in our analysis, given the functional and developmental parallels between the shoulder and pelvic girdles, and to ascertain if there is a privileged potential evolutionary relationship between traits of the shoulder girdle and the basicranium compared with the shoulder and pelvis, or basicranium and pelvis (which should exhibit

the most evolutionary independence). Measurements are mean-standardized prior to analysis. We calculated measures of evolvability and conditioned covariance following the equations of Hansen and Houle (2008). Evolvability indices are estimated using 1000 simulated random selection gradients. Lower evolvability indicates greater evolutionary covariance among traits, and lower conditioned covariance indicates greater constraint among anatomical regions. Our results elucidate evolutionary relationships not previously explored and refine the model of shoulder girdle evolution in primates, while suggesting broader considerations for the selection of traits to model trait evolution in all taxa.

Materials and Methods

We measured all available adult *Colobus* genus specimens in North American museum collections with both cranial and post-cranial skeletal elements necessary for this study, giving a total sample size of 69 individuals: *C. angolensis* (n=4), *C. guereza* (n=53), *C. polykomos* (n=9), and *C. satanas* (n=3). All individuals were adults, as indicated by fully fused epiphyses and spheno-occipital sutures; missing teeth in multiple individuals prevented the use of dental eruption for aging. Due to missing data, these samples are not sufficiently large enough by themselves to accurately estimate evolvability statistics. Pooling species was deemed reasonable as DNA analyses indicate the African colobine monkeys represent a monophyletic assemblage, with genus *Colobus* being more similar within itself than with the other two genera (*Piliocolobus and Procolobus*) (Wang et al 2012). Additionally, ANOVA results indicate no significant difference in the morphological traits among these species ($p > 0.05$; see Table SI.1; all tables and figures are located in Appendix II and Supplementary Information I). Preservation of the crania and os coxa prevented the capture of certain measurements used in this study for several specimens. Due to the non-random nature of this missing data, missing values were not estimated (Allison 2002; Little and Rubin 2002). When the missing data was accounted for, our effective sample size on our pooled sample was reduced to a minimum of 37 and a maximum of 50 individuals. These sample sizes are adequate to accurately

estimate evolvability statistics per the recommendation of Grabowski and Porto (2017), who specify $n \geq 36$ with 10 traits, and $n \geq 37$ with 15 traits.

Interlandmark distances for 21 dimensions from the basicranium, scapula, clavicle, and ilium were calculated from three-dimensional coordinates (see Figure SI.1 and Tables SI.2 - SI.4) captured using an Immersion G2x MicroScribe digitizer. Each coordinate was captured three, non-consecutive times by ERA and subjected to a repeated measures ANOVA (RMANOVA) to assess intra-observer error. Results of the RMANOVA indicated no significant difference among measurement rounds ($p > 0.05$), with an error of less than 1.2mm, so all dimensions were included. All interlandmark distances were mean-standardized within sex prior to all analyses. Both males and females were included in all analyses. Differences due to sex were accounted for by applying a multivariate analysis of variance (MANOVA) and calculating the variance-covariance (VCV) matrix from the resulting residuals.

Body size has been shown to affect how morphological traits respond to directional selection, and can therefore affect estimates of evolvability and obscure non-size related evolutionary relationships among traits (Porto et al 2013). To account for the effect of size on our analyses, we perform each analysis using the VCV matrix derived from our sex-scaled data, and a noise-corrected VCV. Following Porto and colleagues (2013), the size corrected VCV matrix (R) was obtained from the following relationship

$$R = P - VV' \quad (1)$$

where P is the phenotypic VCV matrix, V is the size-related eigenvector, and V' is it's transpose. Estimation of the VCV matrix can be difficult in biological systems due in part to issues with sample size or measurement error; this becomes increasingly difficult when matrix inversion is required (Twede and Hayden 2004; Marroig et al 2012). Small eigenvectors within the VCV matrix will reflect “noise” arising from measurement error more than meaningful variance, and thus transposes of these matrices will exaggerate the effects of the smallest eigenvectors. We control for noise in our VCV matrix estimates by locating the median of the variance of the second derivative derived from

the absolute value of eigenvalues, removing all values below the median, replacing those values with the median eigenvalue, and recalculating the new VCV matrix using these new eigenvalues (Twede and Hayden 2004; Marroig et al 2012). All analyses were performed on noise-controlled VCV matrices.

We used Hansen and Houle's (34) equations to calculate measures of evolvability and conditioned covariance among three anatomical regions: basicranium (skull), shoulder (scapula and clavicle), and pelvis (os coxa). Hansen and Houle's methods are derived from Lande (1979) and colleagues' (1983) equation for the estimation of the average multivariate response to directional selection

$$\Delta\bar{z} = \boldsymbol{G}\beta \quad (2)$$

where $\Delta\bar{z}$ is the average response to selection, $\boldsymbol{G}$ is the genetic variance-covariance matrix, and β is the directional selection gradient. We used the within-group phenotypic variance-covariance ($\boldsymbol{P}$) matrix as a substitute for the $\boldsymbol{G}$ matrix, as most studies indicate the $\boldsymbol{G}$ and $\boldsymbol{P}$ matrices are close to being proportional for morphological traits (Cheverud 1988; Roff 1995, 1996; Roseman 2012; Sodini et al 2018).

Hansen and Houle's (2008) approach uses the selection gradient to estimate the multivariate evolvability. Within the context of Lande's equation, evolvability is the capacity of a multivariate population mean to respond to the strength and direction of selection (Rolian 2009). Essentially, evolvability provides a measure of the potential for a group of traits to respond to directional selection; limitations to trait response to directional selection are imposed by the covariances among traits. Greater evolutionary covariance among traits is indicated by lower measures of evolvability. Evolvability $e(\beta)$ is calculated as

$$e(\beta) \equiv \beta' P \beta \quad (3)$$

where variables are the same as in Equation 2. The conditioned covariance provides a measure of the potential constraint a set of traits under stabilizing selection (x) imposes on a set of traits (y) to respond to directional selection. The conditioned covariance provides an estimate of the conditional

genetic covariance of y given x (Hansen and Houle 2008), and can be thought of as a general measure of the genetic constraints among traits, or suites of traits. Conditioned covariance is calculated as

$$c(y|x) \equiv P_y - P_{yx}P_x^{-1}P_{xy} \quad (4)$$

where P_y is the phenotypic variance in y, P_{xy} and P_{yx} are the column and row vectors of covariances between y and the traits in x, and P_x is the variance matrix of x (Hansen and Houle 2008; Hansen 2003; Hansen et al 2003). In this equation, x denotes those traits being held constant by stabilizing selection, and y denotes traits under directional selection. Conditioned covariance is calculated for each pairing of anatomical regions, with each region acting as both x and y.

Five traits from each anatomical region (basicranium, shoulder girdle, and pelvic girdle) were used to minimize bias on our measures of evolvability. Thus, each analysis of evolvability used a total of fifteen interlandmark distances apportioned equally to the three anatomical regions. Indices of evolvability were calculated for the following groupings of anatomical regions: basicranium and shoulder girdle, shoulder and pelvic girdles, and basicranium and pelvic girdle. Evolvability was also estimated among all three groupings combined, as our sample size is adequate to estimate this measure using 15 traits ($n \geq 37$). Analyzing groupings of anatomical regions allowed us to assess how suites of traits from different anatomical regions affect each other during evolution. To assess the effect of trait choice on our measures of evolvability, 13 different configurations of traits among regions were assessed. Traits that correlated highly with other traits ($r > 0.8$) (Table SI.5), were not included together in the same trait configurations for each analysis. Results on the following configuration of traits are presented in the main body of this paper: basicranium (NR, SCM, SNL, FMW, FML); shoulder girdle (SSL, SBL, VB, GW, CLML); pelvis (AMIB, RAH, ASL, LIH, AW) (see Figure II.1). All other trait configurations for each anatomical region and analysis can be found in the Table SI.6.

To calculate the average evolvability for each grouping of traits in phenotypic space, we subjected the phenotypic variance-covariance matrix to 1000 symmetrically distributed, randomly

generated selection gradients. Selection gradients, which are vectors of partial regression coefficients of relative fitness on each trait in a multivariate system, summarize the direction and magnitude of selection acting on each trait (Lande and Arnold 1983; Hansen and Houle 2008; Rolian 2009). These selection gradients were generated using the 'evolvability' package in R by independently sampling each element of the selection gradient from a univariate, zero-mean Gaussian distribution with a unit variance and normalizing each vector by a unit length (Bolstad et al 2014). 95% confidence intervals (CI's) for both analyses were calculated by resampling each group of traits 1000 times with replacement, calculating the evolvability and conditioned covariance for each resampling, and deriving the 95% interval of the resulting distribution.

All analyses are performed in the R statistical environment (https://cran.r-project.org) using custom scripts and the 'evolvability' package (Bolstad et al 2014). Both data and code are available upon request.

Results

Table II.1 presents a description for each of the fifteen traits used in this study (see Figure II.1). ANOVA results indicate no significant difference between the four species in the sample, however, there is a significant difference between the sexes. Species were therefore pooled within each sex, and then measurements were mean-standardized within sex to allow all individuals to be analyzed together.

Traits were chosen to represent three anatomical regions: the basicranium, the shoulder girdle, and the pelvic girdle. These regions were placed into four groupings for the analysis of evolvability: all fifteen measures (basicranium, shoulder, and pelvis); measures of the shoulder girdle and the basicranium; measures of the shoulder girdle and the pelvic girdle; and measures of the basicranium and pelvic girdle. Table II.2 presents the average estimated evolvability for each grouping of traits for both sex-scaled and noise-corrected data. The mean estimated evolvability for all traits is between the highest and lowest evolvability estimates for pairwise trait groupings for both data treatments.

This is expected, as this analysis incorporates the covariance among all anatomical regions. For both the sex-scaled and noise-corrected data, the shoulder girdle – pelvic girdle grouping has the lowest estimate of evolvability. For the sex-scaled data, the estimate of evolvability is lower for the basicranium – pelvic girdle grouping than the basicranium – shoulder girdle grouping. However, this relationship is reversed when the variance due to size is removed. Our analysis on size corrected data shows that the basicranium – shoulder girdle is slightly less evolvable than the basicranium – pelvic girdle groupings. We interpret this as these regions having similar abilities to respond to directional selection. The 95% confidence intervals (CIs) among the three paired groupings of traits overlap, so while there is a pattern in how these three regions affect each other's potential to respond to directional selection, it is not statistically significant.

Estimates of conditioned covariance were calculated for each pairwise grouping of anatomical regions used in the estimation of evolvability. We executed each pairwise analysis twice, with each anatomical region acting as the traits held constant by stabilizing selection (x) and those responding to directional selection (y) (see Methods for explanations of *x* and *y*), to assess whether one region imposes more constraint on another. The conditioned covariance among anatomical regions are presented in Table II.3. The 95% CIs overlap for these analyses—meaning they are statistically the same—and so we focus on the patterns presented in the results. For both the sex-scaled and noise-corrected data, we observe that the shoulder girdle is less evolvable if the pelvic girdle is under stabilizing selection than when the basicranium is under stabilizing selection. The pelvic girdle is less evolvable when the shoulder girdle, compared to the basicranium, is under stabilizing selection. The basicranium is less evolvable if the shoulder girdle is under stabilizing selection, compared to the pelvic girdle. We observe mutual constraint among anatomical regions, but the basicranium is more evolvable overall. Our results show that the basicranium is not constrained by these other anatomical regions, rather, the basicranium imposes evolutionary constraint on both the shoulder and pelvic girdles. These results indicate the presence of hierarchical patterns of evolutionary constraint among anatomical regions.

As a subset of the total number of traits that were measured for each anatomical region (See Tables SI.2 and SI.3 and Figure SI.1) were used in these analyses, we repeated the estimation of evolvability and conditioned covariance using different compliments of traits within each anatomical region (Table SI.6). This was to test whether we introduced a bias in the traits we chose to include for each anatomical region. Such a bias would be revealed through inconsistencies in the results of these analyses. A similar trend in the patterns of evolvability and conditioned covariance is observed among all trait configurations (see Tables SI.7 and SI.8), suggesting these evolutionary relationships are not limited to only select traits from these anatomical regions. To further assess whether our results were isolated to the genus *Colobus*, we performed all analyses on two additional primate genera: *Macaca* and *Saguinus*. The results for these genera are consistent with, but not as pronounced, as those observed in *Colobus* (Tables SI.9 and SI.10). We also observe that the conditioned covariance among the basicranium and shoulder girdle is more similar in *Macaca,* suggesting mutual constraint among these regions.

Discussion

Our results demonstrate potential evolutionary covariance among traits of the basicranium and shoulder girdle that result in their mutual evolutionary constraint. While the evolvability of the shoulder girdle is similarly constrained by the pelvic girdle, the demonstrated evolutionary covariance of the shoulder girdle with the basicranium is a novel result, even though developmental and mechanical relationships would anticipate such a relationship between these regions. Any evolutionary covariance between the cranium and postcranial elements in primates is heretofore unprecedented. The basicranium is not traditionally considered functionally or evolutionarily covariant with the shoulder girdle, as the base of the skull is not adjacent to the scapula or clavicle, and, outside of some developmental relationships (e.g., PONC), it has separate developmental pathways. And yet, its evolution is tied to these other bones. Therefore, we provisionally answer our two questions raised in the Introduction: (i) the ability of the shoulder girdle and basicranium together

to respond to directional selection is at least as limited as the shoulder girdle with the pelvis; (ii) the shoulder girdle is equally constrained to respond to directional selection by the basicranium and the pelvis, and vice versa. We further conclude that the shoulder girdle and basicranium are examples of what we propose as a functional trait complex, where the developmental and functional integration among traits, in concert with their underlying genetic covariances, create an emergent anatomical complex in which traits mutually constrain independent responses to directional selection. As we discuss further below, these complexes remain hypothetical, but set up future studies that could seek shared regulatory genes or other genomic evidence for shared development, as well as studies incorporating the comparative method.

Mutual constraints in responding to directional selection among the shoulder, basicranium, and pelvis

The evolvability results for the limb girdles were expected. Due to the developmental analogous nature of the limb girdles, evolutionary relationships have previously been proposed for these regions (Sears et al 2015), as they have similar general functions and share many of the same developmental genetic pathways (in addition to similar germ-cell layer origins). It is possible that some of the evolutionary covariance between these regions is also motivated by shared mechanical functions, as the species we chose to study are all quadrupeds.

However, as we note above, no such relationship has been anticipated previously between the basicranium and shoulder girdle. The estimated evolvabilities of the basicranium–shoulder girdle and shoulder girdle–pelvic girdle trait groupings are similar, and significantly lower than the evolvability of all traits combined. Thus, the shoulder girdle is mutually constrained by both the basicranium and the pelvic girdle, and vice versa, and more than the other two groupings we tested. However, we do not know whether the shoulder girdle is potentially more constrained by the basicranium or the pelvis, as our measures of evolvability and conditioned covariance are reporting slightly different patterns. While the question of whether the shoulder girdle is more mutually constrained by the

basicranium or pelvic girdle remains unanswered, our results demonstrate that traits of the basicranium and shoulder girdle and traits of the limb girdles are equally labile in their ability to evolve.

We note that the sample size for these analyses is slightly smaller than recommended by Grabowski and Porto (2017) for measures of conditional evolvability, though we implemented methods to correct for possible biases in calculation of conditioned covariance. Without an adequate sample, measures of conditional evolvability (and thus likely conditioned covariance) estimates are negatively biased, which result in smaller estimated values and perceived stronger genetic constraint among traits (Grabowski and Porto 2017). It is therefore possible that our reported measures of conditioned covariance are biased downward, and therefore lower than the actual conditioned covariances among these traits. Nonetheless, this potential bias would affect all trait groupings alike, thus, our conclusions based on the relative results among these groupings still stand.

One additional confounding factor in our analysis is the effect of body size in shaping the results. Though we scaled by sex and individual measurement means prior to analyses, it is possible that some of the evolvability results we report were motivated by overall size. For this reason, we conducted an additional set of analyses to examine the evolvability of the three anatomical regions under consideration against five dimensions of the humerus (Table SI.11). While shared function links the humerus and the shoulder girdle, the humerus shares no developmental or functional aspects with the basicranium and pelvis. We find that the highest evolvability estimates are associated with the humerus and basicranium, and the lowest are found between the humerus and shoulder girdle. While this does not exclude the potential for size to affect our results, these additional results increase our confidence that the reported evolvability and conditioned covariance estimates reflect real evolutionary potentials.

Functional trait complexes as a framework for modeling evolutionary covariances with the shoulder

In the introduction, we proposed that emergent anatomical complexes arise from developmental, functional, and genetic evolutionary covariances. Unlike modules (Wagner 1996; Schlosser and Wagner 2004; Wagner et al 2007), which are context-dependent and may be applied to multiple levels of organization (cells, tissues, individuals, or populations), functional trait complexes would be limited, and typified specifically by developmental and functional relationships that together yield evolutionary constraint. Developmental processes maintain functional associations among traits, and it is the integration of these two determinants of variation that affect how traits evolve (Hallgrímsson et al 2009). We propose this as the basis for a testable framework for modularity.

Models that predict how variation can be generated or structured through developmental processes can be used to make hypotheses of the patterns of morphological diversity and trait covariance (Young 2017). Previous studies have used this theoretical framework, in which traits that have shared developmental mechanisms and processes may exhibit evolutionary covariance, to assess serially homologous traits. This approach has been successfully applied to traits within the primate hands and feet (Rolian 2009; Rolian et al 2010), limbs (as reviewed in Young 2017) and vertebrae (Williams et al 2015).

While the basicranium and shoulder girdle are not serial homologues, they do share a complex ontogenetic relationship in both developmental mechanisms and mechanical function. These regions share several tissue contributions and genes during development, but most notably PONC forms attachment areas for muscles that span from the head to the shoulder girdle (Matsuoka et al 2005). Among placental mammals, primates display the most variation in their shoulder girdle morphology (Oxnard 1968; Preuschoft et al 2010). The size, shape, and orientation of the muscles attaching to the scapula are a considerable source of variation in the primate shoulder girdle, as its morphological variation reflects the functional demands of the upper limb (Ashton and Oxnard 1964a; Oxnard 1968; Badoux 1974; Roberts 1974; Ashton et al 1976; Young 2008; Preuschoft et al 2010). The foundation of this variation is present at birth and is maintained through ontogeny (Young

2006). Expanding on this evidence, we hypothesize that the variance in shoulder girdle morphology among primates may arise, in part, through the connectivity organized by PONC between the shoulder and adjacent anatomical regions to maintain functionality in the shoulder (Matsuoka et al 2005). Due to myriad overlapping processes that contribute toward trait covariance, it is not possible to ascribe a single process as an explanation for the degree of morphological integration or the variance-covariance patterns among traits (Hallgrímsson et al 2009), and development has been shown to be a robust, nonlinear process that may conceal the contributions of important genes and factors (Green et al 2017). The resulting covariance structure among traits is most likely due to a combination of different causes.

Our results suggest that this concept of a functional trait complex may be fruitfully assessed both for the shoulder girdle and basicranium, as well as for the shoulder girdle and pelvis. We realize that to successfully demonstrate the existence of a functional trait complex researchers would need to satisfactorily show that traits are linked developmentally and mechanically, and that these have exerted evolutionary constraint. Thus, the assessment of functional trait complexes awaits future study, combining phylogenetic comparative methods with experimental developmental biology.

Implications for the study of traits within evolutionary contexts

Our study's implications for shared evolutionary constraint between the shoulder girdle and basicranium, especially in primates, has important applications to modeling the origins of variation among living taxa and for reconstructing evolutionary patterns from fossil remains. This analysis highlights the importance of considering the relation of traits on a genetic, developmental, and functional level simultaneously to model how they are likely to respond to evolution. Most crucial to the study of primate evolution, our results reemphasize that a level of caution should be taken when interpreting the evolution of individual traits in isolation, such as those in the shoulder girdle. For primates in general, including hominids, evolutionary change in one anatomical region will have related effects in areas that share developmental processes and mechanical function. For example,

directional selection acting on the basicranium may have correlated effects on the scapula, though there was no selection acting directly on the scapula. The examination of the scapula or basicranium alone to understand the evolutionary forces that shaped either will fail to capture these evolutionary interactions. Moreover, within an anatomical region, as shown through other studies, individual traits within a functional complex will exhibit different directions and magnitudes of morphological change in response to the same selection pressure, either through direct or correlated responses (Grabowski 2013; Grabowski and Roseman 2015; Savell et al 2016). This phenomenon is visible in the fossil record as mosaic evolution (Schroeder et al 2014), such as among traits that relate to hominin locomotion (Pilbeam 1996, 2004; Young 2003; Moyà-Solà et al 2009; Nakatsukasa 2009; Feuerriegel et al 2017). These relationships cannot be ascertained through the examination of changes in means of morphological traits—patterns of evolution—as these are not good indicators of the evolutionary processes that shaped them (Lande and Arnold 1983; Houle 1991; Arnold 1992; Ackermann and Cheverud 2002; Hansen and Houle 2008; Rolian et al 2010; Grabowski 2013; Savell et al 2016), or the underlying sources of covariation among traits (Hallgrímsson et al 2009; Mitteroecker 2009). Detecting which traits were the target of directional selection, and which complexes of traits are more mutually constrained can only be assessed through a pan-primate comparison. The identification of *patterns* of morphological change within single anatomical regions, or single skeletal elements, and the interpretation of how those relate to functional differences among extinct primates are unaffected by our results and remain important for our understanding of primate evolution. However, our results call for extreme caution in ascribing evolutionary explanations to these patterns.

Conclusions

Our study adds novel evidence that sheds light on the complexities of shoulder girdle evolution. We show that there is strong potential for misleading conclusions in models of shoulder girdle evolution limited to traits of the scapula alone or ascribed to selection acting directly on specific trait

morphologies. Rather, shoulder girdle evolution is tied to the basicranium and the pelvis, as both these regions constrain its evolution, and vice versa. The consistency of our results, regardless of the configuration of traits used, attests to the strength of the conclusions that can be drawn from our data. These results yield important insights for both functionally related traits and models of primate shoulder girdle evolution, as well as implications for the interpretation of morphological changes in shoulder girdle variation within the fossil record. Caution should be exercised in any model of shoulder girdle evolution that examines traits individually, as this implicitly assumes independent evolution. We further propose a method for assessing this evolutionary covariance within a testable framework—the functional trait complex—which explicitly hypothesizes that functional and developmental covariances among these regions affect how they respond to the force and direction of selection. Morphological evolution is a whole-organism problem (Houle et al 2010), and future models of shoulder girdle evolution need to incorporate evolutionarily covariant traits.

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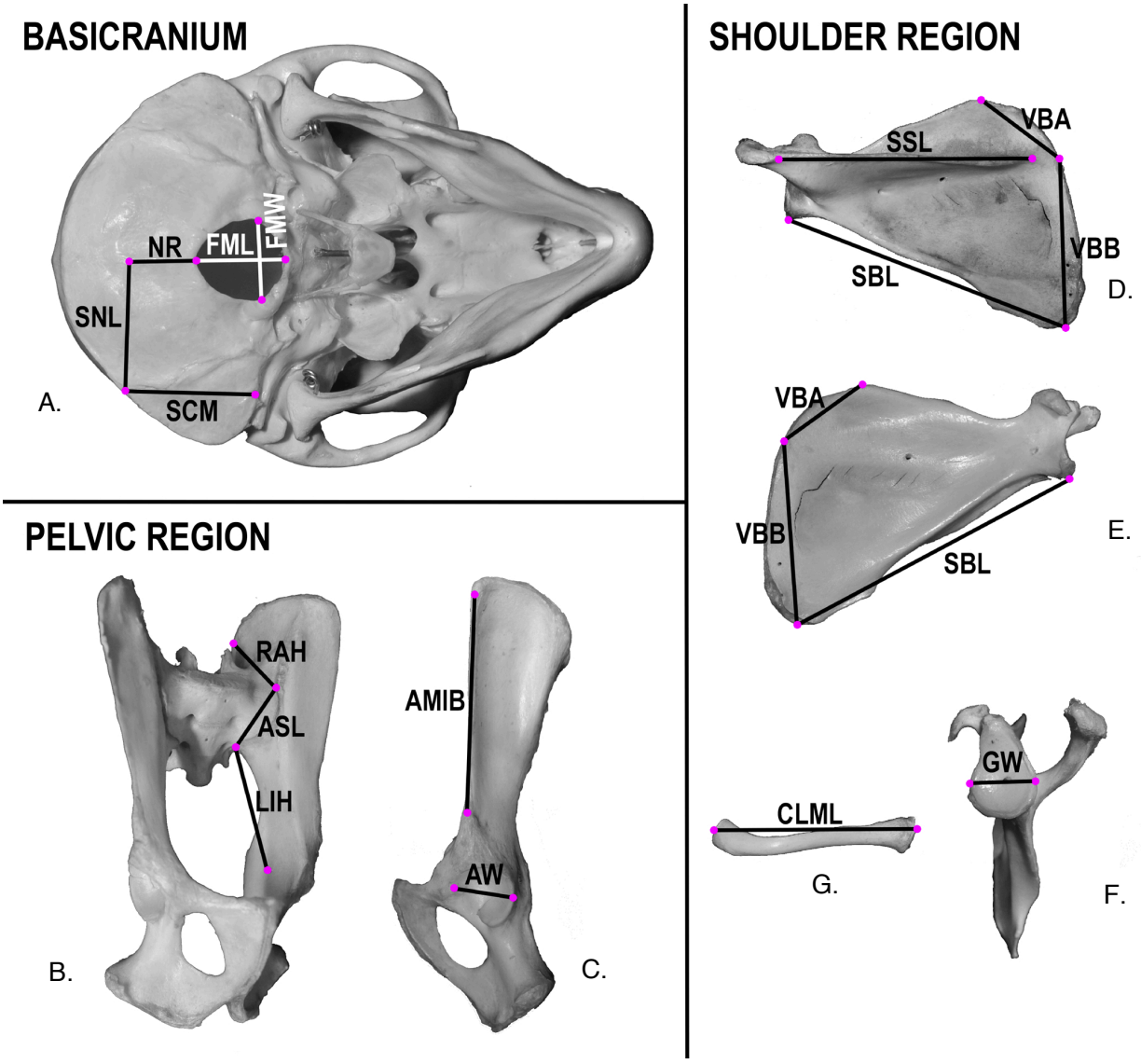


Figure II.1. Linear dimensions collected from each anatomical region: A. caudal aspect of the basicranium; B. medial aspect of os coxa; C. lateral aspect of os coxa; D. dorsal aspect of scapula; E. ventral aspect of scapula; F. lateral aspect of scapula; G. cranial aspect of clavicle. All traits were measured from the left side. Refer to Table II.1 for trait descriptions.

Table II.1. List of traits and trait descriptions for each anatomical region.

Basicranium	
NR	Length of the bony attachment of the nuchal ligament on the basicranium (Richmond et al 2001).
SCM	Length of cranial attachment of sternocleidomastoid (Richmond et al 2001).
SNL	Length of the caudal border of the attachment for cranial-most neck muscles and trapezius muscle (Richmond et al 2001).
FMW	Width of the foramen magnum measured at the greatest curvature of the left and right lateral margins (Moore-Jansen et al 1994).
FML	Ventral to dorsal length of the foramen magnum (Moore-Jansen et al 1994).
Shoulder Girdle	
SSL	Length of the scapular spine – attachment of the trapezius muscle along the scapular spine (Richmond et al 2001; Sears et al 2013).
SBL	Length of scapular blade along lateral border (Martin 1928).
VB	Length of the vertebral border of the scapula. Combined values of VBA and VBB.
GL	Maximum cranial to caudal length of the glenoid fossa (Young 2006).
CLML	Maximum length of the clavicle (Moore-Jansen et al 1994; Martin 1928).
Pelvic Girdle	
AMIB	Anterior margin of iliac blade (Grabowski and Roseman 2015).
ASL	Cranial to caudal length of the auricular surface (Grabowski and Roseman 2015).
RAH	Retro-auricular height, distance from cranial margin of the auricle to posterior superior iliac spine (Grabowski and Roseman 2015).
LIH	Lower iliac height, distance from caudal margin of auricle to the posterior aspect of the central point of the acetabulum (Grabowski and Roseman 2015).
AW	Medial to lateral width of the acetabulum.

Table II.2. Mean evolvability and 95% confidence intervals among pairings of anatomical regions. Estimates for both sex-scaled and sex and noise-scaled are presented.

Trait Group	Sex-scaled	Sex-scaled/Noise-corrected
All Regions	0.0127 (0.0071, 0.0175)	0.0078 (0.0048, 0.01)
Basicranium – Shoulder Girdle	0.0144 (0.0079, 0.0187)	0.0092 (0.0047, 0.0113)
Shoulder Girdle – Pelvic Girdle	0.0107 (0.0056, 0.0157)	0.0053 (0.0036, 0.0085)
Basicranium – Pelvic Girdle	0.0136 (0.0074, 0.0182)	0.0098 (0.0049, 0.0116)

Table II.3. Mean conditioned covariance and 95% confidence intervals among anatomical regions. The anatomical region held constant by stabilizing selection is denoted by (x), whereas the anatomical region under directional selection is denoted by (y).

Trait Group	Sex-scaled	Sex-scaled/Noise-corrected
Basicranium (x) – Shoulder Girdle (y)	0.0523 (0.0186, 0.0772)	0.0181 (0.0022, 0.0199)
Shoulder Girdle (x) – Basicranium (y)	0.0760 (0.0254, 0.0998)	0.0428 (0.0038, 0.0403)
Basicranium (x) – Pelvic Girdle (y)	0.0462 (0.0172, 0.0742)	0.0209 (0.0028, 0.0277)
Pelvic Girdle (x) – Basicranium (y)	0.0780 (0.0315, 0.1027)	0.0562 (0.0048, 0.051)
Shoulder Girdle (x) – Pelvic Girdle (y)	0.0434 (0.0148, 0.0742)	0.0184 (0.0028, 0.0255)
Pelvic Girdle (x) – Shoulder Girdle (y)	0.0500 (0.0186, 0.0783)	0.0135 (0.0025, 0.0252)

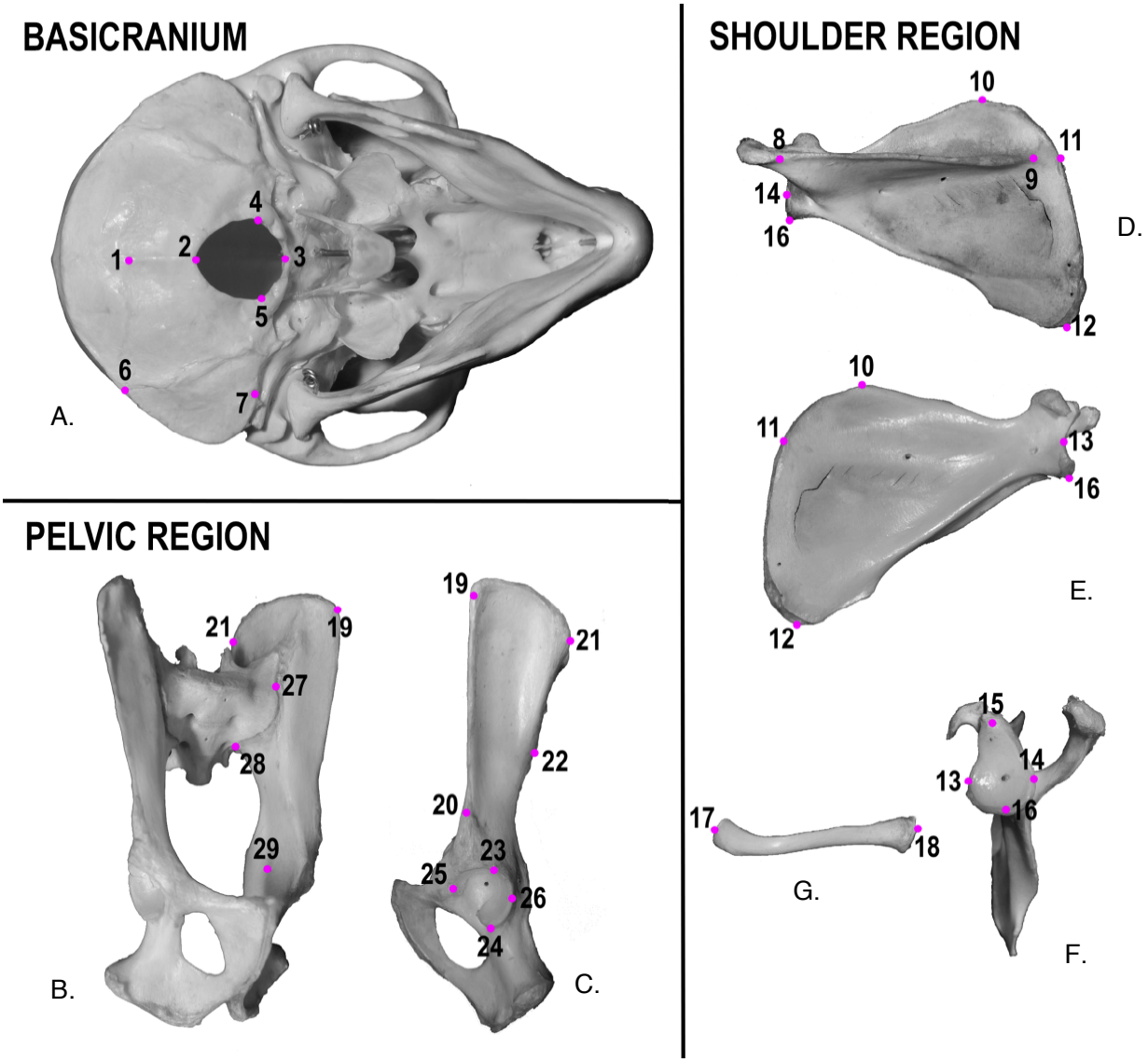


Figure SI.1. Landmarks taken from each anatomical region: A. caudal aspect of the basicranium; B. medial aspect of os coxa; C. lateral aspect of os coxa; D. dorsal aspect of scapula; E. ventral aspect of scapula; F. lateral aspect of scapula; G. cranial aspect of clavicle. All landmarks were taken from the left side. Refer to Table SII.1 for list of landmarks and descriptions. Landmark locations are demonstrated on a macaque specimen and are homologous for colobines.

Table SI.1. ANOVA results among the sexes and among species of colobus monkey for each sex. Bold values are statistically significant ($p < 0.05$).

Analysis		Df	Sum Squares	Mean Squares	F-value	p
Sex * Species	Sex	1	65984	65984	31.169	**3.3e-06**
	Species	2	2126	1063	0.502	0.61
	Residuals	33	69861	2117		
Males: Species	Species	1	2	1.8	0.001	0.977
	Residuals	20	42538	2126.9		
Females: Species	Species	1	2124	2124	1.011	0.333
	Residuals	13	27323	2102		

Table SI.2. List and definitions of landmarks collected.

No.	*Landmark*	*Definition*
		Basicranium
1.	Inion	Location of the intersection of the right and left superior nuchal lines within the external occipital protuberance (White et al 2012).
2.	Opisthion	Midline point of the dorsal margin of the foramen magnum (White et al 2012).
3.	Basion	Midline point of the ventral margin of the foramen magnum (White et al 2012).
4.	Right margin of foramen magnum	Right margin of the foramen magnum at its greatest curvature (Moore-Jansen et al 1994).
5.	Left margin of foramen magnum	Left margin of the foramen magnum at its greatest curvature (Moore-Jansen et al 1994).
6.	Asterion	Point where the lambdoidal, parietomastoid, and occipitomastoid sutures meet (White et al 2012).
7.	Left mastoid	Inferior-most point of the mastoid process (White et al 2012).
		Scapula
8.	Scapular spine lateral border	Point of intersection between the scapular spine and acromion process (Sears et al 2013).
9.	Scapular spine medial border	Medial margin of trapezius attachment along scapular spine (Young 2006).
10.	Superior angle	Intersection of superior and medial borders of scapula (White et al 2012).
11.	Scapular spine vertebral border	Point on vertebral margin where the long axis of the scapular spine and vertebral border meet (Young 2006).
12.	Inferior angle	Intersection of the lateral and medal borders of scapula (White et al 2012).
13.	Ventral margin of glenoid fossa	Ventral margin of glenoid fossa at its greatest width (Young 2006).
14.	Dorsal margin of glenoid fossa	Dorsal margin of glenoid fossa at its greatest width (Young 2006).
15.	Cranial margin of glenoid fossa	Superior-most margin of glenoid fossa (Young 2006).
16.	Caudal margin of glenoid fossa	Inferior-most margin of glenoid fossa (Young 2006).
		Clavicle
17.	Acromial end	Lateral-most point of clavicle on cranial aspect.
18.	Sternal end	Medial-most point of clavicle on cranial aspect.
		Os coxa
19.	Anterior superior iliac spine	Ventral-most point on lateral aspect of iliac crest (Lewton 2012).
20.	Anterior inferior iliac spine	Ventral-most point on anterior inferior iliac spine. If only a bony roughening, the point is taken at the center of this rugosity (Lewton 2012).

Table SI.2 continued

No.	***Landmark***	***Definition***
21.	Posterior superior iliac spine	Medial-most point of the dorsal-cranial border of iliac crest (Lewton 2012).
22.	Posterior inferior iliac spine	Sharp projection posterior and inferior to the auricular surface (White et al 2012).
23.	Cranial margin of acetabulum	Cranial-most point of the margin of the acetabulum (Lewton 2012).
24.	Caudal margin of acetabulum	Caudal-most point of the margin of the acetabulum, directly across from landmark 23 (Lewton 2012).
25.	Medial margin of acetabulum	Medial-most point along margin of the acetabulum.
26.	Lateral margin of acetabulum	Lateral-most point along margin of the acetabulum.
27.	Cranial margin of auricular surface	Central point of the cranial-most margin of the auricular surface.
28.	Caudal margin of auricular surface	Central point of the caudal-most margin of the auricular surface.
29.	Center of acetabulum	Center of the acetabulum, defined as the intersection of the line between landmarks 23 and 24 and landmarks 27 and 28 (Lewton 2012).

Table SI.3. Linear measures calculated from landmarks, measurement descriptions, and descriptive statistics for each measurement for both raw (in mm) and scaled measures. The mean and standard deviation is shown by sex for raw measures and with sexes combined for scaled measures.

Trait	Landmarks	Description	Females		Males		Scaled	
			Mean	SD	Mean	SD	Mean	SD
Basicranium								
NR	1 – 2	Length of the bony attachment of the nuchal ligament on the basicranium (Richmond et al 2001).	17.43	2.51	20.26	2.81	1.00	0.15
SCM	6 – 7	Length of cranial attachment of sternocleidomastoid (Richmond et al 2001).	18.33	1.58	21.76	2.65	1.00	0.11
SNL	1 – 6	Length of the caudal border of the attachment for cranial-most neck muscles and trapezius muscle (Richmond et al 2001).	15.39	3.05	17.99	2.84	1.00	0.19
FMW	4 – 5	Width of the foramen magnum measured at the greatest curvature of the left and right lateral margins (Moore-Jansen et al 1994).	15.16	0.77	16.03	1.00	1.00	0.06
FML	2 – 3	Ventral to dorsal length of the foramen magnum (Moore-Jansen et al 1994).	15.72	1.21	15.73	1.00	1.00	0.07
Shoulder Girdle								
SSL	8 – 9	Length of the scapular spine – attachment of the trapezius muscle along the scapular spine (Richmond et al 2001; Young 2006).	63.43	5.77	73.05	6.98	1.00	0.09
SBL	12 – 16	Length of scapular blade along lateral border (Martin 1928).	72.68	5.94	83.73	5.96	1.00	0.09
SBW	11 – 14	Maximum medial to lateral breadth of scapular blade (Martin 1928; Moore-Jansen et al 1994).	63.23	4.91	72.22	4.53	1.00	0.07
SBH	10 – 12	Cranial to caudal height of scapular blade (Martin 1928; Moore-Jansen et al 1994).	68.62	6.52	80.1	7.39	1.00	0.10
VB	10 – 11 11 – 12	Length of the vertebral border of the scapula. Combined values of VBA (10-11) and VBB (11-12).	78.11	8.29	91.55	9.57	1.00	0.11
GW	13 – 14	Maximum ventral to dorsal width of glenoid fossa (Young 2006).	10.73	0.86	11.66	1.13	1.00	0.09
GL	15 – 16	Maximum cranial to caudal length of the glenoid fossa (Young 2006).	15.65	1.22	17.01	1.34	1.00	0.08
CLML	17 – 18	Maximum length of the clavicle (Martin 1928; Moore-Jansen et al 1994).	53.32	4.81	63.01	4.66	1.00	0.09

Table SI.3 Continued

Trait	Landmarks	Description	Females		Males		Scaled	
			Mean	SD	Mean	SD	Mean	SD
Pelvic Girdle								
AMIB	19 – 20	Anterior margin of iliac blade (Grabowski and Roseman 2015).	59.54	7.89	60.67	9.26	1.00	0.14
PMIB	21 – 22	Posterior margin of iliac blade (Grabowski and Roseman 2015).	42.81	4.37	49.04	3.91	1.00	0.09
ASL	27 – 28	Cranial to caudal length of the auricular surface (Grabowski and Roseman 2015).	23.24	3.6	25.66	4.23	1.00	0.16
RAH	21 – 27	Retro-auricular height, distance from cranial margin of the auricle to posterior superior iliac spine (Grabowski and Roseman 2015).	37.17	4.27	42.11	3.19	1.00	0.10
LIB	19 – 27	Lateral iliac breadth, distance from cranial margin of the auricle to the anterior superior iliac spine (Grabowski and Roseman 2015).	50.7	6.46	56.31	3.59	1.00	0.11
LIH	28 – 29	Lower iliac height, distance from caudal margin of auricle to the posterior aspect of the central point of the acetabulum (Grabowski and Roseman 2015).	44.57	4.97	44.66	4.15	1.00	0.10
AL	23 – 24	Cranial to caudal length of the acetabulum (Lewton 2012).	20.21	1.05	21.48	1.15	1.00	0.06
AW	25 – 26	Medial to lateral width of the acetabulum.	19.02	1.26	20.12	1.2	1.00	0.07

Table SI.4. List of traits and their functional and/or developmental correlates.

Trait	Description
	Basicranium
NR	Length of the bony attachment of the nuchal ligament on the basicranium (Richmond et al 2001). The nuchal ligament serves as an origin for the trapezius muscle (Diogo and Wood 2012), and has paritial contributions from PONC during development (Matsuoka et al 2005).
SCM	Length of cranial insertion of the sternocleidomastoid mastoid muscle (Richmond et al 2001). This muscle and its attachments have PONC contributions during development (Matsuoka et al 2005).
SNL	Length of the caudal border of the attachment for cranial-most neck muscles and trapezius muscle (Richmond et al 2001). The attachment of the trapezius has PONC contribution during development (Matsuoka et al 2005).
FMW	Width of the foramen magnum measured at the greatest curvature of the left and right lateral margins (Moore-Jansen et al 1994). This provides a measure of the intercondylar breadth for the occipital condyles, which are derived from the somites during ontogeny (Pilbeam 2004)
FML	Ventral to dorsal length of the foramen magnum (Moore-Jansen et al 1994). Derived from paraxial mesoderm and somites during development (Pilbeam 2004).
	Shoulder Girdle
SSL	Length of the scapular spine – insertion of the trapezius muscle along the scapular spine (Richmond et al 2001; Young 2006). This point of attachment is derived from PONC during development (Matsuoka et al 2005).
SBL	Length of scapular blade along lateral border (Martin 1928). Combined origin length for teres minor, teres major, latissimus dorsi (in some primates), and long head of the triceps brachii muscles (Diogo and Wood 2012; Zihlman and Underwood 2019).
SBW	Maximum medial to lateral breadth of scapular blade (Martin 1928; Moore-Jansen et al 1994). Roughly corresponds to medial-lateral length of the caudal portion of supraspinatus and cranial portion of infraspinatus muscles.
SBH	Cranial to caudal height of scapular blade (Martin 1928; Moore-Jansen et al 1994). Combined length of the supraspinous and infraspinous fossae, which provide the combined breadth of the supraspinatus and infraspinatus muscles (Diogo and Wood 2012; Zihlman and Underwood 2019).

Table SI.4 continued

Trait	Description
GW	Maximum ventral to dorsal width of glenoid fossa (Young 2006). Maximum width of the shoulder joint surface, derived from the somatopleure during development (Huang et al 2000; Huang et al 2006; Sears et al 2015).
GL	Maximum cranial to caudal length of the glenoid fossa (Young 2006). Maximum height of the shoulder joint surface, derived from the somatopleure during development (Huang et al 2000; Huang et al 2006; Sears et al 2015).
CLML	Maximum length of the clavicle (Martin 1928; Moore-Jansen et al 1994). Part of the bony shoulder girdle, and medial portion is the origin for the sternocleidomastoid muscle and is derived from PONC during development (Matsuoka et al 2005).
	Pelvic Girdle
AMIB	Anterior margin of iliac blade (Grabowski and Roseman 2015). Distance is functionally related to positioning of the lesser gluteal muscles which can aide in pelvic stabilization during the single support phase in bipedal locomotion (Sigmon 1975). Analogous blade measurement to the lateral border of the scapula.
PMIB	Posterior margin of iliac blade (Grabowski and Roseman 2015). Shorter distances place the body's center of mass above the hips during more bipedal locomotion (see McCollum et al 2010). Analogous to the medial blade border of scapula.
ASL	Cranial to caudal length of the auricular surface (Grabowski and Roseman 2015). Functionally related to weight bearing (Berge and Kazmierczak 1986).
RAH	Retro-auricular height, distance from cranial margin of the auricle to posterior superior iliac spine (Grabowski and Roseman 2015). Expansion of this area is related to more upright trunk postures (see Dart 1949; Lovejoy 2005; Stern and Susman 1983; Bramble and Lieberman 2004). Roughly analogous to scapular blade breadth.
LIB	Lateral iliac breadth, distance from cranial margin of the auricle to the anterior superior iliac spine (Grabowski and Roseman 2015). Roughly analogous to scapular blade breadth.
LIH	Lower iliac height, distance from caudal margin of auricle to the posterior aspect of the central point of the acetabulum (Grabowski and Roseman 2015). Longer distances related to lumbar mobility (see Lovejoy et al 2009). Analogous to scapular blade length.
AL	Cranial to caudal length of the acetabulum (Lewton 2012). Analogous measure to GL as part of the joint surface.
AW	Medial to lateral width of the acetabulum. Is an analogous measure to GW as part of the joint surface, and can be used as a proxy for body size (Ruff 2003).

Table SI.5. Correlation matrix for all 21 traits. Highly correlated traits ($r \geq 0.8$) are highlighted in orange.

	AW	AL	LIH	LIB	RAH	ASL	PMIB	AMIB	CLML	GL	
NR		0.745	0.127	0.364	0.194	0.257	0.115	0.242	0.411	0.424	**AW**
SCM	0.187		0.085	0.409	0.202	0.093	0.180	0.158	0.455	0.507	**AL**
SNL	-0.012	0.242		-0.021	-0.242	-0.105	0.160	-0.027	0.424	0.298	**LIH**
FMW	-0.255	0.185	0.111		0.440	0.231	0.207	0.301	0.582	0.437	**LIB**
FML	-0.256	0.249	0.232	0.291		0.250	0.565	-0.018	0.298	0.132	**RAH**
SSL	-0.029	0.163	0.057	0.374	0.162		-0.023	-0.070	0.356	0.078	**ASL**
SBL	0.130	0.384	0.094	0.350	0.058	0.758		-0.017	0.498	0.269	**PMIB**
SBW	-0.032	0.332	0.041	0.337	0.156	0.856	0.901		-0.041	0.101	**AMIB**
SBH	0.063	0.336	0.246	0.347	0.074	0.644	0.864	0.760		0.579	**CLML**
VB	0.028	0.359	0.272	0.256	0.046	0.542	0.756	0.699	0.951		**GL**
GW	0.058	0.405	0.123	0.266	-0.032	0.644	0.572	0.628	0.562	0.507	
GL	-0.022	0.374	0.233	0.411	0.192	0.535	0.439	0.483	0.584	0.523	0.602
CLML	0.207	0.473	0.047	0.456	0.118	0.684	0.774	0.705	0.702	0.584	0.699
AMIB	-0.096	-0.008	0.330	-0.012	0.164	0.069	0.104	0.118	0.204	0.226	-0.012
PMIB	-0.090	0.055	-0.072	0.005	0.192	0.302	0.286	0.333	0.269	0.268	0.305
ASL	0.189	0.566	0.144	0.222	0.061	0.051	0.189	0.160	0.123	0.126	0.304
RAH	0.085	0.177	0.202	-0.046	-0.069	0.004	0.073	0.051	0.179	0.289	0.219
LIB	0.358	0.292	0.165	0.321	0.053	0.493	0.536	0.440	0.614	0.597	0.362
LIH	-0.080	0.159	-0.147	0.152	-0.099	0.338	0.371	0.271	0.219	0.068	0.383
AL	0.253	0.294	0.170	0.266	-0.018	0.283	0.398	0.332	0.548	0.560	0.554
AW	0.241	0.277	0.208	0.255	-0.078	0.171	0.246	0.164	0.355	0.371	0.334
	NR	**SCM**	**SNL**	**FMW**	**FML**	**SSL**	**SBL**	**SBW**	**SBH**	**VB**	**GW**

Table SI.6. List of additional trait configurations.

Configuration Designation	*Basicranium*	*Shoulder Girdle*	*Pelvic Girdle*
1	NR, SCM, SNL, FMW, FML	SSL, SBL, VB, GW, CLML	AMIB, PMIB, ASL, LIH, AL
2	NR, SCM, SNL, FMW, FML	SSL, SBL, SBH, GW, CLML	AMIB, RAH, ASL, LIH, AL
3	NR, SCM, SNL, FMW, FML	SSL, SBL, VB, GL, CLML	AMIB, PMIB, ASL, LIH, AL
4	NR, SCM, SNL, FMW, FML	SSL, GL, VB, GW, CLML	AMIB, PMIB, ASL, LIH, AL
5	NR, SCM, SNL, FMW, FML	SSL, SBL, VB, GW, CLML	AMIB, PMIB, ASL, LIB, AL
6	NR, SCM, SNL, FMW, FML	SSL, SBL, VB, GW, CLML	AMIB, RAH, ASL, LIH, AL
7	NR, SCM, SNL, FMW, FML	SSL, SBL, VB, GW, CLML	AMIB, RAH, ASL, LIB, AL
8	NR, SCM, SNL, FMW, FML	SSL, SBL, GL, GW, CLML	AMIB, RAH, ASL, LIB, AL
9	NR, SCM, SNL, FMW, FML	SSL, SBL, VB, GL, CLML	AMIB, RAH, ASL, LIH, AL
10	NR, SCM, SNL, FMW, FML	SSL, SBL, VB, GW, CLML	AMIB, PMIB, ASL, LIH, AW
11	NR, SCM, SNL, FMW, FML	SSL, SBL, VB, GW, CLML	AMIB, RAH, ASL, LIB, AW
12	NR, SCM, SNL, FMW, FML	SSL, VB, GL, GW, CLML	AMIB, RAH, ASL, LIB, AL

Table SI.7. Mean evolvability and 95% confidence intervals for each configuration of traits. Estimates for both sex-scaled and sex and noise-scaled data is presented. Confidence intervals denoted with '~' indicate analyses that were singular. Traits comprising each configuration are listed in Table SI.6.

Configuration	*Trait Groupings*	*Sex-scaled*	*Sex-scaled/Noise-corrected*
1	All Traits	0.0295 (0.0067, 0.0157)	0.0241 (0.0035, 0.0095)
	Basicranium – Shoulder Girdle	0.0285 (0.0074, 0.0175)	0.0314 (0.0036, 0.0109)
	Shoulder Girdle – Pelvic Girdle	0.0215 (0.0055, 0.0137)	0.0213 (0.0025, 0.0081)
	Basicranium – Pelvic Girdle	0.0302 (0.0065, 0.0163)	0.0296 (0.0037, 0.0107)
2	All Traits	0.0264 (0.0068, 0.0169)	0.0072 (~)
	Basicranium – Shoulder Girdle	0.0107 (0.0074, 0.0181)	0.0084 (~)
	Shoulder Girdle – Pelvic Girdle	0.0068 (0.0054, 0.0151)	0.0047 (~)
	Basicranium – Pelvic Girdle	0.0107 (0.0067, 0.0174)	0.0089 (~)
3	All Traits	0.0111 (0.0069, 0.0171)	0.0063 (~)
	Basicranium – Shoulder Girdle	0.0121 (0.0075, 0.0179)	0.0068 (~)
	Shoulder Girdle – Pelvic Girdle	0.0091 (0.0054, 0.0152)	0.0153 (~)
	Basicranium – Pelvic Girdle	0.0119 (0.0069, 0.0178)	0.0079 (~)
4	All Traits	0.0109 (0.0069, 0.0188)	0.007 (0.0039, 0.0098)
	Basicranium – Shoulder Girdle	0.0122 (0.0074, 0.0196)	0.076 (0.0036, 0.0107)
	Shoulder Girdle – Pelvic Girdle	0.0089 (0.0576, 0.0175)	0.0048 (0.0029, 0.0081)
	Basicranium – Pelvic Girdle	0.0118 (0.007, 0.0194)	0.0089 (0.0041, 0.0111)
5	All Traits	0.0107 (0.0069, 0.0164)	0.0071 (~)
	Basicranium – Shoulder Girdle	0.0127 (0.0075, 0.0179)	0.0081 (~)
	Shoulder Girdle – Pelvic Girdle	0.0089 (0.0051, 0.0145)	0.0059 (~)
	Basicranium – Pelvic Girdle	0.0113 (0.0069, 0.0171)	0.0075 (~)
6	All Traits	0.0127 (0.0071, 0.0183)	0.0089 (0.0043, 0.0099)
	Basicranium – Shoulder Girdle	0.0141 (0.0077, 0.0197)	0.0098 (0.0042, 0.0112)
	Shoulder Girdle – Pelvic Girdle	0.0108 (0.0055, 0.0167)	0.0069 (0.0031, 0.0082)
	Basicranium – Pelvic Girdle	0.0135 (0.0071, 0.0189)	0.0104 (0.0042, 0.0112)
7	All Traits	0.0178 (0.0068, 0.0174)	0.0072 (~)
	Basicranium – Shoulder Girdle	0.0192 (0.0077, 0.0186)	0.0085 (~)
	Shoulder Girdle – Pelvic Girdle	0.0164 (0.0051, 0.0154)	0.0063 (~)
	Basicranium – Pelvic Girdle	0.0187 (0.0068, 0.0181)	0.0072 (~)
8	All Traits	0.0103 (0.0068, 0.0156)	0.0076 (~)
	Basicranium – Shoulder Girdle	0.0122 (0.0076, 0.0171)	0.0083 (~)
	Shoulder Girdle – Pelvic Girdle	0.0088 (0.0049, 0.0137)	0.0067 (~)
	Basicranium – Pelvic Girdle	0.0105 (0.0068, 0.0163)	0.0082 (~)
9	All Traits	0.0126 (0.0072, 0.0189)	0.0065 (0.0038, 0.0096)
	Basicranium – Shoulder Girdle	0.0139 (0.0079, 0.0199)	0.0078 (0.0037, 0.0109)
	Shoulder Girdle – Pelvic Girdle	0.0108 (0.0056, 0.0172)	0.0042 (0.0028, 0.0081)
	Basicranium – Pelvic Girdle	0.0137 (0.0073, 0.0193)	0.0085 (0.0037, 0.0106)
10	All Traits	0.0102 (0.0069, 0.0172)	0.0094 (~)
	Basicranium – Shoulder Girdle	0.0117 (0.0074, 0.0185)	0.0103 (~)
	Shoulder Girdle – Pelvic Girdle	0.0081 (0.0056, 0.0154)	0.0074 (~)
	Basicranium – Pelvic Girdle	0.0108 (0.0069, 0.0176)	0.0104 (~)
11	All Traits	0.0091 (0.0066, 0.0155)	0.0073 (~)
	Basicranium – Shoulder Girdle	0.0112 (0.0074, 0.0169)	0.0083 (~)
	Shoulder Girdle – Pelvic Girdle	0.007 (0.0049, 0.0129)	0.0064 (~)
	Basicranium – Pelvic Girdle	0.0096 (0.0068, 0.0165)	0.0077 (~)
12	All Traits	0.0123 (0.0068, 0.0171)	0.0078 (0.0046, 0.0098)
	Basicranium – Shoulder Girdle	0.0137 (0.0077, 0.0184)	0.0086 (0.0046, 0.0111)
	Shoulder Girdle – Pelvic Girdle	0.0103 (0.0053, 0.0147)	0.0064 (0.0033, 0.008)
	Basicranium – Pelvic Girdle	0.0129 (0.0072, 0.0182)	0.0088 (0.0049, 0.0113)

Table SI.8. Conditioned covariance and 95% confidence intervals for each configuration of traits. Anatomical regions that are held constant by stabilizing selection are denoted by (x), whereas the anatomical regions under directional selection are denoted by (y).

Configuration	*Trait Groupings*	*Sex-scaled*	*Sex-scaled/Noise-corrected*
1	Basicranium (x) – Shoulder Girdle (y)	0.0454 (0.016, 0.0667)	0.0186 (0.0013, 0.0178)
	Shoulder Girdle (x) – Basicranium (y)	0.068 (0.0222, 0.0881)	0.0379 (0.0015, 0.0327)
	Basicranium (x) – Pelvic Girdle (y)	0.0396 (0.0156, 0.0609)	0.0248 (0.0014, 0.0234)
	Pelvic Girdle (x) – Basicranium (y)	0.0724 (0.0268, 0.0934)	0.0458 (0.0021, 0.044)
	Shoulder Girdle (x) – Pelvic Girdle (y)	0.035 (0.0138, 0.0613)	0.0229 (0.0013, 0.0217)
	Pelvic Girdle (x) – Shoulder Girdle (y)	0.0411 (0.0178, 0.069)	0.0160 (0.0015, 0.0225)
2	Basicranium (x) – Shoulder Girdle (y)	0.0313 (0.017, 0.0734)	0.0164 (0.0013, 0.0186)
	Shoulder Girdle (x) – Basicranium (y)	0.0609 (0.0223, 0.0963)	0.0344 (0.0016, 0.0367)
	Basicranium (x) – Pelvic Girdle (y)	0.0330 (0149, 071)	0.0230 (0.0015, 0.0232)
	Pelvic Girdle (x) – Basicranium (y)	0.0672 (0.0277, 0.1001)	0.0515 (0.0023, 0.0474)
	Shoulder Girdle (x) – Pelvic Girdle (y)	0.0292 (0.0136, 0.0707)	0.0165 (0.0013, 0.0212)
	Pelvic Girdle (x) – Shoulder Girdle (y)	0.0286 (0.0173, 0.0756)	0.0123 (0.0016, 0.0211)
3	Basicranium (x) – Shoulder Girdle (y)	0.0394 (0.0152, 0.0747)	0.0112 (0.001, 0.0163)
	Shoulder Girdle (x) – Basicranium (y)	0.0632 (0.0219, 0.0949)	0.0285 (0.0014, 0.0304)
	Basicranium (x) – Pelvic Girdle (y)	0.0409 (0.016, 0.0723)	0.0163 (0.0012, 0.0217)
	Pelvic Girdle (x) – Basicranium (y)	0.0692 (0.0139, 0.0975)	0.0408 (0.0019, 0.0409)
	Shoulder Girdle (x) – Pelvic Girdle (y)	0.0352 (0.0139, 0.072)	0.0116 (0.001, 0.0216)
	Pelvic Girdle (x) – Shoulder Girdle (y)	0.0376 (0.0156, 0.0761)	0.0075 (0.0013, 0.0209)
4	Basicranium (x) – Shoulder Girdle (y)	0.0383 (0.0181, 0.0845)	0.0141 (0.0018, 0.0208)
	Shoulder Girdle (x) – Basicranium (y)	0.0634 (0.0246, 0.1036)	0.0330 (0.0022, 0.039)
	Basicranium (x) – Pelvic Girdle (y)	0.0371 (0.0172, 0.0821)	0.0252 (0.0021, 0.0254)
	Pelvic Girdle (x) – Basicranium (y)	0.0668 (0.0284, 0.1049)	0.0382 (0.003, 0.0466)
	Shoulder Girdle (x) – Pelvic Girdle (y)	0.0314 (0.0156, 0.0834)	0.0191 (0.0018, 0.0246)
	Pelvic Girdle (x) – Shoulder Girdle (y)	0.0332 (0.0187, 0.0857)	0.0118 (0.0018, 0.0218)

Table SI.8 continued

Configuration	*Trait Groupings*	*Sex-scaled*	*Sex-scaled/Noise-corrected*
5	Basicranium (x) – Shoulder Girdle (y)	0.0404 (0.015, 0.0717)	0.0162 (0.0015, 0.0194)
	Shoulder Girdle (x) – Basicranium (y)	0.0609 (0.0245, 0.0965)	0.0194 (0.0023, 0.0385)
	Basicranium (x) – Pelvic Girdle (y)	0.0334 (0.0142, 0.0661)	0.0072 (0.0019, 0.0231)
	Pelvic Girdle (x) – Basicranium (y)	0.0651 (0.0271, 0.0969)	0.0241 (0.0028, 0.0449)
	Shoulder Girdle (x) – Pelvic Girdle (y)	0.0294 (0.0123, 0.0664)	0.0138 (0.0018, 0.0222)
	Pelvic Girdle (x) – Shoulder Girdle (y)	0.0392 (0.0147, 0.0719)	0.0118 (0.0116, 0.0222)
6	Basicranium (x) – Shoulder Girdle (y)	0.0519 (0.0185, 0.0819)	0.0177 (0.0016, 0.0202)
	Shoulder Girdle (x) – Basicranium (y)	0.0756 (0.024, 0.1029)	0.0368 (0.0018, 0.0388)
	Basicranium (x) – Pelvic Girdle (y)	0.0473 (0.0171, 0.0786)	0.0253 (0.0018, 0.0252)
	Pelvic Girdle (x) – Basicranium (y)	0.0782 (0.0306, 0.1037)	0.0534 (0.0026, 0.0486)
	Shoulder Girdle (x) – Pelvic Girdle (y)	0.0446 (0.0147, 0.0789)	0.0238 (0.0014, 0.0238)
	Pelvic Girdle (x) – Shoulder Girdle (y)	0.0492 (0.0188, 0.083)	0.0120 (0.0017, 0.0222)
7	Basicranium (x) – Shoulder Girdle (y)	0.0819 (0.0164, 0.0754)	0.0163 (0.0012, 0.0191)
	Shoulder Girdle (x) – Basicranium (y)	0.1030 (0.023, 0.0999)	0.0205 (0.0018, 0.0374)
	Basicranium (x) – Pelvic Girdle (y)	0.0777 (0.0139, 0.0708)	0.0084 (0.0014, 0.0225)
	Pelvic Girdle (x) – Basicranium (y)	0.1031 (0.0277, 0.1004)	0.0181 (0.0019, 0.0415)
	Shoulder Girdle (x) – Pelvic Girdle (y)	0.0774 (0.0116, 0.0715)	0.0166 (0.0014, 0.0205)
	Pelvic Girdle (x) – Shoulder Girdle (y)	0.0816 (0.0166, 0.0775)	0.0125 (0.0012, 0.021)
8	Basicranium (x) – Shoulder Girdle (y)	0.0415 (0.0156, 0.0668)	0.0201 (0.0016, 0.0191)
	Shoulder Girdle (x) – Basicranium (y)	0.0554 (0.0221, 0.0909)	0.0318 (0.0033, 0.0375)
	Basicranium (x) – Pelvic Girdle (y)	0.0267 (0.0144, 0.0626)	0.0121 (0.0018, 0.0236)
	Pelvic Girdle (x) – Basicranium (y)	0.0584 (0.0259, 0.0916)	0.0200 (0.0032, 0.0462)
	Shoulder Girdle (x) – Pelvic Girdle (y)	0.0231 (0.0124, 0.0625)	0.0157 (0.0018, 0.0218)
	Pelvic Girdle (x) – Shoulder Girdle (y)	0.0369 (0.0153, 0.0671)	0.0193 (0.0016, 0.021)

Table SI.8 continued

Configuration	*Trait Groupings*	*Sex-scaled*	*Sex-scaled/Noise-corrected*
9	Basicranium (x) – Shoulder Girdle (y)	0.0495 (0.0185, 0.0842)	0.0132 (0.0012, 0.0171)
	Shoulder Girdle (x) – Basicranium (y)	0.0740 (0.0248, 0.1072)	0.0302 (0.0016, 0.0345)
	Basicranium (x) – Pelvic Girdle (y)	0.0497 (0.0179, 0.0804)	0.0153 (0.0013, 0.0235)
	Pelvic Girdle (x) – Basicranium (y)	0.0773 (0.0317, 0.1106)	0.0388 (0.002, 0.042)
	Shoulder Girdle (x) – Pelvic Girdle (y)	0.0471 (0.0168, 0.0803)	0.0135 (0.0011, 0.0215)
	Pelvic Girdle (x) – Shoulder Girdle (y)	0.0485 (0.0195, 0.0856)	0.0077 (0.0012, 0.022)
10	Basicranium (x) – Shoulder Girdle (y)	0.0333 (0.0176, 0.0762)	0.0186 (0.0014, 0.0179)
	Shoulder Girdle (x) – Basicranium (y)	0.0577 (0.0223, 0.0961)	0.0384 (0.0019, 0.0359)
	Basicranium (x) – Pelvic Girdle (y)	0.0308 (0.0171, 0.0716)	0.0238 (0.0016, 0.0245)
	Pelvic Girdle (x) – Basicranium (y)	0.0629 (0.0284, 0.0993)	0.0482 (0.002, 0.0483)
	Shoulder Girdle (x) – Pelvic Girdle (y)	0.0229 (0.0146, 0.0702)	0.0239 (0.0015, 0.0221)
	Pelvic Girdle (x) – Shoulder Girdle (y)	0.0264 (0.0181, 0.0779)	0.0178 (0.0015, 0.021)
11	Basicranium (x) – Shoulder Girdle (y)	0.0289 (0.0143, 0.0623)	0.0178 (0.0011, 0.018)
	Shoulder Girdle (x) – Basicranium (y)	0.0467 (0.021, 0.0904)	0.0314 (0.0019, 0.0387)
	Basicranium (x) – Pelvic Girdle (y)	0.0185 (0.013, 0.0573)	0.0122 (0.0014, 0.0226)
	Pelvic Girdle (x) – Basicranium (y)	0.0489 (0.0254, 0.088)	0.0184 (0.0019, 0.0427)
	Shoulder Girdle (x) – Pelvic Girdle (y)	0.0109 (0.0108, 0.0574)	0.0148 (0.0014, 0.0217)
	Pelvic Girdle (x) – Shoulder Girdle (y)	0.0200 (0.014, 0.0635)	0.0108 (0.0012, 0.0207)
12	Basicranium (x) – Shoulder Girdle (y)	0.0492 (0.015, 0.0702)	0.0211 (0.0023, 0.0214)
	Shoulder Girdle (x) – Basicranium (y)	0.0721 (0.0231, 0.0992)	0.0318 (0.0038, 0.0436)
	Basicranium (x) – Pelvic Girdle (y)	0.0436 (0.0134, 0.0673)	0.0109 (0.0028, 0.0242)
	Pelvic Girdle (x) – Basicranium (y)	0.0700 (0.0258, 0.0985)	0.0173 (0.0033, 0.0413)
	Shoulder Girdle (x) – Pelvic Girdle (y)	0.0415 (0.012, 0.0676)	0.0183 (0.0024, 0.024)
	Pelvic Girdle (x) – Shoulder Girdle (y)	0.0456 (0.0159, 0.0718)	0.0181 (0.0022, 0.0214)

Table SI.9. Mean evolvability and 95% confidence intervals for macaques (Macaca mulatta group) and tamarins (*Saguinus oedipus* and *Saguinus fuscicollis illigeri*). Estimates for both sex-scaled and sex and noise-scaled data are presented.

