1 **New endemic platyrrhine humerus from Haiti and the evolution of the Greater Antillean**
2 **platyrrhines**

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Abstract

Much debate surrounds the phylogenetic affinities of the endemic Greater Antillean platyrrhines. Thus far, most phylogenetic analyses have been constructed and tested using craniodental characters. We add to this dialogue by considering how features of the distal humerus support or refute existing hypotheses for the origins of fossil Caribbean primates, utilizing three-dimensional geometric morphometric data in combination with character based cladistic analyses. We also add to the sample of fossil platyrrhine humeri with the description of UF 114718, a new distal humerus from Haiti.

We reconstruct UF 114718 to be a generalized, arboreal quadruped attributed to the species *Insulacebus toussantiana*. Our results from phylogenetic analyses lend some support to the idea that some Greater Antillean fossil taxa including *Xenothrix mcgregori*, *Antillothrix bernensis*, and *Insulacebus toussaintiana* could form a monophyletic clade that is sister to either extant Platyrrhini or basal pitheciids. Based on the distal humeral data, we reconstruct the earliest ancestral platyrrhine to be a generalized, arboreal quadruped that potentially emphasized pronated arm postures during locomotion and may have engaged in some limited climbing, most similar in shape to early anthropoids and some of the earliest Antillean forms. However, aspects of shape and standard qualitative characters relating to the distal humerus seem to be variable and prone to both homoplasy and reversals; thus these results must be interpreted cautiously and (where possible) within the context provided by other parts of the skeleton.

Keywords: Platyrrhini, three-dimensional geometric morphometrics, phylogeny, early anthropoids, platyrrhine evolution, biogeography

1 **Introduction**

2 The platyrrhine radiation is a morphologically and behaviorally diverse group originating
3 from an Eocene African taxon that was likely carried to South America on “rafts” of vegetation
4 or “floating islands” (Hoffstetter, 1974, 1980; Ciochon and Chiarelli, 1980; Houle, 1999). The
5 origins of the modern crown radiation and its relationships to early Miocene fossil platyrrhines,
6 however, remain a matter of debate. Currently, genetic evidence suggests that the three modern
7 families, Atelidae, Cebidae, and Pitheciidae, arose in rapid succession in the Early Miocene
8 (Perelman *et al.*, 2011). Rosenberger and colleagues propose that the Miocene Patagonian
9 platyrrhines can be included within these groups (the long lineage hypothesis; Rosenberger *et al.*,
10 2009; Rosenberger, 2010; Rosenberger and Tejedor, 2013) while Kay and colleagues posit that
11 the Patagonian forms are stem platyrrhines basal to the modern platyrrhine families (the stem
12 platyrrhine hypothesis; see Kay 1990; Kay *et al.*, 2008; Kay and Fleagle, 2010). Within these
13 scenarios, the placement of the endemic extinct Caribbean platyrrhines, found on the Greater
14 Antillean islands of Cuba, Hispaniola, and Jamaica are also debated (see Kay, 2015 for a
15 discussion of this).

16 One of the major problems in platyrrhine paleontology is the paucity of data available
17 from the Eocene and Oligocene, as most fossil platyrrhine remains are dated to the Miocene or
18 Pleistocene of South America and the Caribbean (e.g., Rímoli, 1977; MacPhee and Woods,
19 1982; Flynn *et al.*, 1997; MacPhee *et al.*, 2003; Tejedor *et al.*, 2006; Kay and Cozzuol, 2006;
20 Perkins *et al.*, 2012; Fleagle *et al.* 2012); however there are some notable exceptions from
21 Bolivia and Peru (Hoffstetter, 1969; Rosenberger, 1981; Wolff, 1984; Rosenberger *et al.*, 1991;
22 Takai and Anaya, 1996; Takai *et al.*, 2000; Kay *et al.*, 2002; Bond *et al.*, 2015). Of the available
23 fossil material, the majority is composed of dental remains with many taxa being known only

dentognathically (e.g., *Perupithecus ucayaliensis* [Bond et al., 2015], *Insulacebus toussainatiana* [Cooke et al., 2011]; *Solimoea arcensis* [Kay and Cozzuol, 2006]; *Szalatavus attricuspis* [Rosenberger et al., 1991]; *Mohanimico hershkovitzi* [Lutcherhand et al., 1986], *Branisella boliviana* [Hoffstetter, 1969]). Postcranial remains are scattered and incomplete, but one of the more frequently preserved elements in the skeletons of fossil platyrrhines is the distal humerus (Youlatos and Meldrum, 2011). There are well-preserved, adult distal humeri for *Homunculus patagonicus* (Ameghino, 1891; Fleagle and Kay, 2006), *Cebupithecia sarmientoi* (Meldrum et al., 1990), *Neosaimiri* (Meldrum et al., 1990), and *Cartelles coimbrafilhoi* (Hartwig and Cartelle, 1996; Halenar and Rosenberger, 2013), as well as for most of the extinct Greater Antillean primates, including *Xenothrix mcgregori* (MacPhee and Meldrum, 2006), *Paralouatta varonai* (MacPhee and Meldrum, 2006), and *Antillothrix bernensis* (Rosenberger et al., 2011). Additionally, there are remains of a distal humerus of a juvenile *Caipora bambuorum* (Cartelle and Hartwig, 1996).