Taxon	***Trait Groupings***	***Sex-scaled***	***Sex-scaled/Noise-corrected***
Macaca	*All Traits*	0.0121 (0.0073, 0.0179)	0.0097 (0.0049, 0.0111)
	Basicranium – Shoulder Girdle	0.0123 (0.0076, 0.0184)	0.0097 (0.005, 0.0119)
	Shoulder Girdle – Pelvic Girdle	0.0129 (0.007, 0.0185)	0.0098 (0.0046, 0.0119)
	Basicranium – Pelvic Girdle	0.0115 (0.007, 0.0176)	0.0095 (0.0043, 0.0112)
Saguinus	*All Traits*	0.0046 (0.0029, 0.0059)	0.0029 (0.0018, 0.0038)
	Basicranium – Shoulder Girdle	0.0054 (0.0031, 0.0065)	0.0036 (0.0018, 0.0044)
	Shoulder Girdle – Pelvic Girdle	0.0044 (0.0027, 0.0058)	0.0026 (0.0016, 0.0037)
	Basicranium – Pelvic Girdle	0.0041 (0.0026, 0.0058)	0.0027 (0.0016, 0.0038)

Table SI.10. Mean conditioned covariance and 95% confidence intervals for macaques (Macaca mulatta group, n=72) and tamarins (*Saguinus oedipus* and *Saguinus fuscicollis illigeri*, n=43). Estimates for both sex-scaled and sex and noise-scaled data are presented.

Taxon	***Trait Groupings***	***Sex-scaled***	***Sex-scaled/Noise-corrected***
Macaca	*Basicranium (x) – Shoulder Girdle (y)*	0.0483 (0.0197, 0.087)	0.0257 (0.0029, 0.0304)
	Shoulder Girdle (x) – Basicranium (y)	0.0426 (0.0182, 0.079)	0.0245 (0.0022, 0.028)
	Basicranium (x) – Pelvic Girdle (y)	0.0487 (0.0201, 0.0816)	0.0230 (0.0029, 0.0259)
	Pelvic Girdle (x) – Basicranium (y)	0.0480 (0.022, 0.0828)	0.0281 (0.0028, 0.0317)
	Shoulder Girdle (x) – Pelvic Girdle (y)	0.0397 (0.0152, 0.074)	0.0128 (0.0019, 0.0198)
	Pelvic Girdle (x) – Shoulder Girdle (y)	0.0475 (0.0166, 0.0832)	0.0150 (0.0025, 0.0289)
Saguinus	*Basicranium (x) – Shoulder Girdle (y)*	0.0249 (0.0085, 0.0293)	0.0127 (0.0023, 0.0134)
	Shoulder Girdle (x) – Basicranium (y)	0.0216 (0.0073, 0.029)	0.0146 (0.0018, 0.014)
	Basicranium (x) – Pelvic Girdle (y)	0.0145 (0.0069, 0.0238)	0.0054 (0.002, 0.01)
	Pelvic Girdle (x) – Basicranium (y)	0.0231 (0.0099, 0.0306)	0.0123 (0.0027, 0.0159)
	Shoulder Girdle (x) – Pelvic Girdle (y)	0.0139 (0.006, 0.0232)	0.0043 (0.0017, 0.0092)
	Pelvic Girdle (x) – Shoulder Girdle (y)	0.0250 (0.0092, 0.0299)	0.0095 (0.0023, 0.0143)

Table SI.11. Mean evolvability for pairwise comparisons of anatomical groupings using 20 traits evenly distributed across the following four anatomical regions: basicranium, shoulder girdle, pelvic girdle, and humerus. Traits for the basicranium, shoulder girdle, and pelvic girdle are described in the main text. The five traits from the humerus are measures of maximum length, width of the distal joint surface, distance between the medial and lateral epi-condyles, distance from the medial epicondyle to medial border of distal joint surface, and the distance from the lateral epicondyle to the lateral border of the distal joint surface. Abbreviations for pairings of anatomical regions are as follow: basicranium and pelvic girdle (B-PG), basicranium and shoulder girdle (B-SG), shoulder girdle and pelvic girdle (SG-PG), basicranium and humerus (B-H), pelvic girdle and humerus (PG-H), shoulder girdle and humerus (SG-H).

Anatomical Regions	**B - PG**	**B - SG**	**SG - PG**	**B - H**	**PG - H**	**SG - H**
Mean Evolvability	0.0116	0.0094	0.0097	0.0129	0.0134	0.0108

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Transition from Chapter II to Chapter III

In the previous chapter (Chapter II), I demonstrate that traits of the shoulder girdle, basicranium, and pelvic girdle do not show independent responses to directional selection, but rather mutually constrain each other. Thus, some of the variation observed in the primate shoulder girdle morphology may have arisen through correlational selection on the basicranium or pelvis. Furthermore, I show stronger potential constraint among anatomical regions that have functional and/or developmental relationships, such as the shoulder girdle and basicranium, compared to those that do not have share these relationships, such as the basicranium and pelvic girdle. This suggests a hierarchy to the patterns of evolutionary constraint among anatomical regions. This study highlights the importance of a multivariate framework when assessing the evolution of the shoulder girdle, as patterns of morphological differences among traits do not account for the potential evolutionary constraints imposed by the functional and developmental relationships among anatomical regions.

Chapter III further explores whether the patterns of evolutionary constraints observed in Chapter II vary among different primate taxa, and whether the developmental and functional covariances among anatomical regions may have influenced the observed diversity in primate shoulder girdle morphology. I compare the evolutionary potential and the strength of the covariance among paired groups of traits representing four anatomical regions: the shoulder girdle, basicranium, pelvic girdle, and distal humerus. Comparisons are made using a sample of eight primate taxa. Measures of morphological integration and evolutionary potential are compared between pairs of anatomical regions (i.e. shoulder girdle and basicranium) within each taxon to assess whether the patterns of potential constraint between anatomical regions follow those identified in Chapter II. I also compare these measures across all eight primate taxa to examine whether different primate species have similar potentials to respond to the force of directional selection. Furthermore, I use phylogenetic independent contrasts to demonstrate how individual traits correlated (and thus evolved together) after accounting for the evolutionary relatedness among taxa.

CHAPTER III

MORPHOLOGICAL INTEGRATION AND EVOLUTIONARY POTENTIAL OF THE PRIMATE SHOULDER: VARIATION AMONG TAXA AND IMPLICATIONS FOR GENETIC COVARIANCES WITH THE BASICRANIUM, PELVIS, AND ARM

Abstract

Within the primate order, the morphology of the shoulder girdle is immensely variable among mammals, and reflects the functional demands of the upper limb. The observed morphological variation among extant primate taxa is consequently hypothesized to be driven by selection for different functional demands. Evolutionary analyses of the shoulder girdle often assess this anatomical region, and its traits, individually. Therefore, implicitly assuming independent evolution of the shoulder girdle. However, the primate shoulder girdle has developmental and functional covariances with the basicranium and pelvic girdle that have been demonstrated to influence its evolution. Whether these relationships are similar or even present across primate taxa, and how they may affect morphological variation among primates is unknown. This study evaluates the strength of covariance and evolutionary potential across four anatomical regions: shoulder girdle, basicranium, pelvic girdle, and distal humerus. Measures of morphological integration and evolutionary flexibility are assessed across eight primate taxa. Phylogenetic independent contrasts are also performed to assess the phylogenetically corrected correlations among traits. Results demonstrate patterns of integration and evolutionary flexibility differ among primate taxa, with humans having the highest evolutionary potential overall. These patterns do not follow a straightforward trend, such as the separation of monkeys and apes. Rather, they elucidate more nuanced relationships among taxa that do not necessarily correspond to locomotor function. Therefore, evolutionary hypotheses of primate shoulder girdle morphological variation that evaluate functional demands alone may not account for the effect of these relationships. Furthermore, the corrected covariances among traits show that not all traits within these regions are equally correlated. Thus, results suggest not every trait contributes equally to the relationships among anatomical regions. Taken together, these results suggest differences in genetic covariance among anatomical regions may have contributed to the observable morphological variation among taxa.

Introduction

Among placental mammals, morphological diversity in the shoulder girdle is greatest in primates (Oxnard 1968; Preushoft et al 2010). The observed morphological variation among primates matches the diversity of upper limb functional demands, and corresponds to the size, shape, and orientation of the muscles attaching to the bony elements of the shoulder girdle, especially the scapula (Ashton and Oxnard 1964; Oxnard 1967, 1968; Badoux 1974; Roberts 1974; Ashton et al 1976; Larson and Stern 1986, 1992; Larson 1993, 1995, 2015; Irwin and Larson 2000; Young, 2008; Preuschoft et al 2010). The foundations of functional variation in the scapula are present from birth and are maintained through ontogeny (Young 2006), thus indicating the variation is not solely a plastic response to biomechanical demands encountered during the lifetime of individuals. Nevertheless, whether this variation arose in response to direct selection arising from functional demands on the shoulder, by correlated responses to directional selection on integrated traits (e.g., Rolian et al 2010; Rolian 2015; Grabowski and Roseman 2015), or through neutral processes remains undetermined.

Due to the many muscles associated with upper limb and shoulder movement that attach to the scapula, studies of morphological variation in the primate shoulder girdle are often focused on the scapula alone, with its traits assessed individually (Schultz 1930,1950; Ashton and Oxnard 1961, 1964ab, Oxnard 1963,1967, 1968, 1969; Ashton et al 1965; Roberts 1974; MacLatchey et al 2000; Larson et al. 2007, Feuerriegel et al 2017; Selby and Lovejoy 2017). Two assumptions underlie the conclusions drawn from such studies: 1) Trait differences among taxa are hypothesized to be the result of directional selection acting on those morphologies. 2) Variation within a single trait is given evolutionary explanations that identify differences in trait morphology among primate species as adaptations for particular motor functions that are used to meet the demand of the varied environments primates inhabit. While these conclusions may be merited, the individual assessment of traits inherently assumes their independent evolution, an assumption that is not supported by the evolutionary biology literature for most traits (Lande 1979; Lande and Arnold 1983; Arnold 1983;

Ackerman and Cheverud 2000, Hansen and Houle 2008; Walsh and Blows 2009; Rolian et al 2010; Roseman and Auerbach 2015; Katz et al 2016; Savell et al 2016). Traits within an organism do not exist in isolation. Rather, they covary with whole-organismal traits (such as body size) and with traits from other anatomical regions that share mechanical and developmental variation.

In a recent study cowritten by the author (Agosto and Auerbach, in review), we assessed the potential evolutionary covariance the shoulder girdle has with anatomical regions with which it has mechanical functional and developmental covariance: the basicranium and pelvic girdle. We used a quantitative genetic approach to estimate measures of evolvability within three monkey taxa: colobine monkeys, rhesus macaques, and tamarins. An unprecedented result of this study indicated that traits of the basicranium and shoulder girdle are equally labile in their ability to evolve as traits of the shoulder and pelvic girdles. No prior study had shown evolutionary relationships between any aspect of the cranium and the shoulder. Furthermore, the results suggested the basicranium imposes evolutionary constraint on the shoulder and pelvic girdles, but is not equally constrained by either the shoulder girdle or pelvic girdle. Our study demonstrated that the evolution of the primate shoulder is more complex than previously perceived, uncovering evolutionary covariance with anatomical regions once assumed to be independent (i.e., the basicranium). These relationships, however, are not evident when evaluating the scapula or its traits alone.

The paper by Agosto and Auerbach (in review) established a potential evolutionary relationship between the shoulder girdle, the basicranium, and pelvic girdle. How these relationships relate to the larger breadth of primate shoulder girdle morphological variation remains unanswered. Researchers cannot assume that the results indicated for the three monkey taxa investigated in the aforementioned study are representative of the potential evolutionary relationships among the three anatomical regions for all primates. Other studies (Young 2004; Rolian 2009; Young et al 2010; Lewton 2012) have demonstrated that integration, and thus the evolvability, of postcranial traits vary considerably among primates, and that apes generally are less integrated than monkeys. This has been demonstrated in the major limb elements (Young et al 2010), hands and feet (Rolian 2009),

and scapula (Young 2004). This study therefore investigates whether differences in integration and evolvability of the shoulder girdle, basicranium, and pelvis are present across primate taxa, and thus contributed to the morphological variation noted in the primate shoulder girdle.

Morphological Integration and Evolutionary Covariance

Morphological integration refers to the tendency for traits to covary as a result of the common underlying developmental factors (Hallgrímsson et al 2002; p. 132). This idea was formalized by Olsen and Miller (1951, 1958) using a pattern-based approach that relied on ascribing developmental or functional explanations for high correlation among traits. Cheverud (1995, 1996) brought integration into a quantitative genetic framework (Lande 1979, 1980) when he identified four hierarchical processes underlying morphological integration: two at the individual level, and two at the population level. Within an individual organism, traits can be integrated due to function or development. Functional integration occurs when traits are involved in a common functional and their interaction affects the performance of that function (Cheverud 1996; Rolian 2009). Developmental integration among traits happens when traits share common developmental processes or interact during development. These two types of integration are closely related as functional interactions among traits can be emergent through developmental processes (Cheverud 1996). Morphological integration on the individual level can lead to the integration among traits at the population level. When traits are more often inherited together than with (or to the exclusion of) other traits, they become genetically integrated at the population level (Cheverud 1996). Genetic integration among traits can lead to their evolutionary integration, where they coevolve and experience correlated responses to directional selection (Rolian 2009). The pleiotropic relationship among traits ultimately underlies these genetic covariances (Cheverud 1996).

Phenotypic traits are more integrated on a populational level, as greater covariation among traits leads to a decrease in their ability to respond to the force and direction of selection (Rolian 2009; Rolian et al 2010). This process is reversible, otherwise traits would lose their ability to evolve in

response to directional selection at all. Selection against, or even relaxation on selection for integration, can lead to a reduction in the pleiotropic interactions among traits (Wagner 1996; Wagner and Altenberg 1996). For example, specialized functions arising among traits can lead to their parcellation, and we would expect them to become more evolutionary independent. Individual trait responses to directional selection are therefore reliant on the covariances they have with other traits (Rolian et al 2010), and are a result of different degrees of functional and developmental integration among traits that shape their underlying covariance structure (Hallgrímsson et al 2009; Rolian 2014). These covariances can either constrain or promote evolutionary responses among traits (Schluter 1996). While integration among traits can shape the underlying covariance structure among them, however, the evaluation of the pattern and magnitude of integration does not tell us of the consequences of integration on the evolution of traits (Marroig et al 2009).

To measure the potential evolutionary consequences of trait integration at a population level, researchers depend on estimates of trait covariance within the context of the multivariate breeder's equation (Lande and Arnold 1983, Hansen and Houle 2008). These estimates of evolvability can be used to test the expectations set by patterns of morphological integration (see Rolian 2009). The ability of a trait to respond to the force and direction of selection, its evolvability, is, therefore, reliant on the strength of the developmental and functional covariances it has with other traits. We can think of the evolvability of a trait in terms of the direction and the magnitude of response to a selection gradient, which considers both the variance in a trait and its covariance with other traits. The greater the difference between the multivariate response vector and a selection gradient, the lower the evolvability of a trait due to its genetic covariances. The more divergence there is between these two vectors, the lower the evolvability of a trait due to its genetic covariances.

Thus, evolvability and its related measures (conditional evolvability, respondability, autonomy, and evolutionary flexibility) indicate the potential evolutionary independence in a trait or set of traits to respond to a selection gradient, but do not reflect the actual evolutionary history of a trait. To assess the actual evolutionary processes that led to trait variation, researchers need to use either

experimental biology (e.g., Garland and Rose 2009) or the comparative method (e.g., Harvey and Pagel 1991; Leroi et al 1994; Martins and Hansen 1997; Martins 2000). In this study, one such method—independent contrasts (Felsenstein 1985, Garland et al 1992; Ricklefs and Starck 1996; Price 1997)—is used to consider phylogenetic relationships between taxa when calculating the correlations among traits, as some of the covariance between traits arises from shared ancestry.

By investigating morphological integration and estimates of evolvability, this study seeks to understand how the developmental and mechanical covariance between the shoulder, basicranium, and pelvis varies among primate species, and whether these could have influenced the observed diversity in shoulder girdle morphology. Additionally, measures of the distal humerus are included as a more independent anatomical region under this model. Two questions are asked: 1) Are the evolutionary relationships between the shoulder girdle, basicranium, and pelvic girdle identified by Agosto and Auerbach (in review) present and consistent among primate taxa? 2) Is there evidence for the genetic covariances observed to have affected trait evolution among primates? To assess these questions, the magnitude of integration and a measure of evolvability, evolutionary flexibility, are compared across anatomical groups within and among eight primate taxa. Five traits from each of the following anatomical regions are used: the basicranium, shoulder girdle, pelvic girdle, and distal humerus. It is expected that anatomical regions with clear functional and/or developmental relationships, such as the basicranium and shoulder girdle, will have greater magnitudes of integration and lower flexibility than functionally unrelated traits with each taxon. It is anticipated that these patterns of covariance will be similar across taxa, while the measures of integration and flexibility themselves will differ across taxa, with potentially more independence among apes than monkeys. Finally, I use phylogenetic independent contrasts (PIC) to demonstrate how individual traits covary with each other after accounting for evolutionary relatedness among taxa and interpret these results in light of the evolutionary flexibility estimates. The phylogenetically corrected correlations among traits provided by the PIC allow for estimation of the potential for traits to have correlated evolution that is independent of shared ancestry. I anticipate that traits associated with

shared muscle attachments or functional relationships will have greater covariance and will be highest between pairs of anatomical regions exhibiting the lowest flexibility.

Materials and Methods

Materials

Eight taxa are included in this study: seven catarrhine primates, and one platyrrhine primate (Table III.1; all Tables and Figures are located in Appendix III and Supplementary Information II). The catarrhine primates are equally split among Hominoidea and Cercopithecidae. The primates comprise arboreal, terrestrial, and semiterrestrial taxa that represent a range of functional demands that require different degrees of stability and mobility in the shoulder, including above branch and terrestrial quadrupedal monkeys, suspensory and knuckle-walking apes, and bipedal humans.

Each taxon is represented by a pooled sample of both males and females. All specimens are adults, defined by the fusion of the long bone epiphyses. Only specimens with no visible pathologies affecting trait morphology were measured for this study. When possible, taxa are represented by a single species. Preservation of the crania and os coxa prevented the measurement of several traits in these regions for most taxa, with *Pongo* and *Papio* being the most heavily affected. Missing values could not be estimated because of the non-random nature of missing measurements (Allison 2002; Little and Rubin 2002). Rather, the samples for both *Pongo* and *Papio* are comprised of pooled data from multiple species to achieve the minimum sample sizes recommended by Grabowski and Porto (2017) for estimating evolutionary flexibility ($n \geq 11$ for 10 traits, and $n \geq 21$ for 20 traits). Pooling species for these samples was deemed reasonable as baboon species are known to hybridize in the wild (Rogers et al 2019), and differences among trait covariances are expected to be higher between genera than among closely related species of the same genus. The choice to pool samples was statistically checked using an ANOVA, the results of which show no significant difference among the traits used in this study among species both within *Papio* and within *Pongo* (Table III.2).

Morphological data were derived from the left side of each specimen. If the element or trait (in the case of the basicranium) from the left side was missing, damaged, or showed evidence of healed fracture, the right side of the specimen was measured for all elements. In a few cases (~10), measurements were taken from both the right and left side of the specimen to comprise a 'complete' specimen. A total of twenty linear measurements (Figure III.1, and Tables III.3 and SII.2) were derived from four anatomical regions: basicranium, shoulder girdle, pelvic girdle, and humerus. Each region is represented by five traits, so no one region would overwhelm the model (see below). Potential evolutionary relationships have been demonstrated by Agosto and Auerbach (in review) for these regions in a smaller sample of primates using a different analytical approach. Traits of the shoulder girdle, basicranium, and pelvis were described in detail in Agosto and Auerbach (in review), and the humerus was examined as part of a secondary analysis in that study for the colobine monkeys. Linear dimensions of the humerus are included in this study to characterize an element that has no known developmental or mechanical relationship with the basicranium or pelvis, and thus provides a contrast with the results among the three other anatomical regions.

An Immersion G2X MiscroScribe digitizer was used to capture three-dimensional coordinates from the basicranium, scapula, clavicle, os coxa, and humerus. These coordinates were used to calculate interlandmark distances for the 20 dimensions used in this study. Three non-consecutive measurements were collected for each coordinate and linear measurement, and subjected to a repeated measures ANOVA (RMANOVA) to assess intra-observer error. Results of the RMANOVA show no significant difference between measurement rounds ($p > 0.05$), and less than three percent error for each element within taxa. All subsequent analyses were performed using the average of the three measurement rounds.

Methods

Estimation of Phenotypic VCV Matrices

To optimally perform quantitative genetics analyses, researchers should have knowledge of the additive genetic variances and covariances among traits (the G matrix) (Lande 1979; Hansen and Houle 2008). However, these measures are notoriously difficult to obtain. For morphological traits, the phenotypic variances and covariances among traits have been shown to be close to proportional with their genetic counterparts (Roff 1995, 1996; Cheverud 1988; Roseman 2012; Sodini et al. 2018). As such, the phenotypic VCV matrix, or P matrix, will be substituted for the genetic VCV matrix (G matrix) in this study. VCV matrices were estimated using 20 traits across four anatomical regions (basicranium, shoulder girdle, pelvic girdle, and humerus) for each taxon; the variance and covariance among traits for paired comparisons of regions were acquired from this matrix. Sources of variation not directly associated with genotype-phenotype map (Wagner and Altenburg 1996), sex and species differences in the case of this study, were controlled during matrix estimation by applying a multivariate analysis of variance (MANOVA) to the raw data, and estimating the VCV matrices from the resulting residuals. Accounting for these sources of covariance are important because differences in the trait averages among groups can result in inflated covariance among traits, therefore masking the true relationships among traits (Porto et al 2013).

All analyses of flexibility, integration and trait autonomy (see below) were performed from VCV matrices that account for both size and random noise. Body size is an important factor in mammalian evolution (Marroig et al 2009; Porto et al 2013), so it is imperative to remove size related variation from within species data to ensure evolutionary relationships among traits are driven by similarities in size (Porto et al 2013). Following Porto and colleagues (2013), size corrected VCV matrices (R) were obtained from the following relationship:

$$R = P - VV' \quad (1)$$

where P is the phenotypic VCV matrix, V is the size-related eigenvector and V' is its transpose. Each VCV matrix was also 'noise corrected' to minimize the effect small sample sizes and measurement

error have on matrix estimation, especially in analyses that require matrix inversion (Twede and Hayden 2004; Marroig et al. 2012; Agosto and Auerbach, in review). I controlled for noise in our VCV matrix estimates by replacing values smaller than the median of the variance of the second derivative derived from the absolute value of eigenvalues with the median, and recalculating the new VCV matrix using these new eigenvalues.

Estimating Evolutionary Flexibility and Integration

To analyze evolutionary flexibility and integration among sets of traits, I compared different pairings of traits (e.g., the shoulder girdle and pelvis versus the shoulder girdle and basicranium). Each pairing consists of ten traits—five from each of the two regions—which is the minimum number of traits recommended by Grabowski and Porto (2017) for estimating measures of evolvability. Restricting the analysis to five traits from each region to maximize the sample (avoiding missing data) and to avoid potential bias in estimates of evolvability and morphological integration that may be imposed due to unequal trait representation among anatomical regions.

To assess the consistency of the evolutionary covariance of the shoulder girdle with other anatomical regions, adaptations of Hansen and Houle's (2008) evolvability equations and other measures of integration (Wagner 1984, 1990) were used to assess two measures of morphological integration and evolvability both within and among taxonomic groups. The estimates of integration and evolvability for multivariate traits developed by Hansen and Houle (2008) were based on Lande (1979) and colleagues' (1983) equation for estimating multivariate responses to directional selection

$$\Delta\bar{z} = G\beta \quad (2)$$

where $\Delta\bar{z}$ is the average trait response to selection, *G* additive genetic VCV matrix (replaced by *P* in this study) and β is the directional selection gradient, which is a vector of partial regression coefficients of relative fitness on each trait in a multivariate system (Lande and Arnold 1983, Hansen and Houle 2008). The selection gradient essentially characterizes the direction and magnitude of selection in phenotypic space.

Hansen and Houle (2008) adapted this equation to estimate the capacity of a multivariate (i.e., multi-trait) population mean to respond to the directional selection. This measure, evolvability, provides an estimate of the potential for traits to evolve in phenotypic space, given their covariances with other traits and thus the potential constraints on patterns of variation characterized by the population's VCV matrix (Rolian 2009). Hansen and Houle (2008) define multivariate evolvability, $E(\beta)$, as the length of the projection of evolutionary response vector ($\Delta\bar{z}$) on the selection gradient (β):

$$E(\beta) = |\Delta z(\beta)| cos\theta / |\beta| \quad (3)$$

where cos θ is the angle between the response vector and the selection gradient, and the other variables are the same as in Equation 2. This equation provides a different measure of evolvability for each selection gradient, and therefore is unique in each direction of phenotypic space. The evolutionary potential of the *P* matrix can be assessed by computing its average evolvability over random selection gradients. In phenotypic space, the average trait additive variance is equal to the average eigenvalue (Hansen and Houle 2008). As noted by Rolian (2009), evolutionary potential highly correlates with the total variance within a population, which prevents the comparison of average evolvabilities among species with unequal total variance. This study will use a related measure, evolutionary flexibility, to compare evolutionary potential across taxa.

Evolutionary flexibility, also referred to as the Directional Evolvability Index (Rolian 2009), captures how closely the evolutionary response vector follows the selection gradient in phenotypic space (Marroig et al 2009), and is measured as the cosine of the angle between these two vectors

$$\text{Evolutionary flexibility} = \cos\theta = |\beta| \cdot |\Delta z(\beta)| \quad (4)$$

This is the portion of Hansen and Houle's evolvability that measures the direction of the response of the population mean to the selection gradient, regardless of the magnitude of evolutionary response (Rolian 2009). Essentially, evolutionary flexibility captures the orientation of evolutionary response in phenotypic space (Marroig et al 2009). Measures of evolutionary flexibility range from zero to one, where a measure of zero implies that the response vector is orthogonal to the direction of selection,

and a measure of one is perfectly aligned with selection vector. Thus, a value of one implies that traits are free to respond to any pressure of selection, while measures closer to zero indicate stronger constraint among traits.

The average evolutionary flexibility for each taxon was calculated using 1000 symmetrically distributed, randomly generated selection gradients. These were generated using the 'evolvability' package by independently selecting each element of the selection gradient from a zero-mean Gaussian distribution with a unit variance, and normalizing each selection gradient by a unit length (Bolstad et al 2014). For each selection gradient, evolutionary flexibility was calculated as the cosine of the angle between the response vector ($|\Delta z(\beta)|$) and the normalized selection gradient ($|\beta|$). The average evolutionary flexibility is the average of 1000 cosines. Following Rolian (2009), statistical significance of the differences among taxa were determined by bootstrapping the original data, with replacement, and recomputing the evolutionary flexibility for each iteration of the bootstrapped sample (Manly 1991). Statistical significance was determined by counting how many times the bootstrapped value in the CI of the smaller value exceeded that of the larger value and divided by the number of observations. Pairwise comparisons were performed both between regions and taxa.

Morphological integration among anatomical regions for each taxon were assessed using two methods: the variance of eigenvalues (VE) and trait autonomy. VE provides a measure of the strength of the covariance among traits within a population (Rolian 2009). Higher measures of VE indicate that a small number of principal components with large eigenvalues explain most of the variance in the data. Stronger integration among traits suggests greater covariance among them. The VE method was developed for correlation matrices (Wagner 1984), and Rolian (2009) demonstrated its application to VCV matrices and how it can be adjusted so measures of VE are proportional across taxa of unequal variances. This adjustment entails standardizing eigenvalues by the trace of the VCV matrix, so that each eigenvalue is expressed as a portion of the total variance, where the sum of all eigenvalues is one for each taxon. Statistical differences among taxa were calculated using the same bootstrap strategy described for evolutionary flexibility (1000 iterations).

Trait autonomy reflects the magnitude of morphological integration by estimating the amount of genetic or phenotypic variance of a trait that is independent of the traits with which it covaries (Hansen and Houle 2008). This measure therefore quantifies the constraint on a trait with respect to a set of traits. Trait autonomy for a single trait z_j, with respect to all others, is given by:

$$\text{Trait autonomy} = ([P^{-1}]_{jj}[P]_{jj})^{-1} \quad (5)$$

where P^{-1} is the inverse of the P matrix, and $_{jj}$ distinguishes the jth trait along the diagonal of the matrix (Hansen and Houle 2008). The average autonomy across a suite of traits provides a measure of how parcellated the data is (Wagner and Altenberg 1996). Traits with a lower autonomy have a greater proportion of their potential variance 'locked up' in their covariance with other traits (Rolian 2009). Significance among comparisons of trait autonomy use the same resampling strategy mentioned above (1000 iterations).

As noted above, trait covariance is a product of both evolutionary morphological integration and shared evolutionary history. In making comparisons among the eight taxa examined herein, to better understand how trait correlations relate to morphological integration versus shared evolutionary history, it is important to determine which traits have higher covariances after accounting for phylogenetic relatedness. To examine these correlations, phylogenetic independent contrasts (PICs) were calculated for the paired correlations of traits after considering the phylogenetic relationships among the eight taxa. A custom script using the pic function in the ‘ape’ package for R was used to recalculate the correlations between traits after accounting for evolutionary relationships by using phylogenetic data from version 3 of the *10kTrees Project* (Arnold et al 2010). Phylogenetic relationships were derived from a consensus chronogram constructed using eleven mitochondrial and six autosomal genes across 301 primate species.

All analyses are performed in the R statistical environment (https://cran.r-project.org) using custom made scripts and the 'evolvability' package (Bolstad et al 2014).

Results

Evolutionary Flexibility

The mean evolutionary flexibility among all traits and among paired groupings of anatomical regions are presented in Table III.4 and visually in Figure III.2. The 95% confidence intervals are reported in Table III.4 as well. Rows present a comparison of trait pairings within taxa, while comparisons of the same trait pairings among taxa are in the columns. Significance for mean estimates of evolutionary flexibility and morphological integration both between pairs of anatomical regions and among taxa in Tables SII.5 and SII.6, respectively

Comparisons of mean flexibility within each taxon are expected to have the lowest estimates among anatomical regions that share mechanical function and/or development: the basicranium and shoulder girdle, the shoulder girdle and pelvic girdle, and the shoulder girdle and humerus. In five taxa—*Alouatta*, *Colobus*, *Homo*, *Hylobates*, and *Papio*—this expectation is borne out. Within *Alouatta*, *Colobus*, and *Homo*, the lowest estimated mean evolutionary flexibility is observed in the shoulder girdle-basicranium pair. Values are consistent in *Hylobates*, except for lower flexibility in the shoulder girdle and humerus, and a flexibility greater than 0.8 for the basicranium-humerus pair (0.824). In *Papio*, the shoulder girdle has lower flexibility when paired with the basicranium or the pelvis compared to its flexibility when paired with the humerus. However, the lowest evolutionary flexibility is observed in the basicranium-pelvic girdle pairing. It is of note that the flexibility values among all trait pairings are less than 0.753 for *Papio*, and so compared with other taxa, the baboons have low evolutionary flexibility across all four anatomical regions. In both *Macaca* and *Pan*, the basicranium-pelvic girdle and the pelvic girdle-humerus pairs have similarly low evolutionary potential, followed by the shoulder girdle-pelvic girdle and basicranium-pelvic girdle pairs, respectively. Among orangutans (*Pongo*), the basicranium-humerus pair have the lowest mean evolutionary flexibility (a result only found in orangutans), followed by the basicranium-shoulder girdle, and the basicranium-humerus pairs. For most taxa, pairings that include the humerus have

the greatest estimates of mean evolutionary flexibility, indicating less evolutionary constraint among them compared to the pairings comprising the basicranium, shoulder girdle, and pelvic girdle.

Broadly, among taxa, apes consistently present the highest mean evolutionary flexibility values for any trait pairing compared to the two groups of monkeys. Traits collectively are least constrained within *Homo*, especially for the three pairings made between regions that are developmentally and functionally more independent: the basicranium-pelvis, the basicranium-humerus, and the humerus-pelvis. Conversely, the highest estimated average evolutionary flexibility for the shoulder girdle-pelvic girdle pair, as well as the shoulder girdle-humerus pair, are observed in *Pongo*. As noted above, baboons have the lowest collective evolutionary flexibility estimates, with exceptions in the basicranium-shoulder girdle pair (0.711), and the shoulder girdle-humerus pair (0.747). In contrast, among monkeys, macaques have the highest evolutionary flexibility in all pairings except the basicranium-pelvic girdle pair, and the pelvic girdle-humerus pair (both are higher in *Colobus*). Among monkeys, there is higher evolutionary flexibility in the basicranium-humerus pair than among any other trait pairing.

Among pairings of anatomical regions, then, the basicranium-shoulder girdle pair have low evolutionary potential over all directions in p-dimensional space for most taxa (*Alouatta*, *Colobus*, *Homo*, and *Hylobates*), followed by the basicranium-pelvic girdle pair (*Macaca*, *Papio*, and *Pongo*). The basicranium and humerus, overall, are the least constrained anatomical group pairing among taxa. Notably, in *Pongo*, all three pairings with the basicranium are equally labile in their ability to evolve. The basicranium-shoulder girdle pair are similarly constrained compared to the shoulder girdle-humerus pair in *Homo* and *Hylobates*.

Morphological Integration

The index of integration, given by the trace-adjusted eigenvalues of the VCV matrix, for each paired grouping of anatomical regions and among all 20 traits can be found in Table III.5, statistical significance between pairs of anatomical regions and among taxa can be found in Tables SII.4 and

SII.5. In general, the patterns of morphological integration follow the broad trends presented in Table III.4 of evolutionary potentials among taxa. In all taxa except *Pongo*, morphological integration is lowest between the basicranium and humerus; integration is lowest between the humerus and the two limb girdles for *Pongo*. As found in comparisons of mean flexibility, there is no clear pattern for higher integrations of traits, though amongst the majority of taxa the highest integration, as reflected by VE values, is found between the basicranium and shoulder girdle (*Colobus*, *Homo*, *Hylobates*, and *Pongo*), the shoulder girdle and pelvis (*Alouatta*, *Papio*, and *Homo*), and the basicranium and pelvis (*Alouatta*, *Macaca*, *Pan*, and *Pongo*). The integration among all 20 traits is consistently lower among apes, with the exception of macaques.

These results are reflected in the average trait autonomy for each trait grouping among taxa (Table III.5). The greatest autonomy for any trait pairing within taxa occurs in the basicranium and humerus, matching the integration results reported above. Again, *Pongo* presents the only exception, where the shoulder girdle and humerus have the greatest autonomy. Low trait autonomy values generally relate to the shoulder girdle across all taxa, either between the shoulder girdle and basicranium or shoulder girdle and pelvis.

Phylogenetic Independent Contrasts

Correlations among trait pairs using independent contrasts are presented in Table III.6. Collectively, these correlations indicate that not all traits within anatomical regions are likely equally contributing to the morphological integration trends observed among the regions. Focusing on the correlations of traits between anatomical regions, the highest correlations are between the acetabular width (AW) and all other traits (except for scapular spine length, SSL), as well as the distal width of the humerus (HDW) and most other traits (except, again, SSL, as well as the length of the anterior margin of the iliac blade, AMIB). It is notable that the length of the anterior iliac blade has an inverse relationship with most other traits, with the exception of those of the scapula and nuchal region of the basicranium. Higher correlations ($r < 0.5$) are present between nuchal traits (NR

and SNL) and dimensions of scapular blade size (SBL and VB), as well as the distal dimensions of the humerus. Also notable are the lower correlations between the nuchal region length (NR) with other measures of the basicranium, and the parcellation of regions within the scapula (mediolateral dimensions have lower correlations with superoinferior dimensions). Both the pelvis and humerus show higher correlations among all dimensions, comparatively.

Discussion

The results present both a remarkably consistent pattern of integration, as well as variation in the evolutionary flexibility among primate species in the basicranium, shoulder girdle, pelvic girdle, and humerus. These results answer the first question in the Introduction, and further support previous examinations of the evolvability and constraint on the primate shoulder girdle, basicranium, and pelvic girdle among three primate taxa (Agosto and Auerbach, in review). Pairings of these three regions are more integrated with each other than they are with the humerus, and the shoulder girdle and humerus are more integrated than the basicranium and humerus or pelvic girdle and humerus in all taxa except orangutans. A broad conclusion is that the primate shoulder region, on the whole, is consistently among the least autonomous and more morphologically integrated anatomical regions considered. However, the patterns of evolutionary flexibility are not consistent among the taxa and bear further examination (see *Function and Evolutionary Flexibility* below).

The second question asked in this study concerns the results of the trait correlations made after accounting for phylogenetic relatedness. While these correlations cannot determine the relative contributions of traits to the estimates of evolutionary flexibility or the mean VE estimates, they show that, using independent contrasts, there is evidence for some traits to covary more strongly within and between regions than others. Dimensions that are often associated with body size (Ruff et al. 1991, Ruff 2003)—the width of the acetabulum and the distal breadth of the humerus—covary strongly with almost all traits, with the notable exception of scapular spine length and the length of the anterior iliac blade. That many of the dimensions highly correlate between anatomical regions

and elements suggests that the covariances among these traits did affect the evolution of the variation observed in primate taxa. Thus, while evolutionary flexibility estimates reported in this study show *potential* responses to directional selection given genetic covariances among traits, these covariances could have previously shaped the evolutionary diversification of primates. The details of these results are discussed in more detail below (see *Phylogenetic Independent Contrasts and Realized Potential in Evolutionary Trait Covariance*).

Function and Evolutionary Flexibility

As discussed in the Introduction, shared trait responses to directional selection are ultimately influenced by the developmental and functional relationships among them. This occurs through increased pleiotropy on a population level among traits that are more strongly integrated due to shared developmental processes or engagement in similar functional demands within individuals (Cheverud 1996, Wagner 1996). The relationship among shared function, the strength of integration, and the constraints these may have on trait response to directional selection have been empirically demonstrated among the autopods (Rolian 2009) and limbs (Young et al 2010) of primates. These studies show that traits from anatomical regions that engage in similar functional demands are more strongly integrated, and overall less evolvable than functionally independent traits. The patterns of integration and flexibility, as they relate to function, differ among primate taxa, and thus likely explain some of the differences observed in evolutionary flexibility (Table III.3).

The patterns of morphological integration and flexibility among anatomical regions relates to shared development and function. There is evidence that the shoulder and basicranium share developmental pathways (Matsuoka et al 2005; see also Lieberman et al 2000 and Valasek et al 2010). In many primate species, these two regions are physically connected by muscles of the neck and shoulder, or at least by ligaments and connective tissues (Richmond et al 2001; Diogo and Wood 2012). In addition, the shoulder and pelvic girdle are developmentally linked as analogous morphological regions (limb girdles) (Sears et al 2015), and in quadrupedal species these share

some broad locomotor functions. With both developmental and biomechanical sources of covariance, it is unsurprising the strongest relationships are often found among these regions. As noted above, in most taxa, integration between the distal humerus and these other three regions is smaller than those amongst those three regions. This may in part be an artifact of the use of distal articular dimensions for the humerus; the proximal end of the humerus provides attachment sites for several muscles originating from the scapula (Diogo and Wood 2012), and was excluded.

The observed variation in flexibility estimates among primate species is noteworthy, especially in light of the generally consistent results found among taxa in the morphological integration and autonomy estimates. Summarizing the results presented in Table III.4, the most independence and autonomy is evident for the basicranium-humerus pair in most species, except in *Homo* (where the basicranium-pelvic girdle pairing is as independent) and *Pongo* (where the basicranium and humerus are highly integrated, and the shoulder girdle-humerus pairing has the most independence). These results are broadly supported in the flexibility estimates presented in Table III.3, but there are notable deviations from the integration patterns. Monkeys in general have lower flexibilities than apes except for macaques, which have more ape-like estimates of evolutionary flexibility (especially in the shoulder girdle pairings). *Macaca*, *Pan*, and *Papio* all demonstrate stronger morphological integration and more evolutionary constraint among the basicranium and pelvic girdle than among more developmentally or functionally related anatomical regions; differences among regions are statistically significant in *Pan*. In contrast, humans most closely match the flexibility patterns predicted in the first question as based on the previous study of evolvability in the shoulder region (Agosto and Auerbach in review); the greater flexibility estimates coincide with the pairings outside of the shoulder girdle, with the highest in the pelvic girdle and humerus (which share no direct developmental or functional relationships in *Homo*). It is also notable that humans have the most independence and greatest evolutionary flexibility among the anatomical pairings compared to other primates.

The sample used in this study comprises a group of primate taxa that represent a range of different functional demands placed on the shoulder. Macaques, chimpanzees, and baboons are the only quadrupedal terrestrial or semi-terrestrial taxa represented (see Meyers et al 2019). They also exhibit a similar pattern of flexibility values among paired regions that is distinct from the pattern described for *Alouatta*, *Colobus*, *Homo*, and *Hylobates* (Table SII.3). The upper limbs of terrestrial quadrupedal primates encounter different biomechanical stresses compared to those of arboreal primates. Since the shoulder girdle and upper limb supports much of the body weight during terrestrial locomotion, its morphology promotes stability, as opposed to mobility, of the joint and is positioned to better counteract compressive forces experienced during locomotion (Biewener 1989; Schmitt 1998; Larson and Stern 2007; Preuschoft et al 2010). This could relate the lower flexibility values in these taxa in the shoulder-pelvic girdle pairing, as well as in the pelvic girdle and humerus. It is possible the differences in the patterns of integration and flexibility among anatomical regions observed in these three taxa are related to these biomechanical differences they have with the other primate taxa.

Pongo is the only taxon that substantially deviates from the broad primate pattern (see Table SII.3), though they are similar to other apes in having higher flexibility estimates than monkeys. The evolutionary potential among the basicranium and humerus is as constrained as the shoulder girdle and basicranium, and the lowest flexibility estimate is between the humerus and basicranium. More surprisingly, the shoulder region and humerus are the most independent and flexible among the trait pairings. Among the apes, *Pongo* has disproportionately high intermembral index for its size due to its disproportionately long humerus (Jungers 1985). Forelimb length in *Pongo* scales positively with body size, and to a greater degree than what is observed among other primates (Jungers 1985). It is possible the evolutionary constraint observed here among the humerus and basicranium is related to some underlying covariance with body size that was not removed during the size correction in the VCV matrix. Most likely, the relationship observed here may be due to unrelated similarities in the covariance structures of these two regions that results in their mutual constraint. The exact cause of

this relationship is unknown and warrants further investigation with measurements from other skeletal regions, as well as a better understanding of orangutan development compared with other apes.

Phylogenetic Independent Contrasts and Realized Potential in Evolutionary Trait Covariance

In general, it was anticipated that morphological integration and mean evolutionary flexibility would differ among primates, especially among those engaged in different functional demands for the upper limb and shoulder girdle (for example between terrestrial and arboreal taxa). However, as discussed above, the results of this study do not clearly support this expectation. Among the pairings of anatomical regions, the mean evolutionary flexibility is similar across all eight primate taxa, though there are three clear patterns in which these occur (Table SII.3). A broad conclusion is that the shoulder girdle, pelvic girdle, and basicranium have less evolvability with respect to each other than any have with the humerus in all taxa except *Pongo*. Yet, this does not reflect *realized* evolution in these traits, and it is likely that not all of the traits that comprise each region equally influence the integration of these regions. Phylogenetic comparative methods, using models of Brownian motion or evolutionary optima (e.g., Ornstein-Uhlenbeck processes), are better suited to investigating how evolutionary forces most likely shaped trait evolution. While such analysis is beyond the scope of this study, an examination of how traits covary after accounting for species evolutionary relationships may indicate which traits are evolutionarily covarying, and how they might have shaped evolution given the integration and flexibility results.

The goals of the analyses performed in this study are to assess the evolutionary non-independence of traits and ascertain to what degree the covariance among traits constrains their ability to respond to directional selection. However, traits are inherently evolutionarily non-independent due to shared ancestry (Felsenstein 1985). In this study, we are interested in the covariance due to other sources, such as development, mechanical function, among others that can form pleiotropy. Once accounting for size-related covariance among traits, the application of

phylogenetic independent contrasts allows for the covariance due to shared ancestry to be disentangled from the sources of covariance of interest to this study. By accounting for the variance due to shared ancestry using phylogenetic independent contrasts, what is left is the variance that is independent of ancestry. Thus, allowing for the estimation of the potential for traits to have correlated evolution, where higher correlations among traits implies they have greater potential to co-constrain (high constraint) due to developmental covariance and the other many forms of pleiotropy.

Some of the traits in our analysis strongly covary with size, such as the diameters of the glenoid (GW) and acetabulum (AW, Ruff 2003). If selection on these traits were primarily due to size, we would expect all other traits to get carried along with both these dimensions. They phylogenetically corrected correlations show strong relationships between both GW and AW for all traits except the lengths of the scapular spine (SSL) and lateral border of the scapular blade (SBL). Rather, these traits are more strongly correlated with the lengths of the nuchal region (NR) and the attachment for the sternocleidomastoid (SCM). While all other traits more strongly covary with those that can proxy for body size, the PIC does not elucidate whether correlated evolution due to changes in body size actually occurred – it does, however, provide an in indication of co-constraint that is not due to shared ancestry. Whether these potentials are borne out can be evaluated using phylogenetic comparative methods.

The broad interpretation of the correlations among traits following independent contrasts is that not all traits within a single anatomical region, such as the basicranium, equally contribute towards the patterns of morphological integration and evolutionary potential observed among taxa. For example, there is evidence that there is some parcellation of the basicranium, where the nuchal muscle attachments (represented by the NR and SCM dimensions) are more correlated than either is with the other traits of the basicranium. Moreover, these two traits have lower correlation with dimensions of the shoulder region in general than the rest of the basicranial measurements (with a notable exception of NR and the length of the scapular blade). Likewise, there is evidence for some

parcellation in the scapula, where the two mediolateral dimensions of the scapula are more correlated, while the width of the glenoid fossa and the medial border length of the scapula are more independent of these traits, and the clavicle has low correlation with scapular dimensions except for glenoid width (which is likely a measure reflecting body size given its weight support for the shoulder joint). Finally, the anterior border of the ilium has a uniquely inverse relationship with all of the other traits except the width dimensions of the scapula; this suggests that species with larger dimensions generally have a shorter iliac blade, and it is likely that this pattern is driven by the fact that larger species are also apes, and apes tend to have shorter iliac blades on the anterior margin than monkeys relative to body size. Were all the relationships Thus, not all traits are equally driving the patterns of evolutionary flexibility and morphological integration both within and between anatomical regions, and size-related shape cannot be ignored as a factor behind the evolutionary patterns.

Covariances in a multivariate context are nonadditive, and so it is difficult to relate the patterns from the bivariate PIC to the multivariate covariances among several traits across anatomical regions. Trying to interpret the results of the PIC in light of muscle attachments or shared development, even were it possible with each anatomical area represented by the trait dimensions, would be erroneous. However, the patterns reviewed above suggest that parts of these skeletal elements are hierarchically integrated, so that some parts are more integrated within than all traits are integrated for an element. This has been shown to be the case for the cranium (Cheverud 1982, 1996; Mitteroecker and Bookstein 2008; Singh et al 2012) and for the pelvis (Lewton 2012; Mallard et al. 2017). It is therefore not unexpected that some aspects of anatomical regions may have more influence on the measures of integration and evolutionary flexibility with other regions. Disentangling which traits, or groups of traits, drive the evolutionary patterns reported herein will await future studies.

Furthermore, these results cannot show whether the anatomical regions evolved in response to directional selection, neutral evolutionary forces, or a combination of the two among taxa. It likewise remains unknown if function was a motivating selection factor in shaping both trait covariances and

evolution. The ability of traits to respond to directional selection is dependent on both the covariance structure among traits, and the strength of those connections (see Rolian 2014). Both of these factors were shown to be related to functional differences among the primate hands and feet (Rolian 2009) and limbs (Young et al 2010). However, studies of the axial skeleton indicate similar covariance structures among the face and neurocranium of Catarrhines (Oliveira et al 2009), and the pelvis (Lewton 2012) and scapula (Young 2004) across primates. For the skull and scapula, the strength of the covariance among traits appears to be more influential on the morphological variation among traits. The comparisons across primate taxa performed in this study support these findings. This result was somewhat unexpected, as there is a large degree of morphological variation in the primate shoulder girdle that is reflective of differences in the functional demands of the upper limb (Inman et al 1944; Ashton and Oxnard 1961, 1963; Oxnard 1963; Roberts 1974; Stern et al 1977; Tuttle and Basmajian 1977, 1978; Jungers and Stern 1984; Larson and Stern 1986; Larson et al 1991; Larson 1993, 1998; Whitehead and Larson 1994; Preuschoft et al 2010). Traits with direct connection to the shoulder girdle are all participating in the same basic function: movement of the shoulder and upper limb. Other studies have attributed the maintenance of the covariance structure among traits to not be a remnant of phylogeny, but rather internal stabilizing selection on the determinants of the covariance structure (Marroig and Cheverud 2001).

Conclusions

This study demonstrates that the evolution of the shoulder girdle is potentially affected by other traits, namely the basicranium, pelvic girdle, and to a lesser extent, the distal humerus. While evolutionary covariance is observed these anatomical regions for all taxa, the patterns of the strength of these covariances differ. Measures of morphological integration and evolutionary potential demonstrate these patterns are not a straightforward dichotomy between apes and monkeys. Rather, they reflect more nuanced relationships among taxa that may not be explained by functional variation alone. These results suggest the genetic relationships among anatomical regions

differ among primate taxa, and those differences may have contributed the morphological diversity observed among extant primate taxa. While this study elucidates a previously uninvestigated factor affecting primate morphological variation, these results can only assess the evolutionary potential among traits in response to directional selection. Future analyses using different approaches will be necessary to discern by which evolutionary processes shaped trait variation, and the effect the reported patterns of integration and evolutionary flexibility among anatomical regions had on their morphological evolution.

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Appendix III

Table III.1. Sample composition.

Species	Males	Females	Total
PLATYRRHINES			
Alouatta seniculus	18	23	**41**
CATARRHINES			
Cercopithecoids			
Colobus guereza	27	26	**53**
Macaca mulatta	16	46	**62**
Papio	21	18	**39**
P. anubis	12	8	**-**
P. hamadryas	4	5	**-**
P. cynocephalus	5	5	**-**
Hominoids			
Homo sapiens	56	60	**116**
Hylobates lar	28	24	**52**
Pan troglodytes	42	26	**68**
Pongo	11	31	**52**
P. abellii	2	7	**-**
P. pygmaeus	19	24	**-**

Table III.2 ANOVA results among the sexes and among species of baboons (*Papio*) and orangutans (*Pongo*). Bold values are statistically significant ($p < 0.05$).

Papio						
Analysis		**Df**	**Sum Squares**	**Mean Squares**	**F-value**	**p**
Sex * Species	Sex	1	401222	401222	34.653	**2.99e-05**
	Species	2	79012	39506	3.412	0.0601
	Sex:Species	1	136	136	0.012	0.9152
	Residuals	15	173674	11578		
Pongo						
Analysis		**Df**	**Sum Squares**	**Mean Squares**	**F-value**	**p**
Sex * Species	Sex	1	602000	602000	41.429	**2.23e-06**
	Species	2	9636	4818	0.332	0.721
	Residuals	21	305150	14531		

Table III.3. List of traits and descriptions for each anatomical region.

Basicranium	
NR	Length of the bony attachment of the nuchal ligament on the basicranium.
SCM	Length of cranial attachment of sternocleidomastoid.
SNL	Length of the caudal border of the attachment for cranial-most neck muscles and trapezius muscle.
FMW	Width of the foramen magnum measured at the greatest curvature of the left and right lateral margins.
FML	Ventral to dorsal length of the foramen magnum.
Shoulder Girdle	
SSL	Length of the scapular spine – attachment of the trapezius muscle along the scapular spine.
SBL	Length of scapular blade along lateral border.
VB	Length of the vertebral border of the scapula. Combined values of VBA and VBB.
GL	Maximum cranial to caudal length of the glenoid fossa.
CLML	Maximum length of the clavicle.
Pelvic Girdle	
AMIB	Anterior margin of iliac blade.
ASL	Cranial to caudal length of the auricular surface.
RAH	Retro-auricular height, distance from cranial margin of the auricle to posterior superior iliac spine.
LIH	Lower iliac height, distance from caudal margin of auricle to the posterior aspect of the central point of the acetabulum.
AW	Medial to lateral width of the acetabulum.
Humerus	
HML	Maximum length of the humerus.
MCH	Length of the bony attachment of several flexor muscles of the forearm.
LCH	Length of the bony attachment of several extensor muscles of the forearm.
HEW	Medial to lateral width of distal humerus at the epicondyles.
HDW	Medial to lateral width of the distal articular region of the humerus.

Table III.4. Mean evolutionary flexibility and 95% confidence intervals for paired anatomical regions among taxa: basicranium and pelvic girdle (B-PG), basicranium and shoulder girdle (B-SG), shoulder girdle and pelvic girdle (SG-PG), basicranium and humerus (B-H), pelvic girdle and humerus (PG-H), shoulder girdle and humerus (SG-H). Higher values reflect more flexibility, and thus more evolvability for that grouping of traits compared among trait pairings (rows) or among taxa (columns).

	Taxon	*B - PG*	*B - SG*	*SG - PG*	*SG - H*	*B - H*	*PG - H*
Platyrrhines	***Alouatta***	0.694 (0.560, 0.778)	0.639 (0.597, 0.768)	0.725 (0.595 0.772)	0.693 (0.595, 0.78)	0.801 (0.532, 0.841)	0.751 (0.546,).762)
Cercopithecoids	***Colobus***	0.76 (0.666, 0.828)	0.684 (0.602, 0.742)	0.726 (0.653, 0.771)	0.72 (0.644, 0.775)	0.838 (0.669, 0.844)	0.782 (0.707, 0.832)
	Macaca	0.708 (0.658, 0.846)	0.765 (0.67, 0.833)	0.737 (0.688, 0.812)	0.788 (0.676, 0.839)	0.868 (0.661, 0.88)	0.706 (0.66, 0.806)
	Papio	0.66 (0.492, 0.749)	0.711 (0.593, 0.755)	0.706 (0.484, 0.747)	0.747 (0.545, 0.743)	0.752 (0.08, 0.764)	0.696 (0.428, 0.707)
Hominoids	***Homo***	0.895 (0.761 0.953)	0.757 (0.683, 0.826)	0.757 (0.683, 0.84)	0.758 (0.668, 0.841)	0.896 (0.661, 0.88)	0.91 (0.66, 0.806)
	Hylobates	0.757 (0.681, 0.849)	0.722 (0.651, 0.777)	0.751 (0.673, 0.781)	0.716 (0.645, 0.793)	0.824 (0.722, 0.906)	0.764 (0.695, 0.853)
	Pan	0.671 (0.646, 0.834)	0.766 (0.672, 0.882)	0.742 (0.691, 0.804)	0.793 (0.696 0.889)	0.789 (0.755, 0.939)	0.701 (0.681, 0.853)
	Pongo	0.731 (0.617, 0.779)	0.715 (0.634, 0.779)	0.835 (0.705, 0.875)	0.847 (0.704, 0.888)	0.695 (0.61, 0.78)	0.821 (0.686, 0.884)

Table III.5. Mean variance of the eigenvalues (VE) and trait autonomy (TA) by taxa for all 20 traits, and pairwise trait groupings among anatomical regions: basicranium and pelvic girdle (B-PG), basicranium and shoulder girdle (B-SG), shoulder girdle and pelvic girdle (SG-PG), basicranium and humerus (B-H), pelvic girdle and humerus (PG-H), shoulder girdle and humerus (SG-H). 95% confidence intervals are in parentheses. Greater VE values reflect more integration among the traits, as smaller trait autonomy values also reflect; more autonomy indicates less integration. Comparisons among traits within taxa are in rows, and comparisons of trait groupings among taxa are in columns.

	Taxon	*Analysis*	*All*	*B - PG*	*B - SG*	*SG - PG*	*SG - H*	*B - H*	*PG - H*
Platyrrhines	***Alouatta***	**VE**	0.018 (0.012, 0.028)	0.048 (0.015, 0.064)	0.04 (0.018, 0.068)	0.047 (0.022, 0.063)	0.031 (0.017, 0.064)	0.011 (0.008, 0.063)	0.026 (0.016, 0.039)
		TA		0.019 (1.45E-04, 0.059)	0.026 (3.96E-05, 0.044)	0.012 (1.58E-05, 0.027)	0.017 (2.11E-05, 0.037)	0.05 (1.87E-04, 0.076)	0.016 (4.27E-06, 0.043)
Cercopithecoids	***Colobus***	**VE**	0.012 (0.01, 0.02)	0.02 (0.011, 0.041)	0.042 (0.027, 0.062)	0.03 (0.022, 0.048)	0.037 (0.021, 0.052)	0.01 (0.009, 0.037)	0.017 (0.013, 0.027)
		TA		0.042 (1.89E-04, 0.063)	0.017 (4.91E-05, 0.035)	0.017 (5.98E-05, 0.032)	0.018 (6.84E-05, 0.036)	0.06 (2.59E-04, 0.071)	0.039 (5.65E-05, 0.06)
	Macaca	**VE**	0.008 (0.006, 0.016)	0.023 (0.009, 0.043)	0.018 (0.011, 0.04)	0.021 (0.015, 0.04)	0.017 (0.01, 0.038)	0.006 (0.006, 0.038)	0.012 (0.01, 0.024)
		TA		0.062 (2.20E-04, 0.071)	0.044 (1.73E-04, 0.067)	0.04 (8.00E-05, 0.054)	0.044 (1.46E-04, 0.064)	0.079 (2.63E-04, 0.079)	0.044 (7.43E-05, 0.053)
	Papio	**VE**	0.017 (0.013, 0.033)	0.04 (0.018, 0.075)	0.033 (0.022, 0.072)	0.044 (0.024, 0.077)	0.032 (0.024, 0.075)	0.023 (0.017, 0.073)	0.025 (0.018, 0.046)
		TA		0.01 (2.70E-05, 0.039)	0.012 (6.90E-06, 0.023)	0.005 (8.03E-06, 0.019)	0.007 (9.92E-06, 0.019)	0.011 (5.07E-05, 0.033)	0.005 (6.92E-06, 0.029)
Hominoids	***Homo***	**VE**	0.005 (0.003, 0.01)	0.005 (0.002, 0.017)	0.018 (0.011, 0.032)	0.018 (0.01, 0.03)	0.017 (0.009, 0.029)	0.005 (0.004, 0.016)	0.008 (0.004, 0.016)
		TA		0.079 (0.044, 0.092)	0.039 (0.019, 0.069)	0.041 (0.023, 0.074)	0.042 (0.025, 0.079)	0.079 (0.049, 0.094)	0.078 (0.044, 0.095)
	Hylobates	**VE**	0.01 (0.007, 0.015)	0.017 (0.008, 0.034)	0.039 (0.018, 0.049)	0.029 (0.019, 0.039)	0.035 (0.015, 0.042)	0.009 (0.004, 0.024)	0.016 (0.01, 0.021)
		TA		0.04 (0.011, 0.07)	0.019 (0.004, 0.049)	0.015 (0.006, 0.044)	0.02 (0.006, 0.056)	0.056 (0.012, 0.081)	0.038 (0.005, 0.071)
	Pan	**VE**	0.01 (0.005, 0.013)	0.032 (0.009, 0.038)	0.029 (0.007, 0.045)	0.025 (0.015, 0.034)	0.017 (0.006, 0.032)	0.012 (0.002, 0.019)	0.013 (0.008, 0.018)
		TA		0.023 (0.018, 0.074)	0.024 (0.019, 0.078)	0.02 (0.013, 0.055)	0.031 (0.021, 0.077)	0.043 (0.035, 0.089)	0.026 (0.015, 0.071)
	Pongo	**VE**	0.009 (0.007, 0.017)	0.033 (0.018, 0.055)	0.033 (0.023, 0.053)	0.01 (0.007, 0.028)	0.007 (0.005, 0.028)	0.036 (0.019, 0.054)	0.005 (0.004, 0.016)
		TA		0.029 (0.005, 0.046)	0.028 (0.005, 0.041)	0.051(0.011, 0.072)	0.07 (0.013, 0.078)	0.033 (0.005, 0.048)	0.056 (0.012, 0.078)

Table III.6. Phylogenetically corrected correlations between traits. Values are colored into quartiles: first quartile (lowest value to 0.25) are green, second quartile (0.26 to 0.5) are blue, third quartile (0.51 to 0.75) are yellow, and the fourth quartile (0.76 to highest value) are orange.

	NR	SCM	SNL	FMW	FML	SSL	SBL	VB	GW	CLML	AMIB	RAH	ASL	LIH	AW	HML	MCONDH	LCONDH	HDW	HEW	
NR		0.717	0.471	0.372	0.493	0.330	0.541	0.590	0.741	0.425	0.089	0.464	0.725	0.108	0.574	0.131	0.648	0.608	0.736	0.665	**NR**
SCM	NA		0.493	0.587	0.617	0.043	0.322	0.477	0.711	0.537	-0.212	0.319	0.744	0.028	0.755	0.168	0.459	0.587	0.641	0.380	**SCM**
SNL	NA	NA		0.757	0.778	0.530	0.686	0.886	0.858	0.698	0.154	0.616	0.687	0.523	0.792	0.733	0.783	0.838	0.874	0.760	**SNL**
FMW	NA	NA	NA		0.822	-0.035	0.260	0.602	0.743	0.732	-0.405	0.276	0.643	0.103	0.872	0.455	0.445	0.695	0.654	0.306	**FMW**
FML	NA	NA	NA	NA		0.144	0.389	0.813	0.852	0.684	-0.287	0.598	0.903	0.491	0.980	0.537	0.629	0.716	0.826	0.540	**FML**
SSL	NA	NA	NA	NA	NA		0.681	0.631	0.310	-0.160	0.408	0.648	0.295	0.171	0.142	0.034	0.533	0.273	0.374	0.735	**SSL**
SBL	NA	NA	NA	NA	NA	NA		0.690	0.498	0.342	0.328	0.865	0.349	0.650	0.403	0.399	0.866	0.597	0.691	0.894	**SBL**
VB	NA	NA	NA	NA	NA	NA	NA		0.790	0.497	0.296	0.862	0.702	0.597	0.725	0.575	0.789	0.799	0.831	0.755	**VB**
GW	NA	NA	NA	NA	NA	NA	NA	NA		0.654	0.029	0.796	0.739	0.520	0.852	0.620	0.824	0.922	0.948	0.753	**GW**
CLML	NA	NA	NA	NA	NA	NA	NA	NA	NA		0.011	0.394	0.528	0.602	0.667	0.808	0.670	0.759	0.766	0.541	**CLML**
AMIB	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA		0.094	-0.604	0.005	-0.700	-0.455	-0.158	-0.491	-0.443	0.085	**AMIB**
RAH	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA		0.656	0.651	0.647	0.397	0.830	0.778	0.791	0.747	**RAH**
ASL	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA		0.627	0.763	0.485	0.699	0.598	0.813	0.637	**ASL**
LIH	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA		0.714	0.542	0.615	0.456	0.666	0.446	**LIH**
AW	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA		0.593	0.608	0.777	0.784	0.424	**AW**
HML	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA		0.650	0.574	0.709	0.696	**HML**
MCONDH	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA		0.861	0.941	0.879	**MCONDH**
LCONDH	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA		0.914	0.802	**LCONDH**
HDW	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA		0.860	**HDW**
HEW	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA		**HEW**

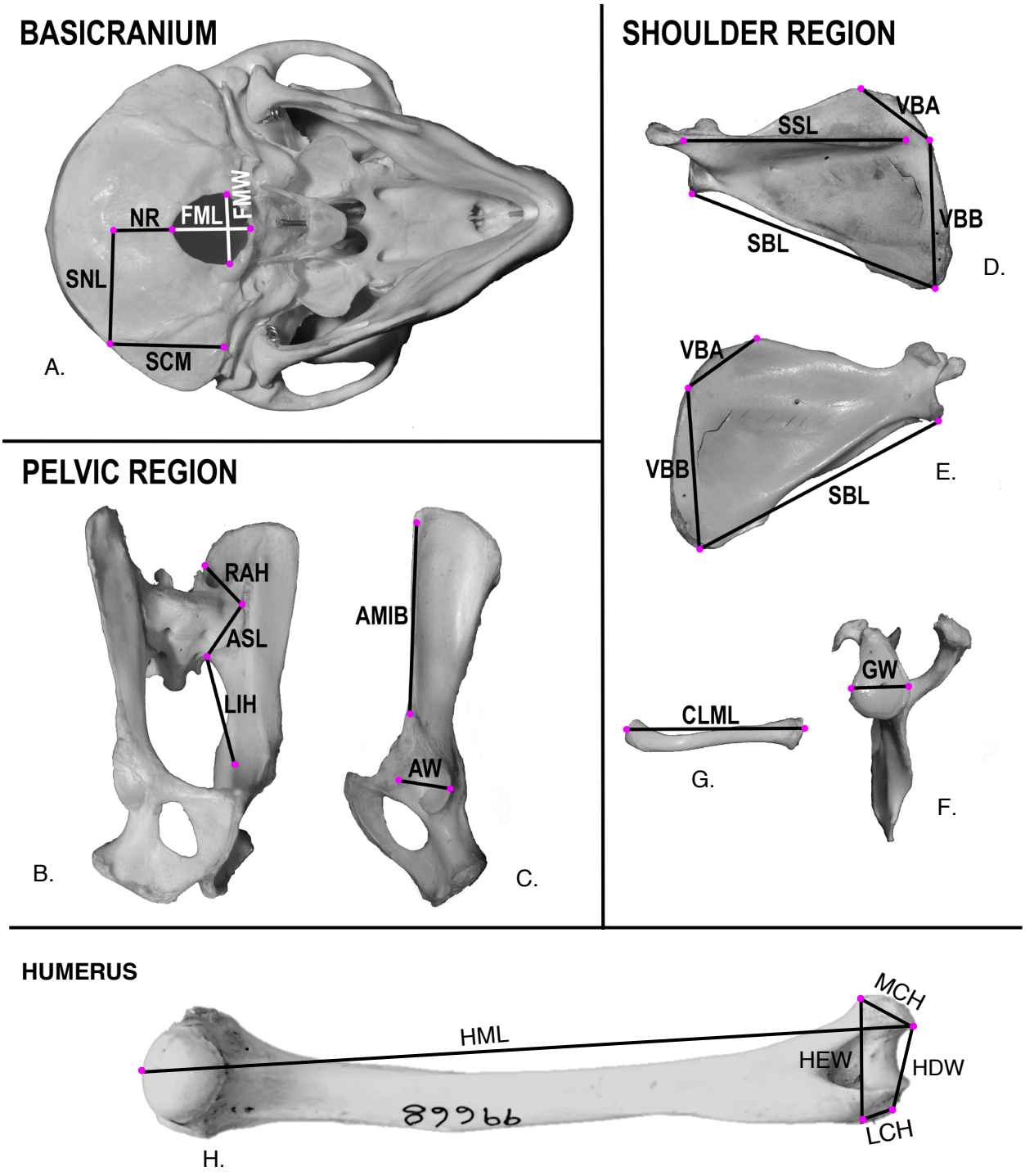


Figure III.1. Linear dimensions collected from each anatomical region: A. caudal aspect of the basicranium; B. medial aspect of os coxa; C. lateral aspect of os coxa; D. dorsal aspect of scapula; E. ventral aspect of scapula; F. lateral aspect of scapula; G. cranial aspect of clavicle; F. ventral aspect of humerus. Trait descriptions can be found in Table III.2. Measurements are demonstrated on a *Macaca mulatta* specimen and are homologous for all taxa

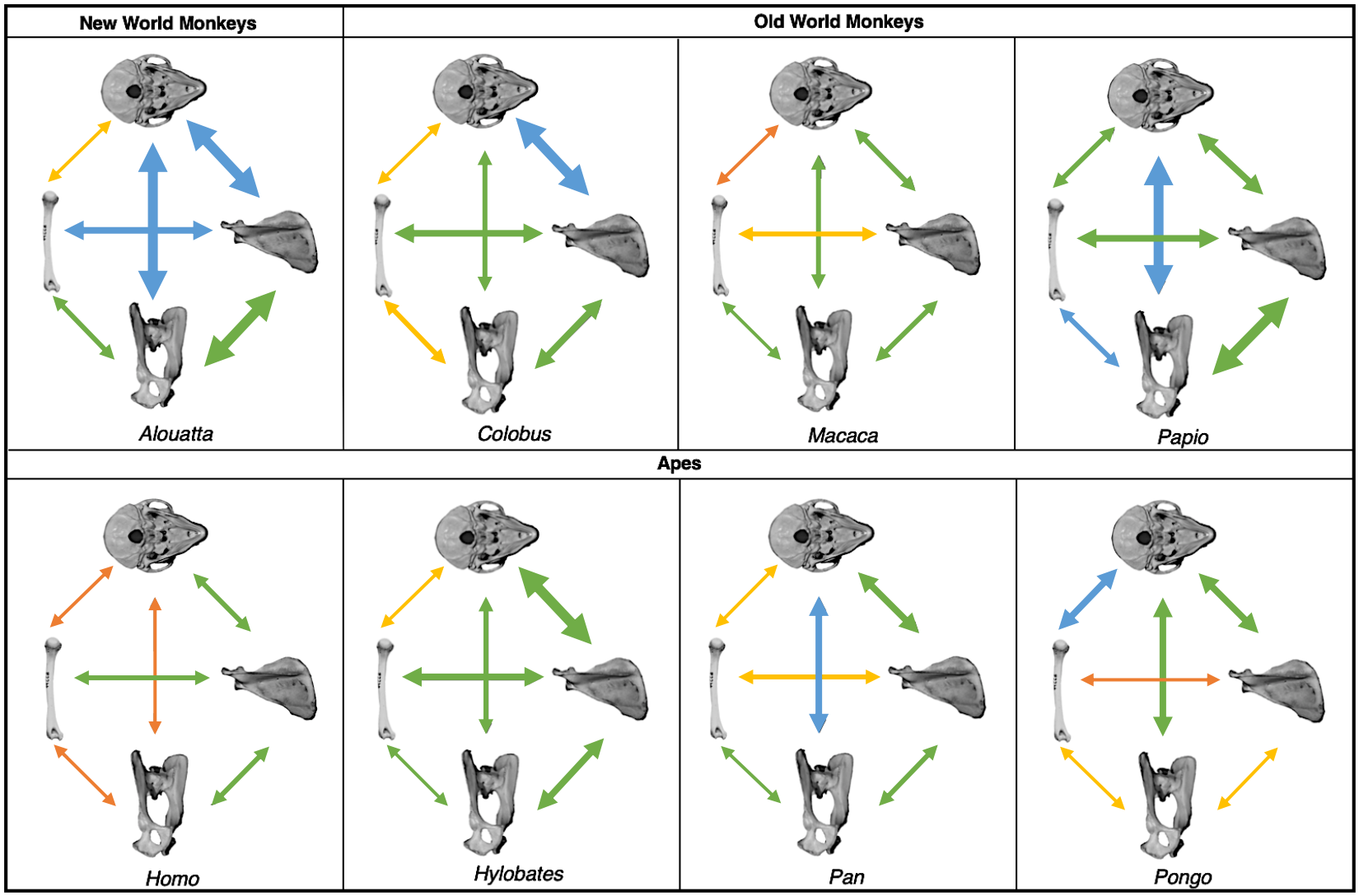


Figure III.2. Visual representation of estimated mean flexibility and morphological integration among pairs of anatomical regions. Colors correspond to the quartiles of evolutionary flexibility: blue (0.63 – 0.7), green (0.71 – 0.77), yellow (0.78 – 0.84), and orange (0.84 – 0.91). Thicker arrows correspond to stronger morphological integration, also grouped by quartiles among all taxa.

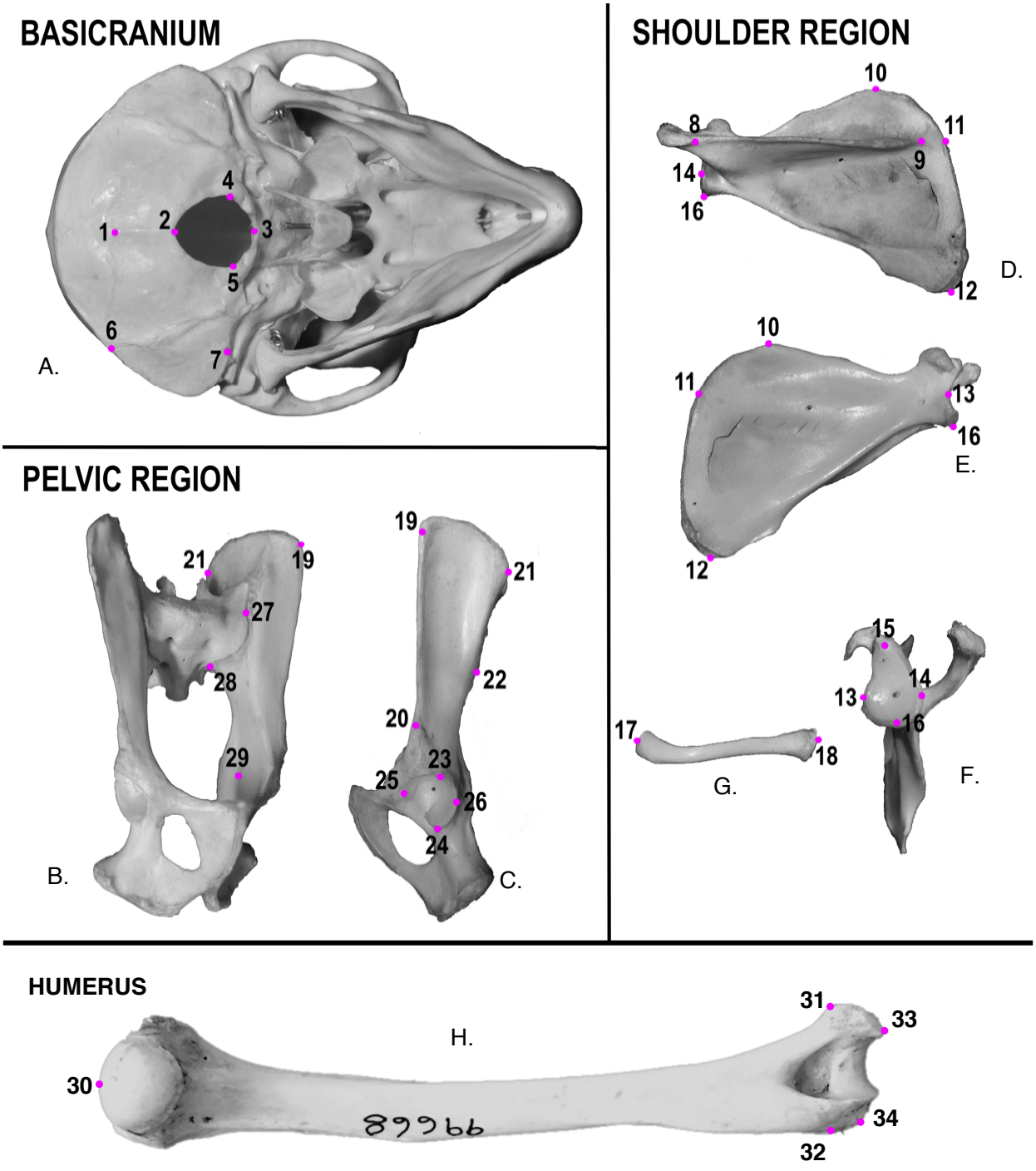


Figure SII.1. Landmarks taken from each anatomical region: A. caudal aspect of the basicranium; B. medial aspect of os coxa; C. lateral aspect of os coxa; D. dorsal aspect of scapula; E. ventral aspect of scapula; F. lateral aspect of scapula; G. cranial aspect of clavicle; F. ventral aspect of humerus. Refer to Table SII.1 for a list of landmarks and descriptions. Landmark locations are demonstrated on a *Macaca mulatta* specimen and are homologous for all taxa.

Table SII.1. List and definitions of landmarks collected.

No.	*Landmark*	*Definition*
	Basicranium	
1.	Inion	Location of the intersection of the right and left superior nuchal lines within the external occipital protuberance (White et al 2012).
2.	Opisthion	Midline point of the dorsal margin of the foramen magnum (White et al 2012).
3.	Basion	Midline point of the ventral margin of the foramen magnum (White et al 2012).
4.	Right margin of foramen magnum	Right margin of the foramen magnum at its greatest curvature (Moore-Jansen et al 1994).
5.	Left margin of foramen magnum	Left margin of the foramen magnum at its greatest curvature (Moore-Jansen et al 1994).
6.	Asterion	Point where the lambdoidal, parietomastoid, and occipitomastoid sutures meet (White et al 2012).
7.	Left mastoid	Inferior-most point of the mastoid process (White et al 2012).
	Scapula	
8.	Scapular spine lateral border	Point of intersection between the scapular spine and acromion process (Sears et al 2013).
9.	Scapular spine medial border	Medial margin of trapezius attachment along scapular spine (Young 2006).
10.	Superior angle	Intersection of superior and medial borders of scapula (White et al 2012).
11.	Scapular spine vertebral border	Point on vertebral margin where the long axis of the scapular spine and vertebral border meet (Young 2006).
12.	Inferior angle	Intersection of the lateral and medal borders of scapula (White et al 2012).
13.	Ventral margin of glenoid fossa	Ventral margin of glenoid fossa at its greatest width (Young 2006).
14.	Dorsal margin of glenoid fossa	Dorsal margin of glenoid fossa at its greatest width (Young 2006).
15.	Cranial margin of glenoid fossa	Superior-most margin of glenoid fossa (Young 2006).
16.	Caudal margin of glenoid fossa	Inferior-most margin of glenoid fossa (Young 2006).
	Clavicle	
17.	Acromial end	Lateral-most point of clavicle on cranial aspect.
18.	Sternal end	Medial-most point of clavicle on cranial aspect.

Table SII.1 continued

No.	Landmark	Definition
	Os coxa	
19.	Anterior superior iliac spine	Ventral-most point on lateral aspect of iliac crest (Lewton 2012).
20.	Anterior inferior iliac spine	Ventral-most point on anterior inferior iliac spine. If only a bony roughening, the point is taken at the center of this rugosity (Lewton 2012).
21.	Posterior superior iliac spine	Medial-most point of the dorsal-cranial border of iliac crest (Lewton 2012).
22.	Posterior inferior iliac spine	Sharp projection posterior and inferior to the auricular surface (White et al 2012).
23.	Cranial margin of acetabulum	Cranial-most point of the margin of the acetabulum (Lewton 2012).
24.	Caudal margin of acetabulum	Caudal-most point of the margin of the acetabulum, directly across from landmark 23 (Lewton 2012).
25.	Medial margin of acetabulum	Medial-most point along margin of the acetabulum.
26.	Lateral margin of acetabulum	Lateral-most point along margin of the acetabulum.
27.	Cranial margin of auricular surface	Central point of the cranial-most margin of the auricular surface.
28.	Caudal margin of auricular surface	Central point of the caudal-most margin of the auricular surface.
29.	Center of acetabulum	Center of the acetabulum, defined as the intersection of the line between landmarks 23 and 24 and landmarks 27 and 28 (Lewton 2012).
	Humerus	
30.	Cranial end of humerus	Cranial-most point of the proximal end of humerus.
31.	Medial epicondyle	Medial-most margin of medial epicondyle of humerus.
32.	Lateral epicondyle	Lateral-most margin of lateral epicondyle of humerus.
33.	Medial margin of distal articular surface	Medial-most margin of distal articular surface of the humerus.
34.	Lateral margin of distal articular surface	Lateral-most margin of distal articular surface of the humerus.

Table SII.2 List of traits and their functional and/or developmental correlates.

Trait	Description
	Basicranium
NR	Length of the bony attachment of the nuchal ligament on the basicranium (Richmond et al 2001). The nuchal ligament serves as an origin for the trapezius muscle (Diogo and Wood 2012), and has partial contributions from PONC during development (Matsuoka et al 2005).
SCM	Length of cranial insertion of the sternocleidomastoid mastoid muscle (Richmond et al 2001). This muscle and its attachments have PONC contributions during development (Matsuoka et al 2005).
SNL	Length of the caudal border of the attachment for cranial-most neck muscles and trapezius muscle (Richmond et al 2001). The attachment of the trapezius has PONC contribution during development (Matsuoka et al 2005).
FMW	Width of the foramen magnum measured at the greatest curvature of the left and right lateral margins (Moore-Jansen et al 1994). This provides a measure of the intercondylar breadth for the occipital condyles, which are derived from the somites during ontogeny (Pilbeam 2004)
FML	Ventral to dorsal length of the foramen magnum (Moore-Jansen et al 1994). Derived from paraxial mesoderm and somites during development (Pilbeam 2004).
	Shoulder Girdle
SSL	Length of the scapular spine – insertion of the trapezius muscle along the scapular spine (Richmond et al 2001; Young 2006). This point of attachment is derived from PONC during development (Matsuoka et al 2005).
SBL	Length of scapular blade along lateral border (Martin 1928). Combined origin length for teres minor, teres major, latissimus dorsi (in some primates), and long head of the triceps brachii muscles (Diogo and Wood 2012; Zihlman and Underwood 2019).
SBW	Maximum medial to lateral breadth of scapular blade (Martin 1928; Moore-Jansen et al 1994). Roughly corresponds to medial-lateral length of the caudal portion of supraspinatus and cranial portion of infraspinatus muscles.
SBH	Cranial to caudal height of scapular blade (Martin 1928; Moore-Jansen et al 1994). Combined length of the supraspinous and infraspinous fossae, which provide the combined breadth of the supraspinatus and infraspinatus muscles (Diogo and Wood 2012; Zihlman and Underwood 2019).
VB	Length of the vertebral border of the scapula. Combined values of VBA (10-11) and VBB (11-12). The vertebral border of the scapula is the location of the insertion of rhomboid major and rhomboid minor muscles (Diogo and Wood 2012; Zihlman and Underwood 2019), and is derived from the somites during development (Valasek et al 2010).

Table SII.2 continued

Trait	Description
GW	Maximum ventral to dorsal width of glenoid fossa (Young 2006). Maximum width of the shoulder joint surface, derived from the somatopleure during development (Huang et al 2000; Huang et al 2006; Sears et al 2015).
GL	Maximum cranial to caudal length of the glenoid fossa (Young 2006). Maximum height of the shoulder joint surface, derived from the somatopleure during development (Huang et al 2000; Huang et al 2006; Sears et al 2015).
CLML	Maximum length of the clavicle (Martin 1928; Moore-Jansen et al 1994). Part of the bony shoulder girdle, and medial portion is the origin for the sternocleidomastoid muscle and is derived from PONC during development (Matsuoka et al 2005).
Pelvic Girdle	
AMIB	Anterior margin of iliac blade (Grabowski and Roseman 2015). Distance is functionally related to positioning of the lesser gluteal muscles which can aide in pelvic stabilization during the single support phase in bipedal locomotion (Sigmon 1975). Analogous blade measurement to the lateral border of the scapula.
PMIB	Posterior margin of iliac blade (Grabowski and Roseman 2015). Shorter distances place the body's center of mass above the hips during more bipedal locomotion (see McCollum et al 2010). Analogous to the medial blade border of scapula.
ASL	Cranial to caudal length of the auricular surface (Grabowski and Roseman 2015). Functionally related to weight bearing (Berge and Kazmierczak 1986).
RAH	Retro-auricular height, distance from cranial margin of the auricle to posterior superior iliac spine (Grabowski and Roseman 2015). Expansion of this area is related to more upright trunk postures (see Dart 1949; Lovejoy 2005; Stern and Susman 1983; Bramble and Leiberman 2004). Roughly analogous to scapular blade breadth.
LIB	Lateral iliac breadth, distance from cranial margin of the auricle to the anterior superior iliac spine (Grabowski and Roseman 2015). Roughly analogous to scapular blade breadth.
LIH	Lower iliac height, distance from caudal margin of auricle to the posterior aspect of the central point of the acetabulum (Grabowski and Roseman 2015). Longer distances related to lumbar mobility (see Lovejoy et al 2009). Analogous to scapular blade length.
AL	Cranial to caudal length of the acetabulum (Lewton 2012). Analogous measure to GL as part of the joint surface.
AW	Medial to lateral width of the acetabulum. Is an analogous measure to GW as part of the joint surface, and can be used as a proxy for body size (Ruff 2003).
Humerus	
HML	Maximum length of the humerus (Moore-Jansen et al 1994).
MCH	Length of the bony attachment of several flexor muscles of the forearm (Zihlman and Underwood 2019).
LCH	Length of the bony attachment of several extensor muscles of the forearm (Zihlman and Underwood 2019).

Table SII.2 continued

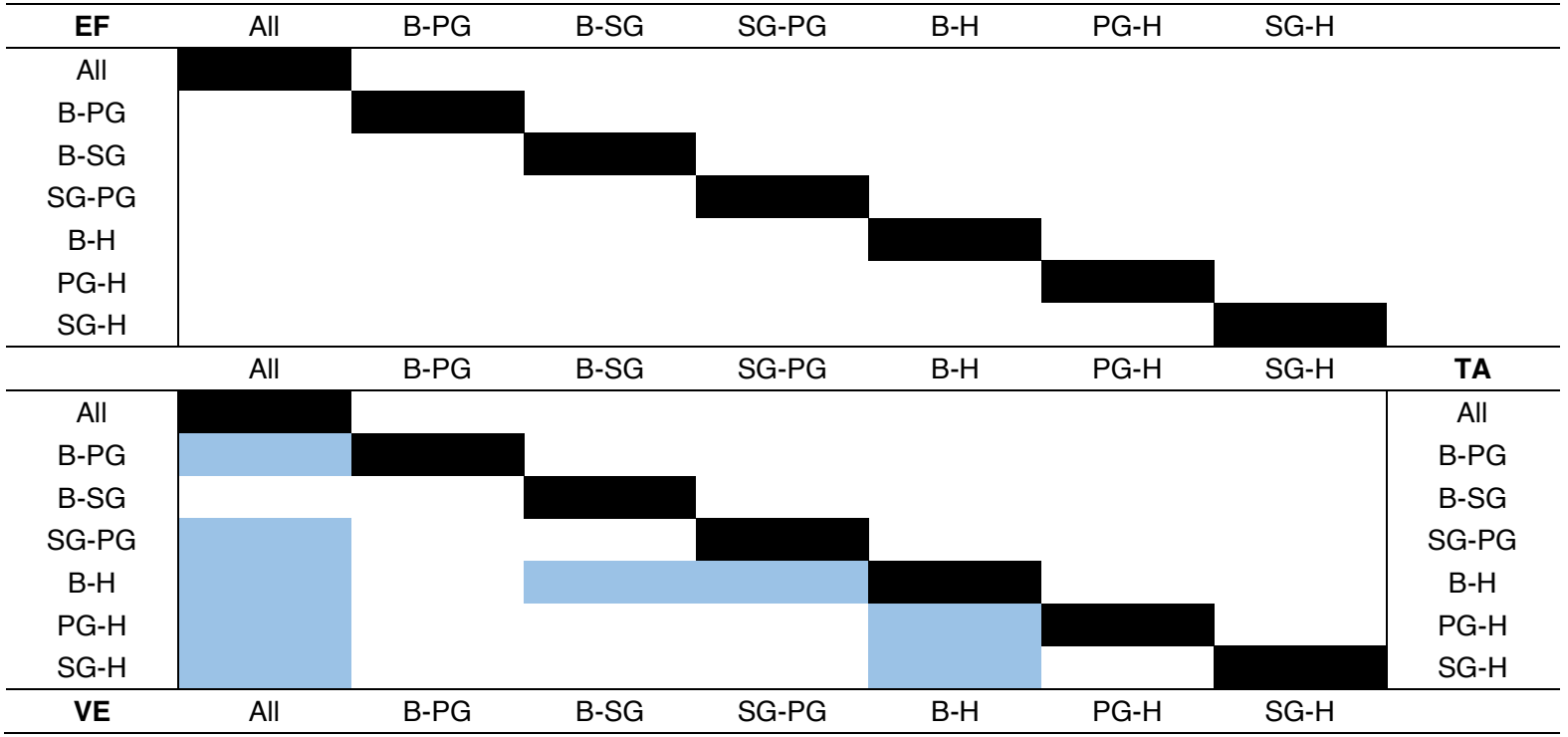
Trait	Description
HEW	Medial to lateral width of distal humerus at the epicondyles (Zihlman and Underwood 2019).
HDW	Medial to lateral width of the distal articular region of the humerus (Zhilmand and Underwood 2019). Articular surface of elbow joint.
HHW	Maximum medial to lateral width of the humeral head (Moore-Jansen et al 1994). Part of the shoulder joint surface on the humerus, and derived from somatopleure during development (Sears et al 2015).

Table SII.3. Mean estimated flexibilities for paired anatomical regions listed in order from smallest to largest within each taxon. Abbreviations are: basicranium and pelvic girdle (B-PG), basicranium and shoulder girdle (B-SG), shoulder girdle and pelvic girdle (SG-PG), basicranium and humerus (B-H), pelvic girdle and humerus (PG-H), shoulder girdle and humerus (SG-H).

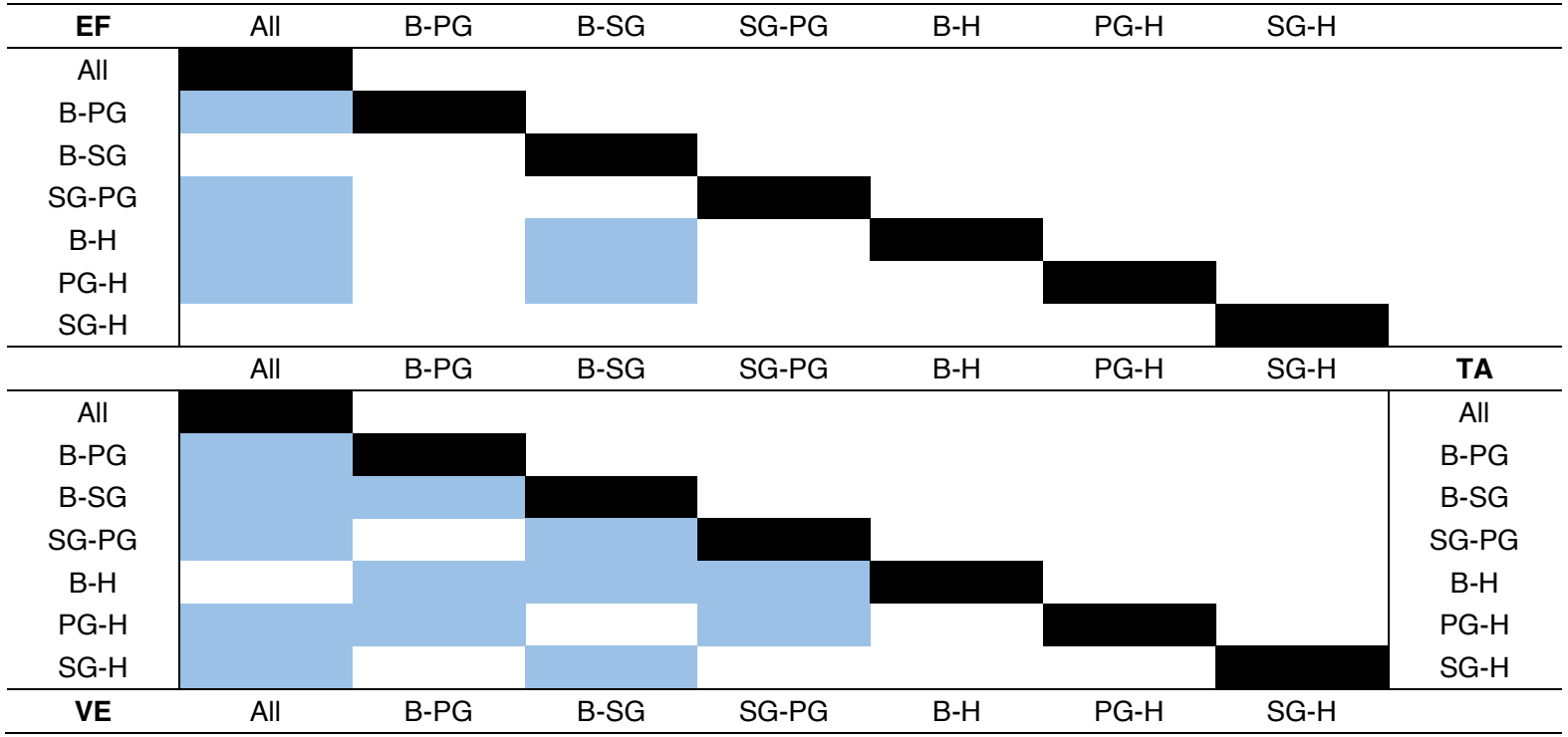
	Taxon	*Flexibility values (smallest – left; largest – right)*					
Platyrrhines	*Alouatta*	B-SG	SG-H	B-PG	SG-PG	PG-H	B-H
Cercopithecoids	*Colobus*	B-SG	SG-H	SG-PG	B-PG	PG-H	B-H
	Macaca	PG-H	B-PG	SG-PG	B-SG	SG-H	B-H
	Papio	B-PG	PG-H	SG-PG	B-SG	SG-H	B-H
Hominoids	*Homo*	B-SG	SG-PG	SG-H	B-PG	B-H	PG-H
	Hylobates	SG-H	B-SG	SG-PG	B-PG	PG-H	B-H
	Pan	B-PG	PG-H	SG-PG	B-SG	B-H	SG-H
	Pongo	B-H	B-SG	B-PG	PG-H	SG-PG	SG-H

Table SII.4 a-h. Significance for measures of mean evolutionary flexibility (EF), mean variance of eigenvalues (VE), and mean trait autonomy (TA) for each taxon between trait groupings: all 20 traits (All), basicranium and pelvic girdle (B-PG), basicranium and shoulder girdle (B-SG), shoulder girdle and pelvic girdle (SG-PG), basicranium and humerus (B-H), pelvic girdle and humerus (PG-H), and shoulder girdle and humerus (SG-H). Comparisons of mean evolvability are in the lower triangle of the upper matrix, comparisons of mean variance of eigenvalues are in the lower triangle of the lower matrix, and comparisons of mean trait autonomy are in the upper triangle of the lower matrix. Significant comparisons, $p < 0.05$, are highlighted blue.

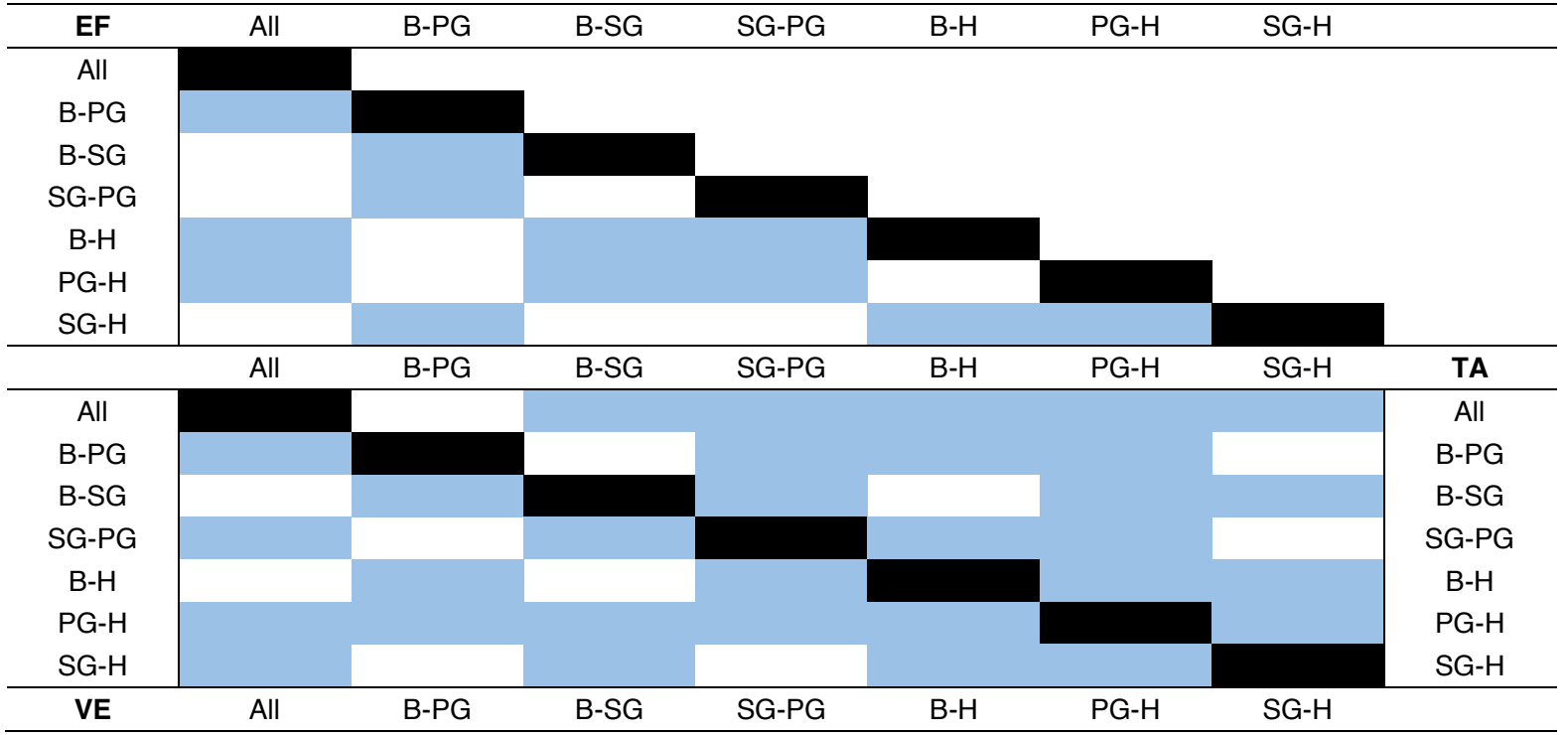
a. *Alouatta*



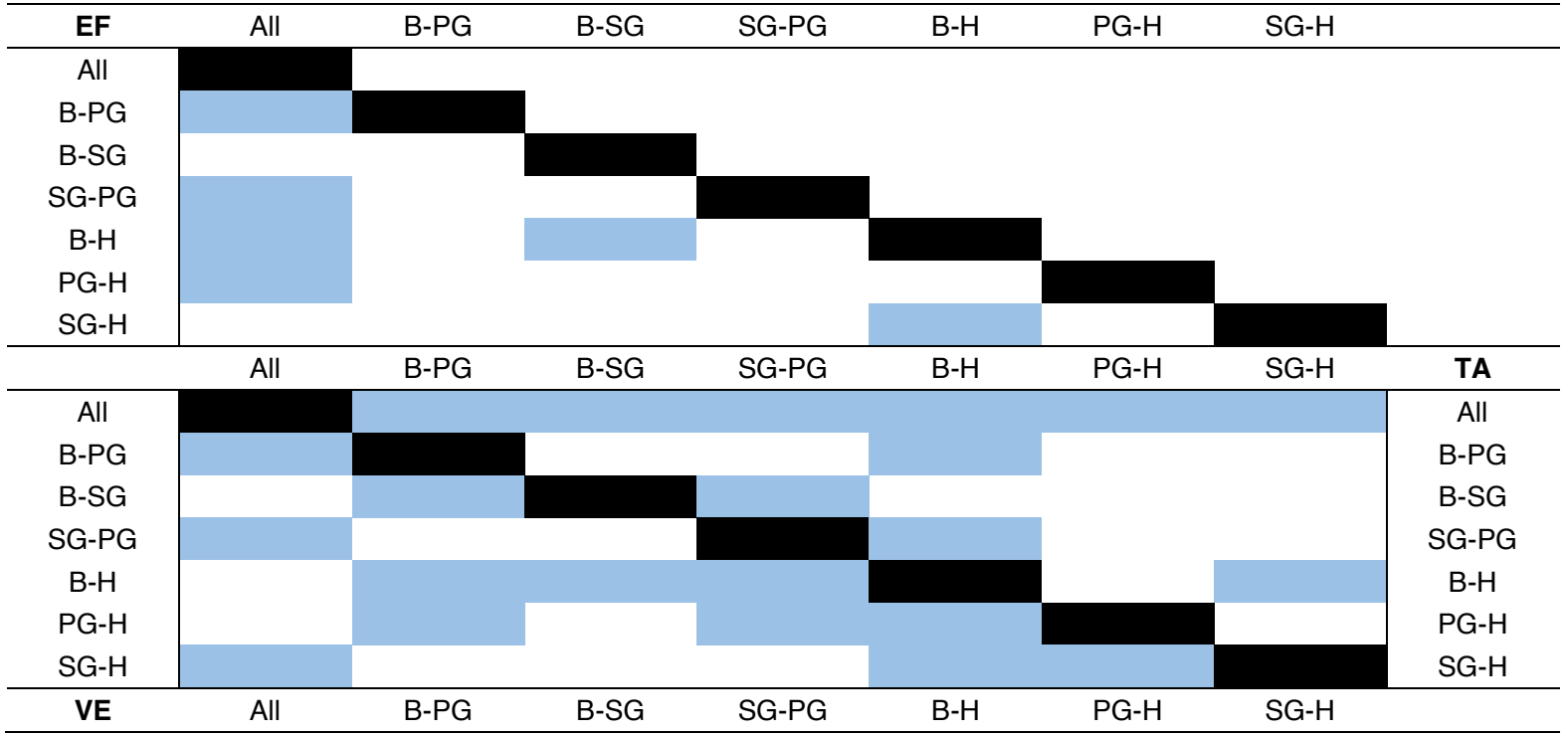
b. *Colobus*


EF
All
B-PG
B-SG
SG-PG
B-H
PG-H
SG-H
All
B-PG
B-SG
SG-PG
B-H
PG-H
SG-H
TA
All
B-PG
B-SG
SG-PG
B-H
PG-H
SG-H
VE
All
B-PG
B-SG
SG-PG
B-H
PG-H
SG-H

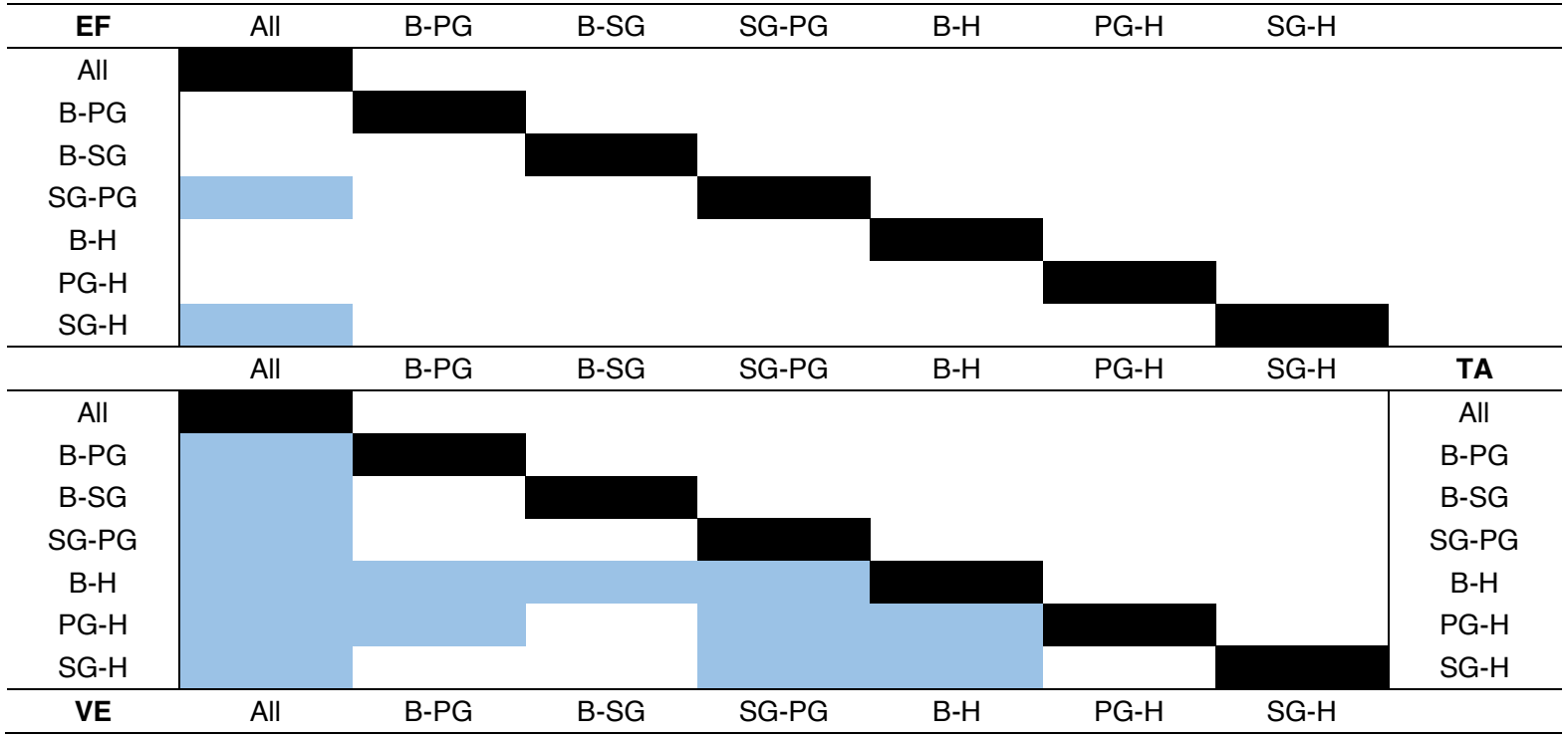
c. *Homo*


EF
All
B-PG
B-SG
SG-PG
B-H
PG-H
SG-H
All
B-PG
B-SG
SG-PG
B-H
PG-H
SG-H
TA
All
B-PG
B-SG
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VE
All
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B-H
PG-H
SG-H

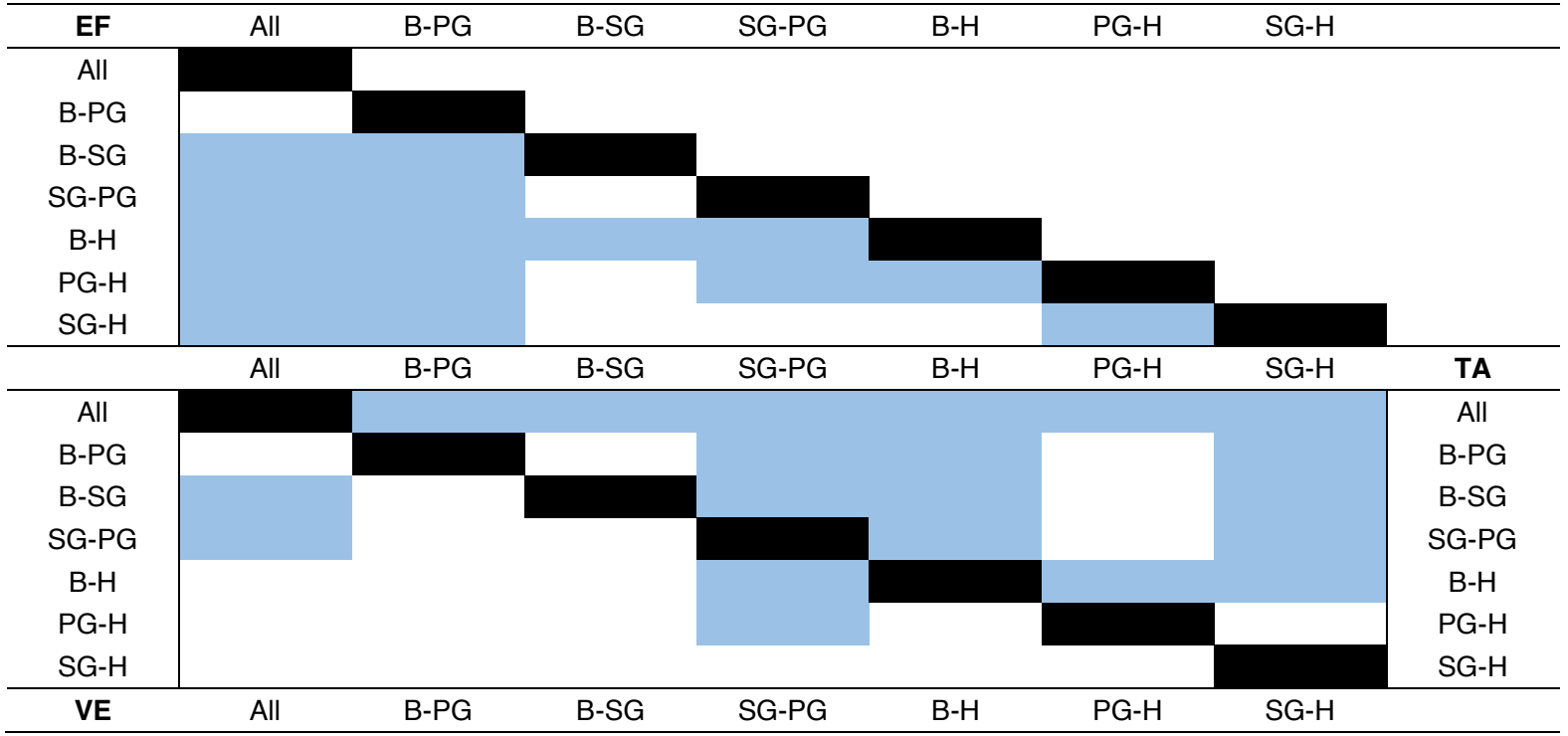
d. *Hylobates*


EF
All
B-PG
B-SG
SG-PG
B-H
PG-H
SG-H
All
B-PG
B-SG
SG-PG
B-H
PG-H
SG-H
TA
All
B-PG
B-SG
SG-PG
B-H
PG-H
SG-H
VE
All
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B-H
PG-H
SG-H

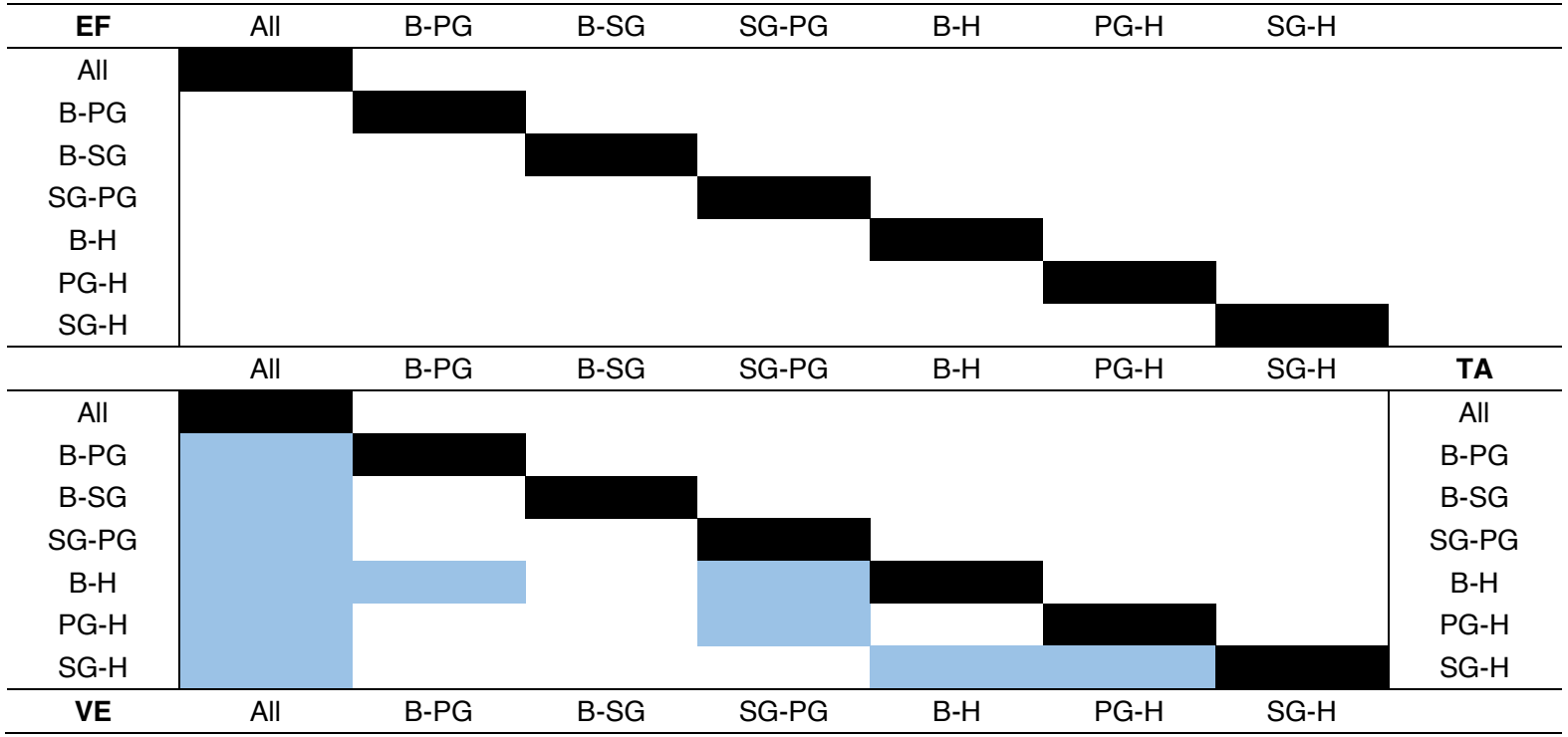
e. *Macaca*


EF
All
B-PG
B-SG
SG-PG
B-H
PG-H
SG-H
All
B-PG
B-SG
SG-PG
B-H
PG-H
SG-H
TA
All
B-PG
B-SG
SG-PG
B-H
PG-H
SG-H
VE
All
B-PG
B-SG
SG-PG
B-H
PG-H
SG-H

f. *Pan*


EF
All
B-PG
B-SG
SG-PG
B-H
PG-H
SG-H
All
B-PG
B-SG
SG-PG
B-H
PG-H
SG-H
TA
All
B-PG
B-SG
SG-PG
B-H
PG-H
SG-H
VE
All
B-PG
B-SG
SG-PG
B-H
PG-H
SG-H

g. *Papio*


EF
All
B-PG
B-SG
SG-PG
B-H
PG-H
SG-H
All
B-PG
B-SG
SG-PG
B-H
PG-H
SG-H
TA
All
B-PG
B-SG
SG-PG
B-H
PG-H
SG-H
VE
All
B-PG
B-SG
SG-PG
B-H
PG-H
SG-H

h. *Pongo*

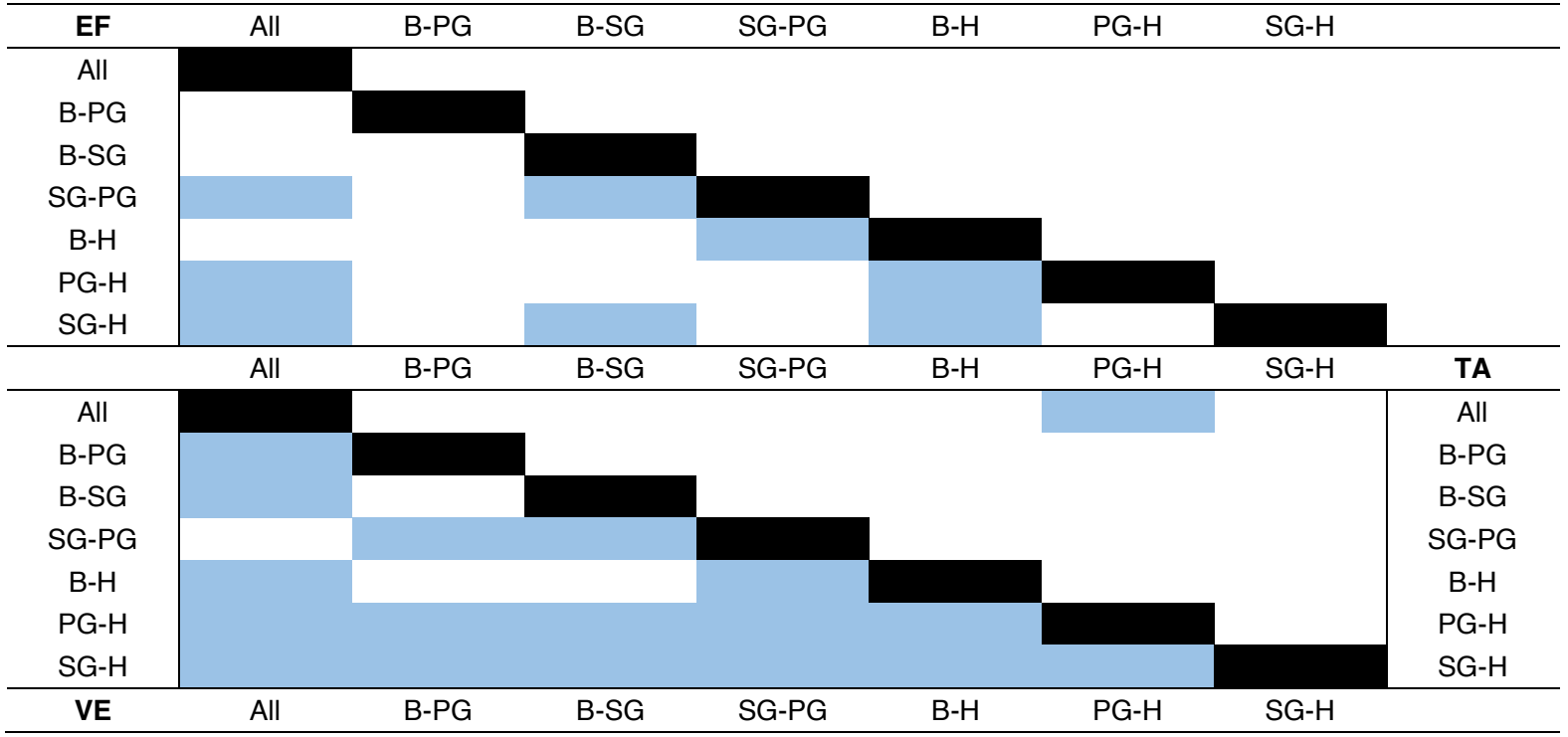
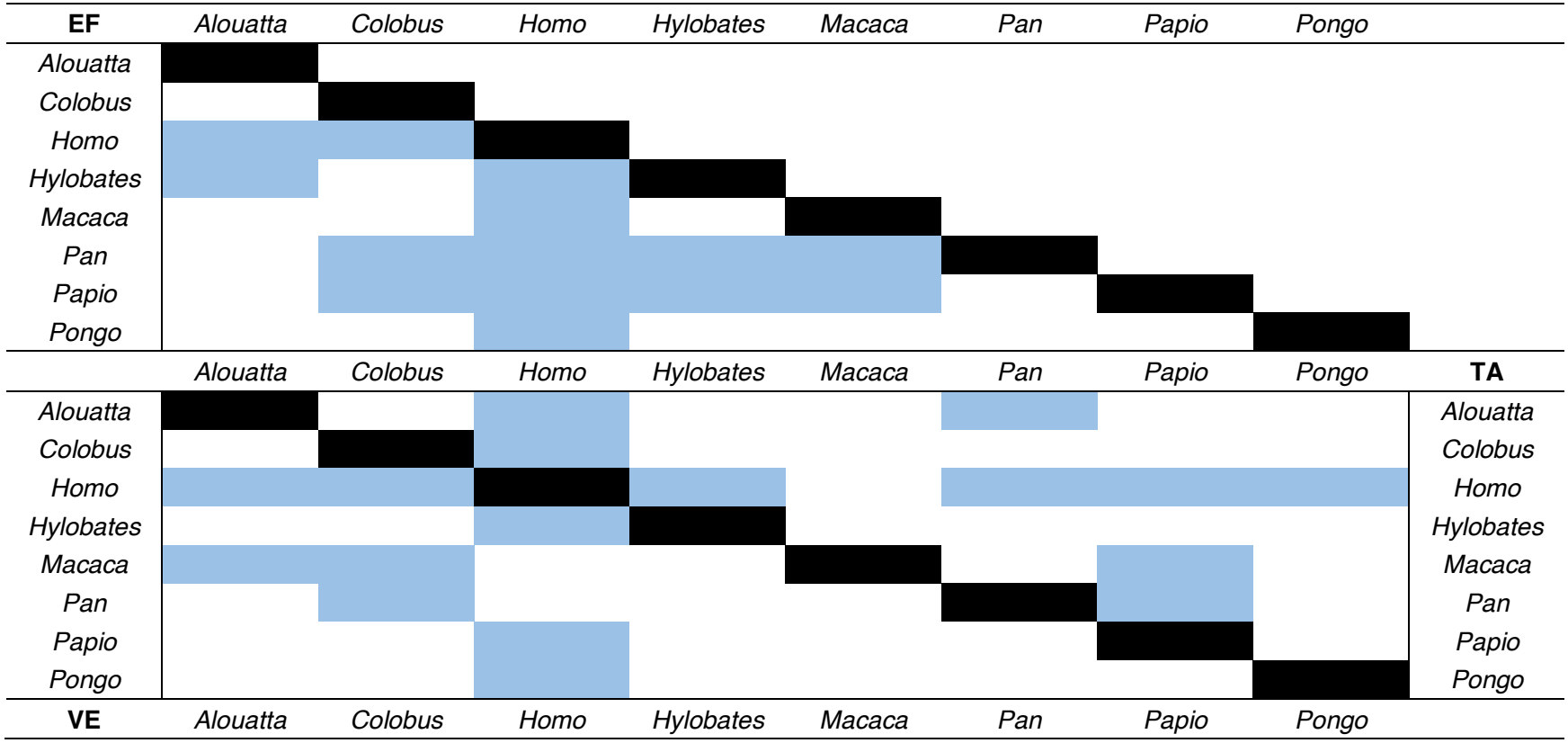

EF
All
B-PG
B-SG
SG-PG
B-H
PG-H
SG-H
All
B-PG
B-SG
SG-PG
B-H
PG-H
SG-H
TA
All
B-PG
B-SG
SG-PG
B-H
PG-H
SG-H
VE
All
B-PG
B-SG
SG-PG
B-H
PG-H
SG-H

Table SII.5 a-g. Significance for measures of mean evolutionary flexibility (EF), mean variance of eigenvalues (VE), and mean trait autonomy (TA) between taxa for each trait grouping: all 20 traits (All), basicranium and pelvic girdle (B-PG), basicranium and shoulder girdle (B-SG), shoulder girdle and pelvic girdle (SG-PG), basicranium and humerus (B-H), pelvic girdle and humerus (PG-H), and shoulder girdle and humerus (SG-H). Comparisons of mean evolvability are in the lower triangle of the upper matrix, comparisons of mean variance of eigenvalues are in the lower triangle of the lower matrix, and comparisons of mean trait autonomy are in the upper triangle of the lower matrix. Significant comparisons, $p < 0.05$, are highlighted blue.

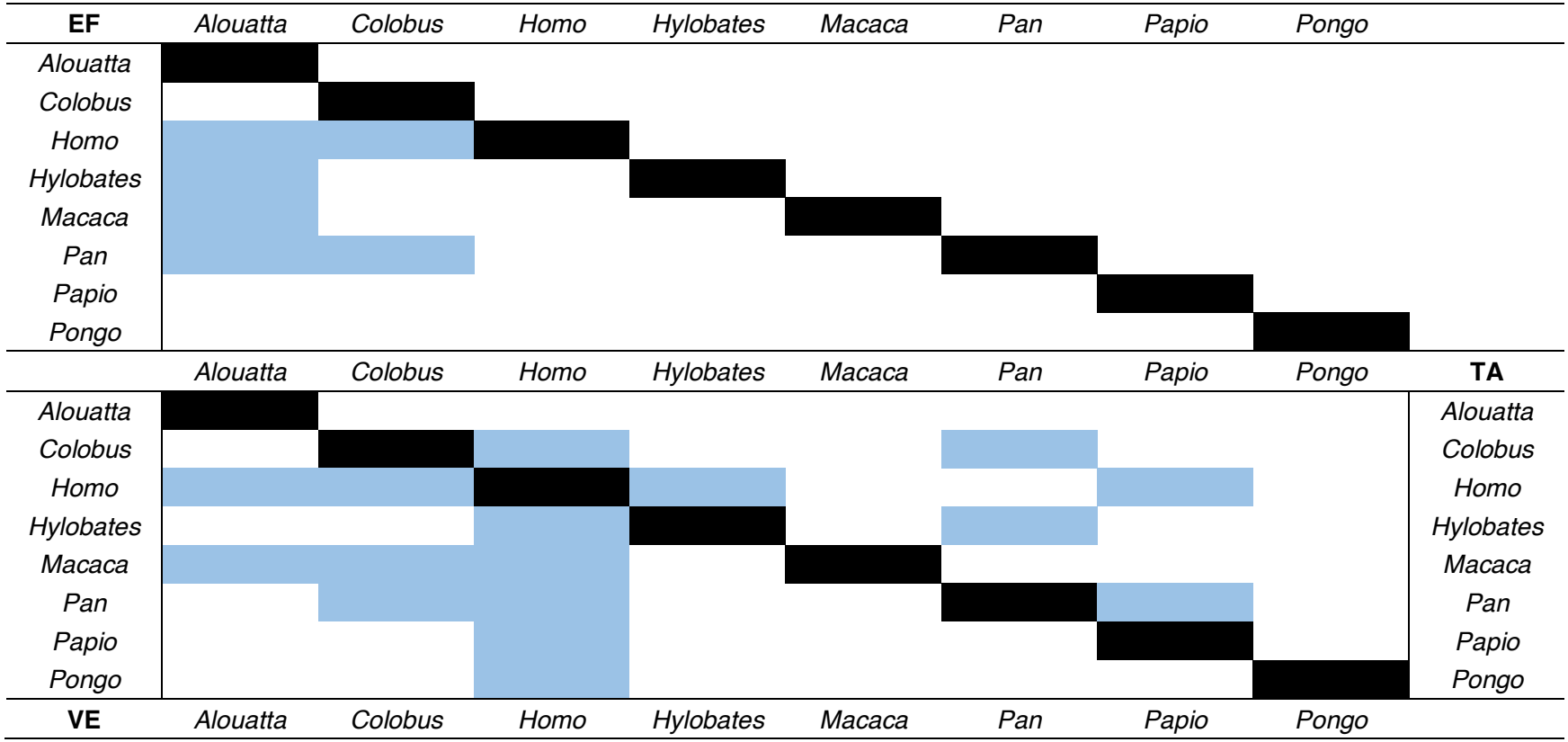
a. All 20 traits

EF	*Alouatta*	*Colobus*	*Homo*	*Hylobates*	*Macaca*	*Pan*	*Papio*	*Pongo*	
Alouatta									
Colobus									
Homo									
Hylobates									
Macaca									
Pan									
Papio									
Pongo									
	Alouatta	*Colobus*	*Homo*	*Hylobates*	*Macaca*	*Pan*	*Papio*	*Pongo*	**TA**
Alouatta									*Alouatta*
Colobus									*Colobus*
Homo									*Homo*
Hylobates									*Hylobates*
Macaca									*Macaca*
Pan									*Pan*
Papio									*Papio*
Pongo									*Pongo*
VE	*Alouatta*	*Colobus*	*Homo*	*Hylobates*	*Macaca*	*Pan*	*Papio*	*Pongo*	

b. Basicranium – Pelvic Girdle



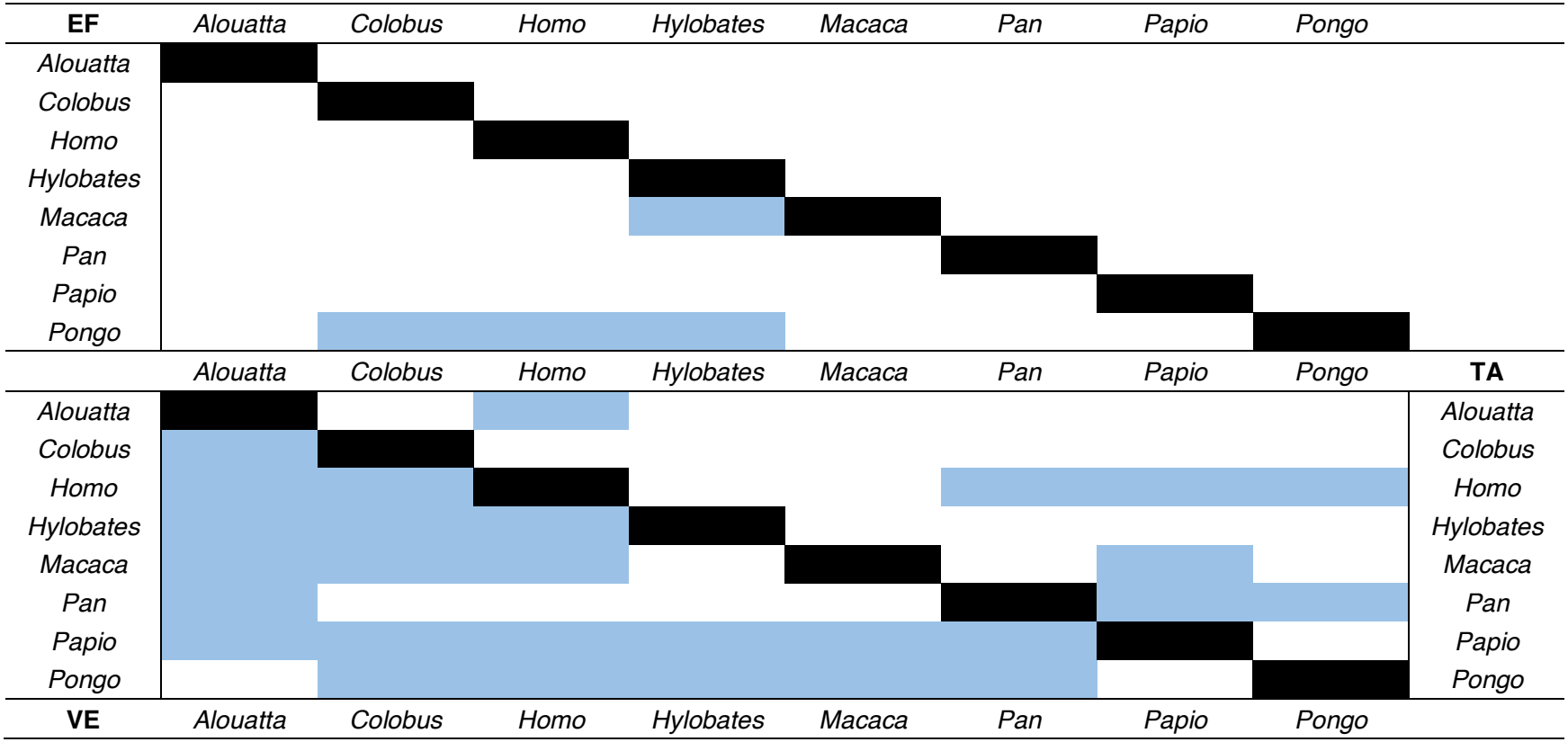
c. Basicranium – Shoulder Girdle



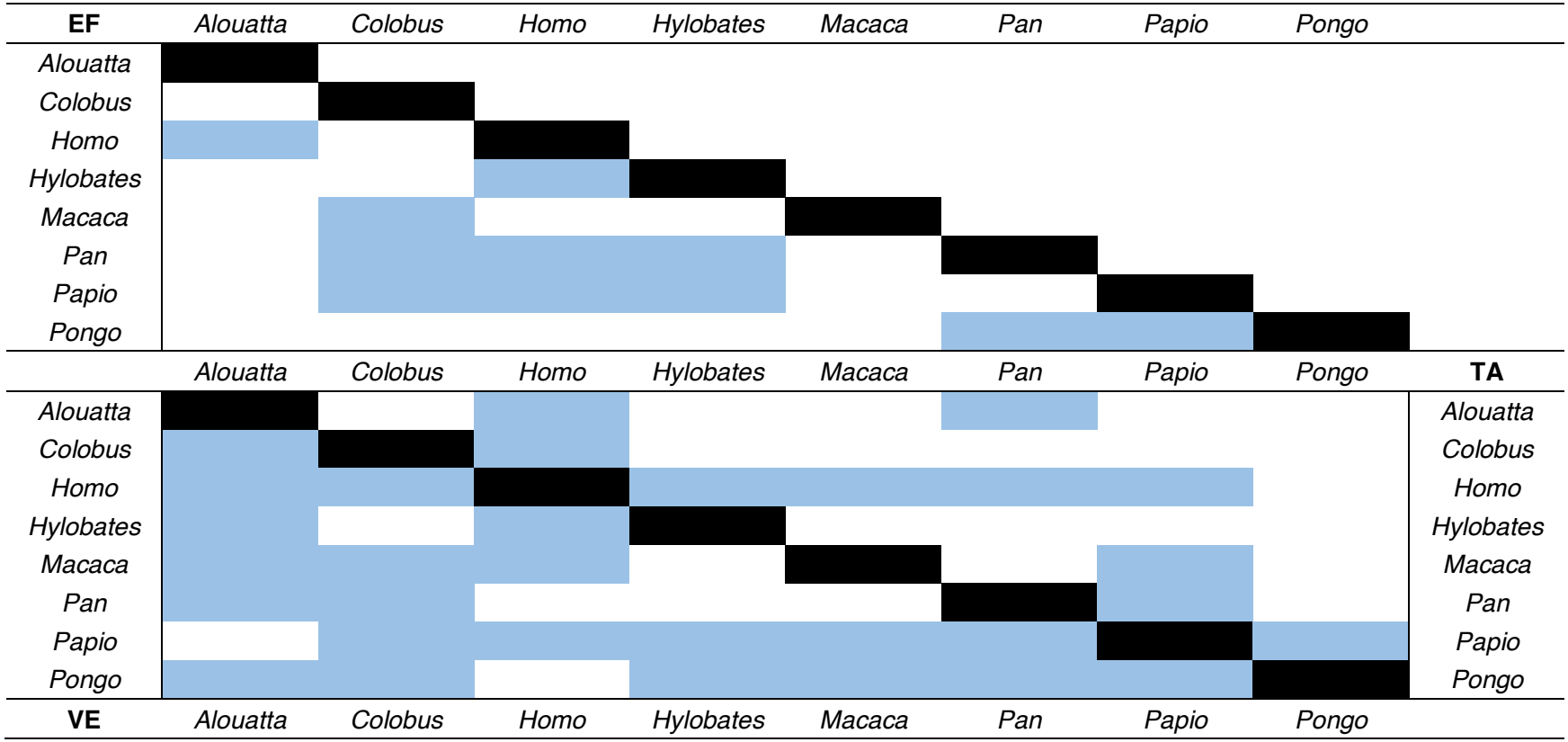
d. Shoulder Girdle – Pelvic Girdle

EF	*Alouatta*	*Colobus*	*Homo*	*Hylobates*	*Macaca*	*Pan*	*Papio*	*Pongo*	
Alouatta	■								
Colobus		■							
Homo			■						
Hylobates				■					
Macaca					■				
Pan						■			
Papio							■		
Pongo							▒	■	
	Alouatta	*Colobus*	*Homo*	*Hylobates*	*Macaca*	*Pan*	*Papio*	*Pongo*	**TA**
Alouatta	■		▒			▒		▒	*Alouatta*
Colobus		■	▒						*Colobus*
Homo	▒	▒	■	▒		▒	▒		*Homo*
Hylobates			▒	■		▒			*Hylobates*
Macaca	▒	▒			■		▒		*Macaca*
Pan	▒					■	▒		*Pan*
Papio			▒		▒	▒	■	▒	*Papio*
Pongo	▒	▒	▒	▒	▒	▒	▒	■	*Pongo*
VE	*Alouatta*	*Colobus*	*Homo*	*Hylobates*	*Macaca*	*Pan*	*Papio*	*Pongo*	

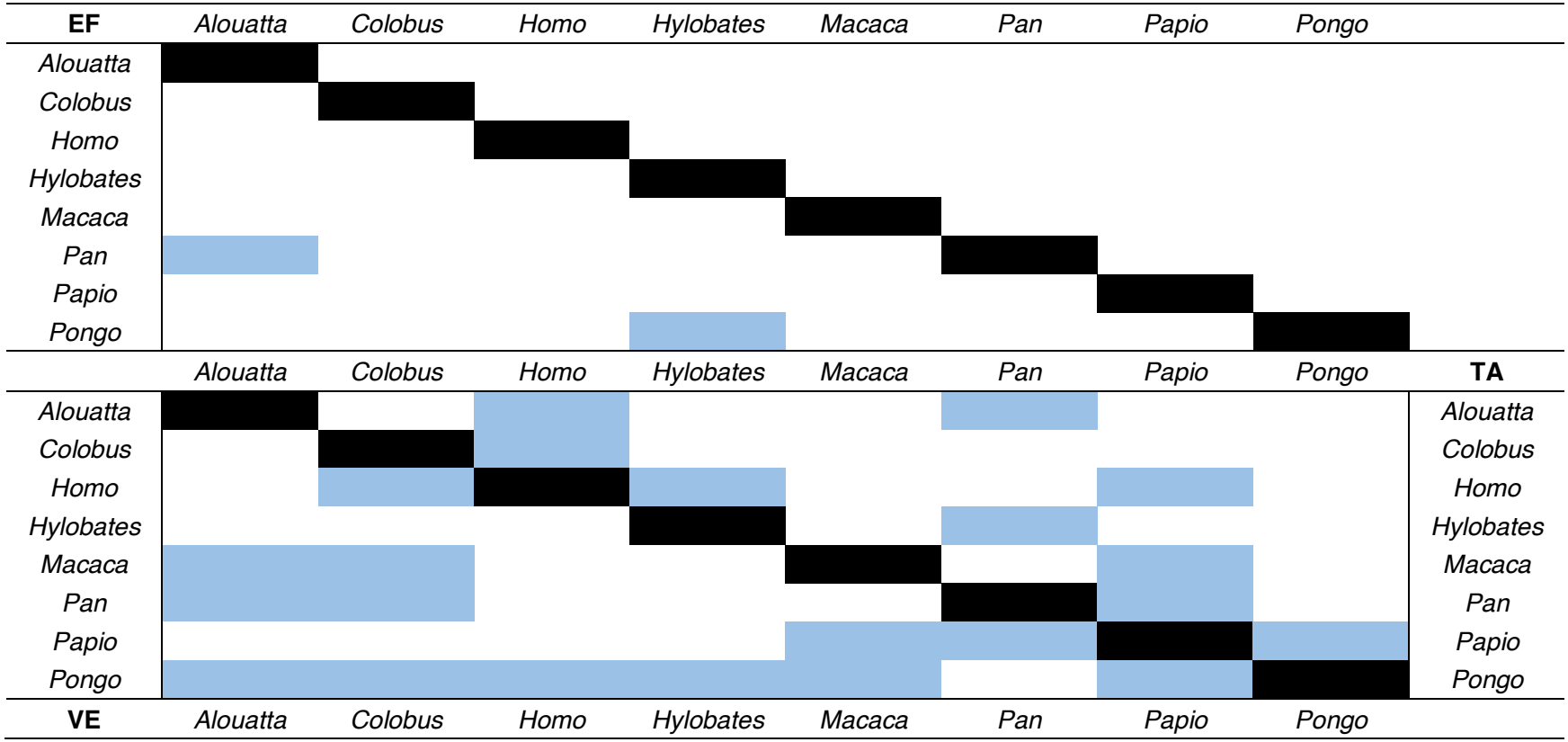
e. Basicranium – Humerus



f. Pelvic Girdle – Humerus



g. Shoulder Girdle – Humerus



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Transition from Chapter III to Chapter IV

Chapter III demonstrates a fairly consistent pattern of hierarchical trait covariance between anatomical regions. Generally, within each primate taxon, paired anatomical regions with functional and developmental relationships tend to have lower evolutionary potential and greater morphological integration compared to other pairs of anatomical regions. Thus, this indicates stronger covariances among these regions that result in more constraint in response to directional selection. While there are similar trends in the patterns of constraint among anatomical regions, the strength of those relationships differs between primate taxa. Therefore, we would expect primate species to have different responses to the same selective pressure. Measures of integration can present researchers with the strength of the covariances underlying characters correlated through genetic and developmental processes, and evolvability provides a depiction of how that covariance is structured. However, estimates of evolvability and integration only provide a framework for the evolutionary potential of traits, but are unable to assess through what processes traits ultimately did evolve and the effect this had on morphological variation.