The distal humerus has often been used to make inferences about the locomotor repertoires of fossil taxa (e.g., Harrison, 1989; Ford, 1988, 1990a,b; Meldrum et al., 1990; Rose 1993; MacPhee and Meldrum, 2006; Halenar, 2011) as it participates in a functionally informative joint with both the radius and the ulna. The distal humerus has also been shown to distinguish modern platyrrhine groups on the basis of locomotor mode (Halenar, 2011). In addition to locomotor reconstruction, the distal humerus is potentially a valuable region for phylogenetic analyses. The postcranium as a whole is often assumed to be homoplastic because of the influence of locomotion on postcranial evolution, however postcranial remains have been shown to be no more prone to homoplasy than craniodental remains in some mammals (Sánchez-Villagra and Williams, 1998), and Young (2003) was able to accurately reproduce portions of the

consensus phylogeny of Primates using cladistic characters derived specifically from the forelimb. He determined that homoplasy in his dataset was low, with convergence of *Ateles* on the great apes accounting for the majority of the homoplasy present. Postcranial morphology has been successfully used in phylogenetic analyses in many primate groups (e.g., Szalay, 1976; Dunlap et al., 1985; Ford and Morgan, 1986; Ford, 1988; Beard, 1988; Harrison, 1989; Gebo et al., 2001; Sargis, 2002a,b; Marivaux et al., 2010). Another benefit of using the distal humerus in phylogenetic analyses is that it is well preserved in the Late Eocene and Oligocene record of Africa in multiple taxa (Simons, 1959; Fleagle and Simons, 1982a,b; Fleagle and Kay, 1987; Fleagle and Simons, 1995; Seiffert et al., 2002; Simons, 2004;). Thus, the African forms from which the platyrrhines likely originated could be used as a comparative group to examine potential phylogenetic relationships and morphological continuity between fossil platyrrhines and early African anthropoids; these primates have been studied regularly in this context (e.g., Conroy, 1976; Ford, 1988; Takai et al., 2000).

Information from the humerus could be especially useful in considering phylogenetic scenarios for the colonization of the Greater Antilles. There is sound geological evidence for the presence of primates in Cuba by the Early Miocene (MacPhee et al., 2003), and MacPhee, Iturralde-Vinent, and colleagues have posited an even earlier Eocene/Oligocene entrance via a landspan connecting northern South America and the Caribbean islands (MacPhee et al., 1995; Iturralde-Vinent and MacPhee, 1999; Iturralde-Vinent, 2006). However, the phylogenetic relationships of these primates are far from resolved. MacPhee and colleagues (1995) argued that the Greater Antillean forms are part of a monophyletic radiation sharing a relationship with the pitheciids. Kay and colleagues (2011; Kay, 2015) support a modified version of this scenario where the Caribbean forms are sister to the living platyrrhines and some species form a

monophyletic clade. An alternate view disputes the monophyly of this group and suggests that there may have been several colonization events that took place during the Miocene with different species of Caribbean forms sharing ancestry with a different mainland species or groups (e.g., Rosenberger, 1977; Ford and Morgan 1986; Ford, 1990b; Rosenberger, 2002; Cooke, 2011; Cooke et al., 2011). However, at the core of these scenarios are really two questions that each hypothesis attempts to address: (1) whether the Caribbean platyrrhines form a monophyletic group; and (2) whether some or all of Caribbean platyrrhines are stem platyrrhines or members of one or more of the extant platyrrhine families. To further complicate this picture, colonization of Latin America via the Caribbean from Africa cannot be excluded. Ocean currents ran in a favorable direction for a colonizing protoplatyrrhine between 10° North and 30° North from the coast of Africa near present day Senegal towards northern Brazil to Venezuela (Houle, 1999). If this northerly route of colonization is accurate, it is possible, although perhaps not the most parsimonious explanation, that the colonizing protoplatyrrhines arrived in the circum-Caribbean region.

Morphological continuity in the distal humerus between fossil Caribbean forms and Fayum primates, Patagonian fossil platyrrhines, or one or more members of the extant platyrrhine families could add support to one of these hypotheses of relationship. The morphological similarities, or lack thereof, among the Greater Antillean platyrrhines will help to elucidate their relationships to each other. As most analyses have been constructed largely using craniodental remains (Rosenberger, 1977; Horovitz and MacPhee, 1999; Rosenberger, 2002; MacPhee and Horovitz, 2004; MacPhee and Meldrum, 2006; Cooke et al., 2011; Kay et al., 2011) adding additional postcranial information will provide another source of data for testing these hypotheses. As some of the Caribbean forms arrived in the Antilles fairly early in the

1 history of platyrrhine evolution and show an amalgam of primitive and derived characters
2 (Horovitz and MacPhee, 1999; MacPhee and Horovitz, 2004; MacPhee et al., 2003; Cooke et al.,
3 2011), disentangling morphological transitions in this lineage is difficult. Nevertheless, we
4 suggest that constructing a humeral ancestral morphotype for all platyrrhines and for the living
5 crown platyrrhines can help inform understanding of the morphological transitions occurring in
6 the Caribbean and the mainland.

7 Finally, we also add to the sample of known fossil platyrrhine humeri with a description
8 of UF 114718. UF 114718 (Fig. 1-2) was collected from Trouing Carfinéyis (+18° 18' 30.00", -
9 74° 0' 30.00") a sinkhole site in the Département du Sud, Haiti, which acted as a natural animal
10 trap. The specimen was recovered on September 14, 1984 by Daniel Cordier working with a
11 team from the University of Florida, Gainesville. In addition to the primate humerus, a nearly
12 complete *Solenodon paradoxus* was collected (UF 125174). The Plain du Formon has twenty-
13 seven sinkholes and caves from which material was excavated by researchers from the
14 University of Florida in the early 1980s including two sites which have yielded primate material:
15 Trou Woch Sa Wo, from which a partial primate mandible (UF 28038, now lost) was recovered
16 (MacPhee and Woods, 1982), and Trouing Jeremie #5, the type site for *Insulacebus*
17 *toussaintiana* (UF 114714, Cooke et al., 2011). One additional Haitian locality in the
18 Département de l'Ouest, Trou Jean Paul, yielded a primate femur (UF 114717, Cooke and
19 Tallman, 2012). As endemic fossil platyrrhine material is quite rare, particularly from the
20 Tiburon Peninsula, the addition of this humerus to the known material doubles the postcranial
21 sample from this region.

22 Thus, this paper has three major goals:

- 1 1. To describe the morphology of UF 114718, create a locomotor reconstruction for this
- 2 individual and assign it taxonomically;
- 3 2. To develop a model for the ancestral platyrrhine morphotype of the distal humerus;
- 4 3. To develop and/or support existing phylogenetic hypotheses for the origin of the
- 5 Greater Antillean primates that take into account the morphology of the distal
- 6 humerus.

8 **Materials and Methods**

9 *Data collection*

10 In order to characterize the morphology of the distal humerus, we employ three
11 dimensional geometric morphometric (3D-GM) techniques, which allow for the actual shape
12 differences among original specimens to be used in multivariate analyses (Rohlf and Slice,
13 1990). Eighteen landmarks on the distal humerus of UF 114718 and a comparative sample of
14 extant and fossil platyrrhines and early anthropoids (Table 1) were collected by M.T. as a series
15 of x,y,z coordinate data (Fig. 3; Table 2).

16 In the extant sample, all individuals were adults and displayed full epiphyseal closure.
17 Where sex was not indicated on the specimen, it was listed as unknown; no zoo specimens were
18 sampled. The extinct platyrrhines sampled were *Cebupithecia sarmientoi*, a Middle Miocene
19 pitheciid from La Venta, Columbia (Stirton, 1951; Meldrum and Kay, 1997), *Paralouatta*
20 *varonai*, a Miocene-sub-recent taxon from Cuba, cranially most similar to *Alouatta* (Rivero and
21 Arredondo, 1991; MacPhee and Meldrum, 2006), *Xenothrix macgregori*, a Pleistocene taxon
22 from Jamaica, variably considered a cebid (Williams and Koopman, 1952), a pitheciid
23 (Rosenberger, 1977 et seq.; MacPhee and Horovitz, 2004), or a stem platyrrhine (Kay, 2015),

1 and previously unpublished humeri from the eastern Dominican Republic attributed to
2 *Antillothrix bernensis*. The extinct early anthropoids sampled were *Apidium phiomense*, an
3 Oligocene anthropoid from the Fayum of Egypt (Simons, 1959) which has been posited to be
4 similar to the ancestral platyrrhine morphotype, most similar to modern *Saimiri* (Fleagle and
5 Simons, 1995), *Aegyptopithecus zeuxis*, an Oligocene anthropoid from the Fayum of Egypt
6 reconstructed to be a primitive, large-bodied arboreal quadruped with similarities to *Alouatta*
7 (Fleagle and Simons, 1982a), *Propithecus chirobates*, an Oligocene anthropoid from the
8 Fayum of Egypt, reconstructed to be an arboreal quadruped with phenetic similarities to modern
9 ceboids (Fleagle and Simons, 1982b), and *Parapithecus grangeri*, an Oligocene early anthropoid
10 from the Fayum of Egypt reconstructed to be a generalized, arboreal quadruped, similar to both
11 extant small platyrrhines and omomyids (Fleagle and Simons, 1995; Simons, 2004).

12 Data on larger bodied taxa were all collected with a Microscribe 3DX digitizer. The
13 specimens were stabilized and oriented using modeling clay and points were taken in the same
14 orientation and sequence on each individual. Where possible, the left side of each element was
15 digitized in order to minimize differences due to slight bilateral asymmetry. All callitrichines
16 were microCT scanned at 30-45 microns and surfaces were rendered from the CT images using
17 the isosurface function in Stratovan Checkpoint (Stratovan Corp., 2012). Landmark data were
18 subsequently collected using Landmark Editor (Wiley et al., 2005). It was not possible to use a
19 microscribe accurately on callitrichine taxa because of their small size. In order to test the
20 comparability of data collected with a microscribe and data collected with Landmark Editor, data
21 on a series of 10 specimens representing most of the genera in this study were collected using a
22 microscribe and three-dimensional surfaces. In all cases, the Procrustes distances between the
23 coordinates from the microscribe and from Landmark Editor were well within the expected