In Chapter IV, I, with coauthors B. O'Meara, C. Roseman, and B. Auerbach, assess different hypotheses of primate morphological diversification to evaluate hypothesized factors (introduced in Chapter I) and evolutionary processes contributing towards observable variation among primate taxa. Phylogenetic comparative methods (PCM) using an Ornstein-Uhlenbeck process to model evolution are used to test ten hypotheses of primate evolution on a sample of 48 primate taxa; hypotheses are based on differences in diet, locomotion, habitat, and patterns of selection driven lineage divergence. We also utilize a Bayesian approach to PCM to create models of trait evolution that are unrestrained by *a priori* hypotheses, to assess the accuracy of these hypotheses in characterizing primate evolution. We take a univariate approach in assessing these models to assess how well these models of trait evolution conform with the results obtained by previous studies of shoulder girdle evolution, which assess traits in isolation, and interpret the outcomes in the context of the prior analyses using indices of evolvability and integration.

CHAPTER IV

EVOLUTION WITHIN THE PRIMATE AXIAL SKELETON: ASSESSING UNIVARIATE MODELS OF TRAIT EVOLUTION USING A PHYLOGENETIC COMPARATIVE APPROACH

A version of this chapter is being prepared for publication by Elizabeth R. Agosto, Benjamin M. Auerbach, Charles C. Roseman, and Brian C. O'Meara as:

Agosto ER, O'Meara BC, Roseman CC, Auerbach BM (2019) Evolution within the primate axial skeleton: assessing univariate models of trait evolution using a phylogenetic comparative approach. *In preparation.*

This chapter is a research chapter. The test of this chapter regularly uses the pronouns "we" and "our" to reference the contributions of my coauthors, Drs. Benjamin M. Auerbach, Charles C. Roseman, and Brian C. O'Meara. It should be noted, however, that in addition to conducting the majority of the research and performing the analyses, I am the author in the ordinary sense.

Abstract

Objectives: Differences in primate shoulder trait morphology are traditionally hypothesized to be adaptive responses to different locomotor functions ultimately driven by diet or habitat. Recently, it has been proposed that primate shoulder girdle morphology may be influenced by correlated responses to directional selection with developmentally and functionally covariant traits in the basicranium and pelvic girdle. Differences in the strength of these connections can influence how traits can respond to directional selection, thus affecting morphological variation among primates. However, these hypotheses have not been tested to assess the accuracy of these models in characterizing primate evolution.

Methods: We test ten hypotheses of primate diversity using phylogenetic comparative methods using 15 traits from the shoulder girdle, basicranium, pelvic girdle, and humerus across 48 primate taxa and tree shrews. A Bayesian model of primate trait evolution is also tested, and phylogenetically corrected correlations among traits are calculated.

Results: Primate diversity evolved in response to selection. Of the *a priori* hypotheses tested, diet and locomotion models best fit the data, however, a model of selection creating divergence in lineages at major nodes produced by the Bayesian analysis most accurately describes the variation among primate taxa. Additionally, pressures shaping relationships among New World monkeys are

driven by size, while shape related functional variance best describes the relationships among Catarrhines.

Discussion: No single selection model—habitat, locomotion, or diet—best explains the factors that motivated trait evolution, especially in the shoulder. Study results instead argue that multiple selection factors, along with trait covariance across the axial and appendicular skeleton, led to primate morphological diversity.

Introduction

Studies of primate shoulder girdle morphology have long held the hypothesis that traits of the shoulder girdle, and primarily the scapula, are adapted for locomotor function (Ashton and Oxnard 1961, 1963, 1964a; Oxnard 1963; Ashton et al 1965ab; Stern et al 1977; Tuttle and Basmajian 1977, 1978; Jungers and Stern 1984; Larson and Stern 1986; Larson et al 1991). To better understand this variation, researchers have examined the association of individual traits with different functional demands encountered within an organism's environment (Stern et al 1977; Tuttle and Basmajian 1977, 1978; Jungers and Stern 1984; Larson and Stern 1986; Larson et al 1991; Larson 1993, 1998; Whitehead and Larson 1994; Gouveia et al 2014; Lynch Alfaro et al 2015; Matsuo 2019). As functional demands differ across environments, researchers have further extrapolated the relationship between morphological variation and habitat to model modes of locomotion, the effects of diet, activity patterns, paleoenvironments, behaviors, and evolutionary relationships from the fossil record. While studies have investigated the relation of scapular morphology to musculoskeletal, locomotor, and/or behavioral variables (Aston and Oxnard 1963; Oxnard 1967, 1968; Ashton et al 1976; Larson and Stern 1986, 1987; Taylor 1997; Preuschoft et al 2010), and placed these relationships in a historical context (see Fleagle 2013), they have not directly addressed hypotheses of scapular evolution or primate diversification. As argued by multiple authors, comparing morphological trends in the fossil record and placing them in a historic or phylogenetic perspective instead allows for the creation of evolutionary hypotheses to test (Weishampel 1995; Lauder 1996;

Ward 2002; Pearson and Lieberman 2004). The patterns resulting from such analyses are not, inherently, direct tests of these hypotheses themselves, and therefore the the effect this had on morphological variation among extant primate taxa. We therefore build on the outcomes from these quantitative genetic approaches in this study by using phylogenetic comparative methods (PCM) to test explicit hypotheses of primate shoulder girdle evolution.

Our previous analyses (Agosto and Auerbach in review; Agosto Chapter III) indicate that none of the anatomical regions under examination evolve independently. Some of the variation we see in the primate shoulder girdle may be driven by changes in the basicranium and pelvic girdle, but it is unknown whether or not this occurred in primate evolution. And yet, we need to determine how individual traits in the scapula evolved with respect to selective regimes before we try to understand how these regions evolved in multivariate space. Covariances in a multivariate context are nonadditive, and so we don't expect the results from this study to be reflective of the effect of genetic covariance among anatomical regions. Rather, we are examining how the variation in individual traits among primate taxa fit models of evolution to better understand how well these models conform with results obtained using the approach of most studies of shoulder girdle evolution, in which trait evolution was examined with each trait in isolation. Results of PCM analyses for individual traits can then be interpreted in the context of multivariate evolvability and integration.

With this provision, in this study we assess ten different hypotheses, described below, using Brownian Motion and Ornstein-Uhlenbeck processes to model trait evolution for 15 traits from the shoulder girdle, basicranium, pelvic girdle, and humerus. We further compare the best fitting hypotheses for each trait against an unrestrained model of character evolution that is derived from the data itself, using a reversible-jump Bayesian approach to identify the location and number of adaptive regimes and adaptive optima for each trait. Finally, we use phylogenetic independent contrasts to demonstrate how traits covary with each other after controlling for the evolutionary relationships among taxa and interpret them in the context of the PCM. By these approaches, we examine three questions: 1) As noted above, researchers hypothesize that responses to selection

motivated by habitat, by diet, or by locomotion, best explain diversification in morphology; is there support for these models among traits of the shoulder girdle, basicranium, pelvic girdle, and humerus? 2) Has the evolution in morphological diversity among primates been motivated by size, or size-related shape differences in traits? 3) Do anatomical regions evolve in response to selection? We anticipate that traits for which we have found more evolutionary covariance (Agosto and Auerbach in review; Agosto Chapter III) will follow similar evolutionary trajectories.

Hypothesized Factors Influencing Primate Shoulder Evolution

Differences in shoulder girdle morphology among primates have been demonstrated to closely reflect the functional demands of the upper limb (Inman et al. 1944; Ashton and Oxnard 1961, 1963; Oxnard 1963; Roberts 1974; Stern et al 1977; Tuttle and Basmajian 1977, 1978; Jungers and Stern 1984; Larson and Stern 1986; Larson et al 1991; Larson 1993, 1998; Whitehead and Larson 1994; Preuschoft et al 2010). Due to the immense variation in the primate shoulder girdle, it is hypothesized that changes in shoulder morphology were a major driver of primate evolution, especially the diversification of apes and monkeys (Miller 1932; Washburn 1951; Grand 1972). Broadly, the functional variation that relates to this diversity of morphology is thought to relate to the breadth of habitats—terrains, diets, and other aspects—in which primates exist.

The origin of the Primate order is hypothesized to be driven by diet (Sussman 1991; Sussman and Raven 1978; Sussman et al 2013, see also Silcox et al 2015). Diet-driven hypotheses persist for the diversification of primate genera and species (see Scott 2019), but these largely focus on cranial adaptations (Fish and Lockwood 2003; Allen and Kay 2012), with changes in the postcrania happening subsequently and even concurrent with cranial changes (Cartmill 1974, 1992; Sussman and Raven 1978; Bloch and Boyer 2002; Kirk et al 2003; Sussman et al 2013; see also Silcox et al 2015). Therefore, hypotheses of primate postcranial evolution concentrate on adaptations to meet the functional demands of different ecological niches (Schultz 1930; Ashton et al 1976; Hunt 1991; Oxnard 1963; 1967; 1968; Robinson 1972; Roberts 1974; Lovejoy 1975; Fleagle and Anapol 1992;

Anemone 1993; Bramble and Lieberman 2004; Gouveia et al 2014; Tran 2014; Hunt 2016; Selby and Lovejoy 2017; Matsuo et al 2019). In association with dietary specialization, the evolutionary success of primates is thought to be due, in part, to their ability to inhabit various environments. Primates can be found in dense forests, savannahs, and in every level of the forest canopy (see Silcox et al 2015 and Zihlman and Underwood 2019), and the morphology of the shoulder girdle aligns with the manner in which primates navigate these different environments (Oxnard 1967, 1968; Matsuo et al 2019).

Numerous studies have been conducted to better understand the functional relationships of traits of the scapula (Miller 1932; Inman et al 1944; Davis 1949; Smith and Savage 1956; Ashton and Oxnard 1963, 1964ab, Erikson 1963; Oxnard 1963; Müller 1967; Roberts 1974; Corruccini and Ciochon 1976; Fleagle 1976; Kimes et al 1981; Shea 1986; Taylor 1997; Krause 2008). This information has been utilized to infer function in the fossil record (MacLatchey et al 2000; Larson et al. 2007; Larson 2013; Feuerriegel et al 2017; see also Oxnard 1967). Individual traits of the scapula are often used for these inferences, and the patterns of morphological difference are often attributed to selection acting on individual traits and their biomechanical function. However, patterns of morphological difference are poor representations of the evolutionary forces that formed them (Lande and Arnold 1983; Houle 1991; Arnold 1992; Ackerman and Cheverud 2002; Hansen and Houle 2008; Mitteroecker 2009; Rolian et al 2010; Grabowski 2013; Katz and Weaver 2016; Savell et al 2016). Traits may have evolved in response to directional selection, or traits may have evolved through correlated responses to directional selection that are not oriented toward an adaptive optimum associated with the most fit functionality. Individual trait responses to directional selection are thus partially reliant on the covariances they have with other traits (Rolian et al 2010). Shared development, in the form of similarities in germ-layer origins, genetic pathways, and coordinated growth between structures, and participation in shared functions among traits can lead to their integration on a population level due to pleiotropic relationships among traits (Cheverud 1996). Pleiotropy can ultimately lead to genetic covariances among traits that result in their correlated

responses to directional selection (Rolian 2009). The stronger these relationships are among traits, the less likely they will be able to independently respond to the force of directional selection. Correlated responses to directional selection will result in suites of traits that maximize functions associated with adaptive optima (i.e. fitness). Thus, functional demands on morphology will favor some groups of traits to the exclusion of others. This can ultimately affect morphological differences among taxa, as different abilities to evolve can constrain the areas of phenotypic space occupied by different species (see Young 2017).

Selection Regimes, Optima, and Morphospace

The approaches used within this study test explicit evolutionary models by translating different hypotheses of adaptation to selective regimes (also referred to as adaptive regimes or zones). Selective regimes refer to a group of species that share a common selective factor, or OU optimum (Uyeda and Harmon 2014). These optima can be thought of as the 'ideal' trait value that will maximize organismal fitness. Difference in selective regimes may be due to differences in different ecological factors, such as diet, locomotion, habitat, among others (Hansen 1997). Selective regimes, however, are not static, as changes in an organism's environment can affect what traits, or trait expressions, are better for surviving the new environment (i.e. 'more fit'). Thus, organisms are under ongoing selective pressures to adapt to a continually shifting environment (Van Valen 1973; Lewontin 2000). As organisms concurrently experience a variety of conflicting selective demands that may require different phenotypes, thus their current state is reflective of a compromise of those demands (Hansen 1997).

In addition to ecological factors, phenotypic expression within an organism is affected by the genetic, developmental, and functional covariances among traits (Cheverud 1995, 1996; Wagner 1996; Wagner and Altenberg 1996; Rolian 2009; Rolian et al 2010). These factors can have considerable effects on the frequency of observed phenotypes in a population. How these factors constrain the possible directions these phenotypes can evolve is referred to as a morphospace

(Mitteroecker and Huttegger 2009). Morphospaces are a useful tool to describe and compare organismal phenotypes and is an underlying concept to many comparative approaches.

Hypotheses of Primate Shoulder Girdle Morphological Evolution Tested in This Study

In this study, we evaluate ten different *a priori* hypotheses of primate shoulder girdle morphological evolution. Phylogenetic branching patterns have been shown to be important to understand shape variation in the crania of Platyrrhines (Perez et al 2011), Cercopithecoidea (Cardini and Elton 2008a), and various mammalian groups (Polly 2001; Álvarez et al 2011). Given the importance of shared ancestry on primate cranial evolution, seven of the ten hypotheses examined in this study are based on the branching patterns among different taxonomic levels. The differences among the models parallel the timing of different levels of taxonomic diversification among primate groups (see Perelman et al 2011). The other three hypotheses are based on habitat, locomotor behavior, and primary diet. Each model makes different assumptions of the adaptive or selective regimes taxa experience; we follow Uyeda and Harmon's (2014) definition of regime to denote a set of lineages that share an OU optimum. Model descriptions are provided below, and regime designation for each species per hypothesis can be found in Table SIII.1 (all Tables and Figures are located in Appendix IV and Supplementary Information III). Visual representations of the Habitat, Locomotion, Diet, and Family Hypotheses can be found in Figure IV.1, whereas all others are located in the Supplementary Appendix, Figure SIII.1.

Mammal: The first hypothesis we test is a null model of primate evolution; it creates a naïve model of trait evolution. This hypothesis assumes all taxa are mammals and the morphological differences among them are simply different solutions to the same selective pressure to be mammals (Figure SIII.1a).

Primate vs. Other (PvO): The PvO hypothesis is also a naïve model of primate evolution. It assumes that after the split from mammals 80-90 MYA (Goodman et al 1998; Wilson and Reeder 2005), primate diversification across North America, Asia, Europe and Africa occurred under a single adaptive regime, with non-primate species occupying a separate morphospace. The shift in regimes would occur at the node between tree shrews (non-primate outgroup) and primates (Figure SIII.1b).

Monkey-Ape-Prosimian-Other (MAPO): The MAPO hypothesis places regime shifts among major taxonomic groups of primates. It assumes a different selective regime for the origination of the Primate Order from other mammals (tree shrew acting as the 'other'), a regime for Prosimians (galagos, lemurs, lorises, and tarsiers), a regime shift approximately 81 MYA with the branching of Simiiformes (Catarrhines and Platyrrhines; Perelman et al 2011), and a final regime shift during the branching of Apes (orangutans, chimpanzees, gorillas, and humans) from other Catarrhines (Old World monkeys) 20.4 MYA (Perelman et al 2011) (Figure SIII.1c).

Monkey-Ape-Lemur-Loris-Tarsier-Other (MALLTO): The MALLTO hypothesis is similar to the MAPO hypothesis, but rather than treating Prosimians as a single group, it splits them into their constituent taxa (Lemurs, Lorises, and Tarsiers). This model assumes more diversification among Prosimian species compared to other primates (Figure SIII.1d). The diversification of the Prosimians is hypothesized to have occurred before major diversifications among monkeys and apes (Perelman et al 2011).

Parv.Order: The Parv.Order hypothesis groups taxa together at the level of Order for tree shrews, each Infraorder of Prosimian (Lemuriformes and Tarsiiformes), and parvorders among Simiiformes (Platyrrhini and Catarrhini). This model does not separate monkeys and apes, for a

total of five selective regimes (Figure SIII.1e). This model most closely models the early diversification patterns among primate groups (Perelman et al 2011).

Ape-NWM-OWM-Prosimian-Other (ANOPO): This hypothesis posits separate adaptive regimes for Hominoidea, Platyrrhines, Cercopithecoidea, Prosimians, and tree shrews (Figure SIII.1f). This model posits the diversification among Simiiformes is driving primate evolution, which would be captured in the branching of Catarrhines from Platyrrhines 43.5 MYA, and Hominoidea from other Catarrhines 20.4 MYA (Perelman et al 2011).

Family: This hypothesis suggests that adaptive regimes would be comprised of individuals of the same Family. For some groups, such as OWM, the level of Family is the lowest taxonomic level where branching patterns among taxa are clear (see Groves 2001, Tosi et al 2003; Xing et al 2007), and so we test a model based on diversification being driven at the Family level. A total of ten regimes are present: Tupiadae, Galigade, Lemuridae, Tarsiidae, Cebidae, Atelidae, Pitheciidae, Hylobatidae, Hominidae, and Cercopithecidae (Figure IV.1a).

Habitat: The Habitat model places all taxa into one of three regimes based on the three basic types of environments primates are found: terrestrial, semi-terrestrial, and arboreal (Figure IV.1b). This model is based on those studies that posit environmental factors as a driving force to primate diversification. Here we present the most simplistic form of that model, based on habitat categorizations explained in the Methods.

Locomotion: Locomotion may be considered an aspect or consequence of habitat but allows for more specificity in categorizing groups than is afforded by the Habitat model. This hypothesis posits that locomotion is a primary driver of primate diversification in the shoulder girdle, and thus associated traits in the basicranium, pelvis, and humerus. The model assumes an adaptive

regime for seven different modes of locomotion defined in the literature: scansorial (climbing and scurrying), saltatorial (leaping), arboreal quadrupedalism, terrestrial quadrupedalism, arboreal/terrestrial quadrupedalism, brachiation/suspension, and bipedalism (Figure IV.1c). Locomotor function is a primary hypothesis used to explain primate morphological diversification, and the basis for defining locomotion categories for species is explained in the Methods.

Diet: Like locomotion, diet is in part an aspect of the habitat, though again it has some overlap with and independence from the environment in which organisms live. This hypothesis posits that diet is a primary driver of primate diversification, and that differences in resource acquisition will be reflected in shoulder girdle morphology as a manifestation of resource acquisition. This hypothesis assumes different adaptive regimes for the six different primary diets present for the taxa within this study (Figure IV.2d). The following diets are represented: 1) Omnivore: diet consists of a mixture of both plants and animals; 2) Insectivore: diet consists primarily of insects; 3) Herbivore: diet consists of a mixture of leafy foliage and fruit; 4) Folivore: diet consists mainly of leaves; 5) Frugivore: diet consists mainly of fruits; 6) Granivore: diet primarily composed of seeds. All dietary information was provided by Meyers and colleagues (2019), and the definition of categories is provided in the Methods.

Materials

Sample

A total of 914 individuals were measured, representing 49 species (Table IV.1). This sample is composed of a broad range of specimens across the Primate Order (Prosimians, Platyrrhines, and Catarrhines), and one out-group (tree shrews, *Tupaia*). Tree shrews are often used as an out-group to primates in phylogenetic analyses due to their close affinity to the Primate Order (Shoshani et al 1996; Seiffert et al 2003; Sargis 2004). All species were selected based on the availability of complete data for both males and females. A total of 13 specimens of unknown sex are also

included in this sample. These specimens were included to prevent the loss of 9 clades across the phylogeny and retain Prosimians in this study. Individuals of unknown sex are included in both the male and female analyses. All specimens included in our sample are adults, as defined by the fusion of long bone epiphyses, with no visible pathologies affecting trait morphology.

Data

Fifteen traits from the basicranium, shoulder girdle, pelvic girdle, and humerus are included in this study (Table IV.2, Figure IV.2). These traits represent attachment points for muscles that affect movement at the shoulder (Diogo and Wood 2012), shoulder joint dimensions, or have biomechanical relevance for locomotion (Jungers 1985; Grabowski and Roseman 2015). These traits also share developmental molecular pathways or cell lineages (Matsuoka et al 2005; Huang et al 2006; Valasek et al 2010) and interact during the growth and development, or in the case of the pelvis and scapula, are developmental analogues (Sears et al 2015).

Three dimensional coordinates were captured from the left side of each specimen using an Immersion G2X MicroScribe digitizer. In cases where the left side was unavailable, the right side of the specimen was measured. Linear dimensions were calculated from homologous landmarks for each of the fifteen traits used in this study (see Figure SIII.2.). Due to their small size, linear measurements for *Callithrix, Galago, Saguinus, Tarsius,* and *Tupaia* were collected using Mitutoyo Absolute IP 67 sliding digital calipers. Three non-consecutive rounds were collected for each coordinate and linear measurement, and subjected to a repeated measures ANOVA (RMANOVA) to assess intra-observer error. Results of the RMANOVA show no significant difference between measurement rounds ($p > 0.05$), with an error rate below three percent within genera for each skeletal element. Subsequent analyses are performed on the average of the three measurement rounds.

Prior to analysis, data for each sex were scaled by the average species body mass (kg) and then log transformed to reduce the effects of body size and non-linear relationships many traits have with

size (Nakagawa et al 2017). Species-specific body mass data was compiled from Ernest (2016) and Meyers and colleagues (2019). For sexually dimorphic species, the average body mass for each sex was used to scale the data. Males and females are assessed separately for all analyses. See Tables SIII.3 and SIII.4 for summary statistics for each trait across species.

Methods

Phylogenetic Tree

We use a molecular phylogeny to infer the relationships among taxa. Phylogenetic relationships were derived from a consensus chronogram in version 3 of the *10kTrees Project* (Arnold et al 2010). The primate consensus tree is constructed using eleven mitochondrial and six autosomal genes across 301 primate species. The outgroup, *Tupaia*, was appended to the consensus chronogram using the ape package (Paradis and Schliep 2019) in R. Edge length for *Tupaia* was taken from Kumar and colleagues (2017), and represents the estimated divergence time between *Tupaia* and extant primate species (82 MY). The full phylogenetic tree can be found in Table SIII.5.

Primate Classifications

The ability to meet different ecological challenges has been hypothesized as a key factor for the evolutionary success of primates. Primates inhabit a wide variety of environments, and the postcranial morphology of primates aligns with the way species navigate the challenges presented by their environment. However, linking specific aspects of morphology to particular behaviors associated with different ecological niches is difficult due to the wide array of observable behaviors. Currently, for example, there are 32 primate positional modes that are divided into 52 postural sub-modes and 74 possible locomotor sub-modes (see Hunt et al 1996) that are used to describe how primates interact with their environment. While more specific and standardized methods are necessary to understand the intricacies of primate locomotor behaviors within a given ecological context, such studies have not been completed for all taxa. Thus, more generalized habitat groups,

such as arboreal, semi-terrestrial, and terrestrial, are used to frame these hypotheses. These designations were sourced from Meyers and colleagues (2019) and are based on whether the primate species spends a majority of its time on the ground (terrestrial) compared to in the trees (arboreal). A designation of 'semiterrestrial' is provided to those species that spend a similar amount of time in both environments.

A similar approach was taken for classifications of locomotion and diet due to the variation that exists in these categories. Primary dietary information was sourced form Meyers and colleagues (2019), and are based on the primary resource consumed by a species. Instances when there was no clear preference, or where diet substantially changes based on season, a more general term, like 'herbivore' was used.

Locomotor classifications also represent fairly broad categories among primates; many primates engage in a wide variety of behaviors, thus generalized terms are used in this study. Locomotor classifications were based on those presented by Selby and Lovejoy (2017), Nyakatura and colleagues (2008), Sargis (2004) Meyers and colleagues (2019), and Schmitt (2003).

Analyses

The ten models based on *a priori* hypotheses of trait evolution, in addition to an unrestrained (*bayou*) model (see below), are tested using Brownian Motion (BM, Felsenstein 1973, 1985) and Ornstein-Uhlenbeck (OU, Hansen 1997) processes to model trait evolution (described below) for each of the 15 traits. Hypotheses were 'painted' on the phylogenetic tree using the R package *bayou* (Uyeda et al 2018) to obtain the parameter values for the location and number of adaptive regime shifts for each hypothesis. Under Brownian motion, trait evolution is modeled as a stochastic process motivated by random evolutionary forces. For example, BM processes can result from the neutral drift of adaptive peaks, drifting adaptive zones, or the neutral genetic drift of trait means (Uyeda and Harmon 2014, p. 903). Alternatively, the optima under an OU model may represent adaptive zones in which adaptive peaks drift stochastically, or broad ranges where adaptive zones

evolve (Hansen 1997; Butler and King 2004; Uyeda and Harmon 2014). Since OU processes allow for both the effect of random processes and multiple evolutionary optima, they represent a more realistic way to model phenotypic evolution, as these models are consistent with phenotypic evolution under both selection and drift (Butler and King 2004). The OU process expresses the change in a quantitative character, $d\bar{z}$, with respect to the intensity of random fluctuations in the evolutionary process (σ), the rate of adaptation (α), and the optimum value (θ) calculated using the following differential equation:

$$d\bar{z} = \alpha(\theta - \bar{z}) + \sigma dW \quad (1)$$

where $\bar{z}$ is the trait mean and *W* is a continuous-time Wiener process (Uyeda and Harmon 2014). If α = 0, the process reduces to a BM process. Hypothesis testing was performed using the R package *OUwie* (Beaulieu et al 2012), using a BM model with different rate parameters for each state on a tree (BMS) and an OU model that allows for multiple α and σ^2 acting on all regimes (OUMVA). These models include a standard error term for each trait, which represents the average standard error across species for each trait. Model fit is assessed using both Akaike Information Criteria (AICs) and the corrected AIC (AICc), where a lower score denotes a better fit of the model to the data. Parameters from the models with the best fit were used to then inform the number of shifts and ranges of α and σ^2 when constructing the prior for the unrestrained models.

As noted in the Introduction, in addition to the assessment of our ten hypotheses, we examine unrestrained models of trait evolution using the *bayou* package (Uyeda et al 2018) in R. The *bayou* package uses a reversible-jump Bayesian method that estimates the location, number, and magnitude of adaptive optima from phylogenetic comparative data (Uyeda and Harmon 2014). The OUMVA model is used by *bayou* to model evolution. A prior on the number of shifts between adaptive regimes was placed using a Poisson distribution, with the maximum number of shifts equal to the number of tips in the phylogeny, with the most likely number of shifts equal to the number of regimes in the best-fitting *a priori* hypothesis (i.e., five for Parv.Order). A normal prior was placed for the adaptive optima, and a half-Cauchy distribution was assigned to α and σ^2. Using a half-Cauchy

distribution will give higher likelihoods for values closer to zero, though with a finite likelihood for values at zero. Each branch was assigned an equal probability of having a shift, with one shift allowed per branch. Markov Chain Monte Carlo (MCMC) algorithms were executed for 1,000,000 steps, with the first 30,000 steps discarded as burn-in, and a thinning interval of every 1000 steps. Summary statistics for the *bayou* parameters for each trait can be found in Tables SIII.6 and SIII.7. As *bayou* does not provide AIC scores, we use the best likelihood from the MCMC chain to calculate these values using the following equations

$$\text{AIC} = -2\,(\ln(\text{likelihood})) + 2K \tag{2}$$

$$\text{AICc} = -2\,(\ln(\text{likelihood})) + 2K * (n/(n - K - 1) \tag{3}$$

where n is the sample size, and K is the number of parameters in the model (number of regimes, plus sigma and alpha). *Bayou* optimizes the placement of the regimes, and this could be considered a discrete parameter. However, we don't know exactly how to penalize for regime placement, as it effectively increases the number of free parameters, but to what degree is unknown. As such, our calculations of AIC and AICc do not account for this free parameter.

Adaptive regimes and adaptive optima were assessed for the *bayou* models using a posterior probability cut off value of 0.3. Under this criterion, clades with a posterior probability above 0.3 were assigned to distinct adaptive regimes. To assess whether the body size was a motivating factor in the patterns of regime shifts among taxa, we compared the adaptive regimes and the species that comprise them for each trait against the adaptive regimes for two traits closely associated with body size: the diameters of the humeral head (HHW) and acetabulum (AW) (Ruff 2003). While these are imperfect proxies for body size, these traits are known to scale closely with body size, as they support and transmit body mass across joint surfaces, and so provide more detail than mean species body mass values obtained from published sources. Consistencies in regimes among traits with HHW and/or AW would suggest the variation observed among species within the regime is likely driven by body size. In contrast, differences among regimes would suggest a signal due to another factor, such as shape related to function.

Phylogenetic independent contrasts (PIC, Felsenstein 1985) were used to obtain phylogenetically corrected correlations among traits. PIC was performed using the *ape* (Paradis and Schliep 2019) and *geiger* (Harmon et al 2008) packages.

All analyses are performed in the R statistical environment (https://cran.r-project.org/) using custom scripts and the *OUwie* (Beaulieu et al 2012), *bayou* (Uyeda et al 2018), *geiger* (Harmon et al 2008, and *ape* (Paradis and Schliep 2019) packages. Custom scripts are provided upon request.

Results

Model Testing

Ten evolutionary hypotheses were tested using OU and BM models of trait evolution (Tables SIII.8 and SIII.9). For both males and females, all traits evolved in response to a combination of directional selection and random processes, as an OU model that assumes different state means and multiple values of the rate of adaptation (α) and intensity of random fluctuations in the evolutionary process (σ^2) – OUMVA – best fit the data. In males, a Locomotion model is the best fit (as indicated by AICc score) for most traits. RAH is best explained by a Habitat model, whereas NR, SNL, HML, and HHW equally fit Habitat, Diet, and Locomotion models, and GW by Locomotion and Diet models. In females, a Diet is the best fit for most traits. In females, a Diet model is the best fit, with a Locomotion model being the best fit for SBL, and LIH, whereas for CLML and RAH are equally explained by the Locomotion and Diet models. For AMIB, the Parv.Order provides the best fit.

When the hypothesis-driven models are compared to an unrestrained *bayou* model, the *bayou* model is a better fit for all traits except VB and RAH for males, and AMIB for females (Tables IV.3 and IV.4). These results indicate that for most traits, the best fitting hypotheses of morphological evolution of the primate shoulder girdle (phylogenetic relationships, or habitat, locomotion, and diet models) are unable to fully explain the variance observed among extant primates. For those traits where the unrestrained *bayou* model was not the best fit, it is possible that these hypotheses truly

capture how these traits evolved in response to selection, or the parameters in the *bayou* models for these traits have unknown errors that result in their comparatively poor fit.

Unrestrained Models of Primate Morphological Evolution

The results of the unrestrained models of evolution derived from *bayou* reveal several trends regarding primate evolution as a whole. To make the results interpretable against the previous studies that have examined multivariate trait evolvability and integration (Agosto and Auerbach in review, Agosto Chapter III), we focus on those related to the eight taxa discussed in Agosto (Chapter III): *Alouatta*, *Colobus*, *Macaca*, *Papio*, *Homo*, *Hylobates*, *Pan*, and *Pongo*. Other trends are noted as appropriate Results for traits NR, SBL, and LIH for males are in Figure IV.3, and results for traits SNL, RAH, and AMIB for females are in Figure IV.4. Full results from these analyses are located in Figures SIII.3 and SIII.IV and Tables SIII.10 and SIII.11.

The unrestrained *bayou* models estimate variation in adaptive optima across the phylogenetic tree. For most regimes, multiple optima are observed among the different species within a lineage, as indicated by changes in color among species on the phylogenetic tree (see Figures IV.3 and IV.4). We focus on those results pertaining to Hominidae, as these are unexpected compared with the patterns observed amongst monkeys and prosimians; all other results are presented in Supplementary Information III. Of note is that lack of differences in adaptive optima for gibbons and siamangs compared with Old World monkeys, despite the suite of traits that distinguish Hominoidea from monkey taxa, some of which are included in our analysis. Within Hominidae, *Pongo* and *Pan* tend to have the most distinct adaptive optima, whereas *Homo* and *Gorilla* tend to share optima. *Pongo* has distinct adaptive optima for VB in both males and females, and for NR, SNL, FMW, SBL, and AW in males. *Pan* has distinct adaptive optima for NR, SNL, FMW, VB, GW, LIH, AW, HML, and HHW in males, and SSL, CLML, and RAH in females. *Gorilla* and *Homo* have different optima for SNL, AMIB in females, SCM, SBL, CLML, RAW, AW in males, and HHW in both sexes; all other traits share adaptive optima.

Evolutionary change related to body size is not the major signal identified by the *bayou* model for most traits or taxa. Across all taxa, when the adaptive regimes identified for each trait are compared to those of AW and HHW (which we use as proxies for body size), we find that the evolution of only the basicranial origin for the sternocleidomastoid muscle (SCM) is most consistent with body size. It is therefore possible that the variation in this trait among primates provides little information related to functional variation in either sex, unless the muscle function is correlated with overall body size.

Among the eight focal taxa, the *bayou* model does not support trait evolution in association with or response to body size for most traits among species, and there are few consistent patterns. Only the Atelidae (*Alouatta* and *Ateles*) consistently present an adaptive regime across traits that is closely associated with body size. Traits where the phylogenetic relationship among Atelidae and other taxa, especially the other Platyrrhines, are not strongly associated with size are two basicranial dimensions—NR and SNL—and the maximum clavicular length (CLML) in males, as well as scapular blade length (SBL) and anterior iliac blade length (AMIB) in females. Size-related adaptive regimes are not observed among either *Macaca* or Colobine monkeys for either males or females, suggesting size is not a primary driver of the trait evolution between these taxa and the other species in this analysis. *Papio* males are associated with size-related adaptive regimes for SCM, GW, RAH, and VB. Size-driven relationships also appear among Hominidae females in all traits except NR, SSL, SBL, RAH, and LIH. In contrast, Hominidae males show size-related evolution only in SCM, except for RAH and LIH, respectively, in Hylobatidae and *Pan* males.

There are also three additional size-related regimes persistent among the unrestrained *bayou* models. A regime consisting of *Tupaia, Galago,* and *Tarsius* is present in all traits except HML and SSL in males, and AMIB in males and females. Lemuridae comprise a regime in all traits except SSL, and CLML in males, and AMIB in both sexes. *Miopithecus* is observed to form its own size-related regime in all traits except FMW and SSL in males, and AMIB in both sexes.

Phylogenetic Independent Contrasts

The results of the PIC demonstrate a range of phylogenetically corrected correlations among traits for both sexes (Table IV.5). In males, the correlation among traits range from 0.636 to 0.967, whereas in females this range is broader (0.43 to 0.971). While females appear to have weaker correlations among traits compared to males, correlations below 0.63 are all concentrated within a single trait: AMIB. The correlations among other traits are similar to, if not larger in females than males.

Despite the differences in the corrected correlation values, the relationships among anatomical regions are similar between males and females. Traits of the shoulder girdle and humerus are most strongly correlated, followed by the basicranium and humerus, pelvic girdle and humerus, basicranium and shoulder girdle, and basicranium and pelvic girdle, respectfully. High correlations among the shoulder girdle and humerus are somewhat expected due to their biomechanical relationship.

Discussion

The results of our study, the first to subject primate shoulder girdle evolution to models using PCM approaches, reveal broad evolutionary patterns, including several previously unidentified trends in primate evolution. We draw three primary conclusions. First, the evolution of the traits we examine in association with the shoulder girdle, as well as related traits in the basicranium and pelvis, follow the major patterns of selection-driven lineage divergence among families and genera. Second, among most primates, trait evolution does not present a pattern that indicates selection in response to body size. Finally, while our analyses of the traits we examined show that primates evolved in response to a combination of directional selection and random processes, the patterns of evolution in traits do not always correspond with expectations drawn from preceding analyses of integration and evolvability. Specifically, as we discuss below, traits may have evolved more independently than estimations of their integration would suggest they could, and the rate of

adaptations may not reflect the relative evolvabilities shown between taxa. Considered together, our conclusions suggest shared function and development among anatomical regions may play an important role in primate morphological evolution of the shoulder girdle, basicranium, and pelvic girdle, but that these did not occur in similar patterns or toward the same selective optima among primate species. We also caution that, as univariate models of trait evolution are unable to capture the interactions among traits during evolution, even when contextualizing results within the findings of studies that incorporated estimates of genetic evolutionary covariances among traits, multivariate PCM models of trait evolution are necessary to fully understand how traits evolved.

Modeling Primate Morphological Evolution

Primate morphological diversity in the shoulder, basicranial, and pelvic regions evolved in response to directional selection. Models where OU processes were used to characterize evolution across our sample better fit the variation in all traits than models based on stochastic processes alone (BM models). We expect this result, given the phylogenetic and temporal scale in which this study is based. These results further suggest that primates did not evolve in response to randomly changing adaptive optima, which given sufficient time would appear as a Brownian process; adaptive optima changed within clades, but not stochastically with respect to the initial optima that drove cladistic speciation. While selective forces acted on all traits in this study across the Primate order, it is possible that on more local scales, such as within species, traits may have (and likely) evolved in response to neutral evolutionary forces. Our analyses cannot ascertain whether the selection under which traits evolved was direct or through correlated responses, and so it is also possible that some or many of the traits we observe evolved through correlational selection due to pleiotropic effects. We see evidence of these processes in the evolution of the human cranium (Roseman 2016; Schroeder and Ackermann 2017) limb evolution (Savell et al 2016) and among select traits in the pelvis (Grabowski and Roseman 2015). As phylogenetic relationships among several primates, especially Cercopithecoidea, are tenuous below the Family level (see Groves

2001; Tosi et al 2003; Xing et al 2007), we would be hesitant to apply this finding to specific instances of morphological diversification at the species, or even genus level. A more focused analysis of trait evolution should be performed at these taxonomic levels to better characterize the evolutionary processes involved.

Attributing a single selective factor for fitness in some or all of the traits we test within primate morphological evolution is shown to be misleading by our analyses. Models based on both locomotion and diet, and at times habitat, most broadly explain the observable variance in primate morphology. This aligns with the primary hypotheses of locomotor function (Ashton and Oxnard 1961, 1963, 1964ab; Oxnard 1963; Ashton et al 1965ab; Stern et al 1977; Tuttle and Basmajian 1977, 1978; Jungers and Stern 1984; Larson and Stern 1986; Larson et al 1991) or diet (Cartmill 1972, 1974, 1992, 2012; Sussman 1991; Sussman and Raven 1978; Sussman et al 2013) driving primate morphological diversity, especially in the scapula. Due to the combined model fits, our results most closely resemble ecological niche hypotheses (see Lewontin 2000), as we broadly categorized locomotion, diet, and especially habitat in this study. “Habitat” is a multi-factorial classification that overlaps with both locomotor function and diet, among other factors. Locomotor functions and resource acquisition are not independent from each other, as the types of locomotor functions in which an organism can engage will influence the dietary resources they can access (see Grand 1972). Primates are found in an array of environments (Lynch Alfaro et al 2015; Silcox et al 2015; Zihlman and Underwood 2019), that impose different functional demands that are related to both effective locomotion within the environment and resource acquisition. Thus, our results show that, while it is logical to hypothesize primate shoulder girdle morphology evolved in response locomotor demands, single factor explanations, like locomotion, are ill-advised for explaining this variation, as they are subsumed in the intertwining factors that comprise habitat and, more broadly, niches.

Overall, our results show even the best hypotheses of factor associations with fitness in primate morphological evolution are not necessarily the most accurate models of trait evolution. The

unrestrained *bayou* models indicate most shifts in adaptive regimes occur in locations where selection has driven lineage divergence that produced the phylogenetic branching patterns observed among primate taxa. A similar phenomenon has been observed among cranial traits in primates (Cardini and Elton 2008a; Perez et al 2011). The location of shifts in the OU optima at points of lineage divergence may suggest selective pressures that push for changes in the primate bauplan manifest at higher taxonomic levels, such as Parvorder. Morphological distinctions at the level of genus or species may be a result of how these groups of organisms are able to respond to the selective pressure to modify the bauplan. This would suggest a fairly conserved fundamental morphology among primates, where diversity among extant taxa are a result of differences in evolvability and integration among traits (Agosto Chapter III), but may also could be driven by stochastic processes (Uyeda and Harmon 2014).

Primate Diversification and Size-Related Variance

Body size is an important factor in mammalian evolution (Marroig et al 2009; Porto et al 2013), but it is not the most important evolutionary factor driving morphological diversity among primates. We do, however, observe several phylogenetic groups where size-related variance explains their evolutionary relationship with other taxa; this is most prominent in Platyrrhines. Size-related variance as a driver of New World monkey diversification has been supported for the crania (Marroig and Cheverud 2004, 2005), and is further demonstrated among basicranial and post-cranial traits in this study. The earliest radiations (Pitheciidae and Atelidae) exhibit small to medium body sizes, while size variation among Cebidae follows a pattern of phyletic dwarfism (Ford 1980; Ford and Davis 1992; Perelmen et al 2011). A case for phyletic dwarfism is also argued for the Platyrrhine genus *Miopithecus* (Shea 1992; Bianco et al 2017), a result that is mirrored in our study and may explain the relationship among *Miopithecus* within Cercopithecini.

For most other taxa in our study, morphological diversity is not primarily explained by selection in response to body size. Rather, other factors, such as shape-related mechanical function, likely

underlie the observable variation among extant primates. For example, the selective regimes and adaptive optima of the lower iliac height (LIH, Figure IV.3c), the distance of which is associated with differences in center of gravity and muscle torque to control balance (Stern and Susman 1983) and lumbar mobility in humans (Lovejoy et al 2009ab), do not correspond well with those of the width of the acetabulum (AW, Figure SIII.3j), which is used as a proxy for size in this study. This finding strengthens the argument we make in previous studies (Agosto and Auerbach in review; Agosto Chapter III) that evolutionary potential and constraint observed among the shoulder girdle, basicranium, and pelvic girdle are not simply reflective of similarities in size among traits. While all traits within an organism will have an underlying ontogenetic signal to maintain body size and proportions, and that body size will therefore have an influence on trait evolution, trait evolution among primates is not well-modelled on size alone. The results of this study reinforce previous conclusions that the evolutionary relationships among anatomical regions, namely the shoulder girdle, basicranium, and pelvic girdle, are most likely reflective of shared locomotor function and/or developmental programs.

These results are further supported by the PIC correlations, where strong correlations observed among all anatomical regions with the humerus may, in part, be due to the close affinity with body size observed in the length of the humerus (HML, Jungers 1985), and humeral head diameter (HHW, Ruff 2003) in primates. Similar degrees of correlation are also observed among all traits with the diameter of the acetabulum (AW), which has been shown to have a strong relationship with body mass and can be used as a proxy for this measure (Jungers 1988; Hammond et al 2013). These dimensions are, as we noted in the Methods, imperfect proxies of body mass, but nonetheless have a long-standing relationship with body mass established in the primate and hominid evolution literature. One caveat that we should note, however, is that all of these dimensions—humeral length, the diameter of the humeral head, and acetabular width—have independent and non-isometric relationships with body mass, despite their high covariance with body mass. Therefore, it is possible that our results are reflective of these allometric relationships, rather than of body mass itself. That

we obtained similar results in relation to both the humeral head and acetabulum, however, lends support to our conclusions, despite the different scaling relationships these dimensions have with body mass (Jungers 1985).

Realized Evolution in the Context of Integration and Evolvability

As we note in the Introduction, this study complements and adds to other recent analyses of integration and evolvability among the traits we examine (Agosto and Auerbach in review; Agosto Chapter III), as the PCM model fitting we perform better indicates how evolution actually unfolded in traits. Studies of integration and evolvability can only demonstrate evolutionary potential in a multi-trait framework were a suite of traits subjected to selective factors. As our study has focused on model fitting for individual traits, relating these results to studies of multi-trait evolutionary potential is tenuous. Nevertheless, it is useful to examine the results of our analyses within the context of evolvability and integration to determine where individual trait evolution deviates from what we would expect given the integration of traits, or the relative evolutionary flexibility found among species (Agosto Chapter III).

Alouatta, despite being a New World genus, has previously shown a pattern of integration and of relative evolutionary flexibility among anatomical regions similar to Old World monkeys (*Colobus*) and apes (*Hylobates* and *Homo*) (Agosto Chapter III). Our results further support this pattern, as Atelidae often share an adaptive optimum with many Old World monkeys and Hylobatidae. Atelidae are more similar in size to Cercopithecines than with other Platyrrhines. In their study of body size evolution among primates, Grabowski and Jungers (2017) note that Old World monkeys, hominoids, and Atelidae all share a similar body mass selective regime, which they interpret as a possible ancestral condition for all catarrhines. Although we are unable to determine ancestral from derived character states with our approach, it is of interest that we see a similar optimum across these taxa for several of our traits. Likewise, a similar trend is also observed among Hylobatidae and Hominoidea in our study, a relationship also noted by Grabowski and Jungers (2017), which they

interpret as evidence for a gibbon-like ancestor for all apes (see also Keith 1923; Tuttle 1981; Alba et al 2015). These trends in our results may be due to these taxa responding to similar ecological factors that resulted in a similar optimum state for these traits. It may also be possible that Atelidae also share the ancestral character state of catarrhines, and gibbons the ancestral state for apes among several traits in our analysis. Further investigations are necessary to better clarify the implications of these results.

Of the primates evaluated by Agosto (Chapter III), *Pongo* has the most distinct pattern of integration and evolutionary potential among the shoulder girdle, basicranium, pelvic girdle, and humerus. In this study, we observe that *Pongo* has responded to the shared selective regime that comprises Hominidae in a different manner than the other apes. This may be a result of the different ecological demands orangutans encountered compared to gorillas, chimpanzees, bonobos, and humans. In general, orangutans are unlike these other great apes; they are also large bodied, but they are arboreal, suspensory primates (Zihlman and Underwood 2019). Currently, they are only found on the islands of Borneo and Sumatra, but once inhabited all of Southeast Asia (Steiper 2006), whereas other members of Hominidae have biogeographic origins in Africa (Stumpf 2011; Hunley et al 2015; Reyes-Centeno et al 2015; Zihlman and Underwood 2019). The African apes are all either semi-terrestrial or terrestrial, while orangutans are arboreal (see Meyers et al 2019); arboreal habitats impose a wider range of functional demands on organisms compared to terrestrial habitats (Nyakatura 2019). It is possible the different adaptive optima observed for orangutans reflects the differences in the ecological factors they encountered in their environment. Another possible explanation is that the distinctive adaptive optima for orangutans reflects the unique evolutionary potential of this species compared to the African apes, inherent in a divergent genetic covariance matrix compared with other apes. Overall, though, the results of this study are in line with our general expectations of how *Pongo* might respond to the same selective pressure as the rest of Hominidae, based on the previously found patterns of integration and evolvability.

Like *Pongo, Pan* also has adaptive optima, and at times separate selective regimes, for several traits that differ from the rest of Hominidae. *Pan* also has a unique, un-ape-like, pattern of integration and evolutionary potential (Agosto Chapter III) which may contribute to the differences in adaptive rates observed between *Pan* and the rest of Hominidae. Given this context, it is unsurprising that *Pan* has different adaptive optima from Hominidae. The unexpected result from this analysis, however, is that *Homo* and *Gorilla* often share similar adaptive optima across several traits. It has been hypothesized *Gorilla* represents an ancestral African ape state (Kivell et al 2013; Almécija et al 2015), or that humans and gorillas represent a different pattern of divergence from a common ancestor compared with *Pan*. Given this context, our results may imply humans have a deep ancestral optimum for many traits that has not changed, and have continued to evolve on a similar trajectory as our more ancient ancestors, while *Pan* responded to a different set of optima. As many traits in *Homo* appear to have evolved through neutral processes (e.g., Roseman and Weaver 2007, Grabowski and Roseman 2015, Roseman 2016), it is also possible that the evolution of traits in humans were motivated by selection early in the evolutionary divergence of this taxonomic group (i.e., among *Australopithecines*), followed by more evolution in response to neutral evolutionary processes since. More study specific to apes will be necessary to resolve these potential evolutionary explanations.

These results highlight that not all traits are responding to the OU optima of selective regimes, a phenomenon observed among several taxa. Additionally, the results of the PIC show that traits within anatomical regions have different correlations despite the overall integration among regions. Thus, the covariance of traits within anatomical regions are heterogenous, and so not all traits are contributing to integration between regions.

Throughout our results we note males and females often have different patterns in both selective regimes and the adaptive optima for each species, and this pattern is persistent across most traits. These differences may be the result of different ecological demands faced by males and females of the same species, but may also reflect the effects of sexual selection (see Lande 1980; 1981).

These results may also be, in part, due to different gene-hormone interactions among the sexes that affect trait expression, and possibly, evolution. It is also possible these trends are indicative of differences in the underlying genetic covariance matrix among males and females of a species that affects how they can respond to selection (see Jensen et al 2003; Ingleby et al 2014; McGlothlin et al 2019).

Study Limitations

The application of Bayesian inference on adaptive regimes offers several benefits such as greater certainty in the location of adaptive shifts and compatibility with the current understanding of evolutionary processes (see Uyeda and Harmon 2014). One primary limitation of these methods is the sensitivity of the results of these models to the prior distributions upon which they are based. While no method can provide an automatic determination of whether a model is correct or not, *bayou* heavily relies upon the discretion of the researcher to assess the reasonableness of the results (Uyeda and Harmon 2014). Thus, there will always be a level of uncertainty in whether the priors used to create these models accurately capture the biological reality of the system we wish to explore. As our understanding of the biological and evolutionary context of primates improves, these models will need to be revisited.

Conclusions

Our study provides the first assessment of hypotheses of primate shoulder girdle morphological variation and demonstrates the importance of examining multiple traits to understand these evolutionary processes. Taken together, our results demonstrate that the evolutionary covariances among mechanically functional and developmentally related traits are not driven by size alone. There are factors influencing the morphological diversity of the primate shoulder girdle that have yet to be explored. Models of habitat, locomotion, and diet encompass several factors that may be driving some of this diversity, and more specific models are necessary to fully capture the variance

within the primate shoulder girdle. The modeled optima presented by the diet, habitat, and locomotion models were not met across taxa. This result emphasizes the need to test how the covariances and constraints among traits actually affect the evolution of taxa. Whether this result reflects constraints on independent trait response to selection need to be explored in a multivariate model of trait evolution. Nevertheless, we improved our understanding of univariate trait evolution within the primate shoulder girdle and demonstrate the need to approach the evolution of this anatomical region from a multivariate framework.

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Appendix IV

Table IV.1. List of taxa and number of males, females, and individuals of unknown sex included in the sample.

Genus_species	Males	Females	Unknown	Total
Allenopithecus_nigroviridis		1	1	2
Alouatta_caraya	8	2		10
Alouatta_palliata	15	9		24
Alouatta_seniculus	18	23		41
Aotus_trivirgatus	2	2		4
Ateles_fusciceps	2	2		4
Callithrix_jacchus	55	50		105
Cercopithecus_mitis	2	2		4
Chlorocebus_aethiops	3	3		6
Colobus_angolensis	2	2		4
Colobus_guereza	27	26		53
Erythrocebus_patas	2	1		3
Eulemur_fulvus_fulvus		1	3	4
Galago_senegalensis	2	2		4
Gorilla_gorilla_gorilla	2	2		4
Hapalemur_griseus	1	1	2	4
Homo_sapiens	56	60		116
Hylobates_klossii	1	1		2
Hylobates_lar	28	24		52
Hylobates_muelleri	9	11		20
Macaca_arctoides			1	1
Macaca_cyclopis	1	6	1	8
Macaca_fascicularis			2	2
Macaca_fuscata	1	1		2
Macaca_mulatta	16	46		62
Macaca_nemestrina	1	1		2
Macaca_thibetana	1	1		2
Mandrillus_leucophaeus	2		1	3
Mandrillus_sphinx	4	1		5
Miopithecus_talapoin	1	1		2
Nomascus_concolor	7	3		10
Pan_paniscus	2	2		4
Pan_troglodytes_troglodytes	42	26		68
Papio_anubis	12	8		20
Papio_cynocephalus	5	5		10
Papio_hamadryas	4	5		9
Papio_papio	4	3		7
Papio_ursinus	2	2		4
Pithecia_pithecia		2	1	3
Pongo_pygmaeus	19	23		42
Pygathrix_nemaeus	1	1		2
Rhinopithecus_roxellana	1	1	1	3
Saguinus_fuscicollis	34	35		69
Saguinus_oedipus	31	19		50
Saimiri_sciureus	2	2		4
Symphalangus_syndactylus	3	6		9
Tarsius_bancanus	2	2		4
Theropithecus_gelada	1	2		3
Tupaia_glis	25	21		46
Total	***459***	***450***	***13***	***922***

Table IV.2. List of traits and descriptions for each anatomical region.

Basicranium	
NR	Length of the bony attachment of the nuchal ligament on the basicranium.
SCM	Length of cranial attachment of sternocleidomastoid.
SNL	Length of the caudal border of the attachment for cranial-most neck muscles and trapezius muscle.
FMW	Width of the foramen magnum measured at the greatest curvature of the left and right lateral margins.
Shoulder Girdle	
SSL	Length of the scapular spine – attachment of the trapezius muscle along the scapular spine.
SBL	Length of scapular blade along lateral border.
VB	Length of the vertebral border of the scapula. Combined values of VBA and VBB.
GL	Maximum cranial to caudal length of the glenoid fossa.
CLML	Maximum length of the clavicle.
Pelvic Girdle	
AMIB	Anterior margin of iliac blade.
RAH	Retro-auricular height, distance from cranial margin of the auricle to posterior superior iliac spine.
LIH	Lower iliac height, distance from caudal margin of auricle to the posterior aspect of the central point of the acetabulum.
AW	Medial to lateral width of the acetabulum.
Humerus	
HML	Maximum length of the humerus.
HHW	Medial to lateral width of the humeral head.

Table IV.3. Model fit results for males. Log likelihood, AIC, and AICc for the best fitting hypothesis and Bayou model for each trait. Best fitting model is determined by the lowest AICc value. In several instances, the Habitat, Diet, and Locomotion hypotheses provide equally good model fits. These instances are noted, with the values for the hypothesis for the lowest AICc are presented (indicated by bolded abbreviation). Abbreviations are as follow: H = Habitat model, D = Diet model, L = Locomotion model.

Males	**Best Fitting Hypothesis**			**Bayou Model**		
	Model	AIC	AICc	Model	AIC	AICc
NR	H/D/**L**	60.48476	65.10015	Bayou	-6.674556	14.74211
SCM	Locomotion	59.17006	63.78544	Bayou	-19.9107	24.2493
SNL	H/**D**/L	80.76325	84.36325	Bayou	24.41523	74.41523
FMW	Locomotion	59.11249	63.72788	Bayou	-1.407841	15.59216
SSL	Locomotion	50.09587	54.71125	Bayou	23.43182	28.0472
SBL	Locomotion	43.7001	48.31548	Bayou	-6.423549	10.57645
VB	Locomotion	40.26059	44.87598	Bayou	2.606411	52.60641
GW	**L**/D	47.47512	52.09051	Bayou	-19.02409	30.97591
CLML	Locomotion	49.21344	53.82883	Bayou	0.6634967	17.6635
AMIB	Locomotion	66.21224	70.82763	Bayou	70.07256	74.68794
RAH	Habitat	-113.001	-111.6057	Bayou	-24.31086	19.84914
LIH	Locomotion	61.67737	66.29275	Bayou	0.9770808	57.49882
AW	Locomotion	44.86578	49.48117	Bayou	-29.65466	14.50534
HML	**H**/D/L	59.16618	60.56153	Bayou	2.709715	19.70971
HHW	H/D/**L**	48.49693	53.11232	Bayou	-4.43408	45.56592

Table IV.4. Model fit results for females. Log likelihood, AIC, and AICc for the best fitting hypothesis and Bayou model for each trait. Best fitting model is determined by the lowest AICc value. In several instances, the Habitat, Diet, and Locomotion hypotheses provide equally good model fits. These instances are noted, with the values for the hypothesis for the lowest AICc are presented (indicated by bolded abbreviation). Abbreviations are as follow: D = Diet model, L = Locomotion model.

Females	**Best Fitting Hypothesis**			**Bayou Model**		
	Model	AIC	AICc	Model	AIC	AICc
NR	Diet	51.02342	54.62342	Bayou	-15.2896	4.452332
SCM	Diet	52.44578	56.04578	Bayou	-6.183265	13.55867
SNL	Diet	67.26332	70.86332	Bayou	-31.06206	-11.32013
FMW	Diet	40.28812	43.88812	Bayou	-10.41581	9.326124
SSL	Diet	39.41103	43.01103	Bayou	-37.39409	6.765913
SBL	Locomotion	28.08155	32.69694	Bayou	-30.86552	-11.12358
VB	Diet	41.89707	45.49707	Bayou	-7.465628	9.534372
GW	Diet	28.95791	32.55791	Bayou	-17.36587	2.376064
CLML	L/**D**	38.58378	42.18378	Bayou	-10.65133	9.090601
AMIB	Parv.Orer	-129.9023	-107.1023	Bayou	48.15919	52.77458
RAH	**L**/D	36.17578	40.79116	Bayou	-53.99963	-31.19963
LIH	Locomotion	42.20611	46.82149	Bayou	-18.23447	1.507465
AW	Diet	26.74166	30.34166	Bayou	-24.11798	-4.376046
HML	Diet	32.90747	36.50747	Bayou	-13.56989	6.172046
HHW	Diet	28.83206	32.43206	Bayou	-30.72194	-10.98

Table IV.5. Phylogenetically corrected correlations between traits. The upper triangle are the results for the males, and the lower triangle are the results for the females. Values are colored into quartiles using the male values to compare between sexes. First quartile (lowest value to 0.72) are green, second quartile (0.73 to 0.8) are blue, third quartile (0.81 to 0.89) are yellow, and the fourth quartile (0.9 to highest value) are orange.