variability of a single species. A precision test was also undertaken prior to data collection. A test sample of 10 replicate landmark sets from a single individual was collected. In order to assess the error at each individual landmark, the mean, minimum, and maximum Procrustes distances from each individual landmark to the consensus landmark were calculated. The mean percentage error for each landmark was calculated as each mean landmark error divided by the mean distance between the consensus landmark coordinates and its centroid, multiplied by 100 (Singleton, 2002). In all cases, the percent error was below 1%, which was considered acceptable. Specimens were registered with respect to one another using a generalized Procrustes analysis (GPA) in *morphologika*² (O'Higgins and Jones, 2006). A GPA minimizes the sums of squared distances between the landmark configurations of each specimen by centering all landmark configurations on a common origin (the centroid), rotating them about this point, and adjusting them for size (Rohlf and Slice, 1990). The Procrustes aligned coordinates were then subjected to standard multivariate statistics. In all statistical analyses, changes in shape from one individual to another were visualized as thin-plate spline deformations from a reference to a target specimen (Bookstein, 1991; Adams et al., 2004). These deformations were conducted using Landmark Editor (Wiley et al., 2005), in which a three-dimensional scan can be warped to match the landmark configuration of a target configuration. For consistency in visualization, the distal humerus of *Saguinus*, rendered from CT scan data, was used as the reference for deformation in all cases. All analyses were performed on the full set of landmarks, and some were performed on a reduced set eliminating points on the lateral epicondyle and capitulum (Fig. 3), which allowed for the inclusion of *Paralouatta varonai*.

Canonical variates analyses

Canonical variates analyses (CVA) were performed using the GPA-aligned coordinates from both the full and reduced landmark sets in SPSS v20 (Chicago, IL) in order to determine which aspects of distal humeral morphology best separate the extant groups. Each CVA was conducted twice; once with groups designated at the level of the subfamily, and once with groups designated at the level of the genus. In each case, the fossil anthropoids were also given their own group. Fossil platyrrhines were left ungrouped and were therefore classified by the analysis. While each of the Oligocene fossil anthropoids presents a unique morphotype (Fleagle and Simons 1982a,b; 1995), it is not the purpose of this paper to describe their morphometric affinities. Their commonality is morphology in the distal humerus that should be plesiomorphic as compared to extant platyrrhines and catarrhines. Placing the early anthropoids as a single group allows for the fossil platyrrhines to be classified as such, which would theoretically indicate the presence of a more primitive postcranial morphology than seen in the extant radiation (Fleagle and Simons 1982a,b; 1995; MacPhee and Meldrum, 2006). Mahalanobis distances between the fossils and their nearest group centroid were compared to the distribution of Mahalanobis distances of group members around their own centroid in order to determine how closely the fossils resembled their classified groups. If a fossil has a greater distance from the centroid than 95% of group individuals around their centroid, it can be concluded that while that particular fossil might be most similar to a particular group, it is not likely to be a member of that group. Shape changes along the major canonical axes were calculated by multiplying the loadings for each observation by the maximum and minimum of each axis and adding it to the consensus configuration (Polly, 2008).

Cladistic analyses

1 In order to incorporate qualitative characters into the analysis, we scored all species
2 included in this study for the humeral characters outlined in Ford (1986, 1988, 1994), Fleagle
3 and Kay (1987), and Ross et al. (1998) as well as for several characters newly identified here
4 (Table 3; Supplementary Online Material [SOM] Figures 1-18). Seven to eight individuals for
5 each extant genus except *Brachyteles* were scored by both M.T. and S.B.C. in order to account
6 for intragenetic variability in each trait and intraobserver error in character scoring. *Brachyteles*
7 was omitted from these analyses as insufficient skeletal material was available. All available
8 fossil individuals were also scored by both M.T. and S.B.C., including partial and damaged
9 specimens, in order to account for variability in the fossil taxa. If the morphology of a particular
10 character was not preserved, it was scored as missing data. In addition to the humeral characters,
11 a data matrix of craniodental characters taken from Kay (2015) was included in this analysis; this
12 matrix was made available by Kay (2015) as supplementary material and is available for
13 download. Given the variability present in humeral characters, we chose to limit our character
14 matrix to the craniodental characters that we thought may have lower levels of polymorphism.
15 *Cartelles* was excluded from these analyses as the original material was inaccessible at the time
16 of data collection.

17 Phylogenetic analysis was conducted using PAUP* (Swofford, 2002) using and
18 parsimony methods with a molecular scaffold employed for the living taxa from Perelman et al.
19 (2011), who based their primate phylogeny on 54 nuclear genes. The Fayum taxa were set as the
20 outgroup. For the parsimony analysis, a branch and bound search was conducted. Branches were
21 collapsed if the maximum length was zero and characters were ordered. Again tree topology was
22 not affected if characters were ordered or unordered. One most parsimonious tree was found,
23 which was then bootstrapped using the full heuristic search with 1000 replicates. The branch-

swapping algorithm was tree-bisection-reconnection. Finally, using Mesquite (Maddison and Maddison, 2011) an ancestral state reconstruction analysis was performed to determine hypothetical ancestral states and to examine where along the tree state changes might have occurred.

Several characters included in this study show polymorphism (Table 3). As PAUP* (Swofford, 2002) treats polymorphic characters as either missing data or as uninformative and assigns a state a posteriori depending on where the taxon falls on the tree, an alternative coding scheme is used here where the polymorphic condition receives its own code. While non-polymorphic characters are ideal, in most morphological studies some degree of polymorphism exists. Wiens (2000) found including this diversity in coding produced more accurate trees. When coding each humeral character, the frequency of each state in the sample was recorded (Table 4) and taxa that showed polymorphism were coded as such (see humeral character matrix, SOM Table 1). Trees produced were visualized in Mesquite (Maddison and Maddison, 2011). After the phylogenetic trees were produced, trait changes were mapped across both phylogenetic trees using the trait history function in Mesquite. This allowed for a reconstruction of the ancestral platyrrhine humeral morphotype.

Phylogenetic analyses of shape

In order to both estimate the morphology of the ancestral platyrrhine and determine the direction of shape changes in the distal humerus over the course of platyrrhine evolution, a phylogenetic tree for the modern taxa, including branch lengths, was constructed using genetic data from Perelman et al. (2011). This tree was imported into MorphoJ (Klingenberg, 2011) and landmark configurations (using the full configuration) for the hypothetical taxonomic units

(HTUs) in the phylogenetic tree were computed using weighted squared-change parsimony (Maddison, 1991) in order to visualize the direction of shape change within the tree. The phylogenetic tree was rooted for the purposes of this analysis.

The amount of homoplasy in the morphometric data was assessed by calculating the shape consistency and shape retention indices, as outlined by Klingenberg and Gidaszewski (2010). The shape consistency index is defined as s/m , where s is the length of the genetic tree as represented by the sum of squared shape changes along the branches and m is the shortest possible tree that fits the shape data. The shape retention index is defined as $(g-s)/(g-m)$, where s and m are as defined above, and g is the maximum possible length of a tree. The maximum tree length assumes a star configuration in which each extant taxon branch comes from a single root and all traits are homoplastic. Thus, for three-dimensional data, g can be calculated as the sum of the Procrustes distances of each individual to the mean configuration. The minimum tree was calculated using FindSteinerTree, available at <http://www.flywings.org.uk/FindSteinerTree/index.htm>. Both shape consistency index and shape retention index vary from 0 to 1, with larger values for shape consistency index indicating less homoplasy and larger values for shape retention index indicating greater synapomorphy in the dataset (Klingenberg and Gidaszewski, 2010).

Finally, the parsimony tree generated from the qualitative data was also imported into MorphoJ (Klingenberg, 2011), and shapes for each HTU and root of each tree were calculated using weighted-squared change parsimony. This has the benefit of including fossils in the analysis to refine the potential shape at the root of the tree; however, this also introduces a degree of uncertainty as bootstrap values were not high for all branches (see below). Shape consistency and shape retention indices were not calculated for this tree as the number of taxa and number of

landmarks made the operation too computationally intensive to find the Steiner tree. Permutation tests of 10,000 replicates against the null hypothesis of no phylogenetic signal were performed using MorphoJ to determine if there was a significant phylogenetic component to the data. MorphoJ randomly reconfigures the tips of the tree, recalculates the tree length 10,000 times, and compares the randomized tree lengths against the actual tree length to determine significance (Klingenberg and Gidaszewski, 2010). Pairwise Procrustes distance between the shape of the HTU representing the root was calculated in order to determine the degree of difference in the reconstructed shapes between the parsimony and molecular trees. This pairwise Procrustes distance was compared to the distribution of pairwise Procrustes distances among individuals of the same species across the sample to assess the magnitude of the differences in the reconstructed root. This determines whether inclusion of fossil taxa makes a significant impact on ancestral reconstruction at the root of the tree.

Data from the operational taxonomic units (OTUs – the “tips” of the tree) of the parsimony tree were analyzed in a principal components analysis (PCA), and nodes and lines representing the phylogenetic trees were projected into this space to create a “phylomorphospace” as a way to visualize directions of shape change in different lineages. This projection was accomplished by excluding the HTUs from the covariance matrix used to construct the PCA, and then calculating scores for each HTU post hoc (Rohlf, 2002; Sidlauskas, 2008). In this space, areas where branches from different lineages converge would indicate instances of parallelism for those traits, whereas areas that are occupied by a single lineage would indicate traits that are unique to that clade. Individuals or nodes that fall closest to the root would have more ancestral characteristics, whereas those that fall furthest away would be most derived. Shape changes among the groups were computed by multiplying the loadings for each

observation by the desired position in space and adding it to the consensus configuration and were visualized in Landmark Editor (Wiley et al., 2005) using warped laser scans as in the previous analyses.

Results

Fossil description

UF 114718 (Fig. 1) is a nearly complete humerus, 108.3 mm long (Fig. 2), lacking only the humeral head, which is broken close to the surgical neck. The diaphysis is circular in shape and flattens anteroposteriorly towards the distal epiphysis. The deltopectoral eminence is broad and robust, with obvious lateral and anterior borders that taper to form a v-shape. The anterior border is formed by a ridge that projects anteromedially 2mm from the diaphysis. The deltopectoral eminence is situated anterolaterally such that in anterior view, the diaphysis seems to be angled outward. The crest for the insertion of teres major is robust and projecting. This arrangement of muscular insertions is most similar to modern *Cebus* and *Saimiri* (Fig. 1). The lateral border of the humerus is sharp and clearly defined in the distal third of the diaphysis although the brachioradialis flange is only weakly developed. The lateral epicondyle is distinct, rounded and rolled slightly posteriorly, most like *Pithecia*, but similar as well to *Chiropotes*, *Alouatta*, *Cebus*, *Saimiri* and *Aotus* (Fig. 1). The medial epicondyle is moderately short, gently rounded and slightly posteriorly flexed with a distinct dorsal epitrochlear fossa on the posterior aspect, most similar to *Pithecia* and *Alouatta*. The posterior retroflexion is not as great as in *Cebus* or *Chiropotes* but greater than in *Callithrix*, *Cebuella* and *Ateles* (Fig. 1). The trochlea and the capitulum are of almost equal mediolateral width in the anterior aspect. The capitulum is slightly rounded anteriorly, mediolaterally broad and the articular surface is somewhat distally