	NR	SCM	SNL	FMW	SSL	SBL	VB	GW	CLML	HHW	HML	AMIB	RAH	LIH	AW	
NR		0.786	0.767	0.807	0.855	0.840	0.802	0.855	0.781	0.851	0.800	0.682	0.673	0.774	0.829	**NR**
SCM	0.778		0.797	0.925	0.846	0.860	0.846	0.910	0.890	0.918	0.885	0.635	0.763	0.828	0.938	**SCM**
SNL	0.806	0.843		0.851	0.783	0.797	0.816	0.835	0.791	0.871	0.840	0.816	0.786	0.790	0.859	**SNL**
FMW	0.821	0.906	0.826		0.864	0.889	0.846	0.933	0.921	0.928	0.932	0.719	0.794	0.904	0.967	**FMW**
SSL	0.795	0.826	0.776	0.863		0.963	0.889	0.926	0.881	0.915	0.909	0.795	0.814	0.860	0.885	**SSL**
SBL	0.817	0.838	0.782	0.892	0.959		0.895	0.950	0.921	0.934	0.937	0.837	0.856	0.897	0.916	**SBL**
VB	0.710	0.822	0.742	0.836	0.833	0.802		0.905	0.875	0.915	0.872	0.691	0.786	0.793	0.891	**VB**
GW	0.802	0.903	0.864	0.910	0.919	0.925	0.848		0.950	0.967	0.955	0.752	0.809	0.881	0.960	**GW**
CLML	0.796	0.914	0.815	0.906	0.857	0.897	0.797	0.937		0.949	0.947	0.706	0.782	0.854	0.948	**CLML**
HHW	0.830	0.911	0.888	0.919	0.902	0.913	0.867	0.971	0.946		0.948	0.757	0.836	0.866	0.957	**HHW**
HML	0.805	0.883	0.821	0.919	0.911	0.935	0.825	0.960	0.952	0.954		0.786	0.831	0.918	0.941	**HML**
AMIB	0.548	0.504	0.430	0.657	0.682	0.722	0.599	0.645	0.606	0.646	0.684		0.701	0.810	0.724	**AMIB**
RAH	0.666	0.817	0.807	0.856	0.881	0.874	0.832	0.891	0.828	0.904	0.840	0.579		0.757	0.844	**RAH**
LIH	0.707	0.825	0.714	0.908	0.845	0.891	0.802	0.879	0.885	0.887	0.921	0.760	0.829		0.895	**LIH**
AW	0.837	0.930	0.872	0.943	0.899	0.907	0.850	0.964	0.954	0.968	0.948	0.578	0.872	0.888		**AW**

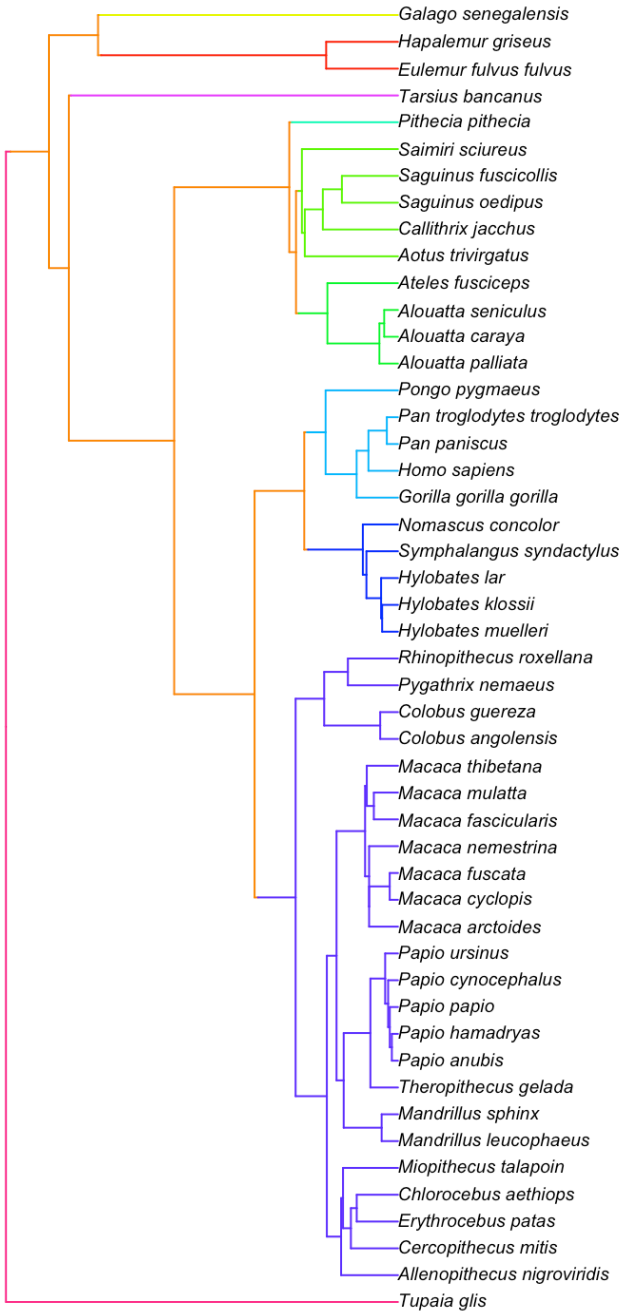
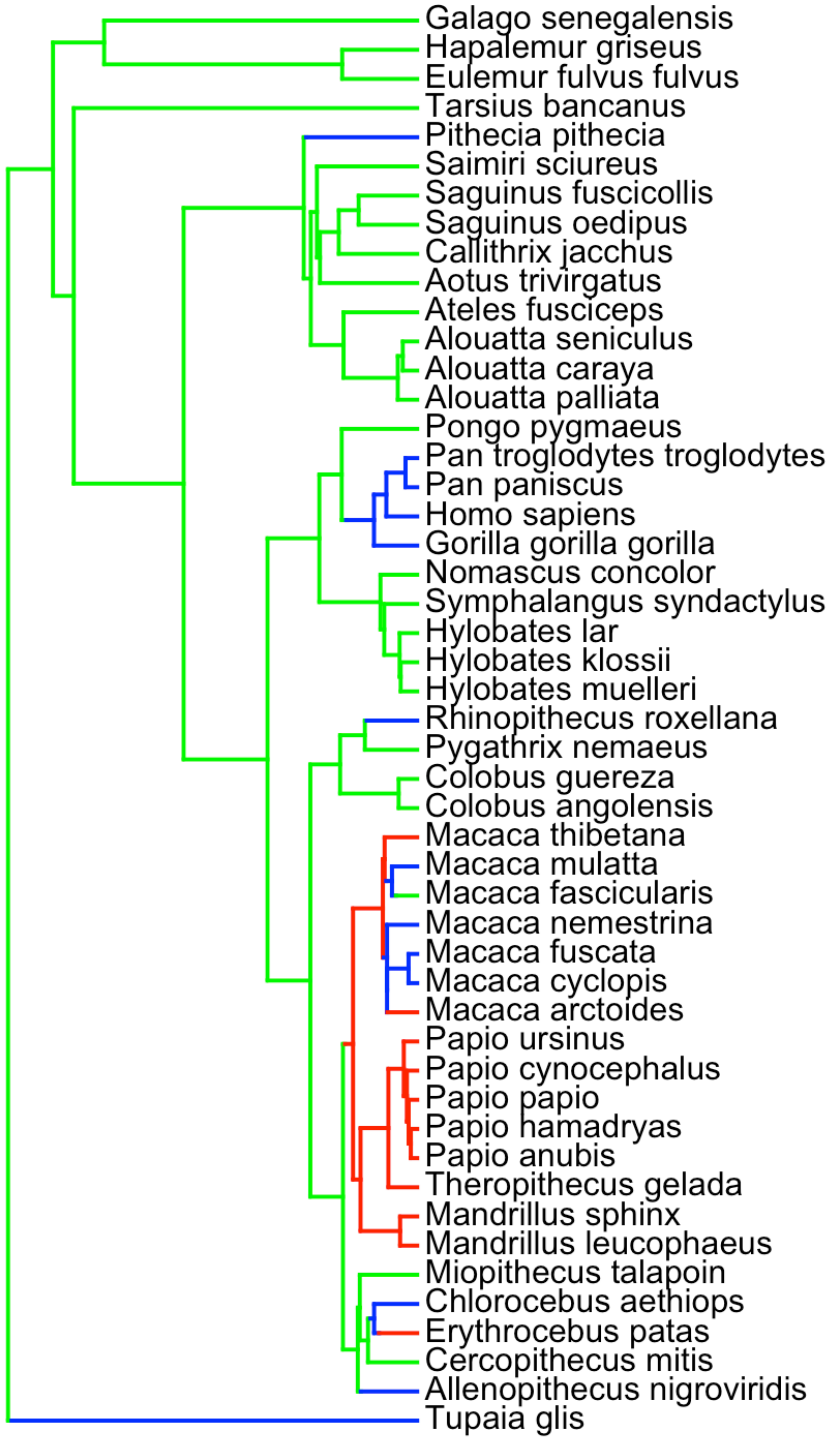
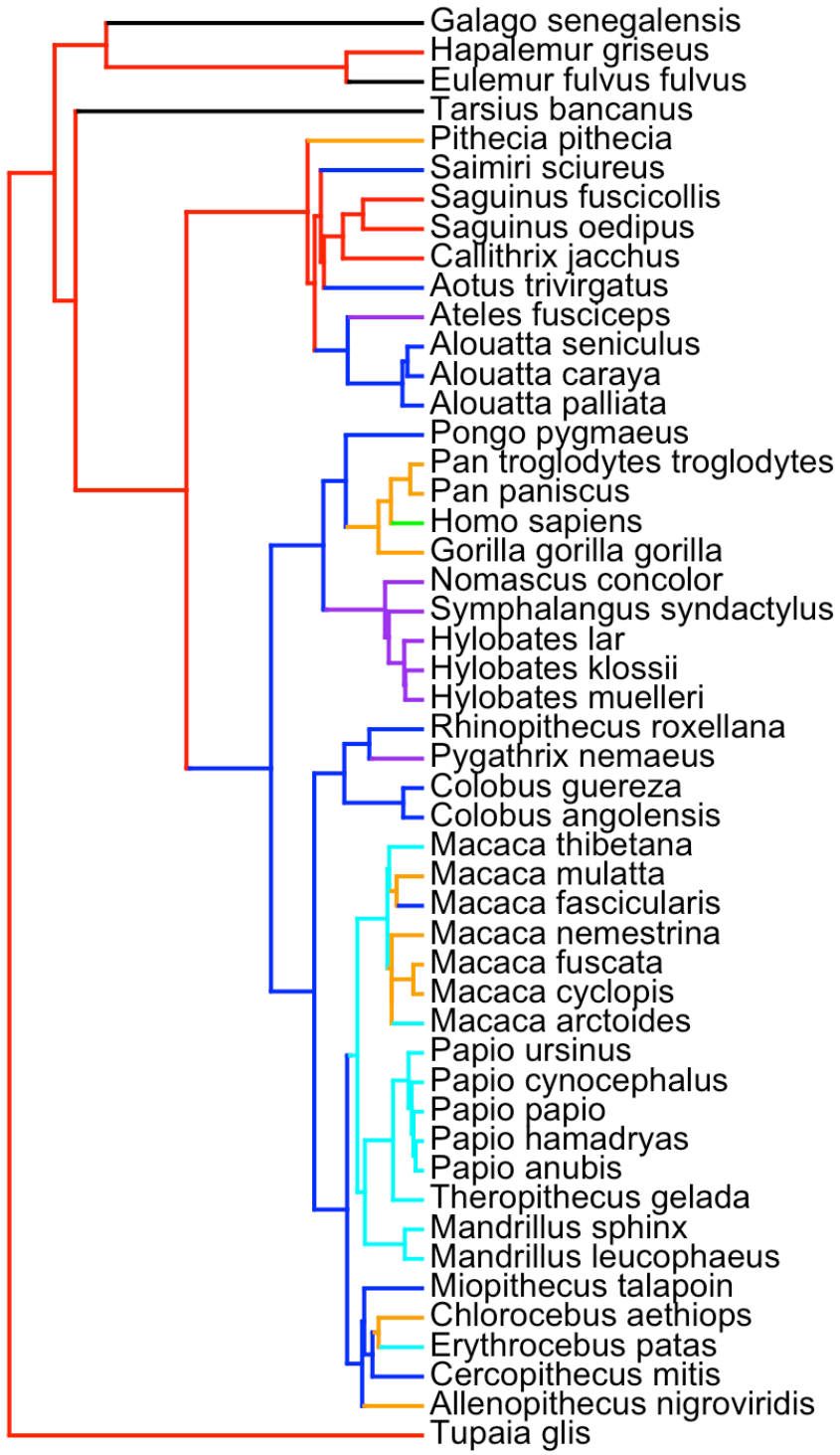


Figure IV.1 a-d. Visual representation for four of the evolutionary hypotheses of primate diversification tested in this study.

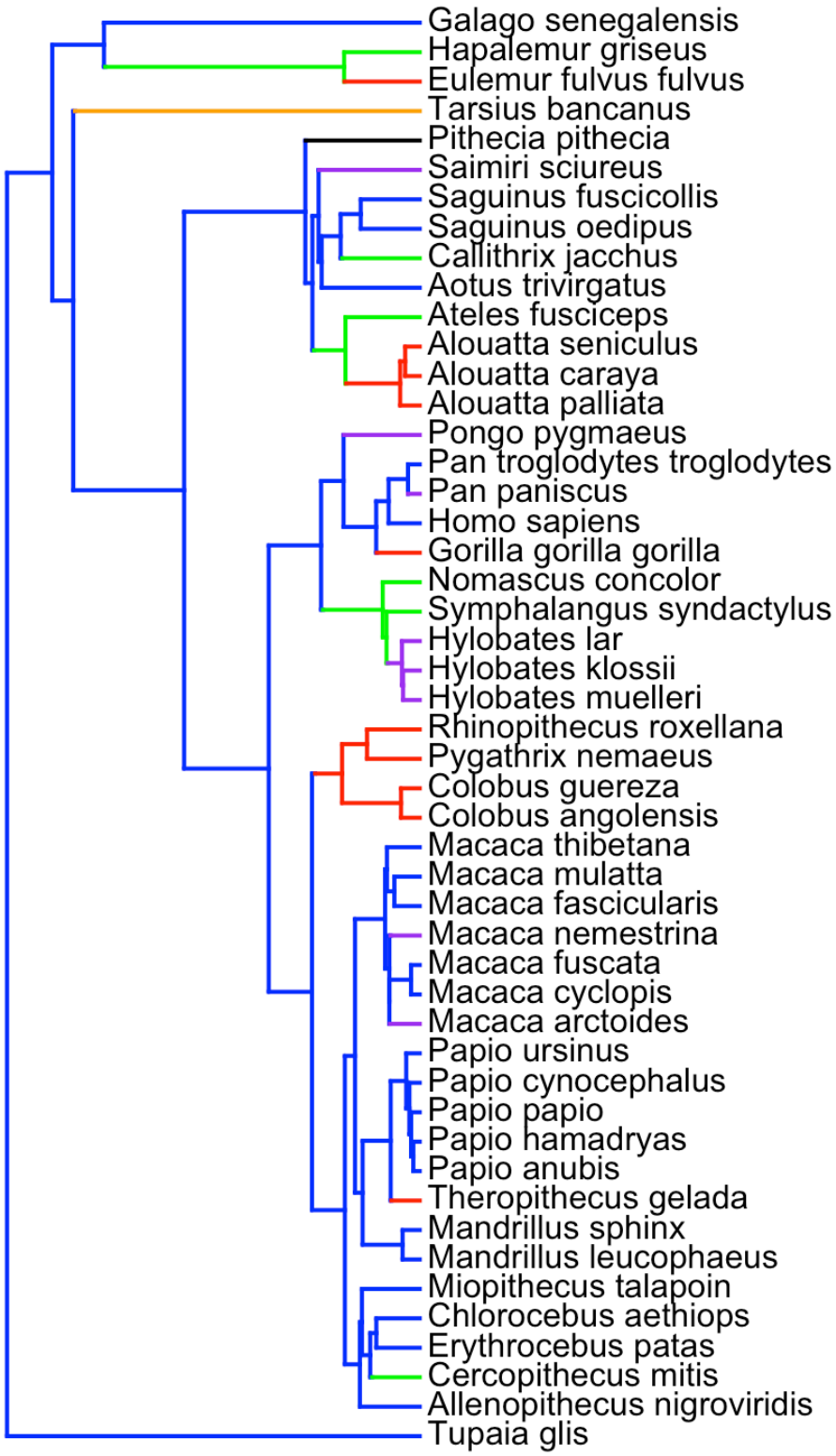
a. Family Hypothesis: Tupiadae (pink), Galigadae (yellow), Lemuridae (red), Tarsiidae (light purple), Cebidae (light green), Atelidae (green), Pitheciidae (aqua), Hylobatidae (dark blue), Hominidae (light blue), and Cercopithecidae (dark purple).



b. Habitat: arboreal (green), semiterrestrial (blue), terrestrial (red).



c. Locomotion: saltatorial (black), scansorial (red), semiterrestrial quadruped (orange), arboreal quadruped (blue), brachiation/suspension (purple), bipedalism (green), terrestrial quadruped (cyan)



d. Diet: omnivore (blue), folivore (red), herbivore (green), frugivore (purple), insectivore (orange), granivore (black).

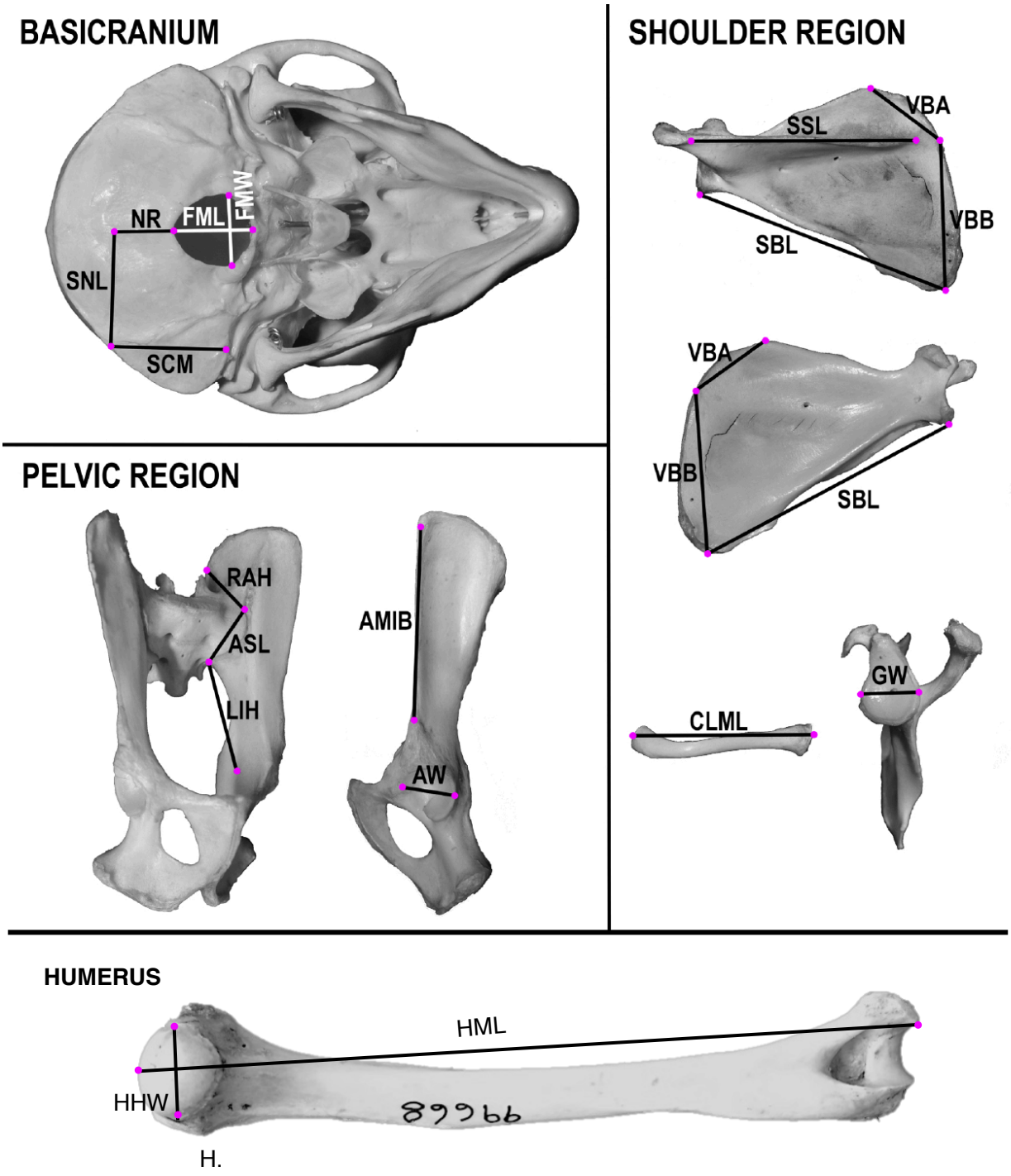


Figure IV.2. Linear dimensions collected from each anatomical region: A. caudal aspect of the basicranium; B. medial aspect of os coxa; C. lateral aspect of os coxa; D. dorsal aspect of scapula; E. ventral aspect of scapula; F. lateral aspect of scapula; G. cranial aspect of clavicle; F. ventral aspect of humerus. Trait descriptions can be found in Table SX. Measurements are demonstrated on a *Macaca mulatta* specimen and are homologous for all taxa.

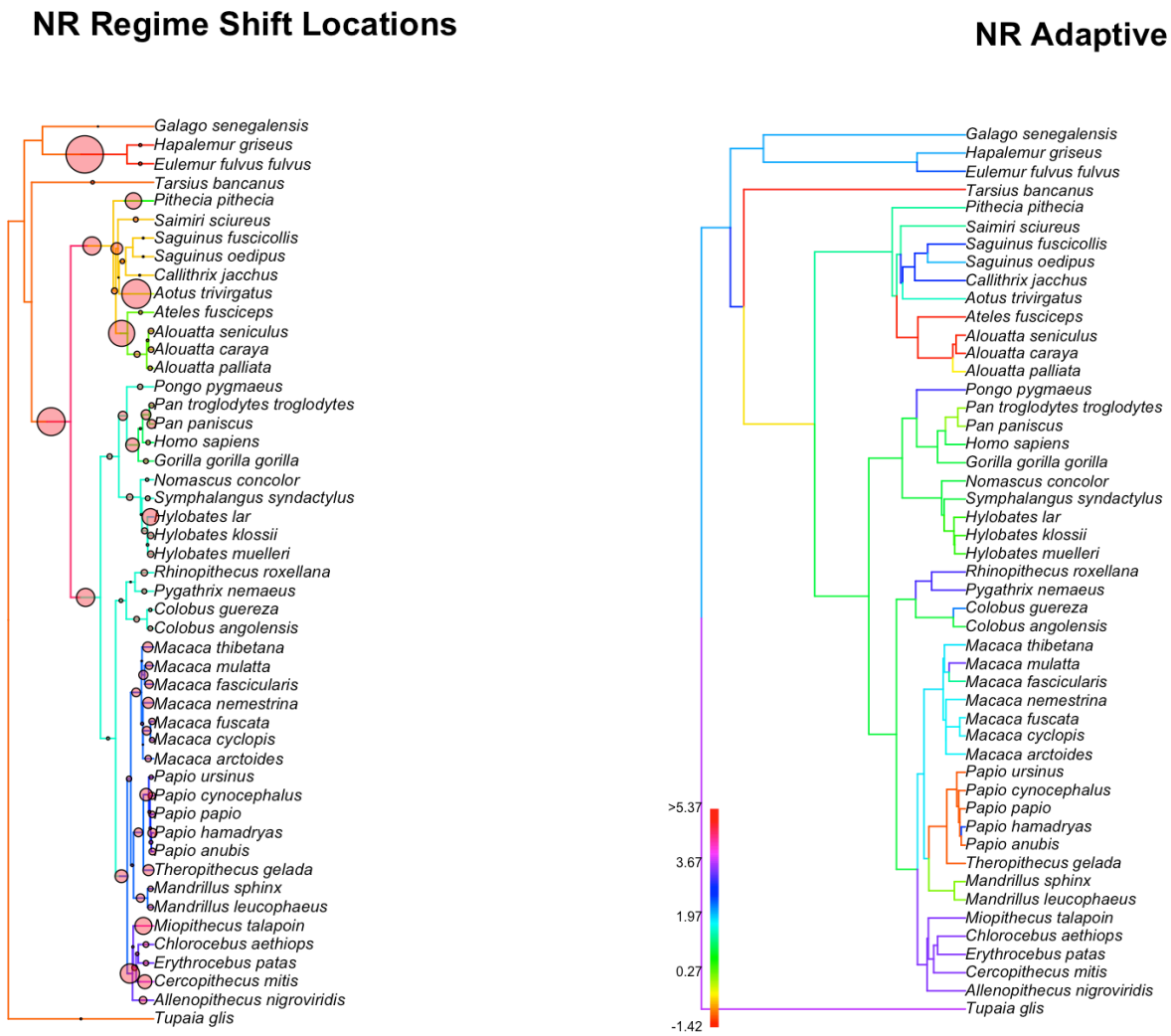
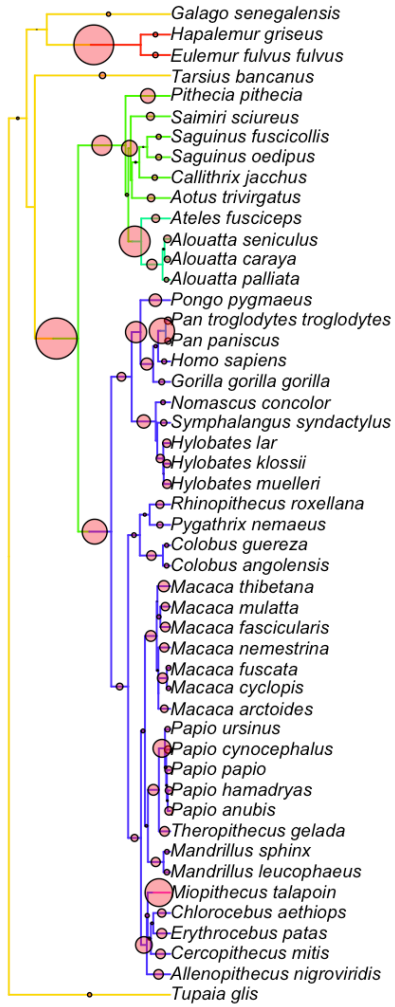


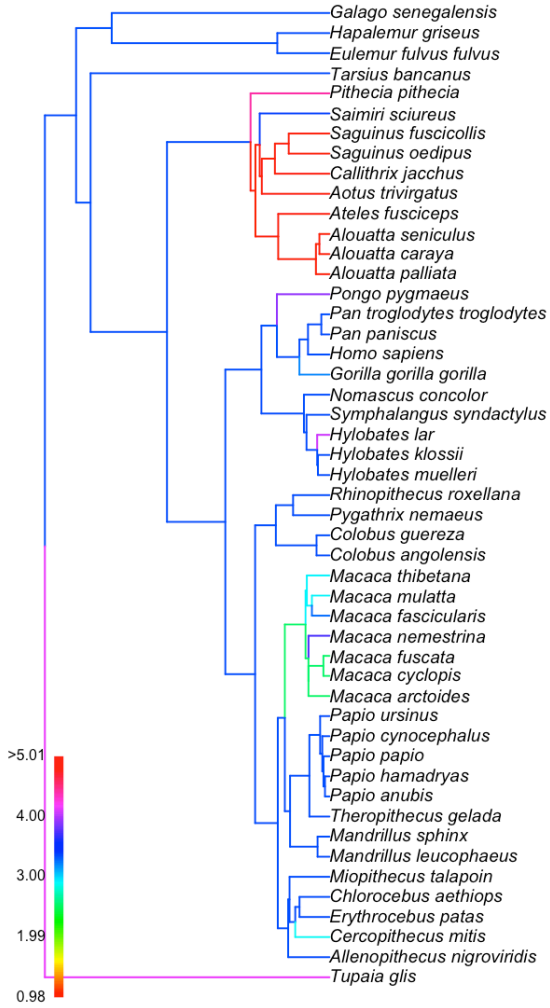
Figure IV.3 a-c. Selective regimes and shift locations (left) and Adaptive Optima (right) of each trait for males. Selective regimes and adaptive optima are indicated by different colors; the size of the red circles is related to the posterior probability of the shift location and scale bars indicate optima values.

a. Nuchal Region (NR) Males

SBL Regime Shift Locations

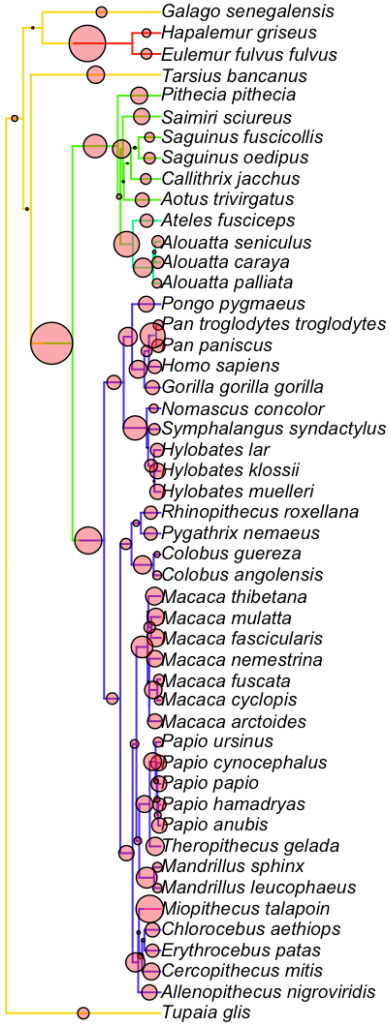


SBL Adaptive Optima

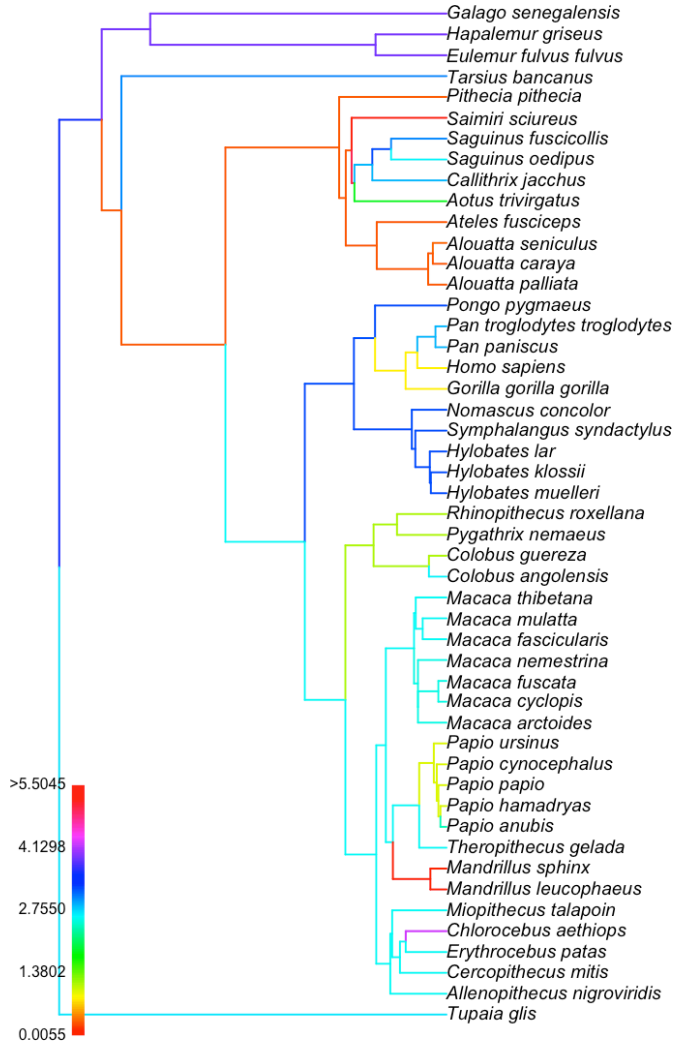


b. Scapular Blade Length (SBL) Males

LIH Regime Shift Locations



LIH Adaptive Optima



c. Lower Iliac Height (LIH) Males

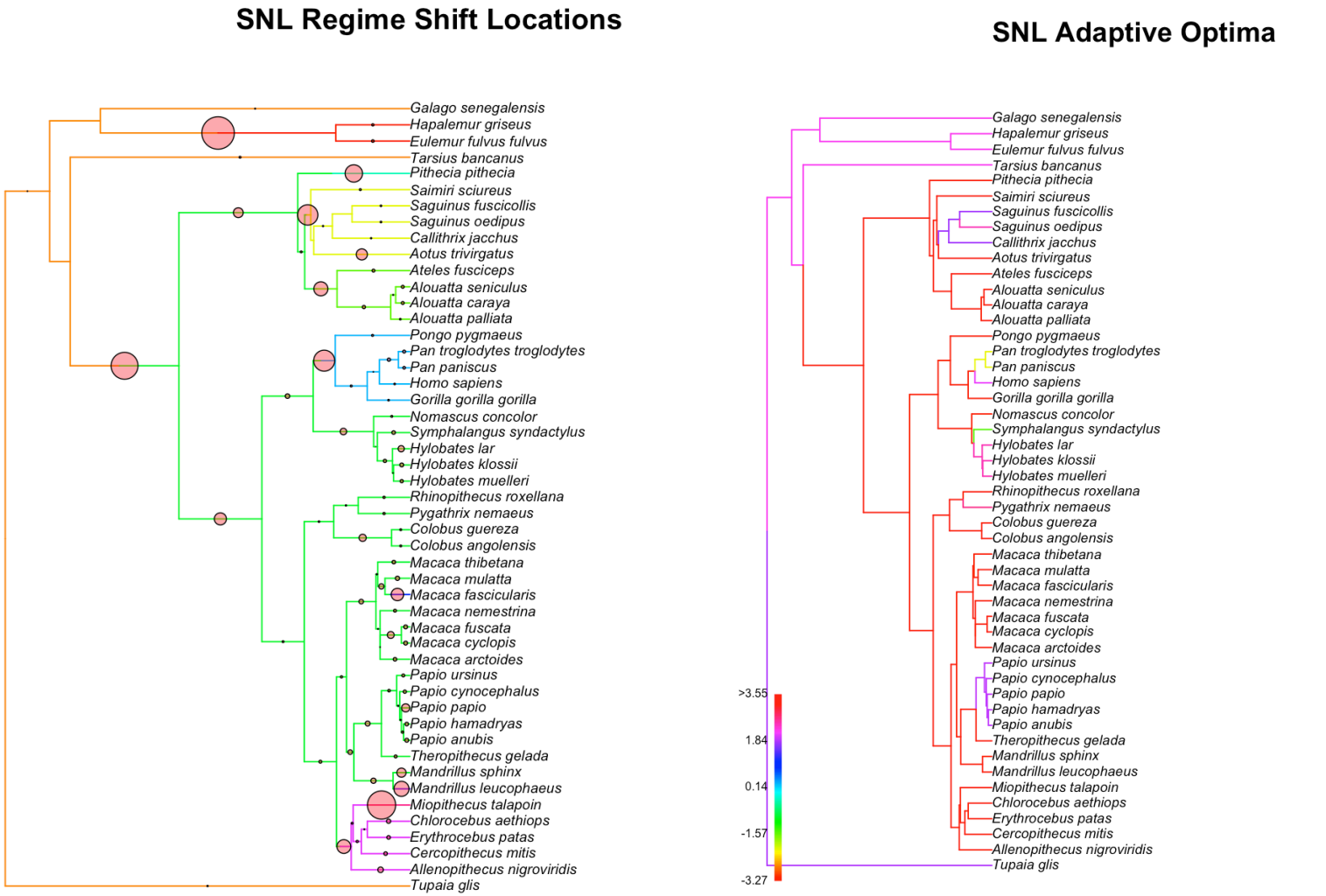
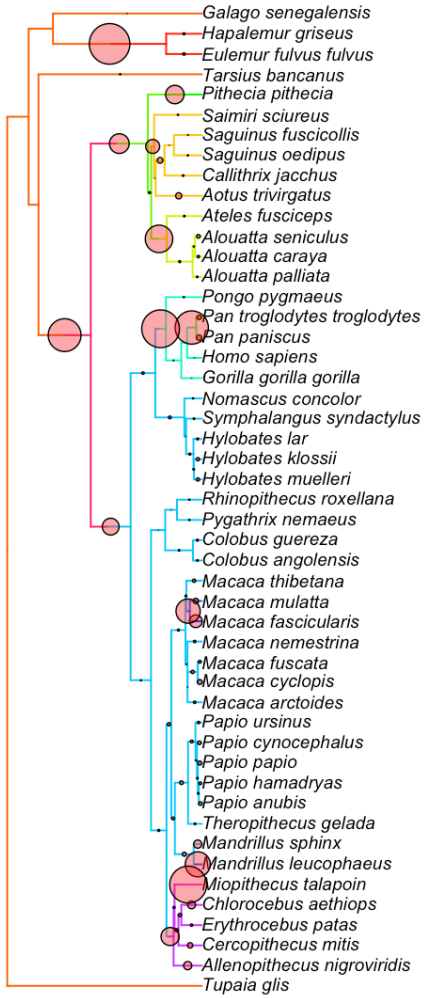


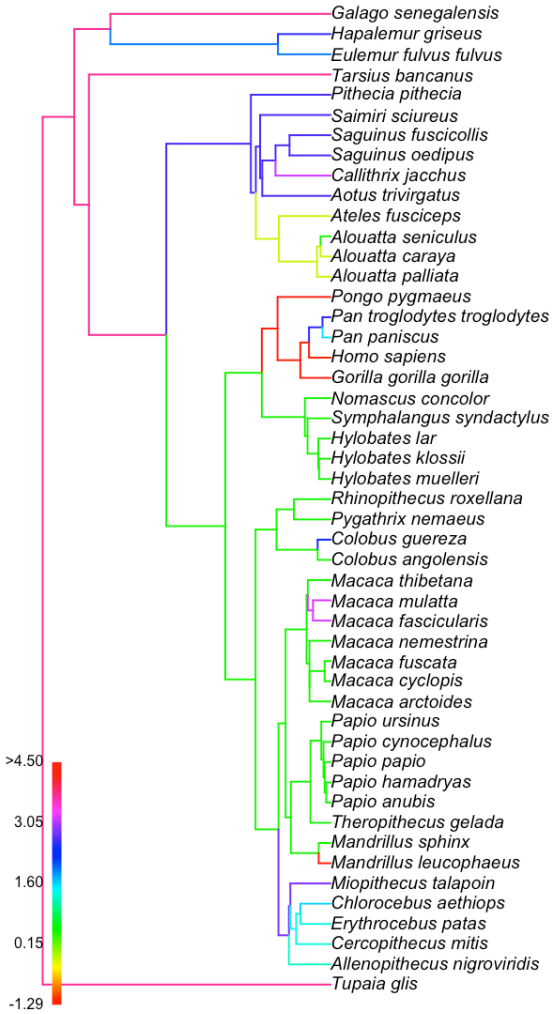
Figure IV.4 a-c. Selective regimes and shift locations (left) and Adaptive Optima (right) of each trait for females. Selective regimes and adaptive optima are indicated by different colors; the size of the red circles is related to the posterior probability of the shift location and scale bars indicate optima values.

a. Superior Nuchal Line (SNL) Females

RAH Regime Shift Locations

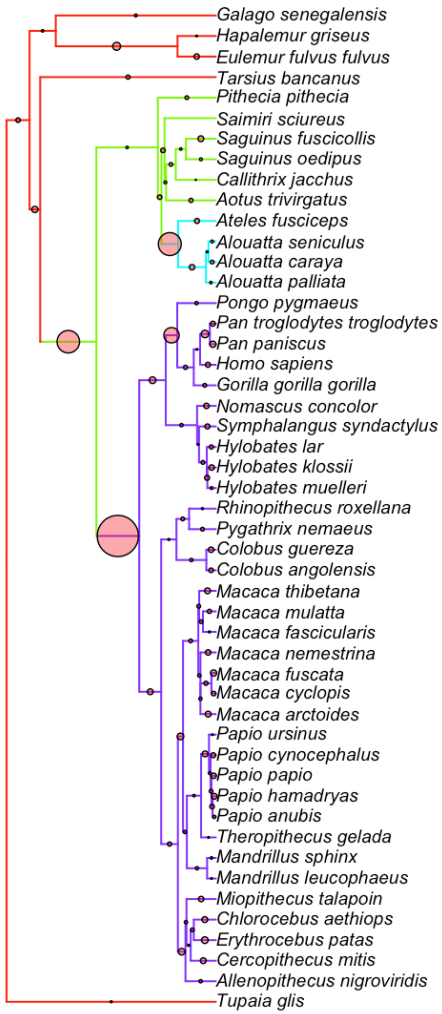


RAH Adaptive Optima

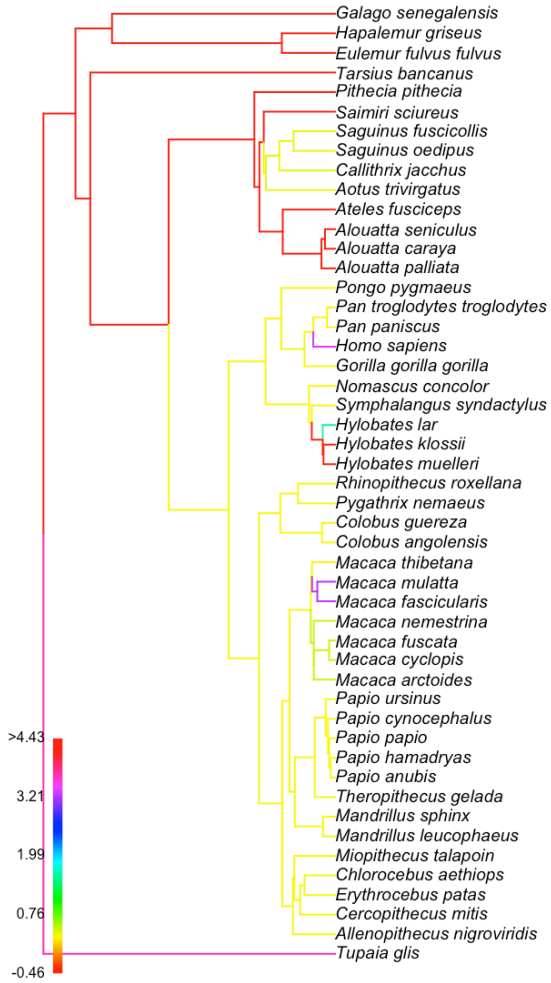


b. Retroauricular Height (RAH) Females

AMIB Regime Shift Locations



AMIB Adaptive Optima



c. Anterior Margin of Iliac Blade (AMIB) Females

Supplementary Information III

Table SIII.1. List of hypotheses tested, and selective regime for each species. Abbreviations are as follows: New World Monkey (NWM), Old World Monkey (OWM), arboreal quadrupedalism (AQ), semiterrestrial quadrupedalism (ATQ), and terrestrial quadrupedalism (TQ).

	HYPOTHESES TESTED									
Genus_species	**Mammal**	**PvO**	**MAPO**	**MALLTO**	**Parv.Order**	**ANOPO**	**Family**	**Habitat**	**Locomotion**	**Diet**
Allenopithecus_nigroviridis	Mammal	Primate	Monkey	Monkey	Catarrhini	OWM	Cercopithecidae	Semiterrestrial	ATQ	Omnivore
Alouatta_caraya	Mammal	Primate	Monkey	Monkey	Platyrrhini	NWM	Atelidae	Arboreal	AQ	Folivore
Alouatta_palliata	Mammal	Primate	Monkey	Monkey	Platyrrhini	NWM	Atelidae	Arboreal	AQ	Folivore
Alouatta_seniculus	Mammal	Primate	Monkey	Monkey	Platyrrhini	NWM	Atelidae	Arboreal	AQ	Folivore
Aotus_trivirgatus	Mammal	Primate	Monkey	Monkey	Platyrrhini	NWM	Aotidae	Arboreal	AQ	Omnivore
Ateles_fusciceps	Mammal	Primate	Monkey	Monkey	Platyrrhini	NWM	Atelidae	Arboreal	Brachiation	Herbivore
Callithrix_jacchus	Mammal	Primate	Monkey	Monkey	Platyrrhini	NWM	Callitrichidae	Arboreal	Scansorial	Herbivore
Cercopithecus_mitis	Mammal	Primate	Monkey	Monkey	Catarrhini	OWM	Cercopithecidae	Arboreal	AQ	Herbivore
Chlorocebus_aethiops	Mammal	Primate	Monkey	Monkey	Catarrhini	OWM	Cercopithecidae	Semiterrestrial	ATQ	Omnivore
Colobus_angolensis	Mammal	Primate	Monkey	Monkey	Catarrhini	OWM	Cercopithecidae	Arboreal	AQ	Folivore
Colobus_guereza	Mammal	Primate	Monkey	Monkey	Catarrhini	OWM	Cercopithecidae	Arboreal	AQ	Folivore
Erythrocebus_patas	Mammal	Primate	Monkey	Monkey	Catarrhini	OWM	Cercopithecidae	Terrestrial	TQ	Omnivore
Eulemur_fulvus_fulvus	Mammal	Primate	Prosimian	Lemur	Lemuriformes	Prosimian	Lemuridae	Arboreal	Saltatorial	Folivore
Galago_senegalensis	Mammal	Primate	Prosimian	Loris	Lorisiformes	Prosimian	Galagidae	Arboreal	Saltatorial	Omnivore
Gorilla_gorilla_gorilla	Mammal	Primate	Ape	Ape	Catarrhini	Ape	Hominidae	Semiterrestrial	ATQ	Folivore
Hapalemur_griseus	Mammal	Primate	Prosimian	Lemur	Lemuriformes	Prosimian	Lemuridae	Arboreal	Scansorial	Herbivore
Homo_sapiens	Mammal	Primate	Ape	Ape	Catarrhini	Ape	Hominidae	Terrestrial	Bipedal	Omnivore
Hylobates_klossii	Mammal	Primate	Ape	Ape	Catarrhini	Ape	Hylobatidae	Arboreal	Brachiation	Frugivore
Hylobates_lar	Mammal	Primate	Ape	Ape	Catarrhini	Ape	Hylobatidae	Arboreal	Brachiation	Frugivore
Hylobates_muelleri	Mammal	Primate	Ape	Ape	Catarrhini	Ape	Hylobatidae	Arboreal	Brachiation	Frugivore
Macaca_arctoides	Mammal	Primate	Monkey	Monkey	Catarrhini	OWM	Cercopithecidae	Terrestrial	TQ	Frugivore
Macaca_cyclopis	Mammal	Primate	Monkey	Monkey	Catarrhini	OWM	Cercopithecidae	Semiterrestrial	ATQ	Omnivore

Table SIII.1 continued

	HYPOTHESES TESTED									
Genus_species	**Mammal**	**PvO**	**MAPO**	**MALLTO**	**Parv.Order**	**ANOPO**	**Family**	**Habitat**	**Locomotion**	**Diet**
Macaca_fascicularis	Mammal	Primate	Monkey	Monkey	Catarrhini	OWM	Cercopithecidae	Arboreal	AQ	Omnivore
Macaca_fuscata	Mammal	Primate	Monkey	Monkey	Catarrhini	OWM	Cercopithecidae	Semiterrestrial	ATQ	Omnivore
Macaca_mulatta	Mammal	Primate	Monkey	Monkey	Catarrhini	OWM	Cercopithecidae	Semiterrestrial	ATQ	Omnivore
Macaca_nemestrina	Mammal	Primate	Monkey	Monkey	Catarrhini	OWM	Cercopithecidae	Semiterrestrial	ATQ	Frugivore
Macaca_thibetana	Mammal	Primate	Monkey	Monkey	Catarrhini	OWM	Cercopithecidae	Terrestrial	TQ	Omnivore
Mandrillus_leucophaeus	Mammal	Primate	Monkey	Monkey	Catarrhini	OWM	Cercopithecidae	Terrestrial	TQ	Omnivore
Mandrillus_sphinx	Mammal	Primate	Monkey	Monkey	Catarrhini	OWM	Cercopithecidae	Terrestrial	TQ	Omnivore
Miopithecus_talapoin	Mammal	Primate	Monkey	Monkey	Catarrhini	OWM	Cercopithecidae	Arboreal	AQ	Omnivore
Nomascus_concolor	Mammal	Primate	Ape	Ape	Catarrhini	Ape	Hylobatidae	Arboreal	Brachiation	Herbivore
Pan_paniscus	Mammal	Primate	Ape	Ape	Catarrhini	Ape	Hominidae	Semiterrestrial	ATQ	Frugivore
Pan_troglodytes_troglodytes	Mammal	Primate	Ape	Ape	Catarrhini	Ape	Hominidae	Semiterrestrial	ATQ	Omnivore
Papio_anubis	Mammal	Primate	Monkey	Monkey	Catarrhini	OWM	Cercopithecidae	Terrestrial	TQ	Omnivore
Papio_cynocephalus	Mammal	Primate	Monkey	Monkey	Catarrhini	OWM	Cercopithecidae	Terrestrial	TQ	Omnivore
Papio_hamadryas	Mammal	Primate	Monkey	Monkey	Catarrhini	OWM	Cercopithecidae	Terrestrial	TQ	Omnivore
Papio_papio	Mammal	Primate	Monkey	Monkey	Catarrhini	OWM	Cercopithecidae	Terrestrial	TQ	Omnivore
Papio_ursinus	Mammal	Primate	Monkey	Monkey	Catarrhini	OWM	Cercopithecidae	Terrestrial	TQ	Omnivore
Pithecia_pithecia	Mammal	Primate	Monkey	Monkey	Platyrrhini	NWM	Pitheciidae	Semiterrestrial	ATQ	Granivore
Pongo_pygmaeus	Mammal	Primate	Ape	Ape	Catarrhini	Ape	Hominidae	Arboreal	AQ	Frugivore
Pygathrix_nemaeus	Mammal	Primate	Monkey	Monkey	Catarrhini	OWM	Cercopithecidae	Arboreal	Brachiation	Folivore
Rhinopithecus_roxellana	Mammal	Primate	Monkey	Monkey	Catarrhini	OWM	Cercopithecidae	Semiterrestrial	AQ	Folivore
Saguinus_fuscicollis	Mammal	Primate	Monkey	Monkey	Platyrrhini	NWM	Callitrichidae	Arboreal	Scansorial	Omnivore
Saguinus_oedipus	Mammal	Primate	Monkey	Monkey	Platyrrhini	NWM	Callitrichidae	Arboreal	Scansorial	Omnivore
Saimiri_sciureus	Mammal	Primate	Monkey	Monkey	Platyrrhini	NWM	Cebidae	Arboreal	AQ	Frugivore
Symphalangus_syndactylus	Mammal	Primate	Ape	Ape	Catarrhini	Ape	Hylobatidae	Arboreal	Brachiation	Herbivore
Tarsius_bancanus	Mammal	Primate	Prosimian	Tarsier	Tarsiiformes	Prosimian	Tarsiidae	Arboreal	Saltatorial	Insectivore

Table SIII.1 continued

	HYPOTHESES TESTED									
Genus_species	**Mammal**	**PvO**	**MAPO**	**MALLTO**	**Parv.Order**	**ANOPO**	**Family**	**Habitat**	**Locomotion**	**Diet**
Theropithecus_gelada	Mammal	Primate	Monkey	Monkey	Catarrhini	OWM	Cercopithecidae	Terrestrial	TQ	Folivore
Tupaia_glis	Mammal	Other	Other	Other	Scandentia	Other	Tupidae	Semiterrestrial	Scansorial	Omnivore

Table SIII.2. List and definitions of landmarks collected.

No.	*Landmark*	*Definition*
	Basicranium	
1.	Inion	Location of the intersection of the right and left superior nuchal lines within the external occipital protuberance (White et al 2012).
2.	Opisthion	Midline point of the dorsal margin of the foramen magnum (White et al 2012).
3.	Basion	Midline point of the ventral margin of the foramen magnum (White et al 2012).
4.	Right margin of foramen magnum	Right margin of the foramen magnum at its greatest curvature (Moore-Jansen et al 1994).
5.	Left margin of foramen magnum	Left margin of the foramen magnum at its greatest curvature (Moore-Jansen et al 1994).
6.	Asterion	Point where the lambdoidal, parietomastoid, and occipitomastoid sutures meet (White et al 2012).
7.	Left mastoid	Inferior-most point of the mastoid process (White et al 2012).
	Scapula	
8.	Scapular spine lateral border	Point of intersection between the scapular spine and acromion process (Sears et al 2013).
9.	Scapular spine medial border	Medial margin of trapezius attachment along scapular spine (Young 2006).
10.	Superior angle	Intersection of superior and medial borders of scapula (White et al 2012).
11.	Scapular spine vertebral border	Point on vertebral margin where the long axis of the scapular spine and vertebral border meet (Young 2006).
12.	Inferior angle	Intersection of the lateral and medal borders of scapula (White et al 2012).
13.	Ventral margin of glenoid fossa	Ventral margin of glenoid fossa at its greatest width (Young 2006).
14.	Dorsal margin of glenoid fossa	Dorsal margin of glenoid fossa at its greatest width (Young 2006).
15.	Cranial margin of glenoid fossa	Superior-most margin of glenoid fossa (Young 2006).
16.	Caudal margin of glenoid fossa	Inferior-most margin of glenoid fossa (Young 2006).
	Clavicle	
17.	Acromial end	Lateral-most point of clavicle on cranial aspect.
18.	Sternal end	Medial-most point of clavicle on cranial aspect.

Table SIII.2 continued

No.	Landmark	Definition
	Os coxa	
19.	Anterior superior iliac spine	Ventral-most point on lateral aspect of iliac crest (Lewton 2012).
20.	Anterior inferior iliac spine	Ventral-most point on anterior inferior iliac spine. If only a bony roughening, the point is taken at the center of this rugosity (Lewton 2012).
21.	Posterior superior iliac spine	Medial-most point of the dorsal-cranial border of iliac crest (Lewton 2012).
22.	Posterior inferior iliac spine	Sharp projection posterior and inferior to the auricular surface (White et al 2012).
23.	Cranial margin of acetabulum	Cranial-most point of the margin of the acetabulum (Lewton 2012).
24.	Caudal margin of acetabulum	Caudal-most point of the margin of the acetabulum, directly across from landmark 23 (Lewton 2012).
25.	Medial margin of acetabulum	Medial-most point along margin of the acetabulum.
26.	Lateral margin of acetabulum	Lateral-most point along margin of the acetabulum.
27.	Cranial margin of auricular surface	Central point of the cranial-most margin of the auricular surface.
28.	Caudal margin of auricular surface	Central point of the caudal-most margin of the auricular surface.
29.	Center of acetabulum	Center of the acetabulum, defined as the intersection of the line between landmarks 23 and 24 and landmarks 27 and 28 (Lewton 2012).
	Humerus	
30.	Cranial end of humerus	Cranial-most point of the proximal end of humerus.
31.	Medial margin of humeral head	Medial-most margin of the head of the humerus.
32.	Lateral margin of humeral head	Lateral-most margin of the head of humerus.
33.	Medial margin of distal articular surface	Medial-most margin of distal articular surface of the humerus.

Table SIII.3. Male trait averages for the scaled, logged data, and average standard error for each trait.

Genus_species	NR	SCM	SNL	FMW	SSL	SBL	VB	GW	CLML	AMIB	RAH	LIH	AW	HML	HHW
Tupaia_glis	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Galago_senegalensis	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Hapalemur_griseus	2	2	2	2	1	2	2	2	2	1	2	2	2	2	2
Eulemur_fulvus_fulvus	2	2	2	2	1	2	2	2	2	1	2	2	2	2	2
Tarsius_bancanus	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Pithecia_pithecia	5	4	8	5	5	7	9	8	5	4	4	7	5	1	10
Saimiri_sciureus	14	14	4	5	3	7	9	8	5	4	15	7	4	1	10
Saguinus_fuscicollis	14	14	4	5	3	7	9	8	5	4	15	7	4	1	10
Saguinus_oedipus	14	14	4	5	3	7	9	8	5	4	15	7	4	1	10
Callithrix_jacchus	14	14	4	5	3	7	9	8	5	4	15	7	4	1	10
Aotus_trivirgatus	3	14	4	5	3	7	9	8	5	4	15	7	4	1	10
Ateles_fusciceps	4	3	3	3	2	3	3	3	5	2	3	3	3	3	3
Alouatta_seniculus	4	3	3	3	2	3	3	3	5	2	3	3	3	3	3
Alouatta_caraya	4	3	3	3	2	3	3	3	5	2	3	3	3	3	3
Alouatta_palliata	4	3	3	3	2	3	3	3	5	2	3	3	3	3	3
Pongo_pygmaeus	13	6	5	4	4	6	8	4	4	3	8	6	7	4	9
Pan_troglodytes_troglodytes	6	6	5	4	4	4	8	4	4	3	5	4	7	4	4
Pan_paniscus	6	6	5	4	4	4	8	4	4	3	6	4	7	4	4
Homo_sapiens	6	6	5	4	4	6	8	4	4	3	8	6	7	4	9
Gorilla_gorilla_gorilla	6	5	5	4	4	6	8	4	4	3	8	6	6	4	9
Nomascus_concolor	13	13	7	5	4	6	8	7	4	3	7	6	13	4	5
Symphalangus_syndactylus	13	13	7	5	4	6	8	7	4	3	7	6	13	4	5
Hylobates_lar	7	13	7	5	4	6	8	7	4	3	7	6	13	4	5
Hylobates_klossii	13	13	7	5	4	6	8	7	4	3	7	6	13	4	5
Hylobates_muelleri	13	13	7	5	4	6	8	7	4	3	7	6	13	4	5
Rhinopithecus_roxellana	13	7	7	5	4	6	8	7	4	3	9	6	8	4	9
Pygathrix_nemaeus	13	13	7	5	4	6	8	7	4	3	14	6	13	4	9
Colobus_guereza	13	13	7	5	4	6	8	7	4	3	14	6	13	4	9
Colobus_angolensis	13	13	7	5	4	6	8	7	4	3	14	6	13	4	9
Macaca_thibetana	12	13	7	5	4	6	8	7	4	3	14	6	13	4	9
Macaca_mulatta	12	8	7	5	4	6	8	7	4	3	14	6	13	4	9
Macaca_fascicularis	12	8	7	5	4	6	8	7	4	3	14	6	13	4	9
Macaca_nemestrina	12	13	7	5	4	6	8	7	4	3	14	6	13	4	9
Macaca_fuscata	12	13	7	5	4	6	8	7	4	3	14	6	13	4	9
Macaca_cyclopis	12	13	7	5	4	6	8	7	4	3	14	6	13	4	9
Macaca_arctoides	12	13	7	5	4	6	8	7	4	3	14	6	13	4	9
Papio_ursinus	8	9	7	5	4	6	5	5	4	3	10	6	9	4	6
Papio_cynocephalus	8	9	7	5	4	6	5	5	4	3	10	6	9	4	6
Papio_papio	8	9	7	5	4	6	5	5	4	3	10	6	9	4	6
Papio_hamadryas	8	9	7	5	4	6	5	5	4	3	10	6	9	4	6
Papio_anubis	8	9	7	5	4	6	5	5	4	3	10	6	9	4	6
Theropithecus_gelada	12	10	7	5	4	6	5	7	4	3	11	6	10	4	6
Mandrillus_sphinx	12	13	7	5	4	6	4	7	4	3	14	6	13	4	9
Mandrillus_leucophaeus	12	13	7	5	4	6	4	7	4	3	14	6	13	4	9
Miopithecus_talapoin	10	11	6	5	4	5	6	6	3	3	12	5	11	4	7
Chlorocebus_aethiops	11	12	7	5	4	6	7	7	4	3	13	6	12	4	8
Erythrocebus_patas	11	12	7	5	4	6	7	7	4	3	13	6	12	4	8
Cercopithecus_mitis	9	12	7	5	4	6	7	7	4	3	13	6	12	4	8
Allenopithecus_nigroviridis	11	12	7	5	4	6	7	7	4	3	13	6	12	4	8

Table SIII.4. Female trait averages for the scaled, logged data, and average standard error for each trait.

Genus_species	NR	SCM	SNL	FMW	SSL	SBL	VB	GW	CLML	AMIB	RAH	LIH	AW	HML	HHW
Tupaia_glis	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Galago_senegalensis	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Hapalemur_griseus	2	2	2	2	2	2	2	2	2	1	2	2	2	2	2
Eulemur_fulvus_fulvus	2	2	2	2	2	2	2	2	2	1	2	2	2	2	2
Tarsius_bancanus	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Pithecia_pithecia	6	5	5	5	5	5	7	5	8	4	5	8	7	8	5
Saimiri_sciureus	5	4	4	4	4	4	3	4	8	4	4	8	7	8	4
Saguinus_fuscicollis	5	4	4	4	4	4	3	4	8	4	4	8	7	8	4
Saguinus_oedipus	5	4	4	4	4	4	3	4	8	4	4	8	7	8	4
Callithrix_jacchus	5	4	4	4	4	4	3	4	8	4	4	8	7	8	4
Aotus_trivirgatus	3	4	4	4	4	4	3	4	8	4	4	8	7	8	4
Ateles_fusciceps	4	3	3	3	3	3	7	3	3	2	3	3	3	3	3
Alouatta_seniculus	4	3	3	3	3	3	7	3	3	2	3	3	3	3	3
Alouatta_caraya	4	3	3	3	3	3	7	3	3	2	3	3	3	3	3
Alouatta_palliata	4	3	3	3	3	3	7	3	3	2	3	3	3	3	3
Pongo_pygmaeus	9	6	6	6	9	7	4	6	5	3	7	5	4	5	6
Pan_troglodytes_troglodytes	7	6	6	6	6	6	4	6	5	3	6	4	4	5	6
Pan_paniscus	7	6	6	6	6	6	4	6	5	3	6	4	4	5	6
Homo_sapiens	7	6	6	6	9	7	4	6	5	3	7	5	4	5	6
Gorilla_gorilla_gorilla	7	6	6	6	9	7	4	6	5	3	7	5	4	5	6
Nomascus_concolor	9	9	11	9	8	9	7	11	4	3	13	7	6	4	9
Symphalangus_syndactylus	9	9	11	9	7	9	7	11	4	3	13	7	6	4	9
Hylobates_lar	9	9	11	9	8	9	7	11	4	3	13	7	6	4	9
Hylobates_klossii	9	9	11	9	8	9	7	11	4	3	13	7	6	4	9
Hylobates_muelleri	9	9	11	9	8	9	7	11	4	3	13	7	6	4	9
Rhinopithecus_roxellana	9	9	11	9	14	9	7	11	7	3	13	7	6	7	9
Pygathrix_nemaeus	9	9	11	9	14	9	7	11	7	3	13	7	6	7	9
Colobus_guereza	9	9	11	9	14	9	7	11	7	3	13	7	6	7	9
Colobus_angolensis	9	9	11	9	14	9	7	11	7	3	13	7	6	7	9
Macaca_thibetana	9	9	11	9	14	9	7	11	7	3	13	7	6	7	9
Macaca_mulatta	9	9	11	9	10	9	7	11	7	3	9	7	6	7	9
Macaca_fascicularis	9	9	7	7	10	9	7	7	7	3	8	7	6	7	9
Macaca_nemestrina	9	9	11	9	14	9	7	11	7	3	13	7	6	7	9
Macaca_fuscata	9	9	11	9	14	9	7	11	7	3	13	7	6	7	9
Macaca_cyclopis	9	9	11	9	14	9	7	11	7	3	13	7	6	7	9
Macaca_arctoides	9	9	11	9	14	9	7	11	7	3	13	7	6	7	9
Papio_ursinus	9	9	11	9	14	9	7	11	7	3	13	7	6	7	9
Papio_cynocephalus	9	9	11	9	14	9	7	11	7	3	13	7	6	7	9
Papio_papio	9	9	11	9	14	9	7	11	7	3	13	7	6	7	9
Papio_hamadryas	9	9	11	9	14	9	7	11	7	3	13	7	6	7	9
Papio_anubis	9	9	11	9	14	9	7	11	7	3	13	7	6	7	9
Theropithecus_gelada	9	9	11	9	14	9	7	11	7	3	13	7	6	7	9
Mandrillus_sphinx	9	9	11	9	14	9	7	11	7	3	13	7	6	7	9
Mandrillus_leucophaeus	9	7	8	9	11	9	5	8	7	3	10	7	6	7	7
Miopithecus_talapoin	8	8	9	8	12	8	6	9	6	3	11	6	5	6	8
Chlorocebus_aethiops	9	9	10	9	13	9	7	10	7	3	12	7	6	7	9
Erythrocebus_patas	9	9	10	9	13	9	7	10	7	3	12	7	6	7	9
Cercopithecus_mitis	9	9	10	9	13	9	7	10	7	3	12	7	6	7	9
Allenopithecus_nigroviridis	9	9	10	9	13	9	7	10	7	3	12	7	6	7	9

Table SIII.5. Full phylogenetic tree used in this study. The tree is comprised of 49 species, 48 nodes, and 96 edges. Tip labels, Edges, and Edge Lengths are listed below.

Tip Labels		Edges			Edge Length	Edges			Edge Length
Tip Number	*Genus_species*	*Edge Number*				*Edge Number*			
1	*Tupaia_glis*	*1*	50	1	82	*49*	76	12	3.714679
2	*Allenopithecus_nigroviridis*	*2*	50	51	9	*50*	75	77	4.960574
3	*Alouatta_caraya*	*3*	51	52	4.162986	*51*	77	42	10.474584
4	*Alouatta_palliata*	*4*	52	53	22.028211	*52*	77	43	10.474584
5	*Alouatta_seniculus*	*5*	53	54	16.811821	*53*	54	78	10.394055
6	*Aotus_trivirgatus*	*6*	54	55	8.589626	*54*	78	79	12.258047
7	*Ateles_fusciceps*	*7*	55	56	6.535196	*55*	79	80	0.749537
8	*Callithrix_jacchus*	*8*	56	57	2.980276	*56*	80	81	3.069395
9	*Cercopithecus_mitis*	*9*	57	2	11.894902	*57*	81	82	0.21945
10	*Chlorocebus_aethiops*	*10*	57	58	0.401789	*58*	82	21	3.309517
11	*Colobus_angolensis*	*11*	58	59	1.644988	*59*	82	19	3.309516
12	*Colobus_guereza*	*12*	59	9	9.848126	*60*	81	20	3.528966
13	*Erythrocebus_patas*	*13*	59	60	1.220881	*61*	80	47	6.598362
14	*Eulemur_fulvus_fulvus*	*14*	60	13	8.627245	*62*	79	32	7.347898
15	*Galago_senegalensis*	*15*	60	10	8.627244	*63*	78	83	4.473491
16	*Gorilla_gorilla_gorilla*	*16*	58	31	11.493113	*64*	83	84	6.480222
17	*Hapalemur_griseus*	*17*	56	61	2.022653	*65*	84	16	8.652233
18	*Homo_sapiens*	*18*	61	62	1.502062	*66*	84	85	2.476353
19	*Hylobates_klossii*	*19*	62	63	7.935259	*67*	85	18	6.17588
20	*Hylobates_lar*	*20*	63	29	3.415204	*68*	85	86	3.842326
21	*Hylobates_muelleri*	*21*	63	30	3.415204	*69*	86	33	2.333553
22	*Macaca_arctoides*	*22*	62	64	5.5813	*70*	86	34	2.333553
23	*Macaca_cyclopis*	*23*	64	49	5.769164	*71*	83	41	15.132455
24	*Macaca_fascicularis*	*24*	64	65	3.090901	*72*	53	87	24.079043
25	*Macaca_fuscata*	*25*	65	66	0.619816	*73*	87	88	1.411478
26	*Macaca_mulatta*	*26*	66	67	0.34864	*74*	88	89	6.56106
27	*Macaca_nemestrina*	*27*	67	68	0.432578	*75*	89	90	10.872024
28	*Macaca_thibetana*	*28*	68	35	1.277228	*76*	90	4	3.888217
29	*Mandrillus_leucophaeus*	*29*	68	37	1.277228	*77*	90	91	1.001745
30	*Mandrillus_sphinx*	*30*	67	38	1.709806	*78*	91	3	2.886471
31	*Miopithecus_talapoin*	*31*	66	36	2.058446	*79*	91	5	2.886471
32	*Nomascus_concolor*	*32*	65	39	2.678262	*80*	89	7	14.76024
33	*Pan_paniscus*	*33*	61	69	5.97453	*81*	88	92	1.228773
34	*Pan_troglodytes_troglodytes*	*34*	69	70	0.840931	*82*	92	93	0.605006
35	*Papio_anubis*	*35*	70	71	0.000001	*83*	93	6	19.487521
36	*Papio_cynocephalus*	*36*	71	22	6.037065	*84*	93	94	3.775269
37	*Papio_hamadryas*	*37*	71	72	4.311865	*85*	94	8	15.712251
38	*Papio_papio*	*38*	72	23	1.7252	*86*	94	95	3.986111
39	*Papio_ursinus*	*39*	72	25	1.7252	*87*	95	45	11.726142
40	*Pithecia_pithecia*	*40*	70	27	6.037065	*88*	95	44	11.726141
41	*Pongo_pygmaeus*	*41*	69	73	0.356891	*89*	92	46	20.092528
42	*Pygathrix_nemaeus*	*42*	73	74	1.475126	*90*	87	40	22.732779
43	*Rhinopithecus_roxellana*	*43*	74	24	5.045978	*91*	52	48	68.840033
44	*Saguinus_fuscicollis*	*44*	74	26	5.045978	*92*	51	96	10.266465
45	*Saguinus_oedipus*	*45*	73	28	6.521104	*93*	96	97	47.716956
46	*Saimiri_sciureus*	*46*	55	75	5.975217	*94*	97	14	15.019595
47	*Symphalangus_syndactylus*	*47*	75	76	11.720478	*95*	97	17	15.019597
48	*Tarsius_bancanus*	*48*	76	11	3.71468	*96*	96	15	62.736554
49	*Theropithecus_gelada*								

Table SIII.6 a-o. Summary statistics for Bayou model parameters for each trait among males.

a. Nuchal Region (NR) Males

NR							
	Mean	*SD*	*Naïve SE*	*Time-series SE*	*Effective Size*	*HPD95Lower*	*HPD95Upper*
lnL	-20.83469	15.20589	0.057472	1.620578734	88.04073	-4.44E+01	4.93353517
prior	-85.21797	12.83651	0.048517	0.327811994	1533.36092	-1.10E+02	-60.00645
alpha	0.037995	0.027151	0.000103	0.002784675	95.06243	4.65E-06	0.08316288
sig2	0.016661	0.006696	2.53E-05	0.00035252	360.80665	4.49E-03	0.02923692
k	20.5096	4.04727	0.015297	0.104866034	1489.54864	1.30E+01	28
ntheta	21.5096	4.04727	0.015297	0.104866034	1489.54864	1.40E+01	29
root.theta	3.418493	0.793376	0.002999	0.06766661	137.47059	1.67E+00	4.41912651
all theta	1.403809	1.560603	NA	NA	NA	NA	NA

b. Sternocleidomastoid (SCM) Males

SCM							
	Mean	*SD*	*Naïve SE*	*Time-series SE*	*Effective Size*	*HPD95Lower*	*HPD95Upper*
lnL	-17.83246	20.0939	5.91E-02	2.9413628	46.66932	-4.51E+01	13.10439959
prior	-83.28632	12.28375	3.62E-02	0.299322275	1684.16254	-1.08E+02	-59.8850038
alpha	0.055668	0.055541	1.63E-04	0.005129505	117.24209	2.49E-10	0.15646911
sig2	0.017336	0.007412	2.18E-05	0.000373877	392.99905	4.48E-03	0.03092845
k	19.75832	4.044779	1.19E-02	0.113156651	1277.70138	1.20E+01	27
ntheta	20.75832	4.044779	1.19E-02	0.113156651	1277.70138	1.30E+01	28
root.theta	3.330337	0.941695	2.77E-03	0.084550691	124.04685	1.53E+00	4.2957877
all theta	1.431551	1.65084	NA	NA	NA	NA	NA

c. Superior Nuchal Line (SNL) Males

SNL							
	Mean	*SD*	*Naïve SE*	*Time-series SE*	*Effective Size*	*HPD95Lower*	*HPD95Upper*
lnL	-37.13383	12.34654	4.67E-02	1.473663442	70.19305	-5.12E+01	-13.3297829
prior	-86.54304	14.31144	5.41E-02	0.362200409	1561.23793	-1.15E+02	-59.1819347
alpha	0.028284	0.037074	1.40E-04	0.003853048	92.58341	4.59E-07	0.09344876
sig2	0.026514	0.00804	3.04E-05	0.000232851	1192.28548	1.15E-02	0.04213223
k	20.37516	4.407883	1.67E-02	0.114634392	1478.53018	1.10E+01	28
ntheta	21.37516	4.407883	1.67E-02	0.114634392	1478.53018	1.20E+01	29
root.theta	2.988068	0.941517	3.56E-03	0.066756293	198.91681	1.30E+00	4.42083157
all theta	1.360636	1.694603	NA	NA	NA	NA	NA

d. Foramen Magnum Width (FMW) Males

FMW							
	Mean	*SD*	*Naïve SE*	*Time-series SE*	*Effective Size*	*HPD95Lower*	*HPD95Upper*
lnL	-34.00748	14.52898	5.49E-02	2.267069188	41.07154	-4.84E+01	0.3137266
prior	-60.64522	13.68262	5.17E-02	0.398191726	1180.74027	-8.71E+01	-33.6987815
alpha	0.023679	0.031863	1.20E-04	0.003798546	70.36291	1.11E-06	0.09193493
sig2	0.023463	0.007348	2.78E-05	0.000294991	620.49163	8.07E-03	0.0372503
k	12.93104	3.369728	1.27E-02	0.088960496	1434.81323	6.00E+00	19
ntheta	13.93104	3.369728	1.27E-02	0.088960496	1434.81323	7.00E+00	20
root.theta	2.741593	0.884177	3.34E-03	0.05242798	284.41453	1.05E+00	4.11019996
all theta	1.101111	1.789598	NA	NA	NA	NA	NA

e. Scapular Spine Length (SSL) Males

SSL							
	Mean	*SD*	*Naïve SE*	*Time-series SE*	*Effective Size*	*HPD95Lower*	*HPD95Upper*
lnL	-36.53662	3.602126	1.36E-02	1.75E-01	425.3867	-4.19E+01	-27.7514314
prior	-27.43746	11.51793	4.35E-02	2.93E-01	1543.3084	-5.18E+01	-8.40012679
alpha	0.006263	0.007418	2.80E-05	3.62E-04	420.6658	6.08E-07	0.02085526
sig2	0.020039	0.004693	1.77E-05	5.77E-05	6616.0388	1.18E-02	0.02925481
k	5.567627	2.329442	8.80E-03	5.88E-02	1569.9037	2.00E+00	10
ntheta	6.567627	2.329442	8.80E-03	5.88E-02	1569.9037	3.00E+00	11
root.theta	3.72812	0.599417	2.27E-03	1.51E-02	1577.5769	2.50E+00	4.84695801
all theta	2.567287	1.609841	NA	NA	NA	NA	NA

f. Scapular Blade Length (SBL) Males

SBL							
	Mean	*SD*	*Naïve SE*	*Time-series SE*	*Effective Size*	*HPD95Lower*	*HPD95Upper*
lnL	-26.63064	13.33222	5.04E-02	1.587521364	70.52873	-4.11E+01	2.99736785
prior	-58.49399	13.04722	4.93E-02	0.343582157	1442.03195	-8.31E+01	-32.162191
alpha	0.024448	0.03112	1.18E-04	0.003236072	92.4818	8.42E-07	0.08907199
sig2	0.017383	0.00534	2.02E-05	0.000185655	827.28393	6.44E-03	0.02727683
k	13.00129	3.338046	1.26E-02	0.086589337	1486.12689	6.00E+00	19
ntheta	14.00129	3.338046	1.26E-02	0.086589337	1486.12689	7.00E+00	20
root.theta	4.156886	0.726668	2.75E-03	0.04328707	281.80961	2.78E+00	5.32989375
all theta	2.636675	1.543181	NA	NA	NA	NA	NA

g. Vertebral Border (VB) Males

VB							
	Mean	*SD*	*Naïve SE*	*Time-series SE*	*Effective Size*	*HPD95Lower*	*HPD95Upper*
lnL	-26.0012	10.53427	3.98E-02	1.134124597	86.27543	-3.80E+01	-4.00867268
prior	-82.80861	13.33253	5.04E-02	0.322596254	1708.07276	-1.09E+02	-57.3754638
alpha	0.019504	0.021389	8.08E-05	0.002129474	100.8897	1.17E-05	0.06252046
sig2	0.015911	0.00455	1.72E-05	0.000128275	1258.26484	7.28E-03	0.02493326
k	20.8427	4.316246	1.63E-02	0.106611228	1639.10368	1.30E+01	29
ntheta	21.8427	4.316246	1.63E-02	0.106611228	1639.10368	1.40E+01	30
root.theta	3.863048	0.65885	2.49E-03	0.033394704	389.24032	2.67E+00	4.9757194
all theta	2.705144	1.399229	NA	NA	NA	NA	NA

h. Glenoid Width (GW) Males

GW							
	Mean	*SD*	*Naïve SE*	*Time-series SE*	*Effective Size*	*HPD95Lower*	*HPD95Upper*
lnL	-21.47825	14.60396	5.52E-02	1.716377171	72.39618	-3.88E+01	7.59177291
prior	-81.85704	13.04456	4.93E-02	0.346307025	1418.84948	-1.08E+02	-57.473696
alpha	0.032717	0.037252	1.41E-04	0.004047659	84.70282	6.02E-06	0.09658382
sig2	0.015752	0.005094	1.93E-05	0.000188976	726.5082	5.78E-03	0.025685
k	20.35975	4.32657	1.64E-02	0.11883087	1325.65035	1.20E+01	28
ntheta	21.35975	4.32657	1.64E-02	0.11883087	1325.65035	1.30E+01	29
root.theta	2.233482	0.722296	2.73E-03	0.047750181	228.81312	8.71E-01	3.29106116
all theta	0.747734	1.398279	NA	NA	NA	NA	NA

i. Clavicle Maximum Length (CLML) Males

CLML							
	Mean	*SD*	*Naïve SE*	*Time-series SE*	*Effective Size*	*HPD95Lower*	*HPD95Upper*
lnL	-31.2157	11.48719	4.34E-02	1.453337214	62.47333	-4.21E+01	-1.19462895
prior	-57.63409	13.3589	5.05E-02	0.36934026	1308.24256	-8.41E+01	-32.3610698
alpha	0.01714	0.023671	8.95E-05	0.002665503	78.86054	7.47E-07	0.07121904
sig2	0.019115	0.005405	2.04E-05	0.00016335	1094.76476	8.01E-03	0.02963668
k	12.80175	3.377517	1.28E-02	0.092356611	1337.39284	6.00E+00	19
ntheta	13.80175	3.377517	1.28E-02	0.092356611	1337.39284	7.00E+00	20
root.theta	3.636564	0.695497	2.63E-03	0.032737858	451.32565	2.43E+00	4.95887601
all theta	2.385316	1.557588	NA	NA	NA	NA	NA

j. Anterior Margin of Iliac Blade (AMIB) Males

AMIB							
	Mean	*SD*	*Naïve SE*	*Time-series SE*	*Effective Size*	*HPD95Lower*	*HPD95Upper*
lnL	-46.42085	2.36501	8.94E-03	7.84E-02	911.0102	-5.07E+01	-41.1739458
prior	-27.23498	11.2242	4.24E-02	2.71E-01	1716.815	-4.76E+01	-4.93501707
alpha	0.006646	0.006782	2.56E-05	2.39E-04	805.4458	2.06E-06	0.01977123
sig2	0.029388	0.006954	2.63E-05	7.82E-05	7909.632	1.74E-02	0.0430202
k	5.318019	2.2571	8.53E-03	5.47E-02	1702.8392	1.00E+00	9
ntheta	6.318019	2.2571	8.53E-03	5.47E-02	1702.8392	2.00E+00	10
root.theta	3.442948	0.631618	2.39E-03	1.16E-02	2945.4394	2.17E+00	4.63286249
all theta	2.323287	1.709938	NA	NA	NA	NA	NA

k. Retroauricular Height (RAH) Males

RAH							
	Mean	*SD*	*Naïve SE*	*Time-series SE*	*Effective Size*	*HPD95Lower*	*HPD95Upper*
lnL	-11.48821	16.77647	6.34E-02	2.257378639	55.23223	-3.96E+01	14.68055602
prior	-79.92	12.12607	4.58E-02	0.330642404	1345.00133	-1.04E+02	-56.8587447
alpha	0.058557	0.059216	2.24E-04	0.006386878	85.96225	2.63E-05	0.13712546
sig2	0.013475	0.005808	2.20E-05	0.000304597	363.63182	3.48E-03	0.02461247
k	19.28246	4.054312	1.53E-02	0.115103344	1240.67642	1.20E+01	27
ntheta	20.28246	4.054312	1.53E-02	0.115103344	1240.67642	1.30E+01	28
root.theta	3.683458	0.646725	2.44E-03	0.053545016	145.88178	2.21E+00	4.49512532
all theta	1.778916	1.433629	NA	NA	NA	NA	NA

l. Lower Iliac Height (LIH) Males

LIH							
	Mean	*SD*	*Naïve SE*	*Time-series SE*	*Effective Size*	*HPD95Lower*	*HPD95Upper*
lnL	-35.91711	11.82606	4.47E-02	1.652538248	51.21259	-4.70E+01	-4.28134582
prior	-85.05881	13.99306	5.29E-02	0.340611627	1687.74363	-1.12E+02	-57.9823037
alpha	0.019859	0.035207	1.33E-04	0.003179881	122.58606	4.35E-06	0.08791732
sig2	0.022889	0.00681	2.57E-05	0.000198877	1172.54574	9.26E-03	0.03704395
k	20.84766	4.42315	1.67E-02	0.110703105	1596.40739	1.20E+01	29
ntheta	21.84766	4.42315	1.67E-02	0.110703105	1596.40739	1.30E+01	30
root.theta	3.250753	0.71677	2.71E-03	0.031835874	506.90496	1.99E+00	4.62668183
all theta	2.113792	1.524779	NA	NA	NA	NA	NA

m. Acetabulum Width (AW) Males

AW							
	Mean	*SD*	*Naïve SE*	*Time-series SE*	*Effective Size*	*HPD95Lower*	*HPD95Upper*
lnL	-10.15615	20.07404	7.59E-02	3.23587709	38.48446	-3.82E+01	22.24624085
prior	-82.02333	12.31893	4.66E-02	0.379564543	1053.35402	-1.07E+02	-58.8987434
alpha	0.05113	0.042477	1.61E-04	0.005197992	66.77894	6.16E-06	0.122679
sig2	0.012777	0.006076	2.30E-05	0.000410407	219.20692	2.50E-03	0.02335533
k	19.87053	4.067542	1.54E-02	0.131278886	960.00703	1.30E+01	28
ntheta	20.87053	4.067542	1.54E-02	0.131278886	960.00703	1.40E+01	29
root.theta	2.996742	0.745312	2.82E-03	0.06372941	136.77181	1.36E+00	3.88374739
all theta	1.203824	1.47746	NA	NA	NA	NA	NA

n. Humerus Maximum Length (HML) Males

HML							
	Mean	*SD*	*Naïve SE*	*Time-series SE*	*Effective Size*	*HPD95Lower*	*HPD95Upper*
lnL	*-30.6356*	8.726014	3.30E-02	8.27E-01	111.43326	-4.05E+01	-11.1958733
prior	-55.64592	13.18962	4.99E-02	3.36E-01	1539.97992	-8.06E+01	-28.9465751
alpha	0.017456	0.026851	1.01E-04	2.88E-03	87.01083	3.05E-06	0.06617034
sig2	0.018584	0.004737	1.79E-05	8.13E-05	3396.27198	1.02E-02	0.02809401
k	12.60151	3.431233	1.30E-02	8.77E-02	1531.68907	6.00E+00	19
ntheta	13.60151	3.431233	1.30E-02	8.77E-02	1531.68907	7.00E+00	20
root.theta	4.434358	0.603711	2.28E-03	2.47E-02	597.09128	3.26E+00	5.56058102
all theta	3.341411	1.424722	NA	NA	NA	NA	NA

o. Humeral Head Width (HHW) Males

HHW							
	Mean	*SD*	*Naïve SE*	*Time-series SE*	*Effective Size*	*HPD95Lower*	*HPD95Upper*
lnL	-22.34907	11.90703	4.50E-02	1.346504098	78.1973	-3.77E+01	-0.00770815
prior	-82.30176	12.87609	4.87E-02	0.313342438	1688.611	-1.08E+02	-57.4291491
alpha	0.026414	0.026698	1.01E-04	0.002460795	117.7046	9.67E-06	0.075593837
sig2	0.015499	0.004558	1.72E-05	0.000141929	1031.2181	6.68E-03	0.024217222
k	20.69534	4.247795	1.61E-02	0.106454554	1592.2037	1.30E+01	29
ntheta	21.69534	4.247795	1.61E-02	0.106454554	1592.2037	1.40E+01	30
root.theta	2.561134	0.710865	2.69E-03	0.047003715	228.723	1.27E+00	3.680538186
all theta	1.130849	1.373591	NA	NA	NA	NA	NA

Table SIII.7 a-o. Summary statistics for Bayou model parameters for each trait among females.

a. Nuchal Region (NR) Females

NR							
	Mean	*SD*	*Naïve SE*	*Time-series SE*	*Effective Size*	*HPD95Lower*	*HPD95Upper*
lnL	-18.74573	14.15706	5.35E-02	1.548569129	83.5766	-4.19E+01	3.25009733
prior	-61.53024	12.35866	4.67E-02	0.376453703	1077.7534	-8.62E+01	-37.2378668
alpha	0.04006	0.029899	1.13E-04	0.002912951	105.3547	1.50E-06	0.09207735
sig2	0.015934	0.005938	2.24E-05	0.000269436	485.7269	5.27E-03	0.02714765
k	13.39985	3.161894	1.20E-02	0.092064395	1179.5363	7.00E+00	19
ntheta	14.39985	3.161894	1.20E-02	0.092064395	1179.5363	8.00E+00	20
root.theta	3.408579	0.703388	2.66E-03	0.049271035	203.8009	1.85E+00	4.39996559
all theta	1.465113	1.624393	NA	NA	NA	NA	NA

b. Sternocleidomastoid (SCM) Females

SCM							
	Mean	*SD*	*Naïve SE*	*Time-series SE*	*Effective Size*	*HPD95Lower*	*HPD95Upper*
lnL	-19.69691	14.0419	5.31E-02	1.501473868	87.46141	-4.31E+01	2.7273987
prior	-61.28925	12.20912	4.61E-02	0.370881036	1083.67657	-8.57E+01	-37.4849889
alpha	0.047106	0.036854	1.39E-04	0.003490814	111.45639	1.17E-06	0.11286304
sig2	0.017802	0.006324	2.39E-05	0.000239664	696.2386	6.66E-03	0.02982174
k	13.19937	3.116591	1.18E-02	0.089652275	1208.47343	7.00E+00	19
ntheta	14.19937	3.116591	1.18E-02	0.089652275	1208.47343	8.00E+00	20
root.theta	3.513152	0.700522	2.65E-03	0.05517687	161.18699	1.85E+00	4.39351661
all theta	1.45995	1.644165	NA	NA	NA	NA	NA

c. Superior Nuchal Line (SNL) Females

SNL							
	Mean	*SD*	*Naïve SE*	*Time-series SE*	*Effective Size*	*HPD95Lower*	*HPD95Upper*
lnL	-25.10151	16.85448	5.20E-02	1.837853092	84.10256	-4.95E+01	2.81354904
prior	-63.99251	13.01485	4.02E-02	0.348274421	1396.48072	-8.98E+01	-38.5400561
alpha	0.049282	0.04521	1.40E-04	0.003969717	129.70344	1.16E-05	0.12943276
sig2	0.0223	0.008781	2.71E-05	0.000343817	652.32684	6.61E-03	0.03861978
k	13.58655	3.247357	1.00E-02	0.076508145	1801.54339	8.00E+00	20
ntheta	14.58655	3.247357	1.00E-02	0.076508145	1801.54339	9.00E+00	21
root.theta	3.524411	0.84769	2.62E-03	0.055475875	233.48843	1.68E+00	4.55029463
all theta	1.538006	1.748869	NA	NA	NA	NA	NA

d. Foramen Magnum Width (FMW) Females

FMW							
	Mean	*SD*	*Naïve SE*	*Time-series SE*	*Effective Size*	*HPD95Lower*	*HPD95Upper*
lnL	-2.543291	6.279797	1.94E-02	0.244585475	659.2193	-14.56366367	9.88851382
prior	-62.33198	10.2706	3.17E-02	0.244381015	1766.2693	-81.56848983	-41.7282427
alpha	0.064007	0.025518	7.87E-05	0.001333146	366.3759	0.022494699	0.114241
sig2	0.011403	0.004095	1.26E-05	0.000115627	1254.2739	0.005040536	0.01940892
k	13.2052	2.723267	8.40E-03	0.063958791	1812.926	8	18
ntheta	14.2052	2.723267	8.40E-03	0.063958791	1812.926	9	19
root.theta	3.813563	0.203515	6.28E-04	0.004870357	1746.1129	3.433148662	4.19444525
all theta	1.328042	1.703341	NA	NA	NA	NA	NA

e. Scapular Spine Length (SSL) Females

SSL							
	Mean	*SD*	*Naïve SE*	*Time-series SE*	*Effective Size*	*HPD95Lower*	*HPD95Upper*
lnL	3.464501	8.503087	2.62E-02	0.388846006	478.1872	-1.33E+01	20.25592092
prior	-79.66964	11.37129	3.51E-02	0.295381268	1482.0178	-1.02E+02	-57.0543131
alpha	0.06187	0.024348	7.51E-05	0.001318622	340.9418	2.65E-02	0.10846192
sig2	0.008827	0.003964	1.22E-05	0.000158982	621.656	2.73E-03	0.01636083
k	19.13775	3.713078	1.15E-02	0.093297379	1583.9057	1.20E+01	26
ntheta	20.13775	3.713078	1.15E-02	0.093297379	1583.9057	1.30E+01	27
root.theta	4.79128	0.306506	9.46E-04	0.014471363	448.5983	4.41E+00	5.17613764
all theta	2.578031	1.425449	NA	NA	NA	NA	NA

f. Scapular Blade Length (SBL) Females

SBL							
	Mean	*SD*	*Naïve SE*	*Time-series SE*	*Effective Size*	*HPD95Lower*	*HPD95Upper*
lnL	0.8632	10.7179	4.05E-02	0.917301937	136.5195	-3.24E+01	15.95059153
prior	-60.94348	10.81354	4.09E-02	0.333880886	1048.9449	-8.25E+01	-40.3195162
alpha	0.055346	0.023945	9.05E-05	0.001629512	215.9272	3.93E-07	0.09536621
sig2	0.009179	0.003859	1.46E-05	0.000190334	411.132	3.10E-03	0.01709877
k	13.49481	2.913025	1.10E-02	0.086950731	1122.3854	8.00E+00	19
ntheta	14.49481	2.913025	1.10E-02	0.086950731	1122.3854	9.00E+00	20
root.theta	4.859899	0.357804	1.35E-03	0.025608621	195.2175	4.14E+00	5.38383804
all theta	2.698191	1.492248	NA	NA	NA	NA	NA

g. Vertebral Border (VB) Females

VB							
	Mean	*SD*	*Naïve SE*	*Time-series SE*	*Effective Size*	*HPD95Lower*	*HPD95Upper*
lnL	-8.936846	9.970428	3.08E-02	0.726637695	188.2746	-3.46E+01	3.98109664
prior	-57.67888	10.94301	3.38E-02	0.248207231	1943.77	-7.90E+01	-36.6323656
alpha	0.055608	0.032635	1.01E-04	0.001930327	285.8339	7.22E-06	0.11206101
sig2	0.012713	0.004807	1.48E-05	0.000145211	1096.0631	5.02E-03	0.02194273
k	12.63499	2.954874	9.12E-03	0.064133186	2122.8158	7.00E+00	18
ntheta	13.63499	2.954874	9.12E-03	0.064133186	2122.8158	8.00E+00	19
root.theta	4.458667	0.580448	1.79E-03	0.037682269	237.275	2.85E+00	5.24813711
all theta	2.811234	1.45974	NA	NA	NA	NA	NA

h. Glenoid Width (GW) Females

GW							
	Mean	*SD*	*Naïve SE*	*Time-series SE*	*Effective Size*	*HPD95Lower*	*HPD95Upper*
lnL	-0.066793	8.896087	3.36E-02	0.556754728	255.3114	-1.79E+01	18.42910514
prior	-59.60954	10.40044	3.93E-02	0.317052428	1076.0713	-7.93E+01	-38.9666785
alpha	0.057406	0.02589	9.79E-05	0.001530218	286.2627	2.05E-04	0.10366682
sig2	0.009557	0.003645	1.38E-05	0.000131239	771.3649	3.67E-03	0.01672163
k	13.38882	2.86751	1.08E-02	0.077637589	1364.1615	7.00E+00	18
ntheta	14.38882	2.86751	1.08E-02	0.077637589	1364.1615	8.00E+00	19
root.theta	2.823986	0.292545	1.11E-03	0.017234643	288.1248	2.25E+00	3.24663759
all theta	0.841834	1.386709	NA	NA	NA	NA	NA

i. Clavicle Maximum Length (CLML) Females

CLML							
	Mean	*SD*	*Naïve SE*	*Time-series SE*	*Effective Size*	*HPD95Lower*	*HPD95Upper*
lnL	-17.45144	12.85641	4.86E-02	1.310894862	96.18412	-3.69E+01	3.76091434
prior	-58.61522	12.31149	4.65E-02	0.350101843	1236.61005	-8.22E+01	-33.3854667
alpha	0.032688	0.025279	9.55E-05	0.002378568	112.95071	6.99E-06	0.07683651
sig2	0.014095	0.004695	1.77E-05	0.000187405	627.66289	5.67E-03	0.02320506
k	13.04053	3.17252	1.20E-02	0.086460977	1346.38278	7.00E+00	19
ntheta	14.04053	3.17252	1.20E-02	0.086460977	1346.38278	8.00E+00	20
root.theta	4.061069	0.636889	2.41E-03	0.044813918	201.97697	2.73E+00	5.00140376
all theta	2.361036	1.506585	NA	NA	NA	NA	NA

j. Anterior Margin of Iliac Blade (AMIB) Females

AMIB							
	Mean	*SD*	*Naïve SE*	*Time-series SE*	*Effective Size*	*HPD95Lower*	*HPD95Upper*
lnL	-44.52115	2.768764	1.05E-02	1.16E-01	568.2548	-4.94E+01	-38.0593243
prior	-26.96804	11.00927	4.16E-02	2.65E-01	1730.1323	-5.11E+01	-8.80515523
alpha	0.007352	0.008099	3.06E-05	3.34E-04	587.0008	3.01E-06	0.02293401
sig2	0.028216	0.006551	2.48E-05	7.84E-05	6986.837	1.70E-02	0.04119839
k	5.34249	2.235547	8.45E-03	5.32E-02	1764.9459	1.00E+00	9
ntheta	6.34249	2.235547	8.45E-03	5.32E-02	1764.9459	2.00E+00	10
root.theta	3.448243	0.614486	2.32E-03	1.14E-02	2901.6568	2.27E+00	4.677309
all theta	2.372524	1.614071	NA	NA	NA	NA	NA

k. Retroauricular Height (RAH) Females

RAH							
	Mean	*SD*	*Naïve SE*	*Time-series SE*	*Effective Size*	*HPD95Lower*	*HPD95Upper*
lnL	11.11515	10.84436	4.10E-02	0.834495086	168.8732	-7.259915093	31.98117092
prior	-63.65945	9.783739	3.70E-02	0.338223616	836.7619	-82.44623593	-44.0247057
alpha	0.082668	0.040639	1.54E-04	0.003232241	158.0839	0.018928146	0.16679029
sig2	0.007707	0.004441	1.68E-05	0.000266449	277.8053	0.001639023	0.01639501
k	14.33139	2.695958	1.02E-02	0.093129855	838.0082	9	19
ntheta	15.33139	2.695958	1.02E-02	0.093129855	838.0082	10	20
root.theta	3.995762	0.197333	7.46E-04	0.01090646	327.3633	3.68860963	4.31921594
all theta	2.045955	1.361801	NA	NA	NA	NA	NA

l. Lower Iliac Height (LIH) Females

LIH							
	Mean	*SD*	*Naïve SE*	*Time-series SE*	*Effective Size*	*HPD95Lower*	*HPD95Upper*
lnL	-21.26771	13.59439	5.14E-02	1.837490774	54.73553	-3.87E+01	0.78468985
prior	-58.97907	12.7204	4.81E-02	0.368950644	1188.68006	-8.33E+01	-33.2383248
alpha	0.031772	0.031612	1.19E-04	0.003181195	98.74411	8.14E-06	0.08676653
sig2	0.015825	0.005194	1.96E-05	0.00020256	657.42733	6.33E-03	0.02562355
k	13.10458	3.248707	1.23E-02	0.089183729	1326.93556	7.00E+00	19
ntheta	14.10458	3.248707	1.23E-02	0.089183729	1326.93556	8.00E+00	20
root.theta	3.753843	0.701248	2.65E-03	0.049727409	198.86182	2.43E+00	4.84304172
all theta	2.240588	1.519231	NA	NA	NA	NA	NA

m. Acetabulum Width (AW) Females

AW							
	Mean	*SD*	*Naïve SE*	*Time-series SE*	*Effective Size*	*HPD95Lower*	*HPD95Upper*
lnL	-3.884705	11.91449	4.50E-02	1.161642844	105.1976	-3.14E+01	11.88426428
prior	-58.45935	10.92696	4.13E-02	0.33309962	1076.0943	-8.03E+01	-38.0495084
alpha	0.053066	0.030974	1.17E-04	0.002468446	157.4566	1.64E-05	0.10655949
sig2	0.010553	0.00397	1.50E-05	0.000168836	552.9913	4.06E-03	0.01838774
k	13.06757	2.93892	1.11E-02	0.085816988	1172.814	7.00E+00	18
ntheta	14.06757	2.93892	1.11E-02	0.085816988	1172.814	8.00E+00	19
root.theta	3.246329	0.440645	1.67E-03	0.030648003	206.7155	2.20E+00	3.82837097
all theta	1.317582	1.411936	NA	NA	NA	NA	NA

n. Humerus Maximum Length (HML) Females

HML							
	Mean	*SD*	*Naïve SE*	*Time-series SE*	*Effective Size*	*HPD95Lower*	*HPD95Upper*
lnL	-9.422361	12.21231	4.62E-02	1.200432183	103.4953	-3.27E+01	7.21127541
prior	-58.07015	11.22553	4.24E-02	0.297598367	1422.8286	-7.98E+01	-35.5800542
alpha	0.044723	0.029513	1.12E-04	0.002370199	155.0465	1.32E-05	0.09395669
sig2	0.011972	0.004218	1.59E-05	0.000169686	618.0123	4.96E-03	0.02007228
k	13.16315	3.011275	1.14E-02	0.078700682	1464.0097	8.00E+00	19
ntheta	14.16315	3.011275	1.14E-02	0.078700682	1464.0097	9.00E+00	20
root.theta	4.973547	0.476	1.80E-03	0.032680581	212.1461	3.92E+00	5.72359768
all theta	3.382801	1.36303	NA	NA	NA	NA	NA

o. Humeral Head Width (HHW) Females

HHW							
	Mean	*SD*	*Naïve SE*	*Time-series SE*	*Effective Size*	*HPD95Lower*	*HPD95Upper*
lnL	-4.801672	13.20946	4.99E-02	1.35971653	94.37861	-3.32E+01	12.95377645
prior	-59.13921	11.50195	4.35E-02	0.357031849	1037.83714	-8.23E+01	-36.7723593
alpha	0.058081	0.039161	1.48E-04	0.003255744	144.68257	4.05E-05	0.12437328
sig2	0.011409	0.004521	1.71E-05	0.000191803	555.61772	4.10E-03	0.02000286
k	13.28929	3.113053	1.18E-02	0.093631213	1105.43113	7.00E+00	19
ntheta	14.28929	3.113053	1.18E-02	0.093631213	1105.43113	8.00E+00	20
root.theta	3.043521	0.471873	1.78E-03	0.034567403	186.3448	1.87E+00	3.64388602
all theta	1.250571	1.378801	NA	NA	NA	NA	NA

Table SIII.8 a-o. Model fit results for males. Log likelihood, AIC, and AICc for both Brownian Motion (BMS) and Ornstein-Uhlenbeck (OUMVA) processes for each trait. Lower AIC score indicates better model fit.

a. Males NR

Models	NR					
	BMS			OUMVA		
	lnL	AIC	AICc	lnL	AIC	AICc
Mammal	-38.92398	81.84797	82.10884	-38.92398	83.84797	84.3813
PvO	-35.57349	79.14698	80.05607	-34.72713	81.45426	83.45426
MAPO	-33.70408	83.40817	87.00817	-32.25926	88.51851	97.18518
MALLTO	-21.52454	67.04909	75.71576	-20.25871	76.51741	99.31741
Parv.Order	-20.19127	64.38253	73.0492	-19.71526	75.43053	98.23053
ANOPO	-32.34441	84.68881	90.47829	-30.35974	90.71947	105.2649
Family	-20.93691	85.87383	124.7969	3.759626	58.48075	208.0807
Habitat	-29.40894	66.81789	67.72698	-27.27949	64.55898	65.95433
Locomotion	-30.2989	76.59781	80.19781	-21.24238	60.48476	65.10015
Diet	-27.1885	68.377	71.10871	-23.58746	63.17492	66.77492
Bayou	~	~	~	27.33728	-6.674556	14.74211

b. Males SCM

Models	SCM					
	BMS			OUMVA		
	lnL	AIC	AICc	lnL	AIC	AICc
Mammal	-40.39429	84.78859	85.04946	-40.39429	86.78859	87.32192
PvO	-36.89494	81.78987	82.69897	-36.57406	85.14812	87.14812
MAPO	-35.57342	87.14684	90.74684	-34.09946	92.19892	100.8656
MALLTO	-26.13891	76.27781	84.94448	-24.173	84.34599	107.146
Parv.Order	-25.50241	75.00482	83.67149	-23.78968	83.57935	106.3794
ANOPO	-34.3301	88.6602	94.44968	-32.77576	95.55151	110.097
Family	-25.90377	95.80755	134.7306	-17.05638	100.1128	249.7128
Habitat	-29.96196	67.92392	68.83301	-29.0764	68.15279	69.54814
Locomotion	-28.61987	73.23973	76.83973	-20.58503	59.17006	63.78544
Diet	-29.19291	72.38583	75.11753	-26.4857	68.9714	72.5714
Bayou	~	~	~	32.95535	-19.9107	24.2493

c. Males SNL

Models	SNL					
	BMS			OUMVA		
	lnL	AIC	AICc	lnL	AIC	AICc
Mammal	-45.71691	95.43383	95.6947	-45.71691	97.43383	97.96716
PvO	-42.50391	93.00783	93.91692	-42.18712	96.37424	98.37424
MAPO	-41.36978	98.73957	102.3396	-39.72298	103.446	112.1126
MALLTO	-33.5182	91.03641	99.70307	-31.44757	98.89515	121.6951
Parv.Order	-32.67923	89.35847	98.02514	-31.147	98.29401	121.094
ANOPO	-40.84545	101.6909	107.4804	38.65641	107.3128	121.8583
Family	-31.07252	106.145	145.0681	-10.41595	86.83189	236.4319
Habitat	-38.19394	84.38789	85.29698	-37.70788	85.41577	86.81112
Locomotion	-38.93274	93.86547	97.46547	-30.91717	79.83434	84.44973
Diet	-34.87571	83.75141	86.48312	-32.38162	80.76325	84.36325
Bayou	~	~	~	11.79239	24.41523	74.41523

d. Males FMW

Models	FMW					
	BMS			OUMVA		
	lnL	AIC	AICc	lnL	AIC	AICc
Mammal	-42.48456	88.96912	89.22999	-42.48456	90.96912	91.50246
PvO	-38.40385	84.80769	85.71678	-38.00733	88.01466	90.01466
MAPO	-36.62378	89.24756	92.84756	-34.9472	93.89439	102.5611
MALLTO	-27.374	78.74801	87.41468	-25.32246	86.64493	109.4449
Parv.Order	-26.99847	77.99694	86.66361	-25.25904	86.51809	109.3181
ANOPO	-35.91405	91.82809	97.61757	-33.65253	97.30505	111.8505
Family	-24.01655	92.0331	130.9562	-13.18462	92.36924	241.9692
Habitat	-32.76963	73.53925	74.44834	-31.95041	73.90082	75.29617
Locomotion	-31.91027	79.82054	83.42054	-20.55625	59.11249	63.72788
Diet	-30.09057	74.18115	76.91285	-25.26143	66.52285	70.12285
Bayou	~	~	~	16.70392	-1.407841	15.59216

e. Males SSL

Models	SSL					
	BMS			OUMVA		
	lnL	AIC	AICc	lnL	AIC	AICc
Mammal	-36.47342	76.94685	77.20771	-36.47342	78.94685	79.48018
PvO	-32.97888	73.95775	74.86685	-32.75681	77.51362	79.51362
MAPO	-30.61136	77.22272	80.82272	-28.81613	81.63225	90.29892
MALLTO	-21.84163	67.68327	76.34993	-19.70313	75.40625	98.20625
Parv.Order	-22.49712	68.99424	77.6609	-20.40867	76.81734	99.61734
ANOPO	-29.67552	79.35104	85.14051	-28.28551	86.57103	101.1165
Family	-20.70176	85.40352	124.3266	-9.506877	85.01375	234.6138
Habitat	-28.6656	65.3312	66.24029	-25.17585	60.3517	61.74705
Locomotion	-27.64715	71.29431	74.89431	-16.04793	50.09587	54.71125
Diet	-24.70643	63.41286	66.14457	-20.59799	57.19598	60.79598
Bayou	~	~	~	-2.715909	23.43182	28.0472

f. Males SBL

Models	SBL					
	BMS			OUMVA		
	lnL	AIC	AICc	lnL	AIC	AICc
Mammal	-35.05621	74.11242	74.37329	-35.05621	76.11242	76.64575
PvO	-31.5974	71.1948	72.10389	-31.25617	74.51235	76.51235
MAPO	-29.18131	74.36262	77.96262	-27.64939	79.29878	87.96544
MALLTO	-20.3153	64.63059	73.29726	-18.5521	73.10419	95.90419
Parv.Order	-20.7359	65.4718	74.13846	-18.88589	73.77178	96.57178
ANOPO	-20.7359	65.4718	74.13846	-18.88589	73.77178	96.57178
Family	-20.3153	64.63059	73.29726	-18.5521	73.10419	95.90419
Habitat	-29.18131	74.36262	77.96262	-27.64939	79.29878	87.96544
Locomotion	-31.5974	71.1948	72.10389	-31.25617	74.51235	76.51235
Diet	-35.05621	74.11242	74.37329	-35.05621	76.11242	76.64575
Bayou	~	~	~	19.21177	-6.423549	10.57645

g. Males VB

Models	VB					
	BMS			OUMVA		
	lnL	AIC	AICc	lnL	AIC	AICc
Mammal	-32.57515	69.15031	69.41118	-32.57515	71.15031	71.68364
PvO	-29.33188	66.66377	67.57286	-29.26311	70.52623	72.52623
MAPO	-28.01974	72.03948	75.63948	-25.99939	75.99877	84.66544
MALLTO	-18.09101	60.18202	68.84869	-16.32696	68.65392	91.45392
Parv.Order	-17.76836	59.53671	68.20338	-16.11138	68.22276	91.02276
ANOPO	-17.76836	59.53671	68.20338	-16.11138	68.22276	91.02276
Family	-18.09101	60.18202	68.84869	-16.32696	68.65392	91.45392
Habitat	-28.01974	72.03948	75.63948	-25.99939	75.99877	84.66544
Locomotion	-29.33188	66.66377	67.57286	-29.26311	70.52623	72.52623
Diet	-32.57515	69.15031	69.41118	-32.57515	71.15031	71.68364
Bayou	~	~	~	22.69679	2.606411	52.60641

h. Males GW

Models	GW					
	BMS			OUMVA		
	lnL	AIC	AICc	lnL	AIC	AICc
Mammal	-33.25128	70.50255	70.76342	-33.25128	72.50255	73.03589
PvO	-29.78487	67.56973	68.47882	-29.47955	70.95909	72.95909
MAPO	-28.03262	72.06525	75.66525	-26.61494	77.22988	85.89654
MALLTO	-19.23605	62.47211	71.13878	-17.41326	70.82652	93.62652
Parv.Order	-19.17635	62.35271	71.01937	-17.41164	70.82328	93.62328
ANOPO	-27.20446	74.40892	80.1984	-25.37794	80.75588	95.30133
Family	-16.40743	76.81485	115.7379	-3.749597	73.49919	223.0992
Habitat	-24.30608	56.61216	57.52125	-23.06787	56.13575	57.5311
Locomotion	-24.47421	64.94843	68.54843	-14.73756	47.47512	52.09051
Diet	-21.65186	57.30371	60.03542	-18.24554	52.49107	56.09107
Bayou	~	~	~	33.51205	-19.02409	30.97591

i. Males CLML

Models	CLML					
	BMS			OUMVA		
	lnL	AIC	AICc	lnL	AIC	AICc
Mammal	-36.1534	76.30681	76.56768	-36.1534	78.30681	78.84014
PvO	-32.58181	73.16363	74.07272	-32.1707	76.34141	78.34141
MAPO	-30.13247	76.26493	79.86493	-29.25723	82.51446	91.18113
MALLTO	-20.91261	65.82523	74.49189	-19.64316	75.28631	98.08631
Parv.Order	-21.17868	66.35736	75.02403	-19.86208	75.72417	98.52417
ANOPO	-28.75454	77.50908	83.29855	-27.92297	85.84594	100.3914
Family	-18.25472	80.50944	119.4325	3.206032	59.58794	209.1879
Habitat	-27.68211	63.36422	64.27331	-26.75433	63.50865	64.904
Locomotion	-26.75647	69.51294	73.11294	-15.60672	49.21344	53.82883
Diet	-25.40747	64.81494	67.54664	-21.69446	59.38891	62.98891
Bayou	~	~	~	15.66825	0.6634967	17.6635

j. Males AMIB

Models	AMIB					
	BMS			OUMVA		
	lnL	AIC	AICc	lnL	AIC	AICc
Mammal	-46.02897	96.05793	96.3188	-46.02897	98.05793	98.59126
PvO	-43.00387	94.00774	94.91683	-42.73438	97.46876	99.46876
MAPO	-39.79149	95.58297	99.18297	-38.83642	101.6728	110.3395
MALLTO	-32.31439	88.62878	97.29544	-30.83612	97.67225	120.4722
Parv.Order	-32.69871	89.39741	98.06408	-31.23134	98.46268	121.2627
ANOPO	-39.07131	98.14263	103.9321	-38.00591	106.0118	120.5573
Family	-32.7449	109.4898	148.4129	-18.44101	102.882	252.482
Habitat	-39.65066	87.30133	88.21042	-33.56631	77.13263	78.52798
Locomotion	-35.64235	87.28471	90.88471	-24.10612	66.21224	70.82763
Diet	-33.653	81.306	84.0377	-34.4914	84.98279	88.58279
Bayou	~	~	~	-26.03628	70.07256	74.68794

k. Males RAH

Models	RAH					
	BMS			OUMVA		
	lnL	AIC	AICc	lnL	AIC	AICc
Mammal	-34.61229	73.22457	73.48544	-34.61229	75.22457	75.75791
PvO	-31.51408	71.02816	71.93725	-31.14508	74.29016	76.29016
MAPO	-29.47976	74.95951	78.55951	-27.80218	79.60436	88.27103
MALLTO	-21.81339	67.62678	76.29344	-19.75662	75.51323	98.31323
Parv.Order	-21.77692	67.55385	76.22051	-20.09032	76.18064	98.98064
ANOPO	28.51176	77.02352	82.81299	-26.27789	82.55579	97.10124
Family	-15.15378	74.30755	113.2306	-7.354042	80.70808	230.3081
Habitat	-18.85196	45.70391	46.613	61.50052	-113.001	-111.6057
Locomotion	-23.17557	62.35114	65.95114	-15.55968	49.11936	53.73475
Diet	-21.32364	56.64729	59.379	-17.71983	51.43967	55.03967
Bayou	~	~	~	35.15543	-24.31086	19.84914

l. Males LIH

Models	LIH					
	BMS			OUMVA		
	lnL	AIC	AICc	lnL	AIC	AICc
Mammal	-40.66477	85.32953	85.5904	-40.66477	87.32953	87.86286
PvO	-37.7908	83.58159	84.49068	-37.33684	86.67367	88.67367
MAPO	-34.62466	85.24933	88.84933	-33.78694	91.57387	100.2405
MALLTO	-26.96835	77.93671	86.60337	-25.51328	87.02655	109.8266
Parv.Order	26.95982	77.91965	86.58631	56.49249	-76.98497	-54.18497
ANOPO	-33.47282	86.94564	92.73512	-31.9832	93.9664	108.5119
Family	-24.5524	93.1048	132.0279	-11.40593	88.81186	238.4119
Habitat	-32.16324	72.32649	73.23558	-30.71854	71.43708	72.83243
Locomotion	-27.63889	71.27778	74.87778	-21.83868	61.67737	66.29275
Diet	-29.88126	73.76253	76.49423	-27.71504	71.43009	75.03009
Bayou	~	~	~	24.51146	0.9770808	57.49882

m. Males AW

Models	AW					
	BMS			OUMVA		
	lnL	AIC	AICc	lnL	AIC	AICc
Mammal	-33.4326	70.8652	71.12606	-33.4326	72.8652	73.39853
PvO	-30.21201	68.42401	69.3331	-29.7366	71.4732	73.4732
MAPO	-28.33008	72.66015	76.26015	-27.0009	78.0018	86.66847
MALLTO	-19.36862	62.73723	71.4039	-17.54139	71.08277	93.88277
Parv.Order	-18.83041	61.66082	70.32748	-17.28831	70.57661	93.37661
ANOPO	-27.24432	74.48863	80.2781	-25.28371	80.56743	95.11288
Family	-15.0551	74.1102	113.0333	-7.453492	80.90698	230.507
Habitat	-23.82161	55.64322	56.55231	-22.02832	54.05664	55.45199
Locomotion	-21.72337	9.44675	63.04675	-13.43289	44.86578	49.48117
Diet	-21.59492	57.18984	59.92155	-18.15281	52.30563	55.90563
Bayou	~	~	~	37.82733	-29.65466	14.50534

n. Males HML

Models	HML					
	BMS			OUMVA		
	lnL	AIC	AICc	lnL	AIC	AICc
Mammal	-34.429	72.858	73.11887	-34.429	74.858	75.39134
PvO	-30.72989	69.45978	70.36887	-30.4047	72.80939	74.80939
MAPO	-28.26377	72.52755	76.12755	-27.33348	78.66696	87.33363
MALLTO	-18.73694	61.47387	70.14054	-17.39222	70.78443	93.58443
Parv.Order	-18.96952	61.93903	70.6057	-17.55363	71.10727	93.90727
ANOPO	-27.3265	74.653	80.44248	-26.01514	82.03028	96.57574
Family	-16.83093	77.66185	116.5849	-11.28723	88.57445	238.1745
Habitat	-26.07913	60.15825	61.06734	-24.58309	59.16618	60.56153
Locomotion	-25.67448	67.34895	70.94895	-19.31574	56.63148	61.24686
Diet	-23.52202	61.04404	63.77574	-22.58592	61.17184	64.77184
Bayou	~	~	~	14.64514	2.709715	19.70971

o. Males HHW

Models	HHW					
	BMS			OUMVA		
	lnL	AIC	AICc	lnL	AIC	AICc
Mammal	-32.03919	68.07839	68.33926	-32.03919	70.07839	70.61172
PvO	-27.99652	63.99303	64.90212	-27.59877	67.19754	69.19754
MAPO	-26.46868	68.93736	72.53736	-25.89723	75.79445	84.46112
MALLTO	-16.34102	56.68203	65.3487	-14.65509	65.31017	88.11017
Parv.Order	-15.79317	55.58633	64.253	-14.28612	64.57224	87.37224
ANOPO	-31.9832	93.9664	108.5119	-24.9803	79.96061	94.50606
Family	-15.65374	75.30749	114.2306	-2.51604	71.03208	220.6321
Habitat	-22.51341	53.02683	53.93592	-21.68674	53.37349	54.76884
Locomotion	-24.81131	65.62263	69.22263	-15.24847	48.49693	53.11232
Diet	-19.79103	53.58206	56.31377	-16.85944	49.71887	53.31887
Bayou	~	~	~	26.21704	-4.43408	45.56592

Table SIII.9 a-o. Model fit results for females. Log likelihood, AIC, and AICc for both Brownian Motion (BMS) and Ornstein-Uhlenbeck (OUMVA) processes for each trait. Lower AIC score indicates better model fit.

a. Females NR

Models	NR					
	BMS			OUMVA		
	lnL	AIC	AICc	lnL	AIC	AICc
Mammal	-37.39281	78.78563	79.0465	-37.39281	80.78563	81.31896
PvO	-33.87783	75.75566	76.66475	-33.06462	78.12924	80.12924
MAPO	-31.82709	79.65418	83.25418	-30.76874	85.53747	94.20414
MALLTO	-21.29532	66.59063	75.2573	-19.76604	75.53209	98.33209
Parv.Order	-19.53606	63.07213	71.7388	-18.4404	72.88079	95.68079
ANOPO	-29.39232	78.78465	84.57412	-27.80743	85.61486	100.1603
Family	-16.79727	77.59455	116.5176	5.304877	55.39025	204.9902
Habitat	-29.40894	66.81789	67.72698	-27.27949	64.55898	65.95433
Locomotion	-2.07448	92.14896	1082.149	78.86639	-25.73277	-517.0661
Diet	-7.417806	90.83561	387.2356	78.86586	-43.73172	-778.3984
Bayou	~	~	~	24.6448	-15.2896	4.452332

b. Females SCM

Models	SCM					
	BMS			OUMVA		
	lnL	AIC	AICc	lnL	AIC	AICc
Mammal	-38.75184	81.50368	81.76455	-38.75183	83.50367	84.037
PvO	-34.95114	77.90228	78.81137	-34.70143	81.40285	83.40285
MAPO	-33.79845	83.5969	87.1969	-32.04099	88.08199	96.74865
MALLTO	-24.11704	72.23408	80.90074	-21.86165	79.7233	102.5233
Parv.Order	-23.1079	70.21579	78.88246	-21.11015	78.22029	101.0203
ANOPO	-32.35506	84.71012	90.4996	-30.20482	90.40965	104.9551
Family	-21.64168	87.28335	126.2064	4.649144	56.70171	206.3017
Habitat	-29.96196	67.92392	68.83301	-29.1404	68.2808	69.67615
Locomotion	-28.61987	73.23973	76.83973	-21.41599	60.83197	65.44736
Diet	-29.19291	72.38583	75.11753	-18.22289	52.44578	56.04578
Bayou	~	~	~	20.09163	-6.183265	13.55867

c. Females SNL

Models	SNL					
	BMS			OUMVA		
	lnL	AIC	AICc	lnL	AIC	AICc
Mammal	44.6865	93.373	93.63387	-44.6865	95.373	95.90633
PvO	-40.99089	89.98177	90.89087	-40.54743	93.09486	95.09486
MAPO	-39.15405	94.30811	97.90811	-37.45313	98.90626	107.5729
MALLTO	-29.89159	83.78319	92.44985	-27.71061	91.42123	114.2212
Parv.Order	-29.44476	82.88952	91.55619	-28.11393	92.22786	115.0279
ANOPO	-38.76175	97.5235	103.313	-36.45178	102.9036	117.449
Family	-21.68562	87.37124	126.2943	-2.136725	70.27345	219.8734
Habitat	-38.19394	84.38789	85.29698	-37.02982	84.05964	85.45498
Locomotion	-38.93274	93.86547	97.46547	-25.66678	69.33356	73.94895
Diet	-34.87571	83.75141	86.48312	-25.63166	67.26332	70.86332
Bayou	~	~	~	32.53103	-31.06206	-11.32013

d. Females FMW

Models	FMW					
	BMS			OUMVA		
	lnL	AIC	AICc	lnL	AIC	AICc
Mammal	-36.9106	77.82119	78.08206	-36.9106	79.82119	80.35453
PvO	-32.34144	72.68288	73.59197	-31.79483	75.58967	77.58967
MAPO	-30.67819	77.35638	80.95638	-28.54118	81.08235	89.74902
MALLTO	-20.34554	64.69109	73.35775	-17.80445	71.6089	94.4089
Parv.Order	-19.24841	62.49683	71.16349	-17.41859	70.83717	93.63717
ANOPO	-29.53276	79.06553	84.855	-26.70564	83.41128	97.95673
Family	-14.52866	73.05731	111.9804	-1.163123	68.32625	217.9262
Habitat	-32.76963	73.53925	74.44834	-22.83604	55.67209	57.06744
Locomotion	-31.91027	79.82054	83.42054	-14.32889	46.65777	51.27316
Diet	-30.09057	74.18115	76.91285	-12.14406	40.28812	43.88812
Bayou	~	~	~	22.20791	-10.41581	9.326124

e. Females SSL

Models	SSL					
	BMS			OUMVA		
	lnL	AIC	AICc	lnL	AIC	AICc
Mammal	-33.70138	71.40275	71.66362	-33.70138	73.40275	73.93609
PvO	-29.76511	67.53021	68.4393	-29.61838	71.23675	73.23675
MAPO	-27.32841	70.65683	74.25683	-25.19618	74.39235	83.05902
MALLTO	-17.65154	59.30309	67.96976	-15.08633	66.17266	88.97266
Parv.Order	-18.32431	60.64863	69.3153	-15.6805	67.36099	90.16099
ANOPO	-25.23388	70.46776	76.25724	-22.755	75.51	90.05546
Family	-15.40817	74.81635	113.7394	-9.048268	84.09654	233.6965
Habitat	-28.6656	65.3312	66.24029	-19.09242	48.18484	49.58018
Locomotion	-27.64715	71.29431	74.89431	-12.78109	43.56218	48.17756
Diet	-24.70643	63.41286	66.14457	-11.70551	39.41103	43.01103
Bayou	~	~	~	41.69704	-37.39409	6.765913

f. Females SBL

Models	SBL					
	BMS			OUMVA		
	lnL	AIC	AICc	lnL	AIC	AICc
Mammal	-30.48297	64.96594	65.22681	-30.48297	66.96594	67.49927
PvO	-26.449	60.898	61.80709	-25.97801	63.95601	65.95601
MAPO	-24.02124	64.04248	67.64248	-22.36711	68.73421	77.40088
MALLTO	-14.03216	52.06432	60.73099	-12.03099	60.06198	82.86198
Parv.Order	-13.87647	51.75294	60.41961	-11.96498	59.92996	82.72996
ANOPO	-22.1137	64.2274	70.01688	-20.00264	70.00528	84.55074
Family	-9.866023	74.81635	113.7394	-9.048268	84.09654	233.6965
Habitat	-27.30237	62.60473	63.51382	-14.60124	39.20249	40.59783
Locomotion	-21.6563	59.31259	62.91259	-5.040776	28.08155	32.69694
Diet	-23.8384	61.67681	64.40852	-10.16592	36.33184	39.93184
Bayou	~	~	~	32.43276	-30.86552	-11.12358

g. Females VB

Models	VB					
	BMS			OUMVA		
	lnL	AIC	AICc	lnL	AIC	AICc
Mammal	-32.61706	69.23412	69.49499	-32.61706	71.23412	71.76746
PvO	-29.09913	66.19825	67.10734	-29.07226	70.14452	72.14452
MAPO	-28.125	72.25	75.85	-25.69588	75.39175	84.05842
MALLTO	-19.11803	62.23607	70.90274	-16.20867	68.41733	91.21733
Parv.Order	-17.99531	59.99061	68.65728	-15.86544	67.73087	90.53087
ANOPO	-26.89289	73.78578	79.57525	-24.47252	78.94503	93.49049
Family	-13.46875	70.9375	109.8606	7.95048	50.09904	199.699
Habitat	-23.64838	55.29676	56.20585	-24.04816	58.09631	59.49166
Locomotion	-24.62732	65.25464	68.85464	-13.66192	45.32384	49.93922
Diet	-21.70023	57.40046	60.13216	-12.94854	41.89707	45.49707
Bayou	~	~	~	19.73281	-7.465628	9.534372

h. Females GW

Models	GW					
	BMS			OUMVA		
	lnL	AIC	AICc	lnL	AIC	AICc
Mammal	-28.54668	61.09336	61.35423	-28.54668	63.09336	63.62669
PvO	-24.63637	57.27274	58.18183	-24.2875	60.575	62.575
MAPO	-23.14579	62.29157	65.89157	-21.42162	66.84323	75.5099
MALLTO	-13.74141	51.48282	60.14949	-11.54261	59.08521	81.88521
Parv.Order	-12.86693	49.73386	58.40053	-10.85346	57.70693	80.50693
ANOPO	-21.962	63.92401	69.71348	-19.80239	69.60478	84.15023
Family	-8.5722	61.1444	100.0675	0.2031189	65.59376	215.1938
Habitat	-24.30608	56.61216	57.52125	-20.11697	50.23394	51.62929
Locomotion	-24.47421	64.94843	68.54843	-6.821854	31.64371	36.25909
Diet	-21.65186	57.30371	60.03542	-6.478955	28.95791	32.55791
Bayou	~	~	~	25.68294	-17.36587	2.376064

i. Females CLML

Models	CLML					
	BMS			OUMVA		
	lnL	AIC	AICc	lnL	AIC	AICc
Mammal	-31.96378	67.92755	68.18842	-31.96378	69.92756	70.46089
PvO	-27.99775	63.99551	64.9046	-27.48835	66.9767	68.9767
MAPO	-26.14868	68.29736	71.89736	-25.2402	74.48039	83.14706
MALLTO	-16.21684	56.43367	65.10034	-15.15088	66.30175	89.10175
Parv.Order	-15.66455	55.32911	63.99577	-14.2509	64.5018	87.3018
ANOPO	-24.72762	69.45524	75.24471	-23.40217	76.80434	91.34979
Family	-12.99173	69.98345	108.9065	-1.13144	68.26288	217.8629
Habitat	-27.68211	63.36422	64.27331	-22.48699	54.97398	56.36933
Locomotion	-26.75647	69.51294	73.11294	-11.55103	41.10206	45.71744
Diet	-25.40747	64.81494	67.54664	-11.29189	38.58378	42.18378
Bayou	~	~	~	22.32567	-10.65133	9.090601

j. Females AMIB

Models	AMIB					
	BMS			OUMVA		
	lnL	AIC	AICc	lnL	AIC	AICc
Mammal	-44.35973	92.71945	92.98032	-44.35973	94.71945	95.25279
PvO	-40.55485	89.10969	90.01879	-40.14497	92.28994	94.28994
MAPO	-37.04707	90.09414	93.69414	-36.21561	96.43121	105.0979
MALLTO	-27.77922	79.55843	88.2251	-26.38855	88.7771	111.5771
Parv.Order	-28.75566	81.51132	90.17799	82.95113	-129.9023	-107.1023
ANOPO	-36.47591	92.95182	98.74129	-35.07023	100.1405	114.6859
Family	-31.42731	106.8546	145.7777	-10.60061	87.20122	236.8012
Habitat	-39.65066	87.30133	88.21042	-33.89287	77.78573	79.18108
Locomotion	-35.64235	87.28471	90.88471	-21.62447	61.24894	65.86432
Diet	-33.653	81.306	84.0377	-28.65567	73.31134	76.91134
Bayou	~	~	~	-15.0796	48.15919	52.77458

k. Females RAH

Models	RAH					
	BMS			OUMVA		
	lnL	AIC	AICc	lnL	AIC	AICc
Mammal	-31.44612	66.89223	67.1531	-31.44612	68.89223	69.42557
PvO	-27.9415	63.88299	64.79208	-27.71313	67.42626	69.42626
MAPO	-26.60734	69.21468	72.81468	-24.29652	72.59303	81.2597
MALLTO	-17.98392	59.96784	68.6345	-15.29249	66.58499	89.38499
Parv.Order	-17.28109	58.56218	67.22884	-14.79669	65.59338	88.39338
ANOPO	-25.58818	71.17636	76.96583	-22.88367	75.76735	90.3128
Family	-12.99173	69.98345	108.9065	-1.13144	68.26288	217.8629
Habitat	-18.85196	45.70391	46.613	-19.30629	48.61258	50.00793
Locomotion	-23.17557	62.35114	65.95114	-9.087889	36.17578	40.79116
Diet	-21.32364	56.64729	59.379	-10.72326	37.44652	41.04652
Bayou	~	~	~	44.99982	-53.99963	-31.19963

l. Females LIH

Models	LIH					
	BMS			OUMVA		
	lnL	AIC	AICc	lnL	AIC	AICc
Mammal	-33.90944	71.81889	72.07976	-33.90944	73.81889	74.35222
PvO	-30.39729	68.79458	69.70367	-30.01853	72.03705	74.03705
MAPO	-27.41153	70.82307	74.42307	-26.33147	76.66294	85.32961
MALLTO	-18.01133	60.02266	68.68932	-16.20176	68.40353	91.20353
Parv.Order	-18.56462	61.12923	69.7959	-16.79781	69.59561	92.39561
ANOPO	-26.52893	73.05786	78.84734	-24.90423	79.80845	94.35391
Family	-14.87298	73.74597	112.669	-1.723492	69.44698	219.047
Habitat	-32.16324	72.32649	73.23558	-19.45036	48.90072	50.29607
Locomotion	-27.63889	71.27778	74.87778	-12.10305	42.20611	46.82149
Diet	-29.88126	73.76253	76.49423	-14.95507	45.91014	49.51014
Bayou	~	~	~	26.11724	-18.23447	1.507465

m. Females AW

Models	AW					
	BMS			OUMVA		
	lnL	AIC	AICc	lnL	AIC	AICc
Mammal	-28.66136	61.32272	61.58359	-28.66136	63.32272	63.85605
PvO	-24.73026	57.46051	58.3696	-24.368	60.736	62.736
MAPO	-23.20914	62.41829	66.01829	-21.46103	66.92207	75.58874
MALLTO	-12.93526	49.87051	58.53718	-10.59814	57.19628	79.99628
Parv.Order	-11.86412	47.72824	56.39491	-9.863212	55.72642	78.52642
ANOPO	-21.8832	63.7664	69.55588	-19.56433	69.12866	83.67411
Family	-6.099631	56.19926	95.12234	9.76204	46.47592	196.0759
Habitat	-23.82161	55.64322	56.55231	-18.32401	46.64802	48.04337
Locomotion	-21.72337	59.44675	63.04675	-9.36321	36.72642	41.34181
Diet	-21.59492	57.18984	59.92155	-5.370829	26.74166	30.34166
Bayou	~	~	~	29.05899	-24.11798	-4.376046

n. Females HML

Models	HML					
	BMS			OUMVA		
	lnL	AIC	AICc	lnL	AIC	AICc
Mammal	-29.28335	62.56669	62.82756	-29.28335	64.56669	65.10003
PvO	-25.08349	58.16699	59.07608	-24.67517	61.35034	63.35034
MAPO	-22.91872	61.83745	65.43745	-22.52238	69.04477	77.71144
MALLTO	-12.18688	48.37377	57.04044	-10.79663	57.59326	80.39326
Parv.Order	-12.26831	48.53662	57.20329	-10.71612	57.43224	80.23224
ANOPO	-21.82324	63.64647	69.43595	-20.41202	70.82404	85.36949
Family	-8.074509	60.14902	99.07209	1.376918	63.24616	212.8462
Habitat	-26.07913	60.15825	61.06734	-17.7037	45.40741	46.80275
Locomotion	-25.67448	67.34895	70.94895	-9.57396	37.14792	41.7633
Diet	-23.52202	61.04404	63.77574	-8.453735	32.90747	36.50747
Bayou	~	~	~	23.78494	-13.56989	6.172046

o. Females HHW

Models	HHW					
	BMS			OUMVA		
	lnL	AIC	AICc	lnL	AIC	AICc
Mammal	-29.77464	63.54927	63.81014	-29.77464	65.54927	66.08261
PvO	-25.66661	59.33322	60.24231	-25.2333	62.4666	64.4666
MAPO	-24.33679	64.67358	68.27358	-22.89873	69.79746	78.46412
MALLTO	-14.41579	52.83159	61.49825	-12.53802	61.07603	83.87603
Parv.Order	-13.39206	50.78413	59.45079	-11.87509	59.75019	82.55019
ANOPO	-23.33374	66.66747	72.45695	-21.41066	72.82132	87.36677
Family	-9.195356	62.39071	101.3138	2.461388	61.07722	210.6772
Habitat	-22.51341	53.02683	53.93592	-21.61003	53.22006	54.61541
Locomotion	-24.81131	65.62263	69.22263	-10.75266	39.50531	44.1207
Diet	-19.79103	53.58206	56.31377	-6.416029	28.83206	32.43206
Bayou	~	~	~	32.36097	-30.72194	-10.98

Table SIII.10. List of selective regimes among males for each trait.

Genus_species	NR	SCM	SNL	FMW	SSL	SBL	VB	GW	CLML	AMIB	RAH	LIH	AW	HML	HHW
Tupaia_glis	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Galago_senegalensis	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Hapalemur_griseus	2	2	2	2	1	2	2	2	2	1	2	2	2	2	2
Eulemur_fulvus_fulvus	2	2	2	2	1	2	2	2	2	1	2	2	2	2	2
Tarsius_bancanus	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Pithecia_pithecia	5	4	8	5	5	7	9	8	5	4	4	7	5	1	10
Saimiri_sciureus	14	14	4	5	3	7	9	8	5	4	15	7	4	1	10
Saguinus_fuscicollis	14	14	4	5	3	7	9	8	5	4	15	7	4	1	10
Saguinus_oedipus	14	14	4	5	3	7	9	8	5	4	15	7	4	1	10
Callithrix_jacchus	14	14	4	5	3	7	9	8	5	4	15	7	4	1	10
Aotus_trivirgatus	3	14	4	5	3	7	9	8	5	4	15	7	4	1	10
Ateles_fusciceps	4	3	3	3	2	3	3	3	5	2	3	3	3	3	3
Alouatta_seniculus	4	3	3	3	2	3	3	3	5	2	3	3	3	3	3
Alouatta_caraya	4	3	3	3	2	3	3	3	5	2	3	3	3	3	3
Alouatta_palliata	4	3	3	3	2	3	3	3	5	2	3	3	3	3	3
Pongo_pygmaeus	13	6	5	4	4	6	8	4	4	3	8	6	7	4	9
Pan_troglodytes_troglodytes	6	6	5	4	4	4	8	4	4	3	5	4	7	4	4
Pan_paniscus	6	6	5	4	4	4	8	4	4	3	6	4	7	4	4
Homo_sapiens	6	6	5	4	4	6	8	4	4	3	8	6	7	4	9
Gorilla_gorilla_gorilla	6	5	5	4	4	6	8	4	4	3	8	6	6	4	9
Nomascus_concolor	13	13	7	5	4	6	8	7	4	3	7	6	13	4	5
Symphalangus_syndactylus	13	13	7	5	4	6	8	7	4	3	7	6	13	4	5
Hylobates_lar	7	13	7	5	4	6	8	7	4	3	7	6	13	4	5
Hylobates_klossii	13	13	7	5	4	6	8	7	4	3	7	6	13	4	5
Hylobates_muelleri	13	13	7	5	4	6	8	7	4	3	7	6	13	4	5
Rhinopithecus_roxellana	13	7	7	5	4	6	8	7	4	3	9	6	8	4	9
Pygathrix_nemaeus	13	13	7	5	4	6	8	7	4	3	14	6	13	4	9
Colobus_guereza	13	13	7	5	4	6	8	7	4	3	14	6	13	4	9
Colobus_angolensis	13	13	7	5	4	6	8	7	4	3	14	6	13	4	9
Macaca_thibetana	12	13	7	5	4	6	8	7	4	3	14	6	13	4	9
Macaca_mulatta	12	8	7	5	4	6	8	7	4	3	14	6	13	4	9
Macaca_fascicularis	12	8	7	5	4	6	8	7	4	3	14	6	13	4	9
Macaca_nemestrina	12	13	7	5	4	6	8	7	4	3	14	6	13	4	9
Macaca_fuscata	12	13	7	5	4	6	8	7	4	3	14	6	13	4	9
Macaca_cyclopis	12	13	7	5	4	6	8	7	4	3	14	6	13	4	9
Macaca_arctoides	12	13	7	5	4	6	8	7	4	3	14	6	13	4	9
Papio_ursinus	8	9	7	5	4	6	5	5	4	3	10	6	9	4	6
Papio_cynocephalus	8	9	7	5	4	6	5	5	4	3	10	6	9	4	6
Papio_papio	8	9	7	5	4	6	5	5	4	3	10	6	9	4	6
Papio_hamadryas	8	9	7	5	4	6	5	5	4	3	10	6	9	4	6
Papio_anubis	8	9	7	5	4	6	5	5	4	3	10	6	9	4	6
Theropithecus_gelada	12	10	7	5	4	6	5	7	4	3	11	6	10	4	6
Mandrillus_sphinx	12	13	7	5	4	6	4	7	4	3	14	6	13	4	9
Mandrillus_leucophaeus	12	13	7	5	4	6	4	7	4	3	14	6	13	4	9
Miopithecus_talapoin	10	11	6	5	4	5	6	6	3	3	12	5	11	4	7
Chlorocebus_aethiops	11	12	7	5	4	6	7	7	4	3	13	6	12	4	8
Erythrocebus_patas	11	12	7	5	4	6	7	7	4	3	13	6	12	4	8
Cercopithecus_mitis	9	12	7	5	4	6	7	7	4	3	13	6	12	4	8
Allenopithecus_nigroviridis	11	12	7	5	4	6	7	7	4	3	13	6	12	4	8

Table SIII.11. List of selective regimes among females for each trait.