extensive, but narrows in its most posterior aspect, most similar to *Saguinus*, *Pithecia*, and *Saimiri*. It is not as distally extensive as in *Ateles*, but more so than in *Cebus* or *Chiropotes* (Fig. 1). The proximolateral extension of the capitular surface makes a distinct capitular tail and there is a shallow but defined medial gutter between the lateral margin of the trochlea and the capitulum on the anterior surface. This combination of characters is not found in any extant platyrrhine genus. The flatter contour of the capitulum is most similar to *Saguinus*, but it has a well-developed medial gutter, whereas *Chiropotes* and *Alouatta* have a poorly developed medial gutter as in UF 114718, but in combination with a very anteriorly rounded capitulum. The capitular tail is most like *Alouatta* or *Saguinus* in its degree of development. The trochlea is only moderately keeled on the medial aspect – the medial margin of the trochlea extends slightly past the distalmost extension of the capitulum – whereas the lateral margin is relatively indistinct. There is a crease between the lateral edge of the trochlea and the capitulum on the posterior surface, most similar to *Saguinus* (Fig. 1). There is a clear depression for both the radial and coronoid fossae, and they are separated entirely by a low ridge. The olecranon fossa is short, wide, unfenestrated, and distally located. Like all extant atelids, there is no entepicondylar foramen.

UF 114718 is distinct from the other Caribbean taxa. It differs from MHD 03a (*Antillothrix bernensis*) in that it has: (1) a mediolaterally longer trochlea; (2) a less retroflexed medial epicondyle; (3) a larger, more posteriorly rolled lateral epicondyle; (4) a short and oval olecranon; (5) a less anteriorly projecting capitulum; (6) a less prominent medial gutter; and (7) a less developed posterior lateral trochlear keel, although that difference could be taphonomic (Fig. 4). UF 114718 shares a similar shape and development of the lateral condyle and the crease on the posterior aspect of the trochlea with *Xenothrix macgregori*, but differs in having a short,

1 ovoid olecranon, medially directed medial epicondyle, and a less well-developed medial
2 trochlear keel. UF 114718 also differs from *Xenothrix* in its loss of entepicondylar foramen. UF
3 114817 is extremely different from *Paralouatta varonai* and has few, if any, traits in common
4 with this taxon (Fig. 4).

5 *Canonical variates analyses*

6 The results of a CVA of the full landmark configuration, with groups designated by
7 genus, are presented in Figure 5. Canonical axis (CA) 1 largely separates callitrichines, *Ateles*,
8 and early anthropoids with positive values from pitheciids, *Cebus*, *Saimiri*, *Aotus*, *Alouatta*, and
9 *Lagothrix* with negative values, based on the bi-epicondylar width, height of the olecranon fossa,
10 degree of retroflexion of the medial epicondyle, degree of keeling in the trochlea and
11 anteroposterior width of the trochlea. Taxa that cluster at the negative end of the axis have
12 narrow distal humeri with tall olecranon fossae, narrow and keeled trochleae and retroflexed
13 medial epicondyles whereas those with the most positive values have wide distal humeri with
14 short olecranon fossae, wide and symmetrical trochleae and less retroflexed medial epicondyles.
15 Canonical axis 2 divides *Cebus* and *Chiropotes*, and - to a lesser degree - some early anthropoids
16 from the rest of the sample based on their high degree of retroflexion in the medial epicondyle.
17 *Ateles* and, to a lesser degree, *Callicebus* and *Saimiri*, are divided at more positive values on CA
18 3, based on their anteriorly projecting capitula. The arrangement of the groups along the three
19 axes does not correspond well to phylogenetic relationships. Classification data for the fossil
20 platyrrhines are presented in Table 5. Seventy two percent of cases were correctly classified on
21 cross-validation (for individual classification percentages by genus, see SOM Table 2). UF
22 114718 and *Cebupithecia sarmientoi* (UCMP 38762) were both classified as *Saguinus*,
23 *Antillothrix bernensis* (MHD 03) as *Chiropotes*, and *Xenothrix macgregori* (AMNH 266009) as

1 an early anthropoid, although in all cases the distance of the fossil individual to its classified
2 group centroid was greater than the distance of any extant individual to its own group centroid
3 (Table 6).