Genus_species	NR	SCM	SNL	FMW	SSL	SBL	VB	GW	CLML	AMIB	RAH	LIH	AW	HML	HHW
Tupaia_glis	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Galago_senegalensis	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Hapalemur_griseus	2	2	2	2	2	2	2	2	2	1	2	2	2	2	2
Eulemur_fulvus_fulvus	2	2	2	2	2	2	2	2	2	1	2	2	2	2	2
Tarsius_bancanus	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Pithecia_pithecia	6	5	5	5	5	5	7	5	8	4	5	8	7	8	5
Saimiri_sciureus	5	4	4	4	4	4	3	4	8	4	4	8	7	8	4
Saguinus_fuscicollis	5	4	4	4	4	4	3	4	8	4	4	8	7	8	4
Saguinus_oedipus	5	4	4	4	4	4	3	4	8	4	4	8	7	8	4
Callithrix_jacchus	5	4	4	4	4	4	3	4	8	4	4	8	7	8	4
Aotus_trivirgatus	3	4	4	4	4	4	3	4	8	4	4	8	7	8	4
Ateles_fusciceps	4	3	3	3	3	3	7	3	3	2	3	3	3	3	3
Alouatta_seniculus	4	3	3	3	3	3	7	3	3	2	3	3	3	3	3
Alouatta_caraya	4	3	3	3	3	3	7	3	3	2	3	3	3	3	3
Alouatta_palliata	4	3	3	3	3	3	7	3	3	2	3	3	3	3	3
Pongo_pygmaeus	9	6	6	6	9	7	4	6	5	3	7	5	4	5	6
Pan_troglodytes_troglodytes	7	6	6	6	6	6	4	6	5	3	6	4	4	5	6
Pan_paniscus	7	6	6	6	6	6	4	6	5	3	6	4	4	5	6
Homo_sapiens	7	6	6	6	9	7	4	6	5	3	7	5	4	5	6
Gorilla_gorilla_gorilla	7	6	6	6	9	7	4	6	5	3	7	5	4	5	6
Nomascus_concolor	9	9	11	9	8	9	7	11	4	3	13	7	6	4	9
Symphalangus_syndactylus	9	9	11	9	7	9	7	11	4	3	13	7	6	4	9
Hylobates_lar	9	9	11	9	8	9	7	11	4	3	13	7	6	4	9
Hylobates_klossii	9	9	11	9	8	9	7	11	4	3	13	7	6	4	9
Hylobates_muelleri	9	9	11	9	8	9	7	11	4	3	13	7	6	4	9
Rhinopithecus_roxellana	9	9	11	9	14	9	7	11	7	3	13	7	6	7	9
Pygathrix_nemaeus	9	9	11	9	14	9	7	11	7	3	13	7	6	7	9
Colobus_guereza	9	9	11	9	14	9	7	11	7	3	13	7	6	7	9
Colobus_angolensis	9	9	11	9	14	9	7	11	7	3	13	7	6	7	9
Macaca_thibetana	9	9	11	9	14	9	7	11	7	3	13	7	6	7	9
Macaca_mulatta	9	9	11	9	10	9	7	11	7	3	9	7	6	7	9
Macaca_fascicularis	9	9	7	7	10	9	7	7	7	3	8	7	6	7	9
Macaca_nemestrina	9	9	11	9	14	9	7	11	7	3	13	7	6	7	9
Macaca_fuscata	9	9	11	9	14	9	7	11	7	3	13	7	6	7	9
Macaca_cyclopis	9	9	11	9	14	9	7	11	7	3	13	7	6	7	9
Macaca_arctoides	9	9	11	9	14	9	7	11	7	3	13	7	6	7	9
Papio_ursinus	9	9	11	9	14	9	7	11	7	3	13	7	6	7	9
Papio_cynocephalus	9	9	11	9	14	9	7	11	7	3	13	7	6	7	9
Papio_papio	9	9	11	9	14	9	7	11	7	3	13	7	6	7	9
Papio_hamadryas	9	9	11	9	14	9	7	11	7	3	13	7	6	7	9
Papio_anubis	9	9	11	9	14	9	7	11	7	3	13	7	6	7	9
Theropithecus_gelada	9	9	11	9	14	9	7	11	7	3	13	7	6	7	9
Mandrillus_sphinx	9	9	11	9	14	9	7	11	7	3	13	7	6	7	9
Mandrillus_leucophaeus	9	7	8	9	11	9	5	8	7	3	10	7	6	7	7
Miopithecus_talapoin	8	8	9	8	12	8	6	9	6	3	11	6	5	6	8
Chlorocebus_aethiops	9	9	10	9	13	9	7	10	7	3	12	7	6	7	9
Erythrocebus_patas	9	9	10	9	13	9	7	10	7	3	12	7	6	7	9
Cercopithecus_mitis	9	9	10	9	13	9	7	10	7	3	12	7	6	7	9
Allenopithecus_nigroviridis	9	9	10	9	13	9	7	10	7	3	12	7	6	7	9

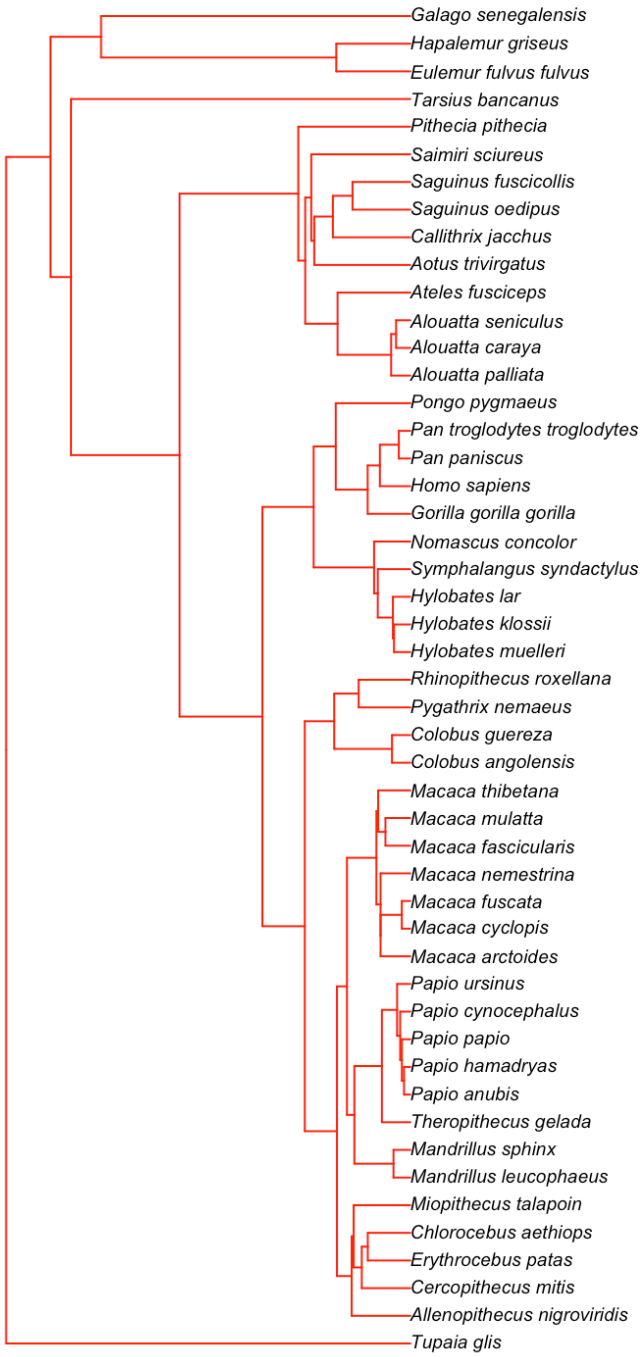
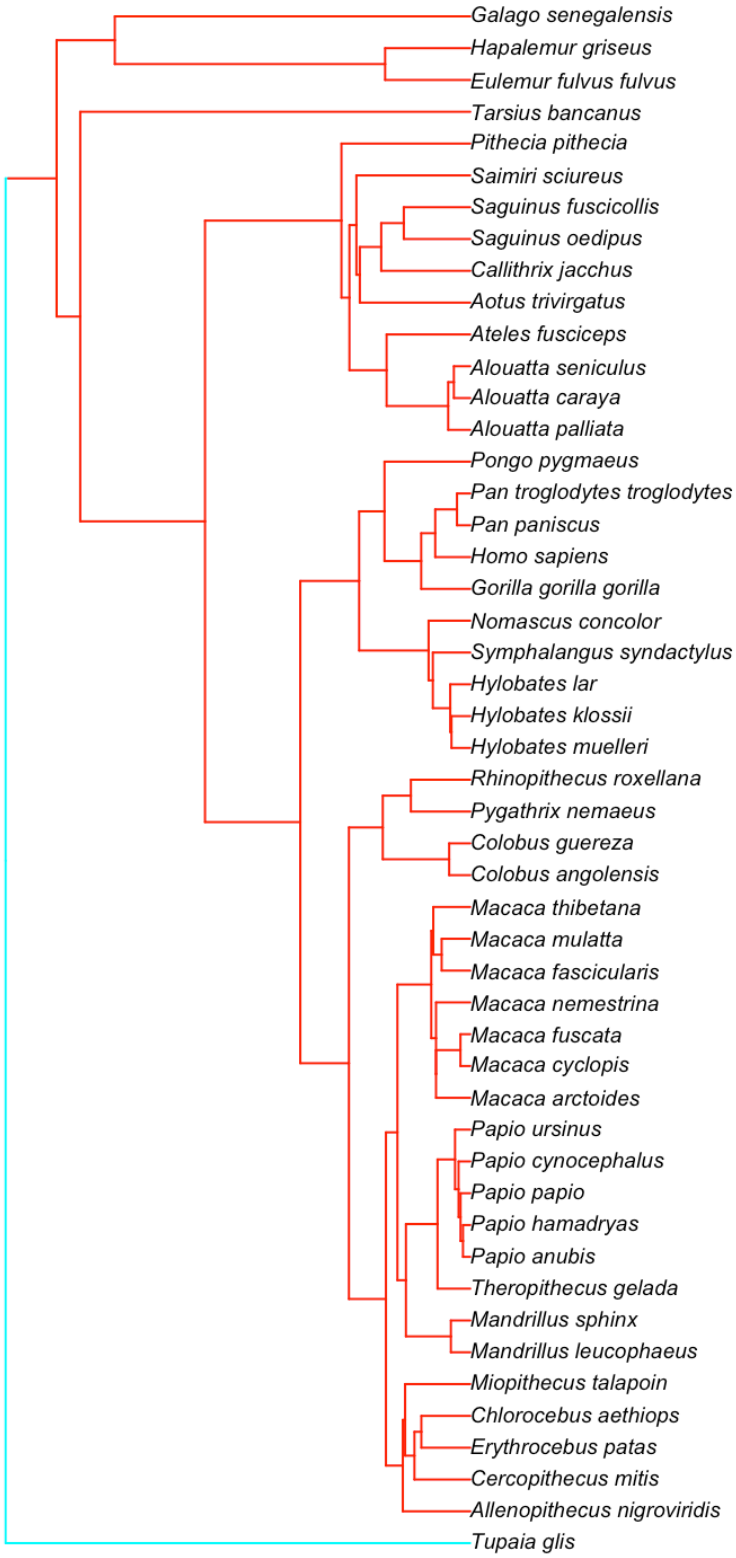
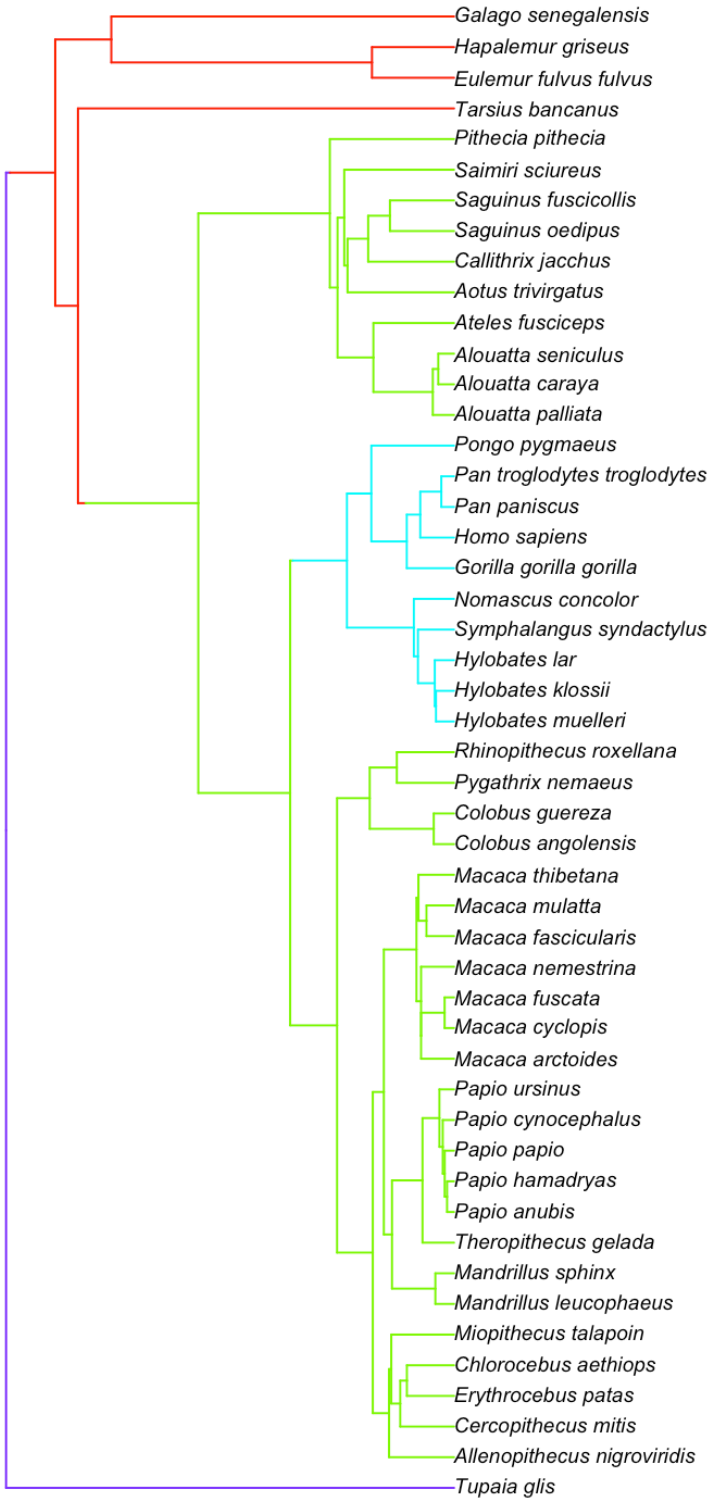


Figure SIII.1 a-g. Visual representation for six of the evolutionary hypotheses of primate diversification tested in this study: Mammal Hypothesis, PvO Hypothesis, MAPO Hypothesis, MALLTO Hypothesis, Parv.Order Hypothesis, and ANOPO Hypothesis. Selective regimes are painted on the phylogeny, where taxa within a single regime are painted similar colors. Written descriptions of each regime can be found in Table SIII.1.

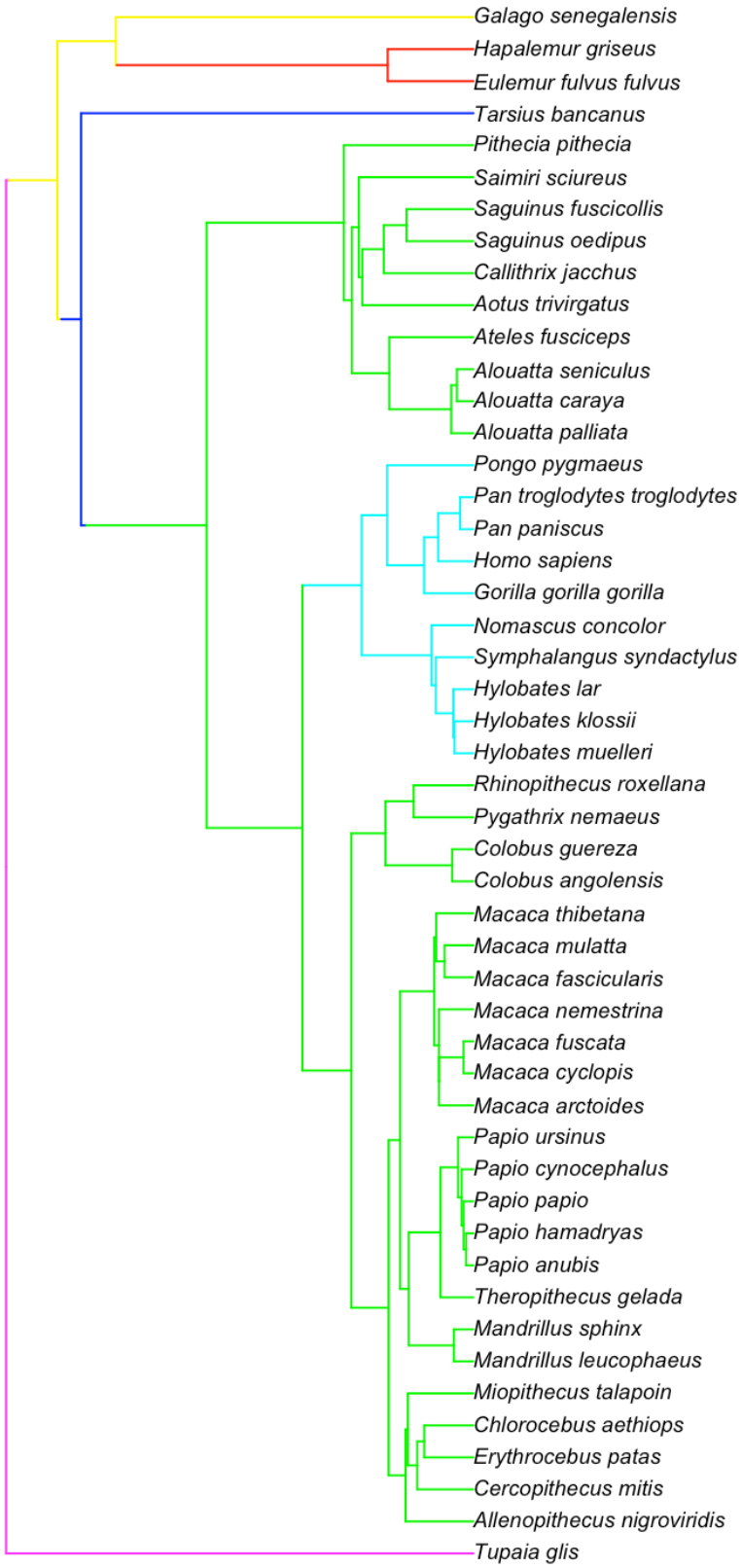
a. Mammal Hypothesis



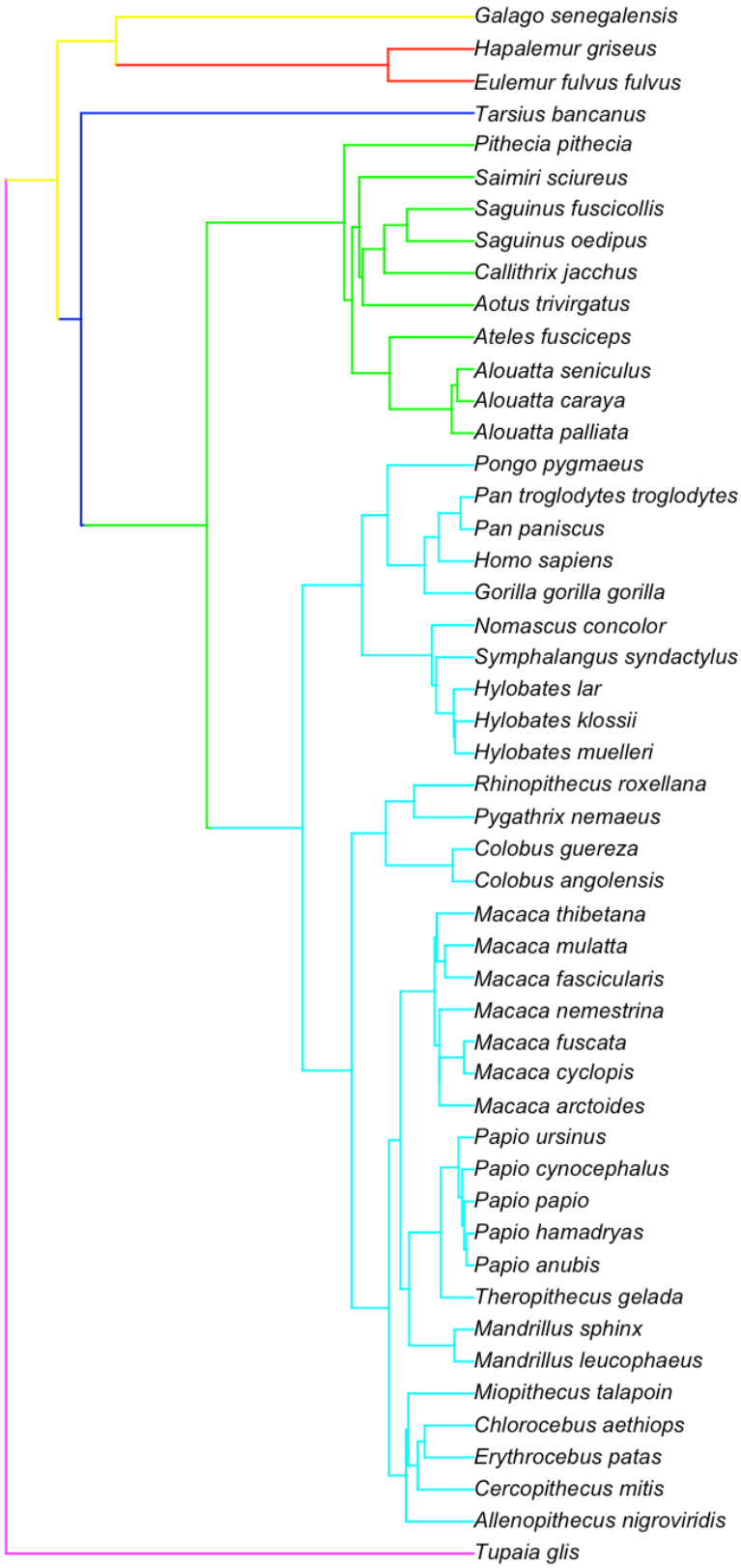
b. PvO Hypothesis



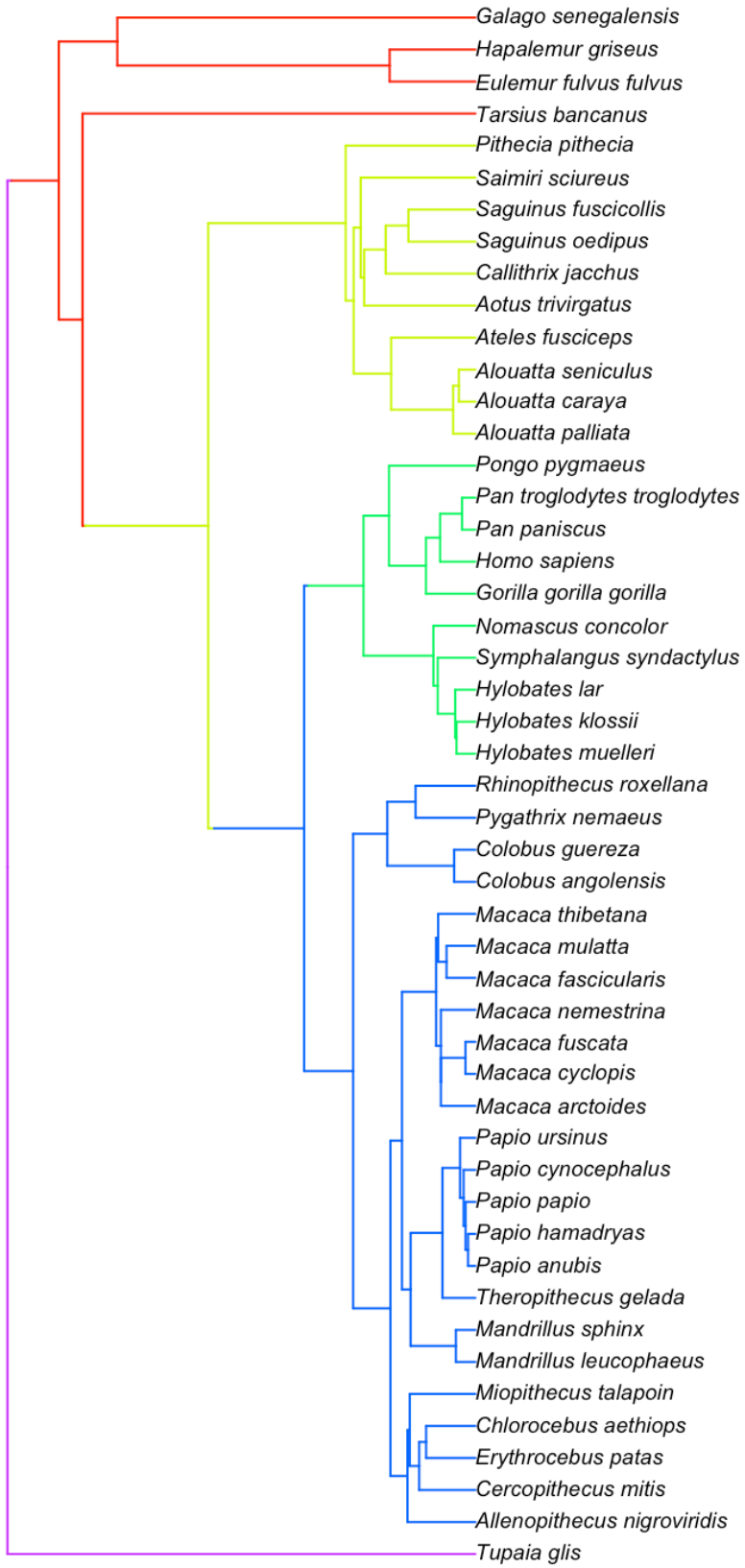
c. MAPO Hypothesis



d. MALLTO Hypothesis



e. Parv.Order Hypothesis



f. ANOPO Hypothesis

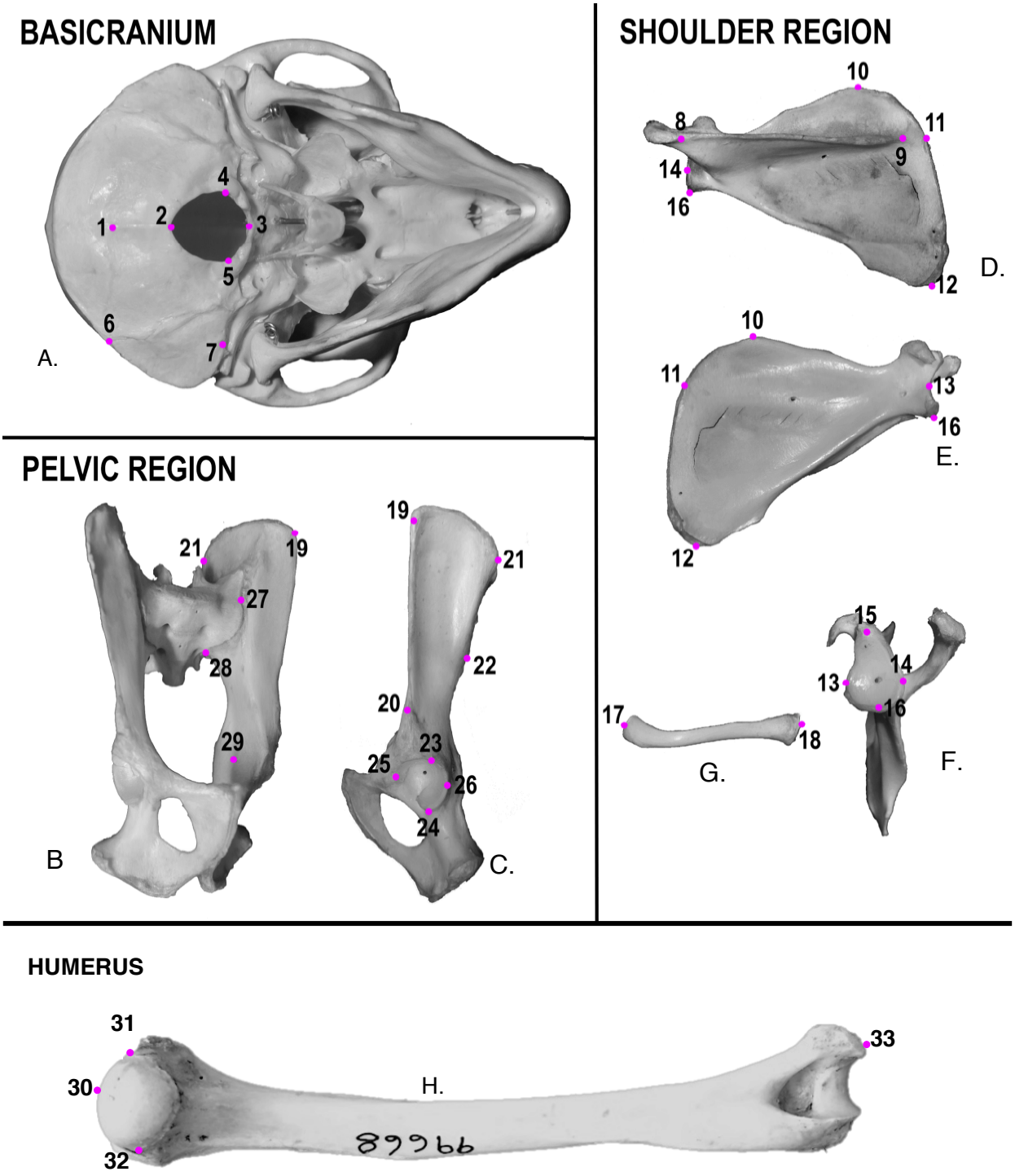


Figure SIII.2. Landmarks taken from each anatomical region: A. caudal aspect of the basicranium; B. medial aspect of os coxa; C. lateral aspect of os coxa; D. dorsal aspect of scapula; E. ventral aspect of scapula; F. lateral aspect of scapula; G. cranial aspect of clavicle; F. ventral aspect of humerus. Refer to Table S1 for a list of landmarks and descriptions. Landmark locations are demonstrated on a *Macaca mulatta* specimen and are homologous for all taxa.

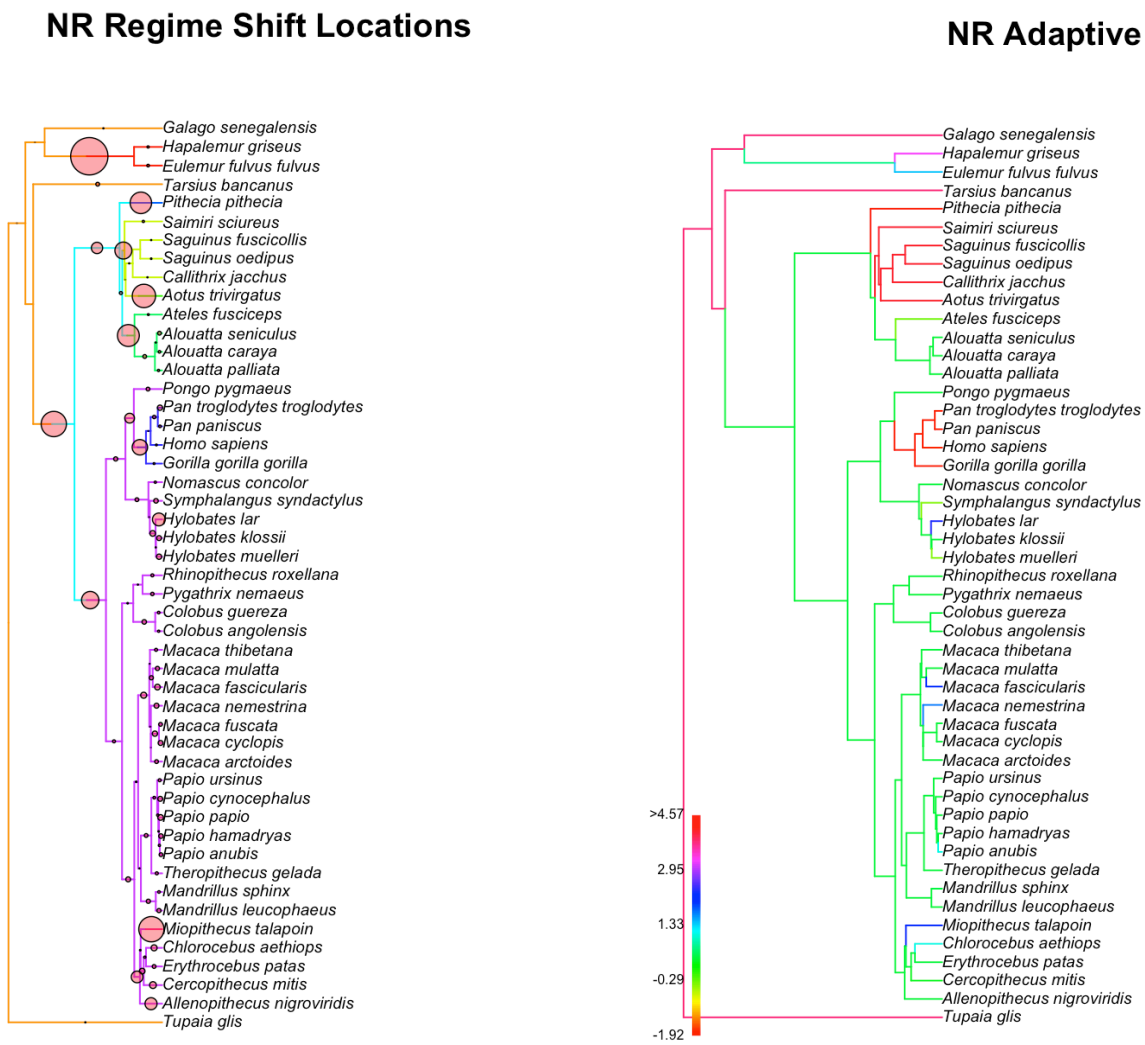
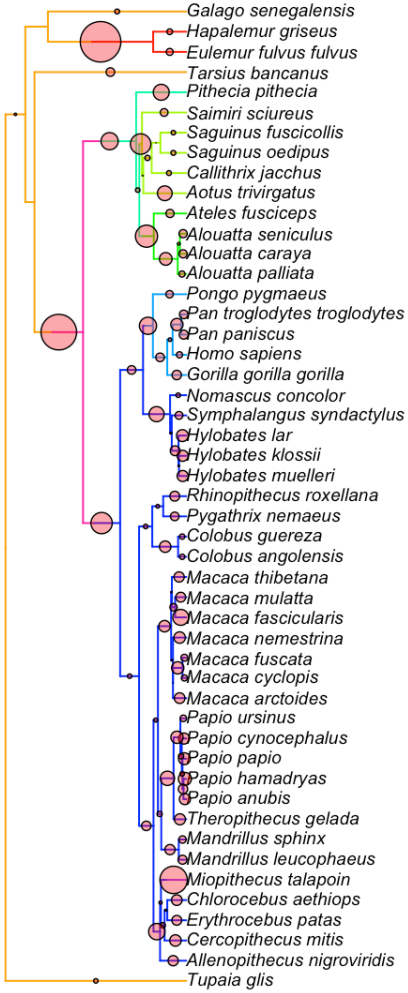


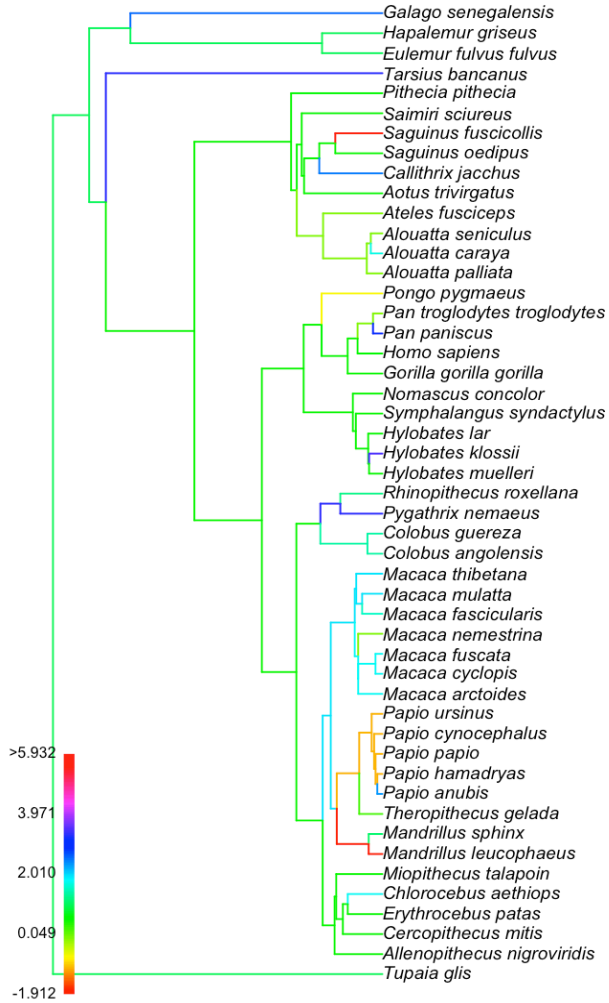
Figure SIII.3 a-l . Selective regimes and shift locations (left) and Adaptive Optima (right) of each trait for males. Selective regimes and adaptive optima are indicated by different colors; the size of the red circle are related to the posterior probability of the shift location and scale bars indicate optima values.

a. Nuchal Region (NR) Males

SNL Regime Shift Locations

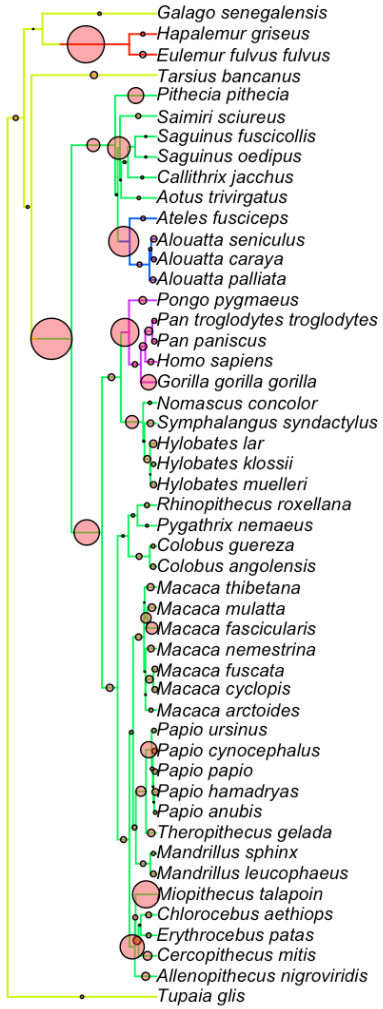


SNL Adpative Optima

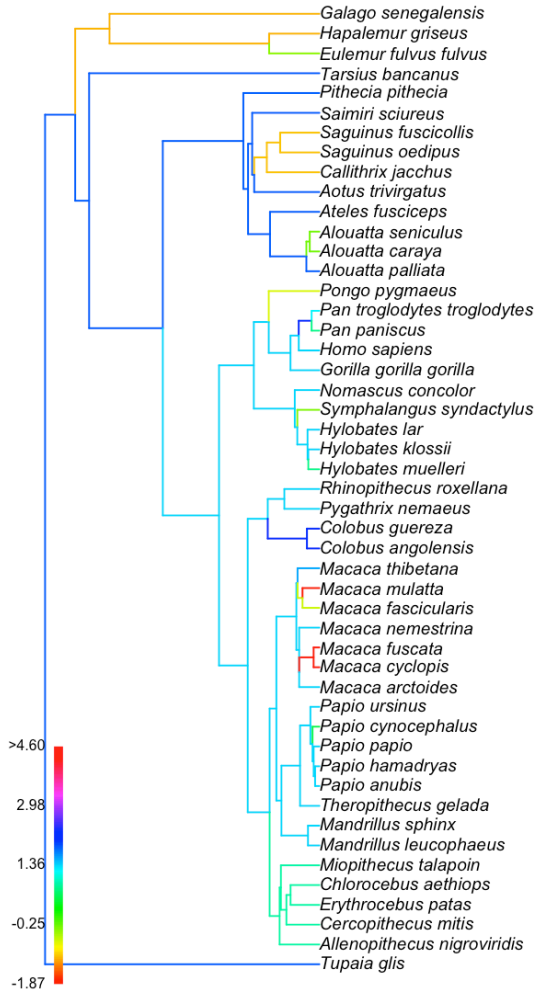


b. Superior Nuchal Line (SNL) Males

FMW Regime Shift Locations

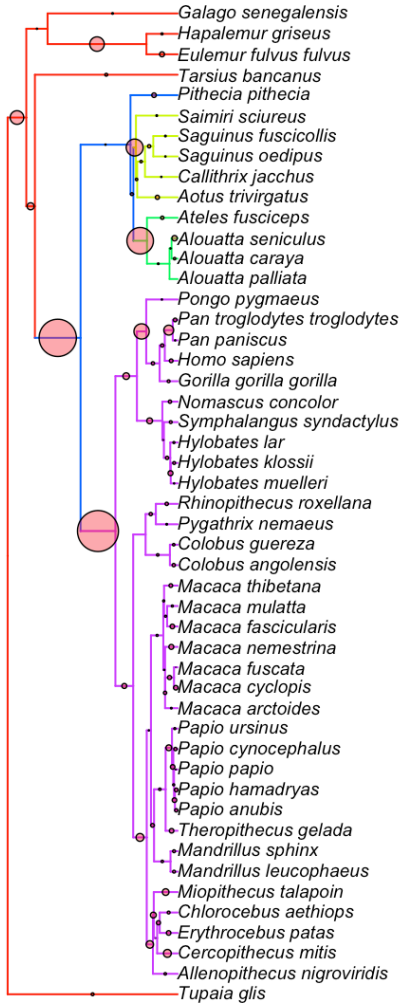


FMW Adaptive Optima

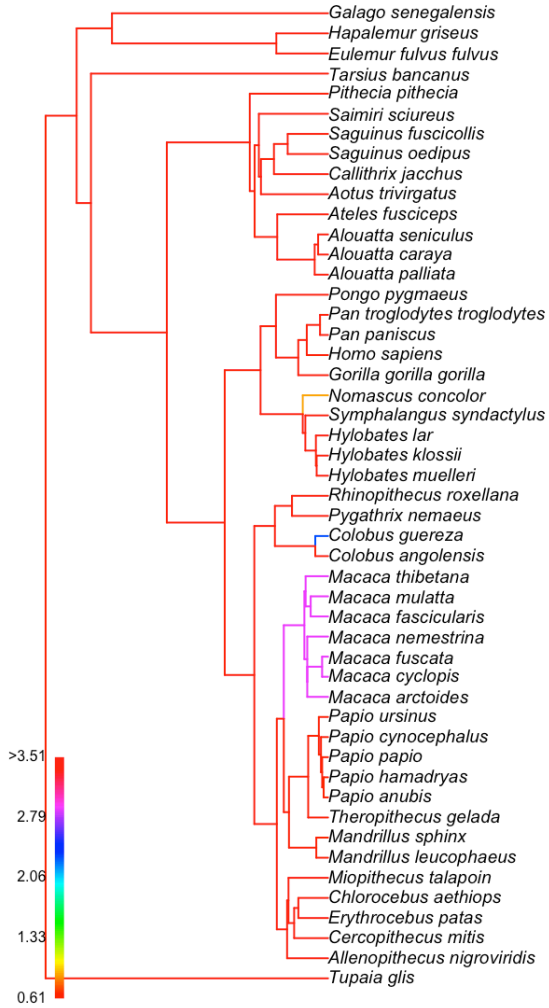


c. Foramen Magnum Width (FMW) Males

SSL Regime Shift Locations

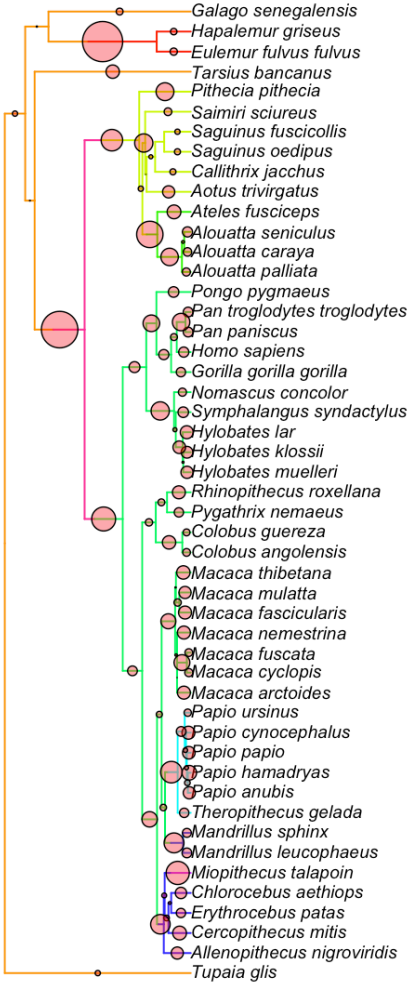


SSL Adaptive Optima

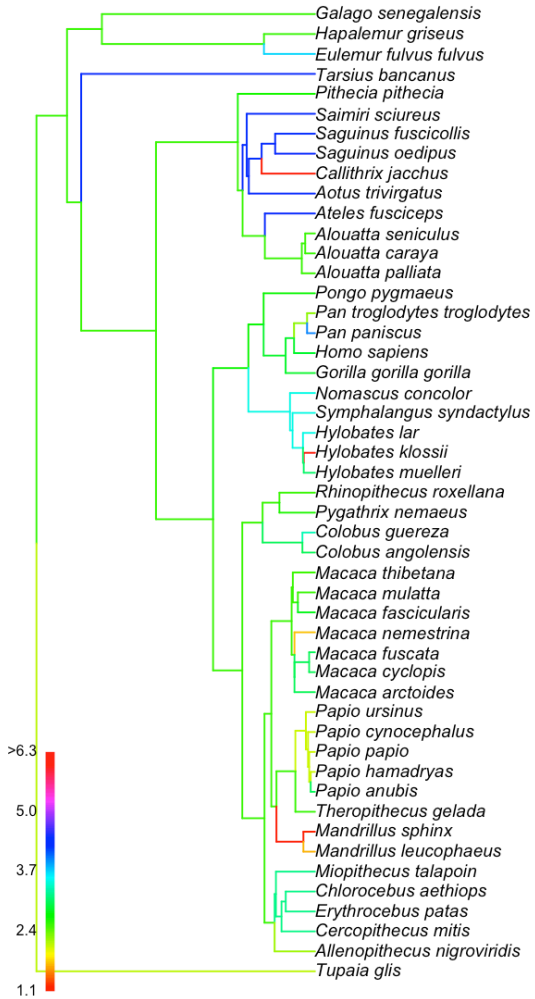


d. Scapular Spine Length (SSL) Males

VB Regime Shift Locations

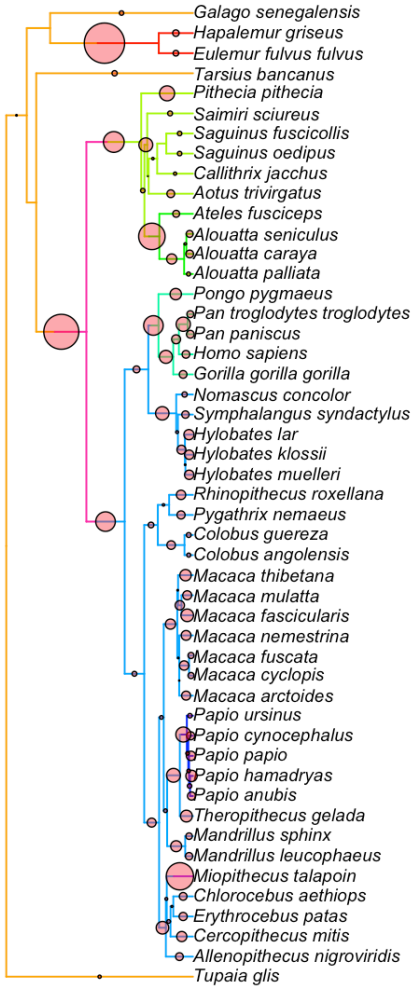


VB Adaptive Optima

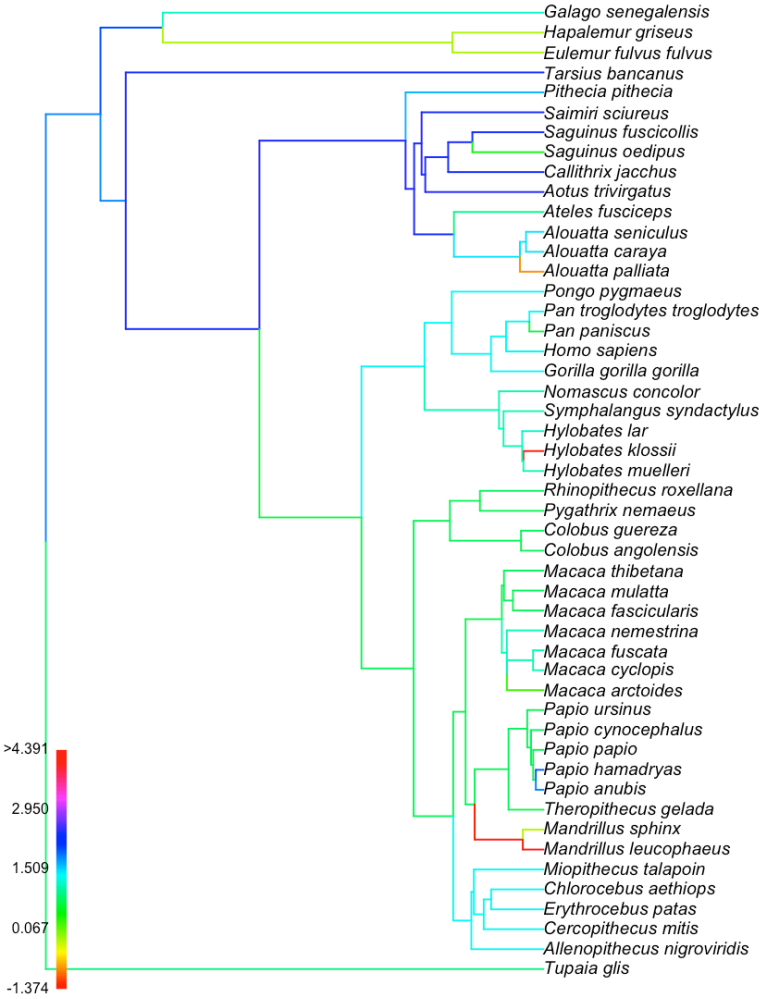


e. Vertebral Border (VB) Males

GW Regime Shift Locations

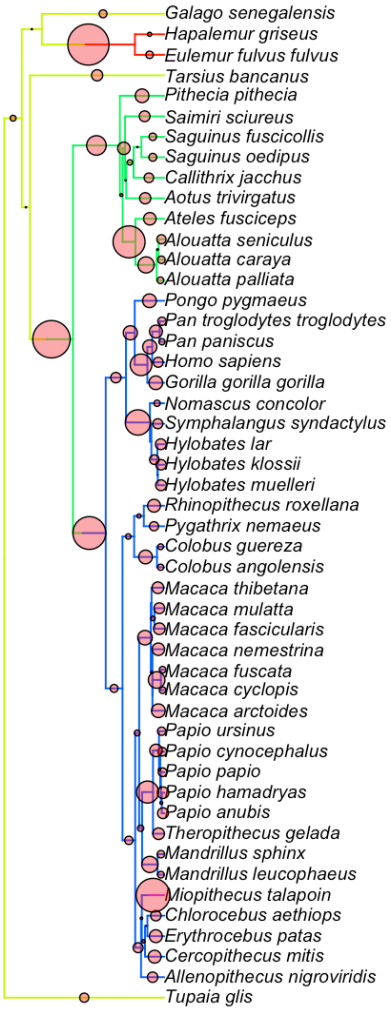


GW Adaptive Optima

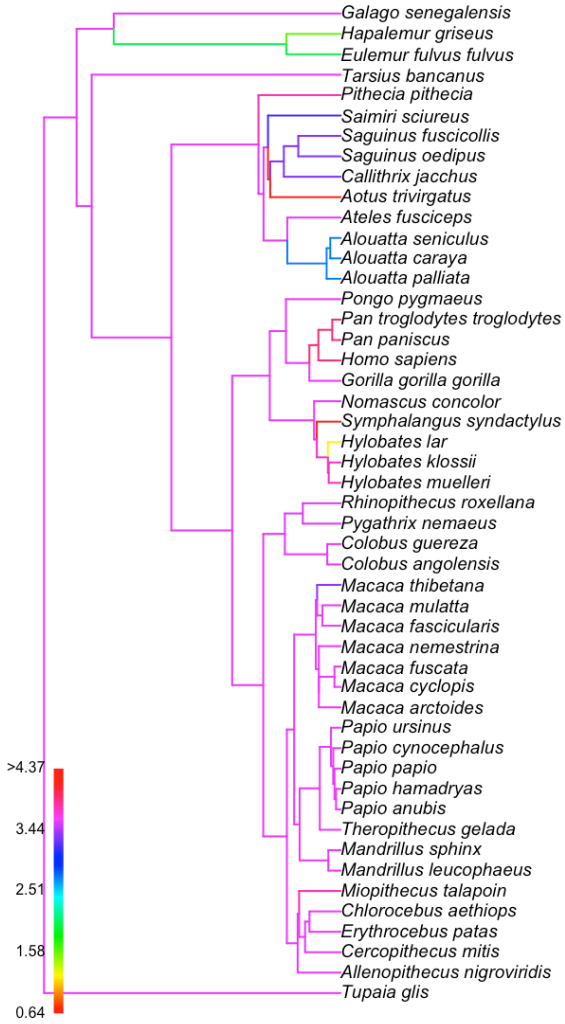


f. Glenoid Width (GW) Males

CLML Regime Shift Location

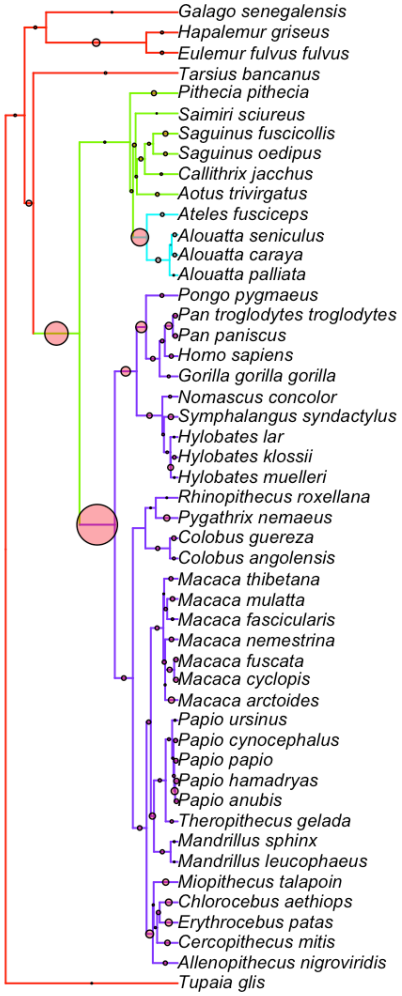


CLML Adaptive Optima

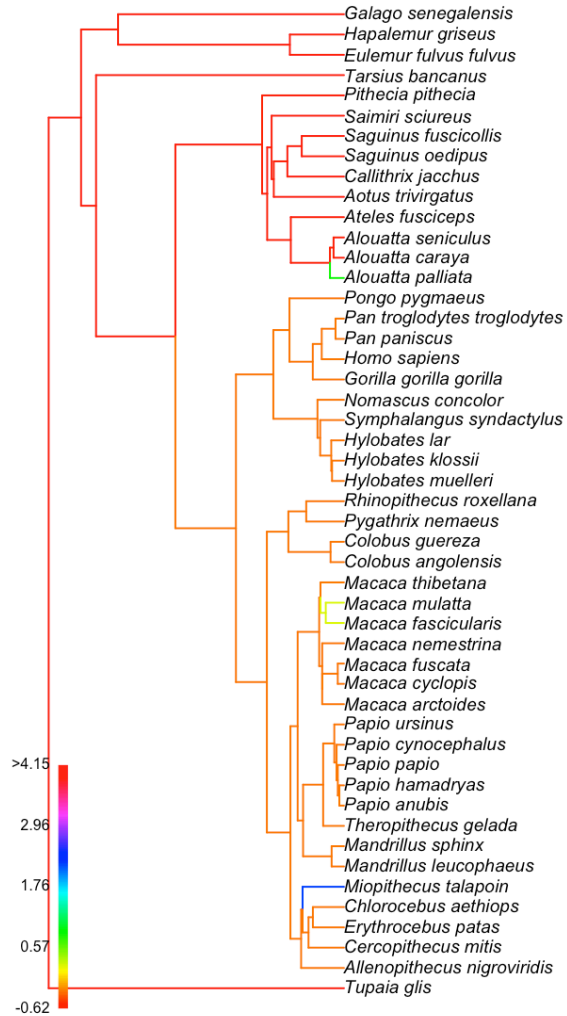


g. Clavicle Maximum Length (CLML) Males

AMIB Regime Shift Locations

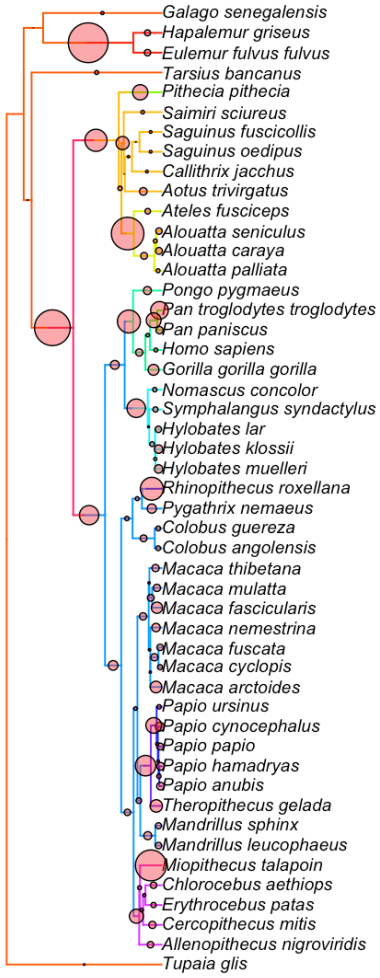


AMIB Adaptive Optima

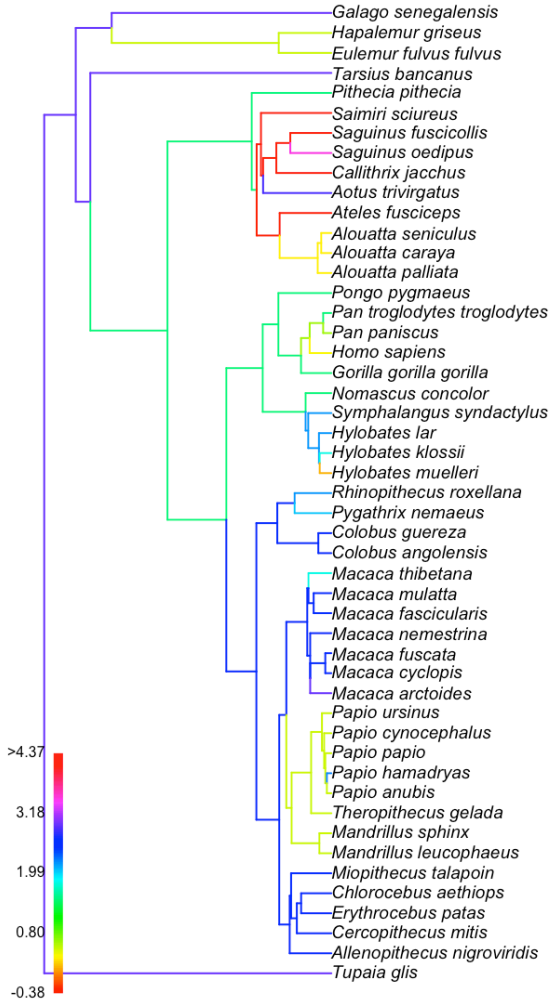


h. Anterior Margin of the Iliac Blade (AMIB) Males

RAH Regime Shift Locations

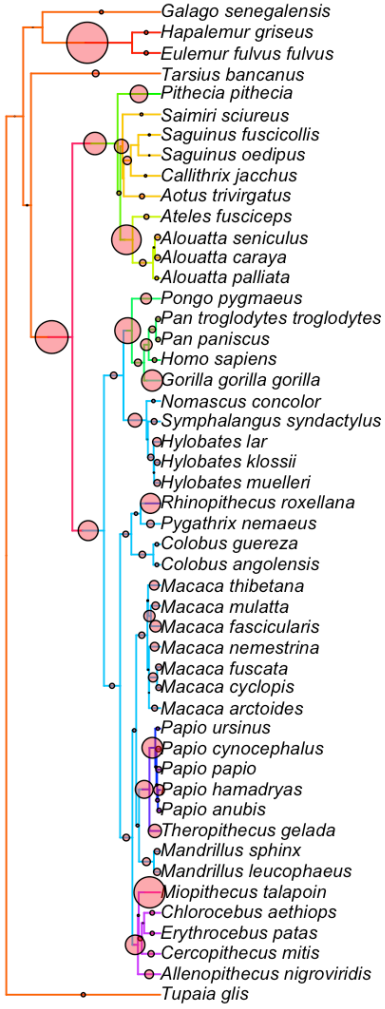


RAH Adaptive Optima

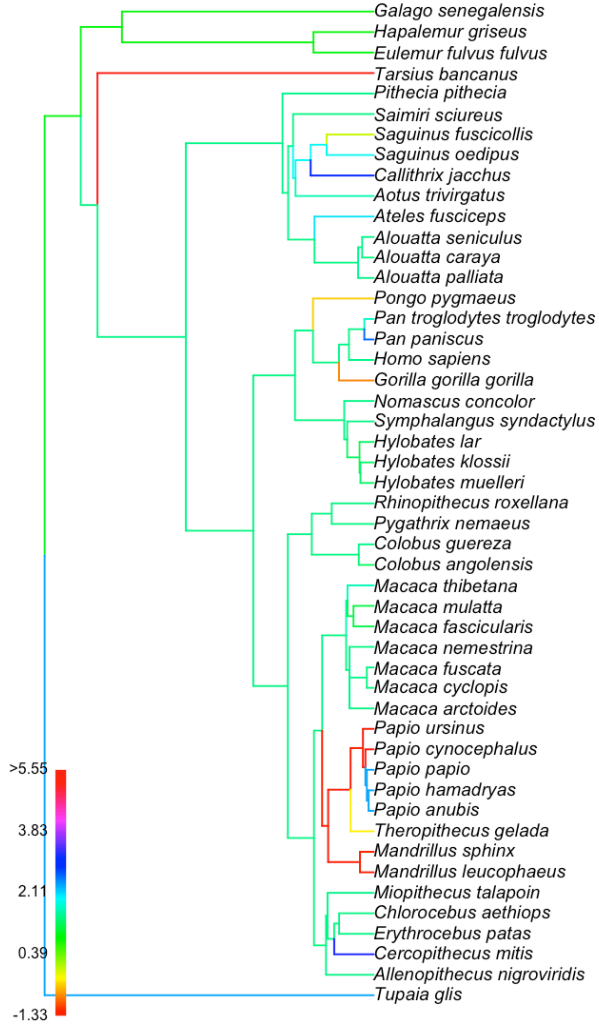


i. Retroauricular Height (RAH) Males

AW Regime Shift Locations

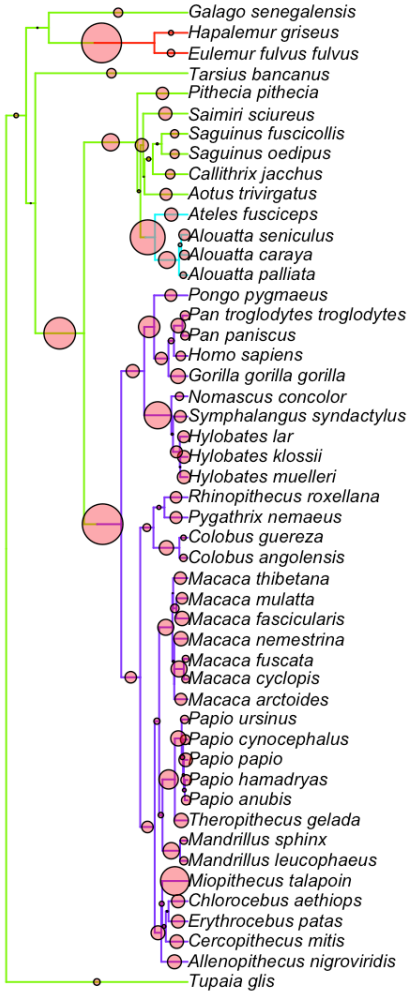


AW Adaptive Optima

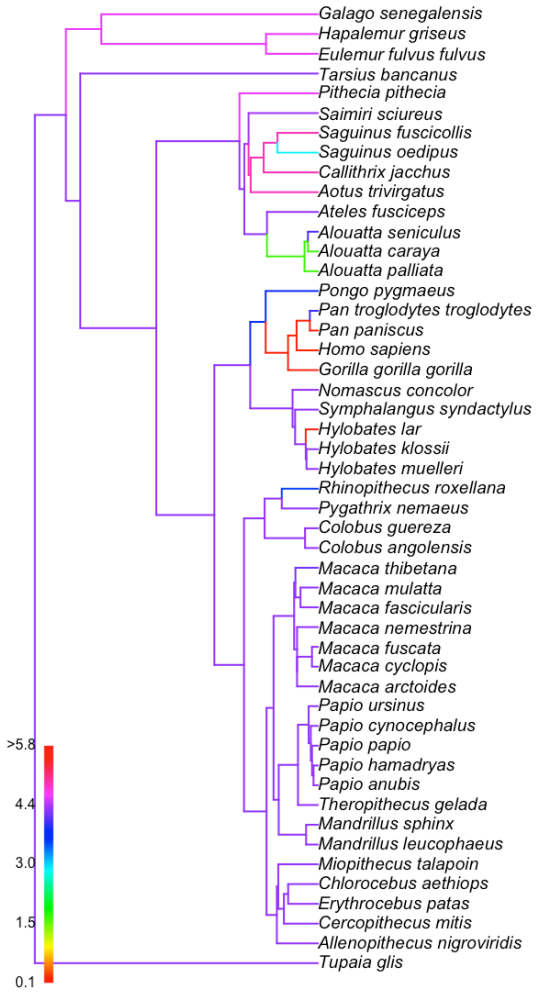


j. Acetabulum Width (AW) Males

HML Regime Shift Locations

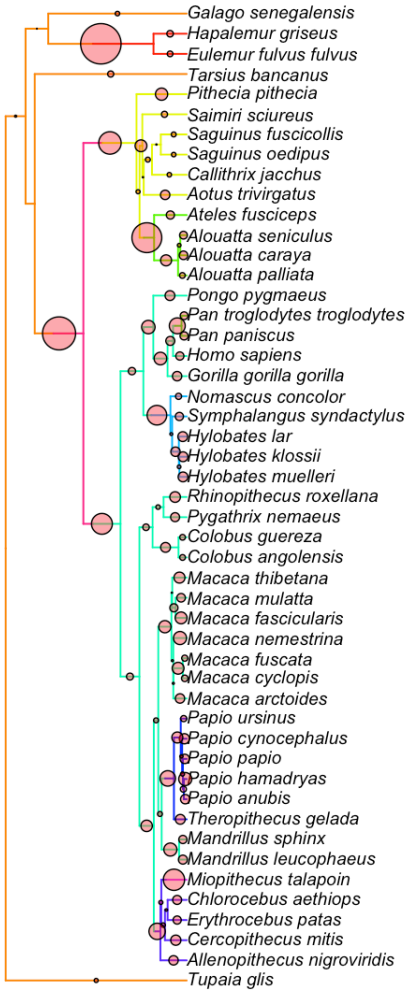


HML Adaptive Optima

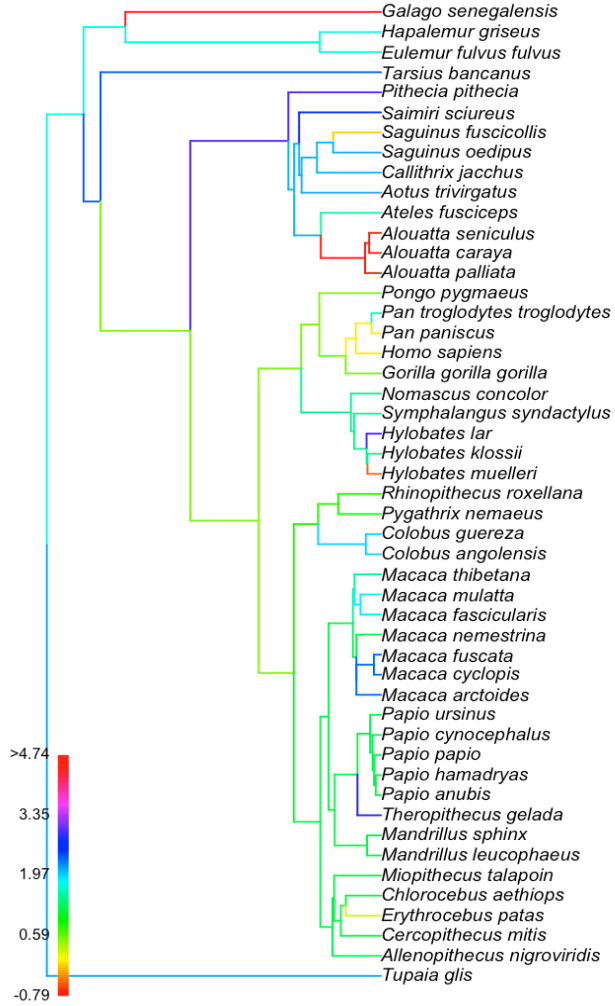


k. Humerus Maximum Length (HML) Males

HHW Regime Shift Locations



HHW Adpative Optima



I. Humeral Head Width (HHW) Males

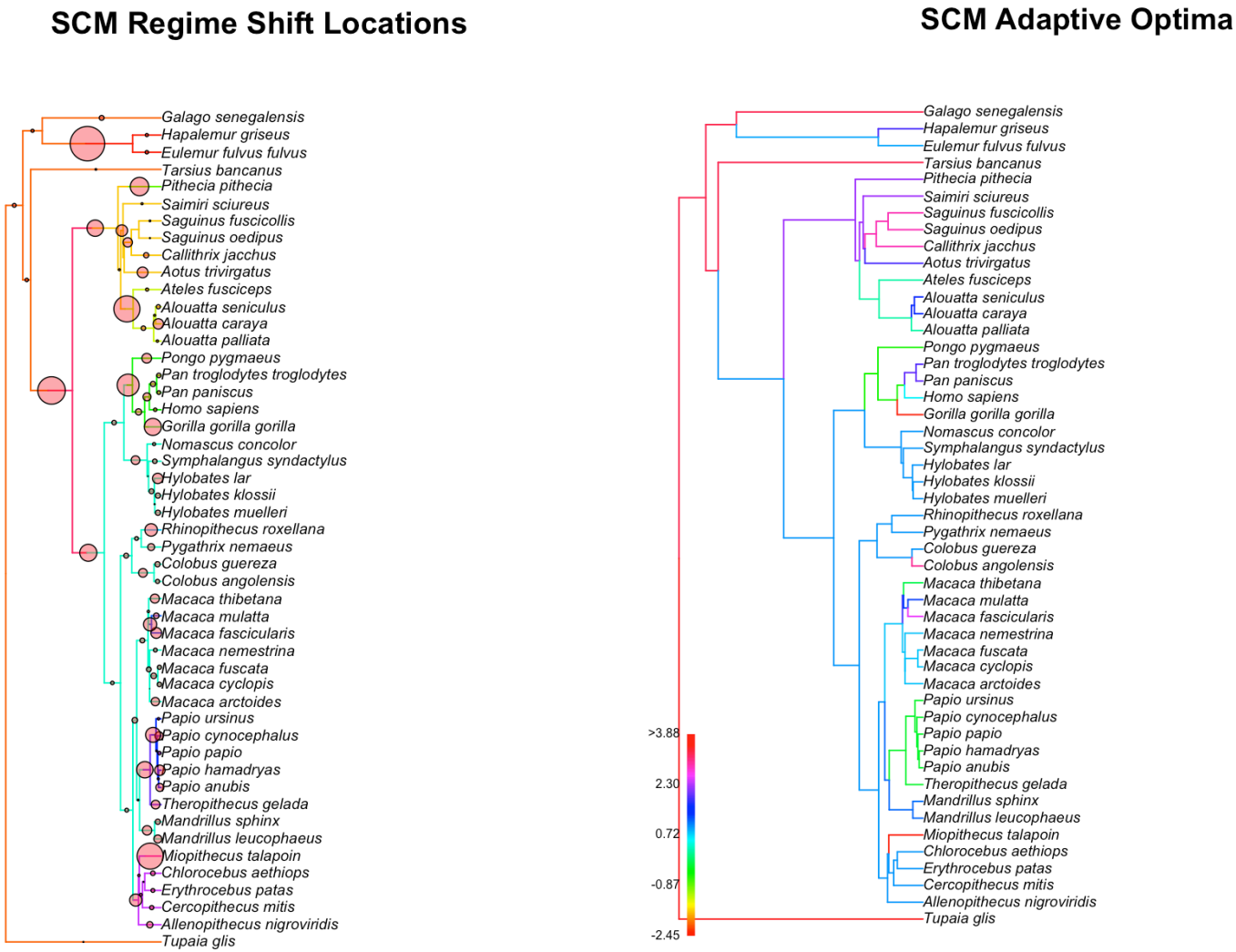
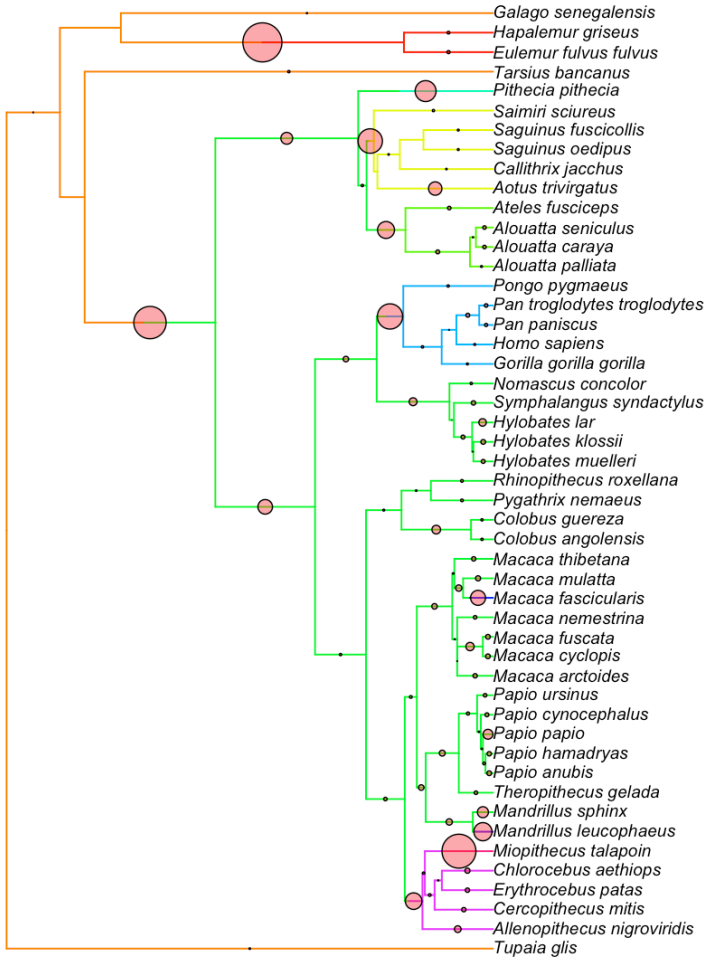