4 Results of a CVA of the partial landmark configuration, with groups designated by genus,
5 are largely similar (Fig. 6). Canonical axis 1 again separates early anthropoids, callitrichines and
6 *Ateles* at positive values and *Saimiri* and *Callicebus* at negative values from the rest of the
7 sample. Canonical axis 1 is driven by all of the same factors as in the previous analysis except
8 for the biepicondylar width; early anthropoids, callitrichines, and *Ateles* all have short olecranon
9 fossae, less keeled and wider trochleae, and less retroflexed medial epicondyles, whereas *Saimiri*
10 and *Callicebus* have the tallest olecranon fossae, more keeled and narrower trochleae, and more
11 retroflexed medial epicondyles. Canonical axis 2 separates *Cebus* and *Chiropotes* from the rest
12 of the sample based on the extreme retroflexion of their medial epicondyles while CA 4
13 separates *Ateles* from the rest of the sample based on its wide and anteriorly projecting capitula.
14 Canonical axis 3 contains 9% of the variance but failed to separate the extant taxa in any
15 meaningful way and is thus not pictured. The arrangement of the groups along the three axes
16 does not correspond well to phylogenetic relationships. Classification data for the fossil
17 platyrrhines are presented in Table 5. Seventy six percent of cases were correctly classified in
18 cross-validation, and the fossil classifications are largely the same (for individual classification
19 percentages by genus, see SOM Table 2). *Cebupithecia* (UCMP 38762) is classified as *Callithrix*
20 for the reduced configuration, while *Paralouatta varonai* (MNHNCu 76.1010) is classified as
21 *Saguinus*. For both MCL 06 and MNHNCu 76.1010, the secondary classification was *Ateles*
22 with, respectively, Mahalanobis distances of 46.4 and 43.2 to the *Ateles* centroid. This change in
23 classification in MCL 06 is likely due to the lack of data on the capitulum, which differentiates

1 the shape of *Ateles/Brachyteles* from the callitrichines in the previous CVA. Also as in the full
2 configuration, the distances between the fossil individuals and their classified group centroids
3 were greater than the distances between group members to their own centroid with the single
4 exception of *Cebupithecia*, which is just inside the maximum distance between a *Callithrix*
5 individual and its group centroid (Table 6).

6 Completing the CVA with groups designated at the subfamily level did not substantially
7 change these results. The percentage of correct classifications of the extant taxa increased in
8 both the full and partial landmark configurations (Table 5; for individual classification
9 percentages by subfamily, see SOM Table 3). In most cases, the fossils were classified into the
10 subfamily that contains the genus level classification given in the previous analyses. Two
11 exceptions are MCL 06 and MNHNCu 76.1010; with groups designated by subfamily, MCL 06
12 is classified as a callitrichine (instead of *Ateles*) and MNHNCU 76.1010 is classified as an
13 ateline (instead of *Saguinus*). For both the full and partial configurations, the Mahalanobis
14 distances between MCL 06 and the centroid for the Callitrichinae is greater than the maximum
15 distance between any callitrichine and its group centroid. Similarly, for the full configuration,
16 the distance between AMNH 266008 and the early anthropoid group centroid is greater than the
17 maximum distance between a member of that group and its centroid. The other fossils fell
18 within the range of variability of each taxon around its centroid in both analyses (Table 7). Three
19 dimensional plots of the first three canonical axes are located in SOM Figure 19.

20 *Cladistic analyses*

21 One most parsimonious tree was returned from the parsimony branch and bound search
22 (Fig. 7, SOM Table 4) (see SOM Fig. 20 for neighbor-joining tree). The bootstrapped tree had a

consistency index (CI) of 0.46 and a retention index (RI) of 0.47. Support values were weak for the clades formed by the fossil taxa and interpretation of these trees should take into account that they are derived in most cases from incomplete character data, while placement of the living taxa was determined by genetic analyses and set as a constraint tree. Fossil platyrrhine taxa were free to move, while extant taxa, whose phylogeny is better known, were not. The Fayum taxa were set as an outgroup and were constrained as well.

Within the consensus parsimony tree, there was a substantial amount of homoplasy for many of the characters (Table 8). Four of eighteen humeral characters showed a CI of 0.50 or greater and thus had a lower degree of homoplasy than other characters used in the analysis. The relative heights of the medial and lateral trochlear margins (character B) was the only character with a CI of 1 and separated the small-bodied callitrichines from the other platyrrhines. Having a small medial epicondyle size (character H, CI = 0.50) was another feature seen in the Caribbean forms *Xenothrix*, *Antillothrix* and variably in *Paralouatta varonai*. Bicipital groove morphology (CI = 0.50) separated the suspensory forms.

While branching patterns at the base of the trees differed between the NJ tree (SOM Fig. 20) and the parsimony tree (Fig. 7), there were some points of congruence. First, both trees support *Cebupithecia* as basal to the living platyrrhine lineage. Second, and of particular interest for this study, is the consistent clade containing *Antillothrix* and UF 147718 as sister taxa; these taxa both lack an entepicondylar foramen (character F), share a moderately waisted trochlea (character E), and possess a dorsoepitrochlear fossa (character K). In the parsimony analysis, *Paralouatta* was basal to this group creating a Caribbean clade that shares three humeral characters: a medially flared trochlear margin (character B), a deep olecranon fossa (character L) and a prominent deltopectoral crest (character Q). However, in the NJ tree the *Antillothrix*-UF

1 114718 clade is basal to all living platyrrhines with *Xenothrix* and *Paralouatta* being the next
2 two branches.