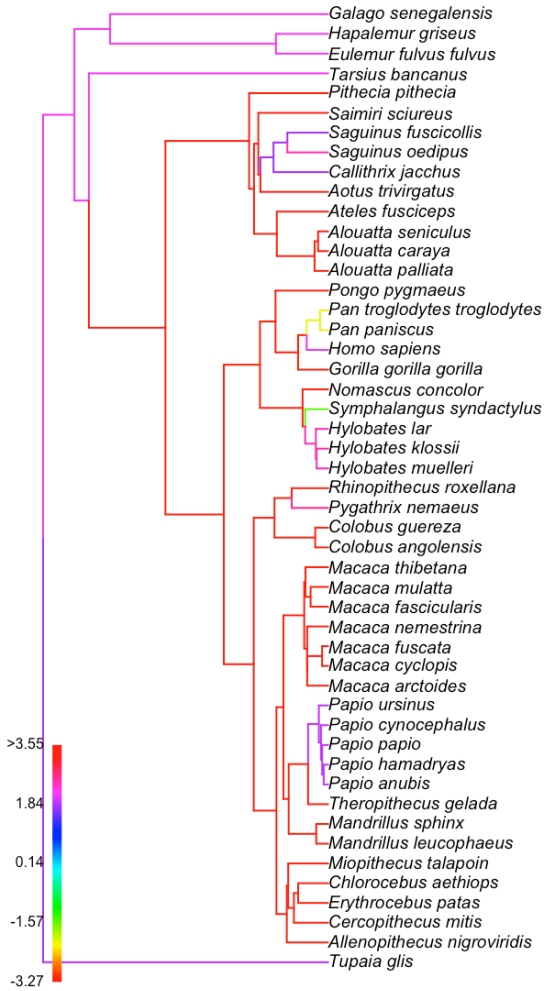
Figure SIII.4 a-l . Selective regimes and shift locations (left) and Adaptive Optima (right) of each trait for females. Selective regimes and adaptive optima are indicated by different colors; the size of the red circle are related to the posterior probability of the shift location and scale bars indicate optima values.

a. Sternocleidomastoid (SCM) Females

SNL Regime Shift Locations

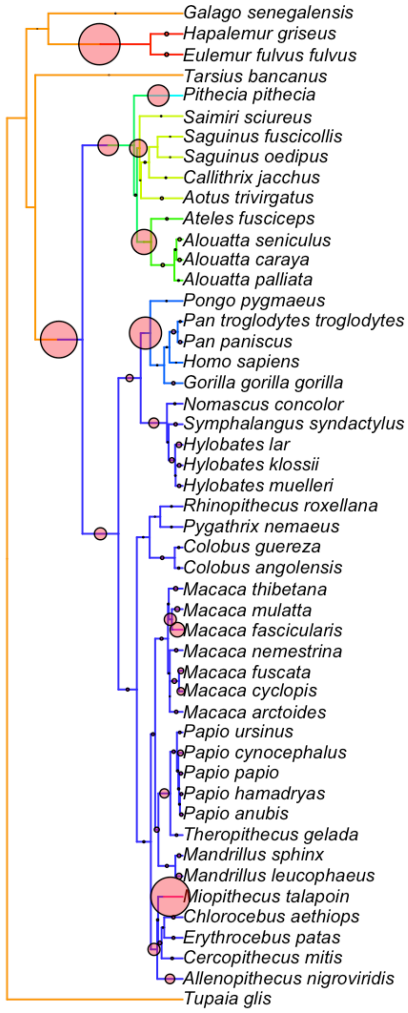


SNL Adaptive Optima

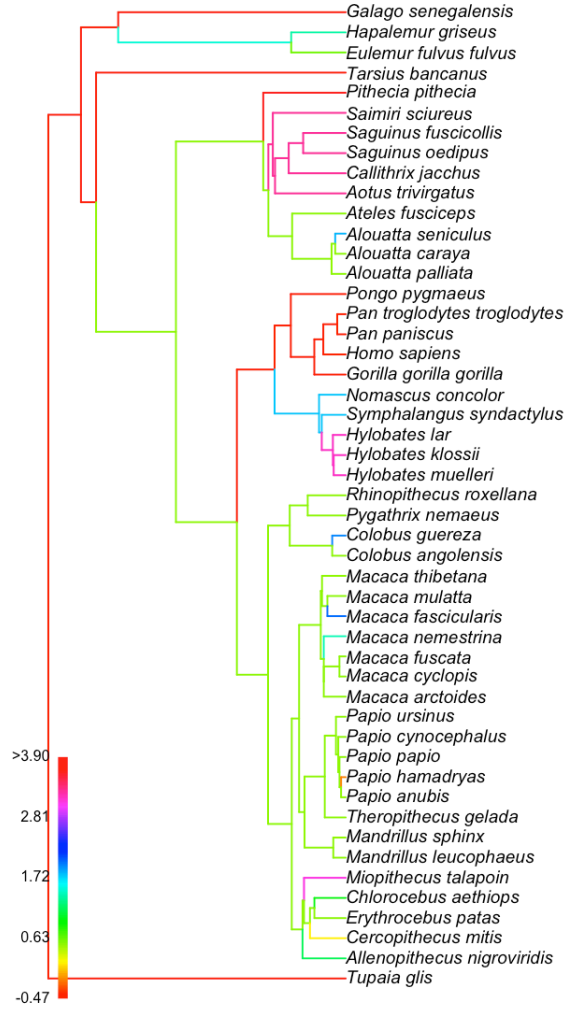


b. Superior Nuchal Line (SNL) Females

FMW Regime Shift Locations

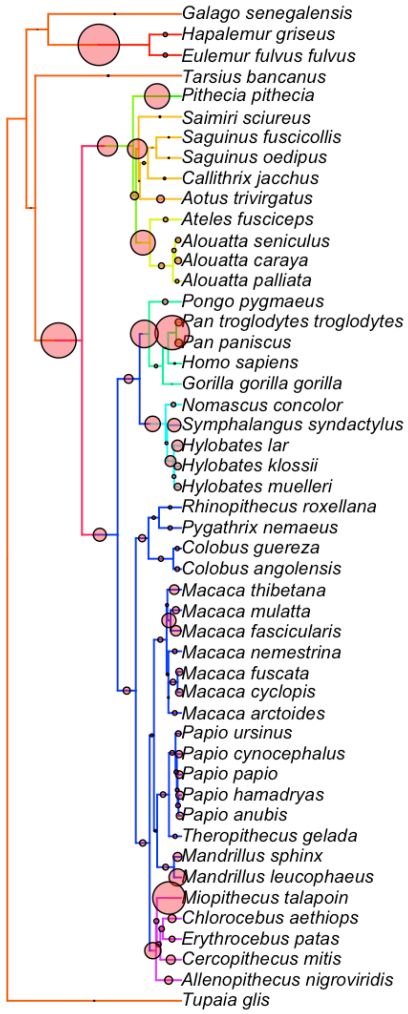


FMW Adaptive Optima

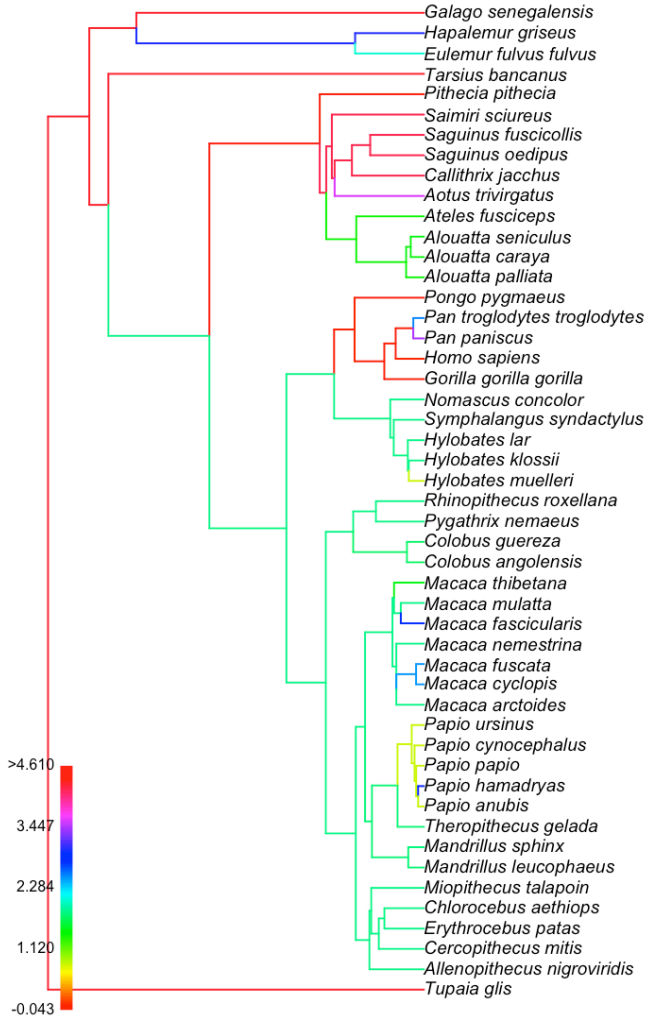


c. Foramen Magnum Width (FMW) Females

SSL Regime Shift Locations

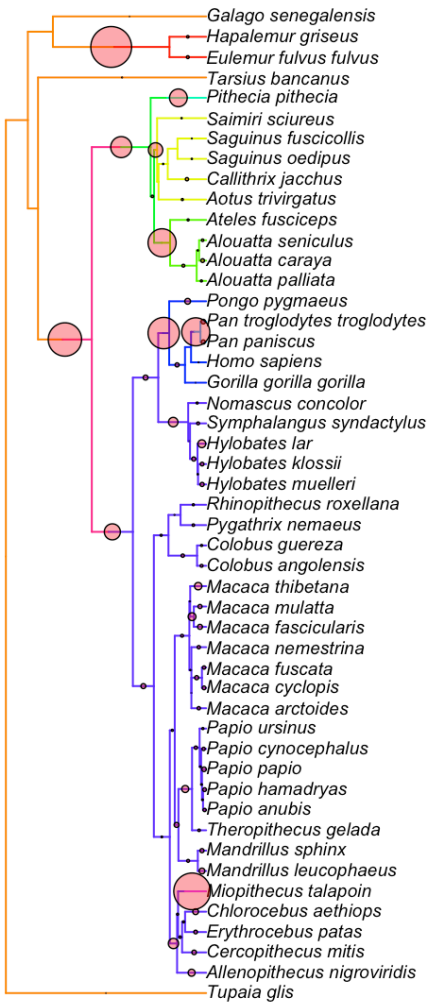


SSL Adaptive Optima

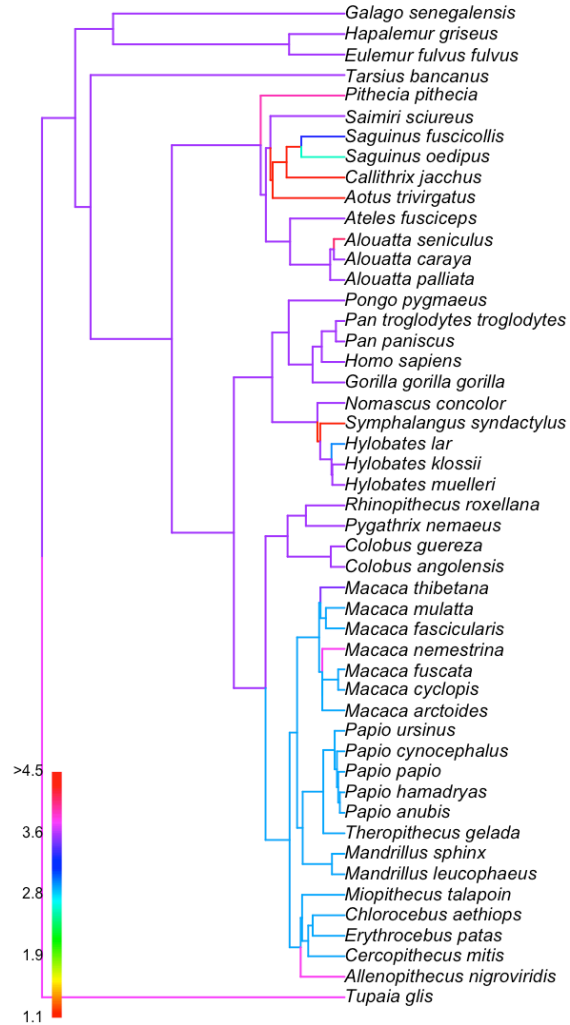


d. Scapular Spine Length (SSL) Females

SBL Regime Shift Locations

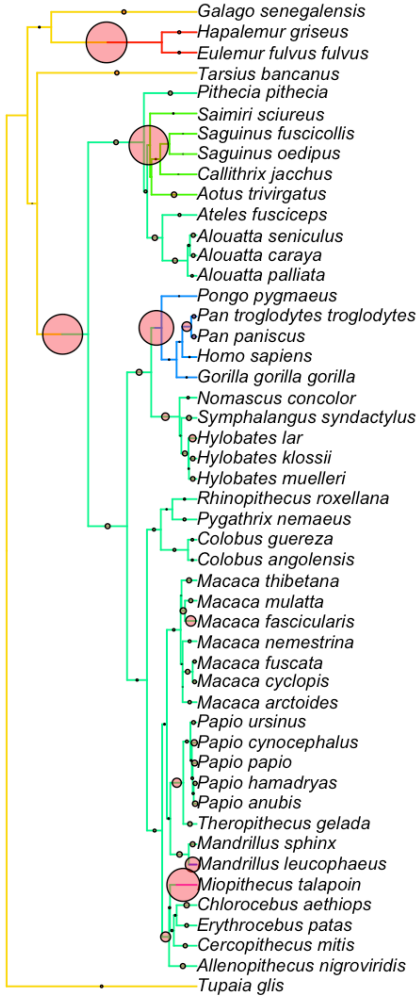


SBL Adaptive Optima

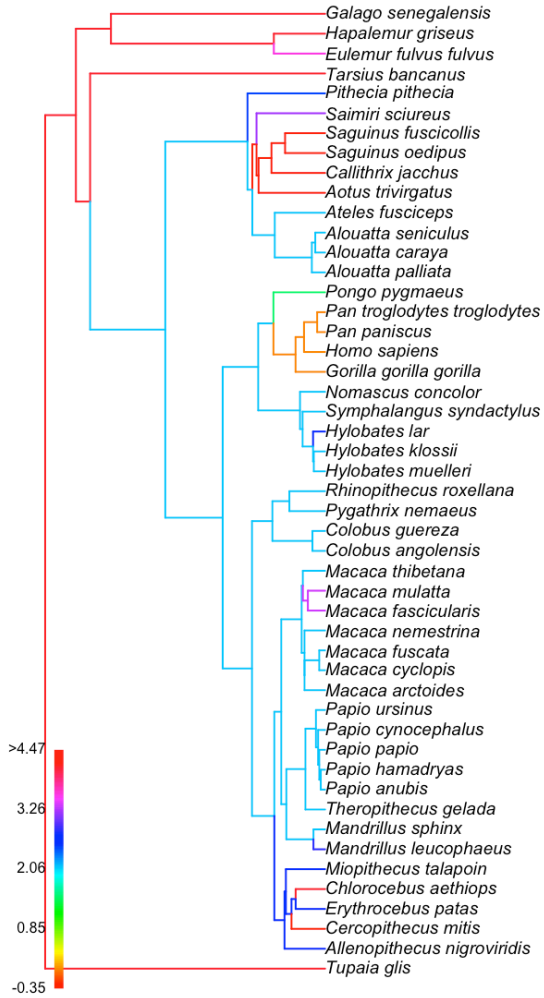


e. Scapular Blade Length (SBL) Females

VB Regime Shift Locations

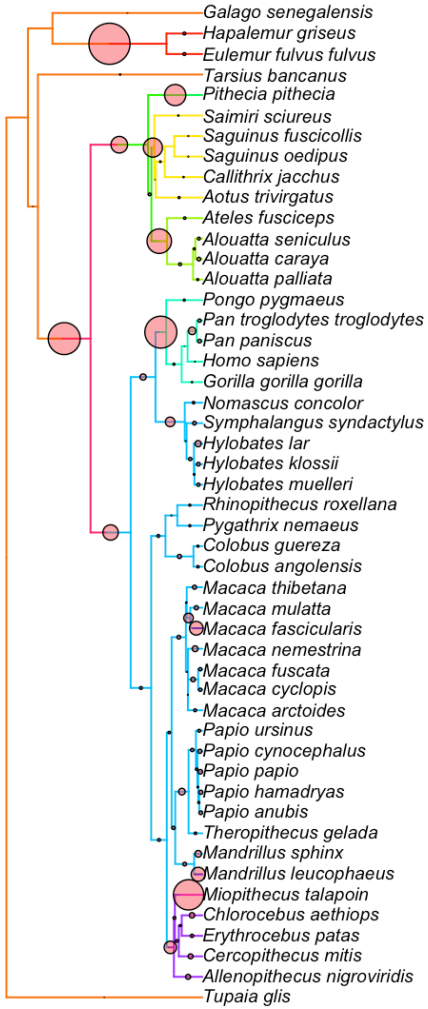


VB Adaptive Optima

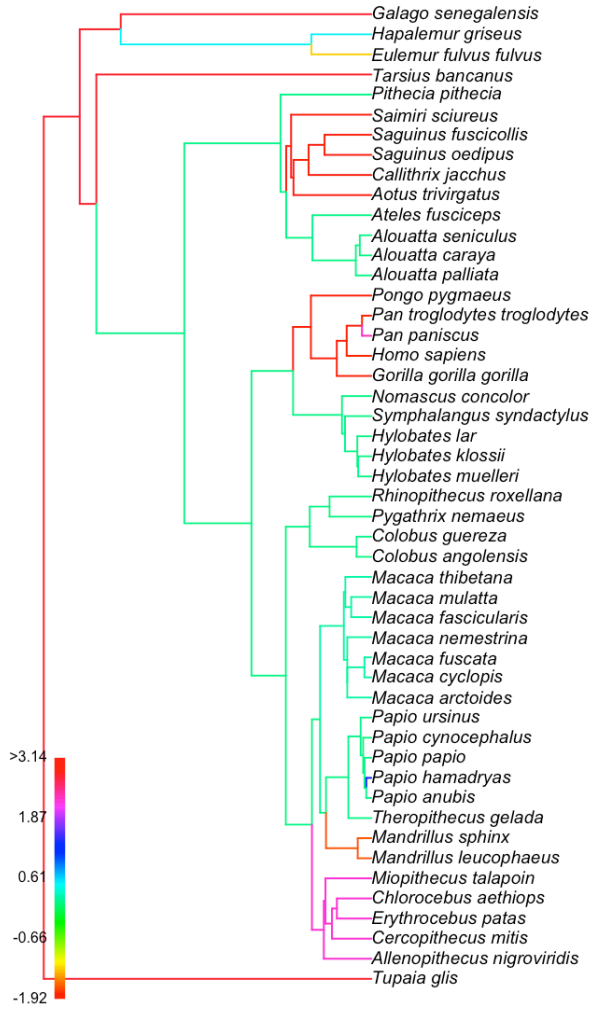


f. Vertebral Border (VB) Females

GW Regime Shift Locations

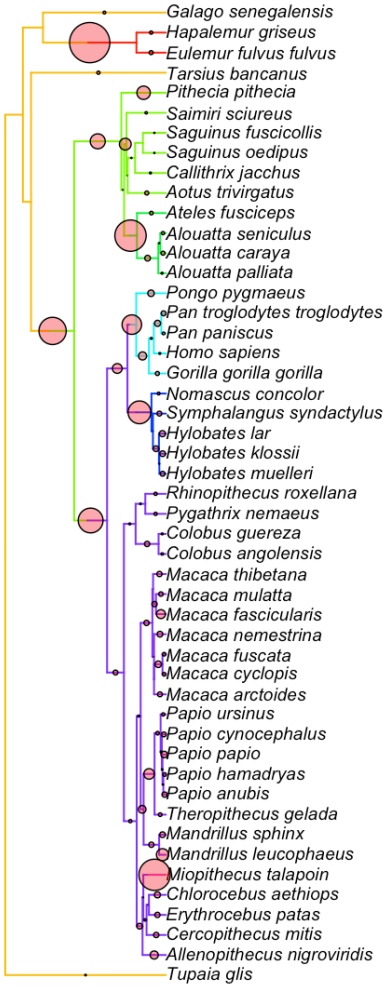


GW Adaptive Optima

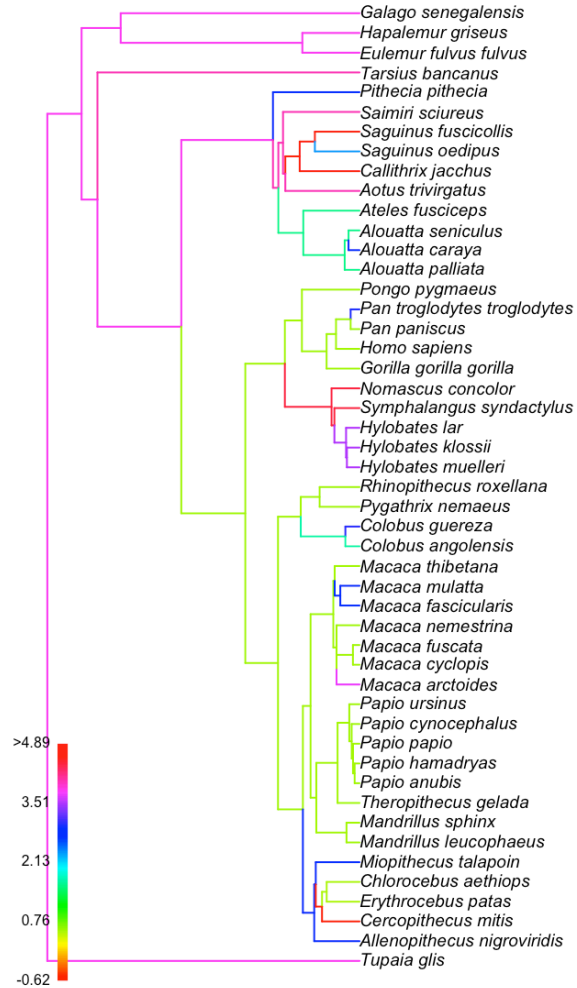


g. Glenoid Width (GW) Females

CLML Regime Shift Locations

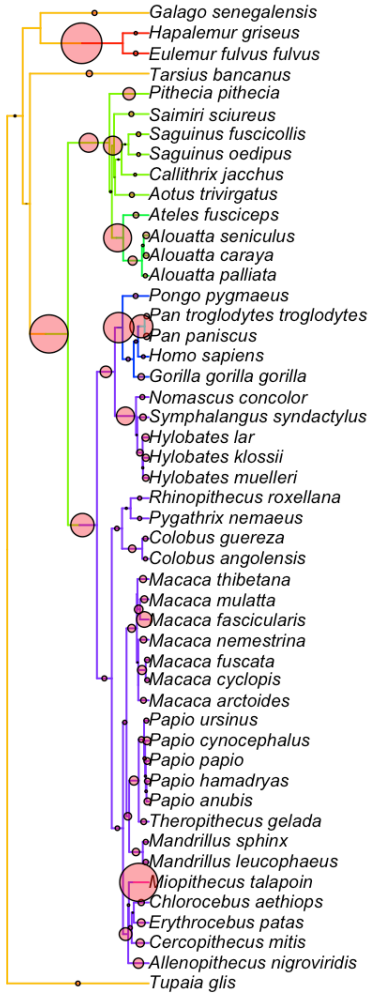


CLML Adaptive Optima

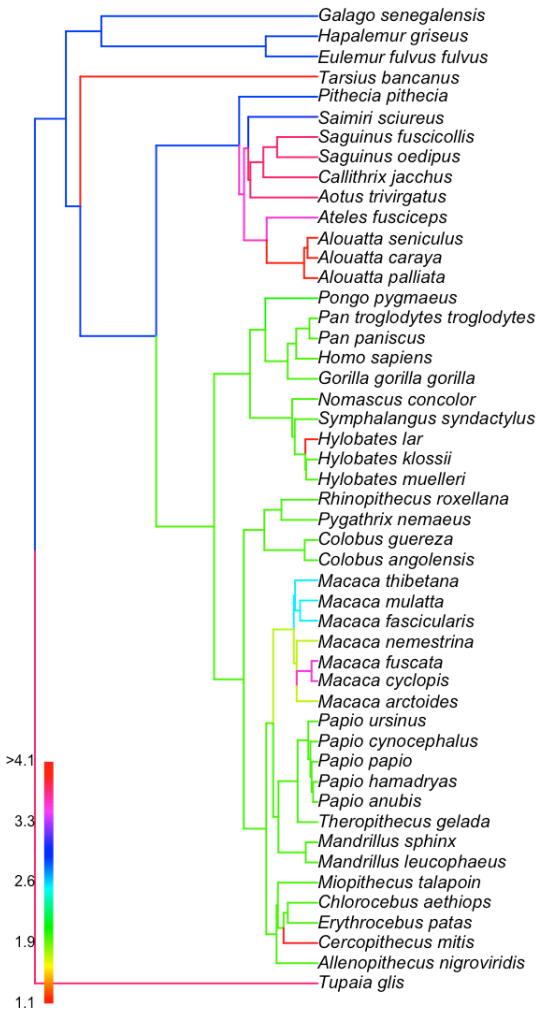


h. Clavicle Maximum Length (CLML) Females

LIH Regime Shift Locations

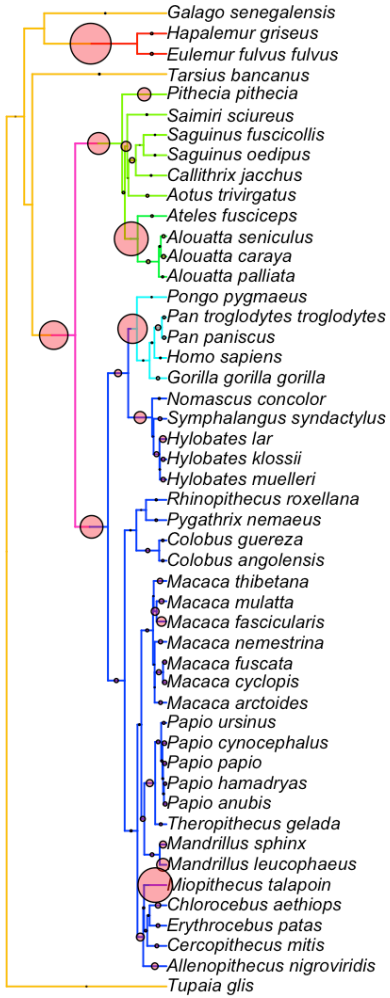


LIH Adaptive Optima

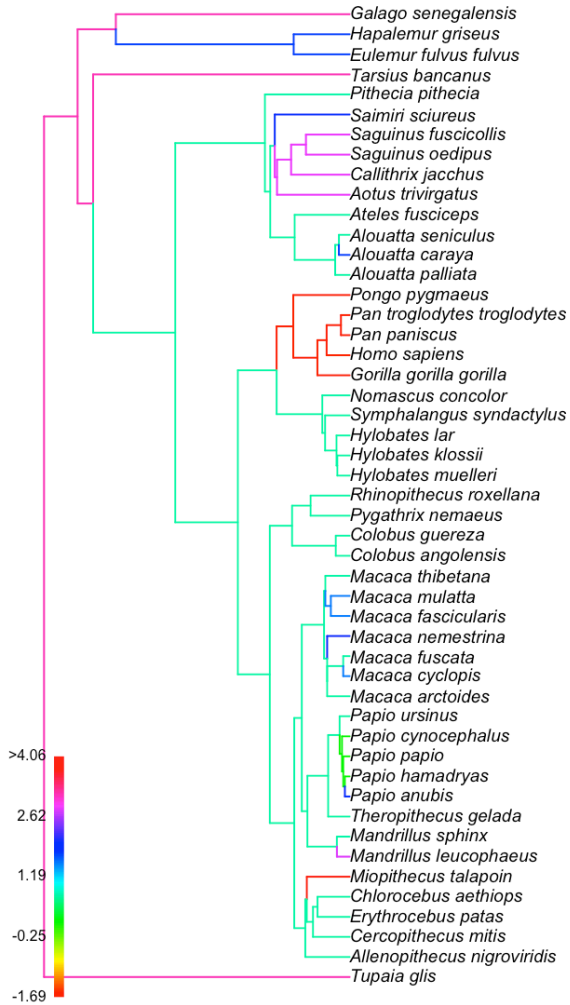


i. Lower Iliac Height (LIH) Females

AW Regime Shift Locations

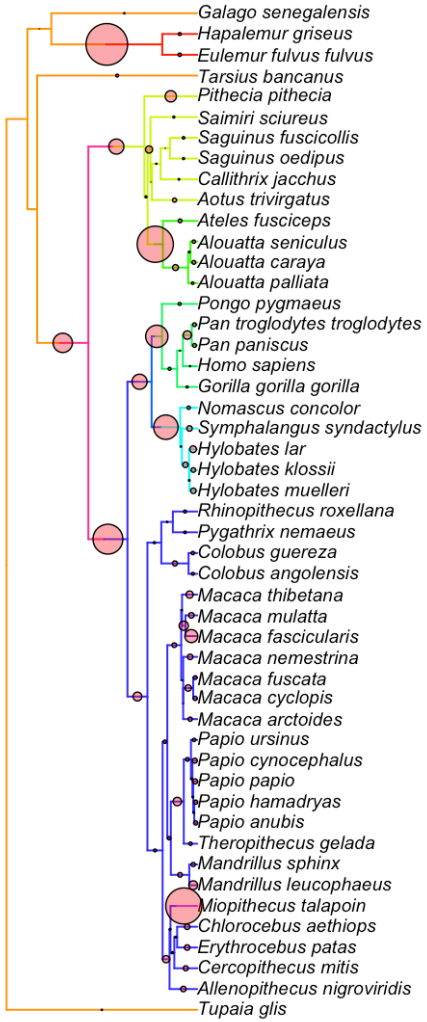


AW Adpative Optima

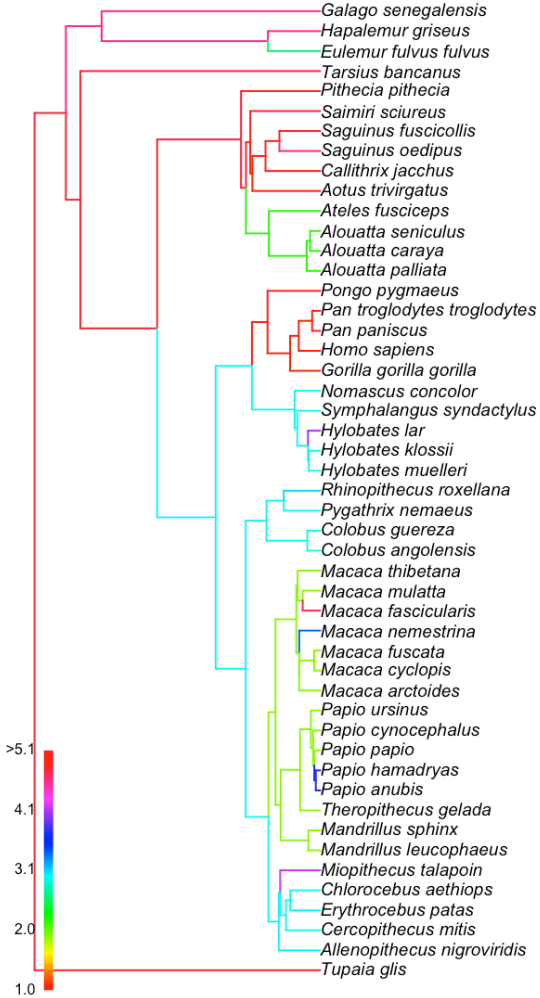


j. Acetabulum Width (AW) Females

HML Regime Shift Locations

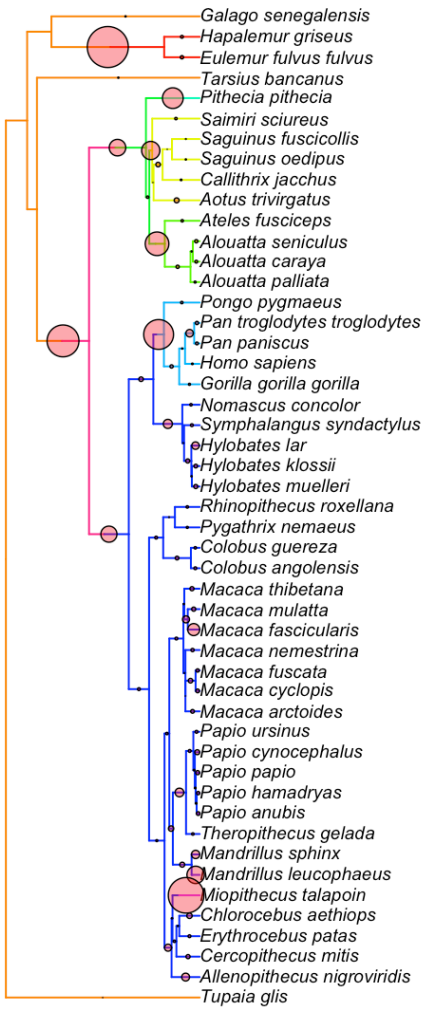


HML Adaptive Optima

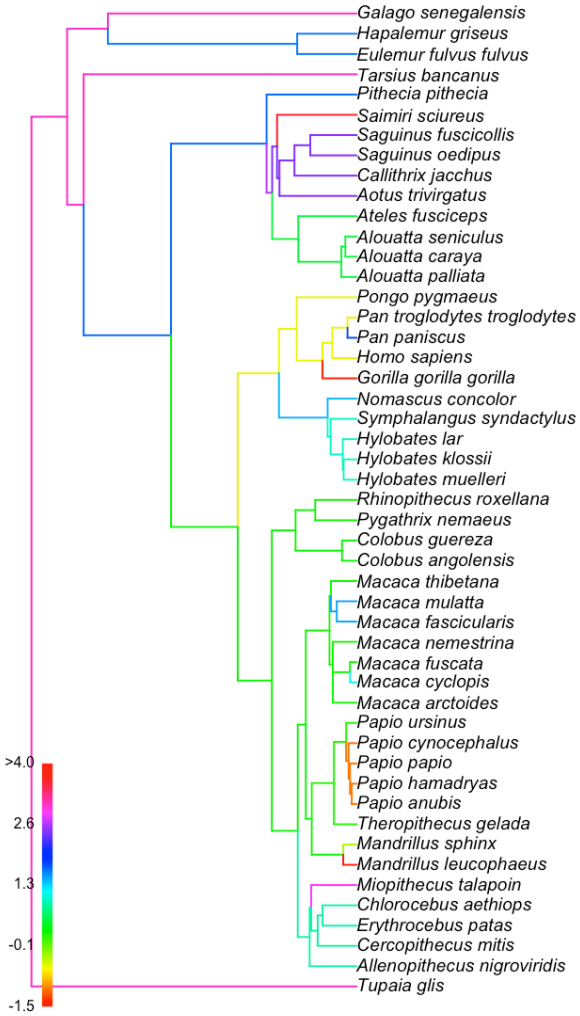


k. Humerus Maximum Length (HML) Females

HHW Regime Shift Locations



HHW Adaptive Optima



I. Humeral Head Width (HHW) Females

References

Lewton KL (2012) Evolvability of the primate pelvic girdle. *Evol Biol* 39:126-139.

Moore-Jansen PM, Ousley SD, Jantz RL (1994) *Data collection procedures for forensic skeletal material: report of investigations No. 48* (Forensic Anthropology Center, Department of Anthropology, The University of Tennessee, Knoxville).

Sears KE, Bianchi C, Powers L, Beck AL (2013) Integration of the mammalian shoulder girdle within populations and over evolutionary time. *J Evol Biol* 26:1536-1548.

White TD, Black MT, Folkens PA (2012) *Human Osteology Third Edition* (Academic Press, San Diego).

Young NM (2006) Function, ontogeny and canalization of shape variance in the primate scapula. *J Anat* 209:623-636.

CHAPTER V

DISCUSSION, LIMITATIONS, AND FUTURE RESEARCH

In this dissertation, I used quantitative genetic and phylogenetic comparative methods to explore how patterns of morphological variation in the primate shoulder girdle were shaped by potential covariances among traits, and broad-scale evolutionary forces for univariate trait evolution. Synthesizing the results of these studies to address three primary questions presented in the Introduction (p. 35-36, Chapter 1), three major points emerge to further our understanding of primate morphological evolution:

1. The shoulder girdle does not evolve independently, rather its evolution is influenced by traits of the basicranium and pelvic girdle.
2. Primates have different patterns of genetic covariance, and therefore different evolutionary potential, among these anatomical regions that affect their ability to respond to directional selection.
3. No single hypothesized evolutionary model – locomotion, resource acquisition, or habitat – best explains what selection factors motivated evolution across all primates.

These key findings are explored in detail below, in addition to their broader implications for the evolution of primate morphological variation. This synthesis is followed by a discussion of the study limitations and avenues for future research.

Non-independent Evolution of the Primate Shoulder Girdle

The various analyses of evolvability among the traits of the shoulder girdle, basicranium, and pelvic girdle, provide evidence of potential evolutionary covariance between these anatomical regions that results in their mutual constraint. Thus, the dimensions considered throughout this

dissertation do not evolve independently across primates. Therefore, differences in trait means across taxa cannot be interpreted as the direct result of selection pushing for specific mechanical functions, as the covariances among them suggest these differences may be the result of both direct and correlated responses to evolutionary forces.

While the relationship between the shoulder girdle and pelvic girdle are somewhat expected due to their analogous roles as limb girdles (see Sears et al 2015), the covariance between the basicranium and shoulder girdle is unprecedented. Olson and Miller (1958) suggested the basicranium and scapula may form an F-group, their designation for a highly correlated group of traits, based on the muscle connections between them. However, just because two anatomical elements or regions share physical connections and soft tissue attachments, and appear to be correlated, it does not mean they are morphologically integrated, nor does it mean there is evolutionary covariance among them. This dissertation is the first study to establish a potential evolutionary relationship between the basicranium and the shoulder girdle. While the results of these analyses are unclear regarding whether the basicranium or pelvic girdle exerts more evolutionary constraint on the shoulder girdle, it is apparent that the basicranium constrains the limb girdles more than either the shoulder girdle or pelvic girdle constrain its ability to respond to directional selection. This result may be indicative of the directionality of trait change that might be expected during primate evolution. Based on these patterns of constraint, we may expect to observe traits from the shoulder girdle and basicranium 'track' each other during primate evolution; where changes in one anatomical region follow changes in the other. There is potential for this phenomenon to occur in primates, as changes in the postcranial skeleton arise both concurrently and subsequently with cranial changes, such as forward-facing orbits and grasping hind feet (Cartmill 1974, 1992; Sussman and Raven 1978; Bloch and Boyer 2002; Kirk et al 2003; Sussman et al 2013; see also Silcox et al 2015). However, multivariate models of trait evolution using phylogenetic comparative analyses are needed to determine whether the traits used throughout this dissertation follow similar evolutionary trajectories.

In humans, the shoulder girdle has traditionally been considered to have an independent evolutionary history from both the basicranium and pelvis, as traits associated with brachiation appeared before those associated with bipedality in the fossil record (see Washburn 1951); this perception has persisted throughout the literature, as reflected in the way these anatomical regions have been studied in both human and non-human primates. Models of primate shoulder girdle evolution are typically restricted to scapula, as a majority of the muscles responsible for movement of the upper limb and stabilization of the glenohumeral joint attach to this bone (Diogo and Wood 2012; see also Stern et al 1977; Tuttle and Basmajian 1977, 1978; Jungers and Stern 1984; Larson and Stern 1986; Larson 1993, 2015). Correlations between muscle function and variation in scapular trait morphology are often used to interpret fossil remains and infer evolutionary relationships based on patterns of morphological difference (see Oxnard 1967; MacLatchy et al 2000; Larson 2007, 2013, 2017). However, the results of the analyses of this dissertation do not support models built around a single element, let alone a single trait. As iterated throughout this dissertation, such models implicitly assume independent evolution of traits, which ignores these covariances, thus resulting in inaccurate models of shoulder girdle evolution. The systematic decapitation of our subjects in analyses of primate shoulder girdle morphological evolution is no longer justified.

The results of the different evolvability measures estimated in this dissertation have major implications for interpretation of the fossil record, as the form-function relationships of scapular traits may not reflect the nuances of the evolution of this element. The identification of morphological change within single anatomical regions, or single skeletal elements, and the interpretation of how those relate to the functional differences among extinct primates are unaffected by these results and remain important for the understanding of primate evolution. However, extreme caution must be taken when ascribing evolutionary explanations to these patterns. Comparisons of morphological trends in the fossil record and placing them in a historic context allows for the creation of evolutionary hypotheses (Weishampel 1995; Lauder 1996; Ward 2002; Pearson and Lieberman

2004), which can be assessed through phylogenetic comparative methods to determine the role of selection in shaping morphological trends.

The potential evolutionary constraint observed among the shoulder girdle, basicranium, and pelvic girdle may arise from multiple causes. It is possible these relationships have arisen from environmental variance in the form of shared function that occurs developmentally. These relationships may also be wholly genetic, as evolutionary covariances can arise through both pleiotropy or linkage disequilibrium (Falconer 1989). Constraint among the shoulder girdle, basicranium, and pelvic girdle is most likely from a combination of these three determinants of variation. Developmental, functional, and genetic evolutionary covariances that result in emergent anatomical complexes form a functional trait complex. While conceptually similar to a module, functional trait complexes are limited, and characterized by the developmental and functional associations among traits. Functional trait complexes afford a potential set of testable hypotheses for how to better determine the structure of evolutionary covariance. However, due to the lack of information regarding the underlying genetic architecture to the developmental and functional relationships between the shoulder girdle, basicranium, and pelvic girdle, the existence of functional trait complexes cannot be assessed through this dissertation. Nevertheless, our results suggest this concept may be fruitfully assessed both for the shoulder and basicranium, and the shoulder and pelvis through combining phylogenetic comparative methods with experimental developmental biology. The work on the primate hands and feet (Rolian 2009; Rolian et al 2010), and limbs (as reviewed in Young 2017) suggest these regions may also comprise functional trait complexes. Evidence for the functional trait complexes have implications for the development of evolutionary models both among primates and other vertebrates.

Patterns of Trait Covariance Across Primate Taxa

The role of the evolutionary constraint in shaping primate morphological variation was further explored by assessing the evolutionary flexibility (potential constraint on trait response to selection)

and morphological integration between the shoulder girdle, basicranium, pelvic girdle, and distal humerus among eight primate taxa: *Alouatta, Colobus, Homo, Hylobates, Macaca, Pan, Papio,* and *Pongo*. Additionally, phylogenetic independent contrasts (PIC) were used to calculated phylogenetically corrected correlations among traits. Results from these analyses demonstrate different estimates of evolutionary flexibility and morphological integration among paired groups of traits; indicating paired regions, such as the shoulder gridle and basicranium, have different potentials to respond to directional selection. This would suggest that within an organism, there exists different degrees of covariance between anatomical regions, that results in unequal constraint between paired groups of regions. When compared among the eight taxa, the strength of the constraint between groups of paired anatomical regions differs for each species. Furthermore, there are several consistent trends to how the variance and co-variance is apportioned between these groups of paired regions among taxa. All together, these results suggest differences in the evolutionary potential among primate taxa may contribute to the morphological variation observed in the primate shoulder. Other studies (Young 2004; Rolian 2009; Young et al 2010; Lewton 2012) have also demonstrated considerable variation in the evolvability and integration of postcranial traits among primates, where less constraint is observed among apes compared to monkeys which has been proffered as an explanation to the divergent morphologies observed among apes.

Of interest are the observed differences among the patterns of evolutionary flexibility among the eight taxa, especially the four apes. *Alouatta, Colobus, Homo,* and *Hylobates* share similar evolutionary flexibility among groups of paired anatomical regions, whereas a different pattern is observed among *Pan, Macaca,* and *Papio,* and *Pongo* has the most divergent pattern. For most taxa, the paired anatomical groups with the lowest evolutionary potential are those with shared developmental and biomechanical associations among them. For example, the development of the scapula relies on the initial patterning of the limb buds (Boulet et al 2004; Min et al 1998), and these two elements are physically connected via musculature that abducts the arm and stabilizes the glenohumeral joint (Diogo and Wood 2012). Furthermore, these two skeletal elements comprise the

shoulder joint itself. These relationships may indicate stronger covariances among them compared to traits that do not interact during development or through mechanical function, like the basicranium and humerus. However, the outgrowth of the limb bud is not necessary for scapular development, as such, a degree of evolutionary independence is possible between these two elements (Boulet et al 2004; Min et al 1998). This may explain why quadrupedal taxa with shoulder girdles more adept for arboreal locomotion, such as *Alouatta, Colobus,* and *Hylobates*, have greater constraint between the shoulder girdle and humerus than those more adept for terrestrial locomotion like *Pan, Macaca,* and *Papio*. The different requirements of muscle stabilization of the glenohumeral joint during arboreal and terrestrial quadrupedalism (Preuschoft et al 2010) may be influencing the patterns of constraint among taxa. Humans are a terrestrial organism; however, the shoulder joint is free from the constraints of locomotion and has maintained a more mobile versus stabile morphology. This may explain why humans share patterns of constraint with the arboreal quadrupedal taxa. Differences in the types of associations among anatomical regions may be contributing to the variation observed in the evolutionary constraint among these regions.

It is also possible the differences between taxa in the morphological integration and evolutionary flexibility observed among paired groups of anatomical regions is indicating underlying differences in the developmental program among these taxa that affect the bauplan of these taxa. Variation in the timing and rate of developmental events (heterochrony) can lead to differences in the size and shape of structures (as reviewed in McKinney 1988; Klingenberg 1998; Schlosser and Wagner 2004). Such differences may be affecting the proportions of traits, such as limb (see Müller 1991) or the somatic patterning of the scapular blade (Huang et al 2006). Differences in development and function may be driving the patterns of evolutionary potential observed among primate taxa, however, it is unknown how these two determinants of variation interact to affect the resulting adult morphology. Different patterns of evolutionary potential among primate taxa may also be due to other factors such as ecological or functional differences. This may be especially true for *Pongo*, as this taxon substantially deviates from the broad primate pattern. The unusually low evolutionary

flexibility between the basicranium and humerus in *Pongo* compared to other primate taxa may be affecting the relationships among traits, body size, and their covariance. *Pongo* has a disproportionately high intermembranal index for its size due to the length of the humerus (Jungers 1985). Additionally, the forelimb of *Pongo* scales positively with body size to a greater degree than other primates (Jungers 1985), and it is possible there is some underlying covariance with body size between the basicranium and humerus that is affecting the results of these analyses. However, the nuanced differences among primate taxa has yet to be determined before any of these explanations can be accepted.

Another potential explanation for the different patterns between primate taxa in morphological integration and evolutionary potential among paired anatomical regions could be the differences in environmental pressures experienced by these different species. Among the taxa sampled for this study, *Pan, Macaca,* and *Papio* are the only semi/terrestrial quadrupeds, and *Pongo* is the only large-bodied suspensory, arboreal primate (Zihlman and Underwood 2019). Different environments present organisms with different selective challenges that may affect the underlying covariances among traits. The genetic variance-covariance matrix (G) underlying the morphological trait covariance is affected by both selection and the environment (Pigliucci 2005, Wood and Brodie 2015). Gradual changes to the G-matrix can occur through traditional evolutionary processes (selection, genetic drift, gene flow, and mutation; Arnold et al 2008), but the direction, magnitude, and geometry of the G-matrix can also be rapidly altered by changes in the environment (Wood and Brodie 2015; reviewed in Sneigula et al 2018). Additionally, suppressed genetic variation can be unlocked with changes to the environment (McGuigan and Sgro 2009), which can then be further affected by selective pressures (Schroeder and Ackermann 2017). The differences in the morphological integration and evolutionary flexibility observed among primate taxa in this dissertation may be due to the combined effects of the environment on the structure G-matrix, and the downstream effects this may have on both the development and function of anatomical regions. The PIC shows different correlations among traits, so it is likely that not all traits are equally playing

roles in the evolutionary covariances and constraint indicated by the estimates of evolutionary flexibility and morphological integration. It is also possible that there is an emergence in multivariate morphospace where individual traits together have important effects that are not visible at the univariate level.

The differences in covariance among the shoulder girdle, basicranium, pelvic girdle, and humerus among primate taxa, and the potential rapid evolution of the G-matrix due to fluctuations in the environment has serious implications for researchers modeling primate morphological evolution. Due to the differences in the ability to respond to directional selection among primate taxa, it would be ill-advised to use a 'model' species to explain how morphological evolution among primates took place. While there is evidence for stronger evolutionary constraint among select anatomical regions, the magnitude of that constraint varies among primate taxa to the extent that it is not possible to predict how one taxon may respond to the force of directional selection based on the responses of another. These results also proffer caution when applying evolutionary trends observed among extant taxa to the fossil record, as it cannot be expected that similar patterns of trait covariance will remain stable across species with different environments and across evolutionary time. Such questions can be addressed, however, through the application of phylogenetic comparative analyses on fossil remains to investigate the evolutionary trajectory of traits among extinct and living primates to assess the role of selective forces in shaping in shaping the observed morphologies.

Shape-related Functional Variance and Primate Morphological Evolution

The phylogenetic comparative methods (PCM) used in Chapter IV of this dissertation show that no single model of selection – habitat, locomotion, or diet – best explains the factors that motivated trait evolution in the primate shoulder. Rather, the results of this study indicate that models of evolution based on macroevolutionary events better fit the evolution of traits than any one of the primary models suggested by previous studies. However, multiple selection factors, along with trait covariances across the axial and appendicular skeleton likely led to primate morphological diversity.

Primate morphological diversity in the shoulder, basicranium, and pelvic regions evolve both in response to selection, and through the correlated responses to selection among genetically covariant traits. Among the single factor hypotheses of primate morphological variation tested, a habitat model offered the best fit for the variation among most of the traits of the shoulder girdle, basicranium, pelvic girdle, and humerus. The way 'habitat' was characterized in this dissertation, it is actually a multifactorial classification that overlaps with both locomotion and diet, and so it more closely resembles an ecological niche model (see Lewontin 2000). As primates are found within a wide variety of environments (Lynch Alfarao et al 2015; Silcox et al 2015; Zihlman and Underwood 2019), it is likely combination of different functional demands contributed to the observable morphological variation among primates. However, when compared to the unrestrained *bayou* model, even habitat fails to fully explain the variance among primate species. This has implications for further studies of primate morphological evolution, as this research has shown that single factor hypotheses do not fully capture the morphological variation present among primates, and will be missing valuable information of how primates evolve.

The best model of primate morphological evolution identified by this dissertation entails selective pressures that push for shifts in the primate bauplan during lineage divergence, primarily at the taxonomic level such as Parvorder. This would imply that morphological differences among species or genera may have occurred under several scenarios. Intergeneric differentiation may be the result of the differences in morphological integration and evolutionary potential causing taxa to have differential responses to similar pressures of selection. It is also possible exposure to different ecological factors drove primate diversity after the initial changes to the bauplan. These changes could also be the result of stochastic processes (see Uyeda and Harmon 2014). Under all of these scenarios, the covariances among traits will contribute to the ultimate morphological variation among primate species. Regardless of which of these scenarios occurred, these results suggest a fairly conserved fundamental morphology among primates. These results contradict hypotheses of specialized evolution for any one primate species, or clades being divergent due to unique selective

optima. Rather, this study reinforces the idea that primates are fairly generalized, at least in a univariate context.

This is an especially interesting result for ape, and primarily human, evolution. The results of the PCM indicate apes are all under a similar OU optimum for most traits assessed in this dissertation, and while there is no way to reconstruct the optimum, it is evident that morphological variation among apes is based on how each species responds to the shared selective pressure. Additionally, there is no specialized selection regime for *Homo*, rather, humans and *Gorilla* share an adaptive optimum for many of the traits assessed in this study. This result may reflect a gorilla-like ancestral character state for apes (see Kivell et al 2013; Almécija et al 2015), or that humans and gorillas represent a different pattern of divergence from a common ancestor compared with *Pan*. It is also possible that humans experienced selection early in their divergence as a taxonomic group, with further evolution being driven by neutral processes (see Roseman and Weaver 2007, Grabowski and Roseman 2015, Roseman 2016). This may imply a deep ancestral optimum for many of the traits in humans that has not changed, and that humans have continued on a similar trajectory as our ancient ancestors.

The results of the PCM also demonstrate that the selective regimes for each of the fifteen traits evaluated in this analysis do not follow a pattern of size-related variance driving the morphological differences among primate species. Size is an important factor driving mammalian evolution (Marroig et al 2009; Porto et al 2013), however, our result suggest it is not the only potential factor driving the variance among primates. Shape-related functional variance also plays a role in the morphological variation in primates, and among the traits of the shoulder, basicranium, pelvis, and arm evaluated throughout this dissertation. This has broader impacts for the results of all three research directives in this dissertation, as it implies that relationships elucidated among anatomical regions are not just reflected similarities in size, rather, there is a signal of the morphological variance due to functional differences among taxa that can be used to explore the intricacies of trait covariance on primate morphological evolution.

Implications for Future Studies of Primate Evolution

The findings of this dissertation have serious implications for the study of primate morphological evolution. This research demonstrates that the shoulder girdle does not evolve independently of other anatomical regions, and the covariance patterns among anatomical regions vary between primate taxa. Furthermore, the evolution of primate morphological diversification of the traits comprising the shoulder girdle, basicranium, pelvic girdle, and humerus cannot be explained by single factor hypotheses. Rather they are best explained by changes in the primate bauplan occurring during selection-driven lineage divergence, followed by subsequent species diversification. Overall, the results of this dissertation suggest that morphological differentiation between different primate genera may have arisen due to the differences in the evolutionary constraint among anatomical regions, that may in turn result in the differential responses to similar pressures of directional selection. The important factor may not be what selection a taxon is subjected to, but rather the taxa of interest and its shared ancestry (i.e., its location on the evolutionary tree).

There is an underlying assumption to the discussion of selection models, that given enough time, if two taxa are subjected to the same selection pressure, you would expect them to converge on similar morphologies. The results of this dissertation do not upend this assumption, rather, they affect how morphological patterns are interpreted in an evolutionary sense. The morphologies of two taxa may converge due to similar selection, but due to shared ancestry and how traits actually covary, they may not be able to respond to the selection pressure. The responds to directional selection may be similar among taxa, but due to differences in the underlying covariance structure among traits, it may take longer for a taxon to respond to selection in the same way. Additionally, similar morphologies do not mean that they arose due to the same evolutionary conditions. Similar morphology does not translate to similar evolution, as correlated responses among traits could result in similar morphologies. Disentangling the interwoven factors that shape the morphological variation of the primate shoulder, can be accomplished through the application of quantitative genetic and phylogenetic comparative methods.

The results of this dissertation emphasize that deterministic hypotheses of primate morphological evolution do not accurately reflect the relationships between traits, elements, anatomical regions, or taxa. Furthermore, the results of the various evolvability measures and phylogenetic comparative analyses throughout this dissertation demonstrate the limitations to the degree evolutionary processes acting on extant primates can be applied to the fossil record. The covariances among the traits of developmentally and mechanically connected anatomical regions, make the assessment of patterns of evolution from individual traits, or within regions, unreliable indicators of the processes that shaped them. Form-function relationships remain important for understanding of the patterns of variation observed among extinct taxa, but these cannot decipher the interwoven factors, such as ecological demands and trait covariances, that produced the observed morphology. Thus, interpretations of evolutionary process from patterns of morphological change in the fossil record will be misleading. Additionally, the differences in the strength of the covariances observed among extant species, and the potential for the genetic covariance matrix to be rapidly altered by the environment, make the translation of the evolutionary forces acting on one primate species to explain the evolution of another ill advised. To better address questions of evolution from the often-fragmentary traits within the fossil record, phylogenetic comparative analyses should be used to directly test the hypotheses created by the patterns of morphological change observed among fossil specimens. Even the application of univariate models for these approaches are beneficial to elucidate how individual traits may evolve, and create a baseline understanding of trait evolution. As additional specimens are recovered, multivariate models can be assessed to determine whether extinct species evolved in similar or different manners compared to living primates.

Limitations of Study

The major limitations to each study are discussed in each chapter. The results of these analyses are limited by the available data. Despite being one of the largest, and most comprehensive, both in terms of taxa and skeletal elements measured, the availability of specimens that had both cranial

and post cranial skeletal elements limited the sample sizes for may taxa. As a result, for the analyses of evolvability and morphological integration, several species of the same genus had to be pooled to achieve the sample sizes recommended by Grabowski and Porto (2017) for evolvability statistics. While the differences in the genetic covariance matrices are presumed to be more different between genera than among species of the same genus, our results indicate the differences in the genetic architecture among closely related species. Thus, the results for those taxa that had to be pooled, may be slightly skewed, and in an unanticipated way. For some taxa, the collection of additional specimens is possible, but for others, I measured all available specimens in North American institutions.

The inclusion of additional skeletal elements may also improve the outcomes of this study. The addition of distal limb elements, such as the phalanges or tibia, would provide skeletal elements that are truly functionally divergent from the shoulder girdle. Thus, providing more independent skeletal elements with which to assess the covariance among traits; this may provide a baseline of covariance that is the result of being from the same organism, but more independent of the functional constraints shared with the shoulder. The inclusion of traits from the thorax may also be of interest, as the close proximity of the shoulder girdle with elements such as the vertebrae and ribs may contribute to covariances among these traits as well.

As discussed in Chapter IV, "Study Limitations", the Bayesian phylogenetic comparative methods used in *bayou* are sensitive to the parameters chosen to produce the prior distribution. While diligent efforts were made to select prior parameters that would produce results that are consistent with the biological reality of primates, it is possible that the parameters for the priors used are producing misleading results. In that instance, the inferences based on the specific ways the different taxa responded to OU optimum may be misinformed. However, I am confident the patterns of regime shifts occurring at major phylogenetic branching are reliable, as a similar result was observed for several different prior parameters. While a level of uncertainty will always persist in the results produced from a Bayesian analysis, the patterns observed in this study fit will with the known

relationships among primates, and any biases caused by the prior are presumed to be minimal. As discussed in Chapter IV, no model will perfectly capture the biological reality of the system explored, and as our understanding of biological and evolutionary context of primates improves, so will our models of trait evolution.

Future Research

This dissertation lends itself to several avenues of future research. As noted throughout this dissertation, there are a number of taxon-specific questions that need investigation, but there are several more broad-scale directions that will be explored here. On a practical sense, the collection of additional data, primarily for distal limb elements, will be beneficial to assess the relationships identified throughout this dissertation. The incorporation of a truly functionally and developmentally distinct element would help provide better context for the extent of the relationships among the axial skeletal elements evaluated. Improving the sample sizes for several primate taxa, such as *Gorilla*, will allow for better representation in the comparison of evolutionary potential across taxa and may help resolve some of the lingering questions of primate evolution unresolved by this dissertation.

Due to the relationship between the shoulder girdle and basicranium elucidated by this dissertation, it would also be of interest to further explore the extent to which the cranium affects the evolution of the shoulder. While the facial cranium and neurocranium have separate developmental pathways from the basicranium (Lieberman et al 2000a), the basicranium influences the shape of the rest of the cranium (Lieberman et al 2000b). Whether or not this relationship translates into evolutionary constraint among the different parts of the cranium, and if there are downstream effects to the shoulder can be investigated through quantitative genetic approaches, and my yield additional information regarding how these anatomical regions evolve.

An important next step to this dissertation is expanding the univariate models of evolution tested herein using phylogenetic comparative methods to multivariate ones. While it was imperative to understand individual trait evolution prior to performing a multivariate analysis, the potential

covariances and constraint among traits identified in Chapters II and III are not reflected in the phylogenetic comparative analysis. In fact, the results of the univariate models tested did not correspond well with the expectations set by the various measures of evolutionary potential performed throughout this dissertation. To assess whether or not these relationships are borne out, a multivariate model of shoulder girdle evolution must be tested.

Within this dissertation, the concept of a functional trait complex has been proposed for the traits of the basicranium and shoulder girdle, as well as those of the shoulder and pelvic girdles due to the functional and developmental covariances among them. To successfully demonstrate the existence of functional trait complexes, the developmental and mechanical covariances must be successfully demonstrated, and that they exerted evolutionary covariance. The combination of phylogenetic comparative methods with experimental developmental biology would provide an avenue by which to assess this concept. Such an endeavor is currently in the works, and I am excited to take the next step to fully investigate the processes by which anatomical traits evolve.

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VITA

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