3 Ancestral character states at the base of the platyrrhine tree and at the base of the crown
4 platyrrhine radiation were calculated in Mesquite (Maddison and Maddison, 2011) using the
5 parsimony criterion (Table 9). The NJ and the parsimony tree produced basal platyrrhine
6 morphotypes that were nearly identical. In each tree, there were, however, some characters
7 which had several equally parsimonious character states; these included: (character D) the length
8 of the trochlear relative to the capitulum, (character E) trochlear waisting, (character I)
9 placement of the medial epicondyle, (character J) posterior trochlear shape, (character N) the
10 supinator crest, and (character R) deltotriceps crest. Characters D, E, I, N, and O all show
11 reversals throughout the tree with little patterning across the three major branches of the
12 platyrrhine tree. Character R, the shape of the deltotriceps crest is low in the atelids, cebines, and
13 pitheciines, while being prominent or polymorphic in *Aotus* and the callitrichines, but while clear
14 patterns exist, an ancestral platyrrhine with either a low or prominent deltotriceps crest is equally
15 parsimonious. Among the extinct platyrrhines, a prominent deltotriceps crest is present in the
16 Caribbean clade forms except for *Paralouatta*.

17 Among the living crown platyrrhines, the ancestral humoral morphotype differs little
18 from that reconstructed for the base of the tree. Major differences included the depth of the
19 olecranon fossa (character L), which is reconstructed in the basal crown platyrrhine to be of
20 intermediate depth and the size of the brachioradialis flange (character O), which is reconstructed
21 as narrow. Several characters (characters C, D, F, I, M, N) had equally parsimonious character
22 state reconstructions, which did not differ from possible character states in the basal platyrrhine.

1 *Phylogenetic shape analyses*

2 Figure 8 illustrates shape transformations among the hypothetical root and nodes (HTUs)
3 in the extant platyrrhine phylogenetic tree and the extant taxa (OTUs). The inferred distal
4 humeral shape at the root of the platyrrhine tree has a long and slightly posteriorly flexed medial
5 epicondyle, a narrow and anteriorly projecting capitulum, and a anteroposteriorly narrow and
6 moderately keeled trochlea; thus, living platyrrhines with these morphological characters have
7 the inferred plesiomorphic pattern for all platyrrhines. The inferred shape for the basal pitheciid
8 is only trivially different from the root, and the inferred shape for the basal cebid differs only in
9 having a slightly wider medial gutter between the capitulum and the trochlea. The greatest
10 change from the root to the base of one of the modern clades is between the root and the basal
11 atelid; as compared to the root, the basal atelid has a less posteriorly flexed medial epicondyle,
12 more anteriorly rounded capitulum and less well-developed medial trochlear keel. The shape
13 consistency index for this dataset is 0.71 and the shape retention index is 0.83, indicating
14 relatively low levels of homoplasy and high levels of synapomorphy in overall shape for this
15 dataset.

16 Including fossils does slightly change the shape of the root of the tree. The root of the
17 parsimony tree differs from the extant-only tree in having a slightly proximodistally shorter
18 trochlea with a more pronounced lateral keel, a mediolaterally narrower and slightly flatter
19 capitulum, and slightly more posteriorly placed medial and lateral epicondyles . However, the
20 Procrustes distance between the two tree roots is 0.13, which is greater than only 1.6% of
21 pairwise Procrustes distances between members of the same species, so these differences are
22 likely within the range of extant variation in a single species. All other nodes are even more
23 similar to one another and thus are not further discussed.

Figure 9 is a three dimensional PCA of the distribution of extant taxon means, HTUs and fossil taxa in phylomorphospace. There is a significant ($p < 0.0001$) phylogenetic signal in this dataset. Principal component 1 accounts for 27.5% of the variability in this sample and separates callitrichines, UF 114718 and *P. chiobates* (DPC 8710) at the most negative values from *Cebus*, *Saimiri*, *Chiropotes* and *Callicebus* at the most positive values. *Aotus* and *Pithecia* also fall towards the positive end of the axis. Principal component 1 is related to degree of development of the medial trochlear keel, shape of the capitulum; proximodistal height of the epicondyles, proximodistal height of the trochlea, mediolateral space between the trochlea and the capitulum, and location of the deepest point of the olecranon fossa. Individuals or nodes that appear nearest to callitrichines on that axis have anteroposteriorly wide trochleae with less well-developed medial trochlear keels. The capitulum is mediolaterally wide on its proximoanterior border (indicating the presence of a capitular tail), and narrows in its more anterior aspect. There is a wide space between the trochlea and capitulum, indicating the presence of a medial gutter. The medial and lateral condyles are proximally placed, and the deepest point in the olecranon fossa is located close to the trochlea. Individuals or nodes that appear closest to *Cebus* and *Saimiri* have trochleae that are anteroposteriorly narrow with a strong medial keel. The capitulum is anteriorly broad with a mediolaterally shorter proximoanterior border. The capitulum and trochlea are close together. The medial and laterally epicondyles are located distally and the deepest point of the olecranon fossa is more proximally located.

Principal component 2 accounts for 18.1% of the variability in this sample. It differentiates *Xenothrix* (AMNH 266008), and, to a lesser degree, *P. chiobates* (DPC 3103), *P. grangeri* (DPC 8710), *Apidium* (DPC 3101), *Antillothrix* (MHD 03a), and UF 114718 from the rest of the sample. These aspects of shape include an increase in posterior size of the lateral

epicondyle, a posterior and distally extensive capitulum and a retroflexed medial epicondyle. Principal component 3 accounts for 13.5% of the variability in this sample and differentiates the extant pitheciids, *Antillothrix* (MHD 03a), *P. chiobates* (DPC 3103) and *P. grangeri* (DPC 8710) at the most negative values from the rest of the sample. It also differentiates *Xenothrix* (AMNH 266008) at the most positive value. The variability on PC 3 is related to the length of the medial epicondyle and development of posterolateral lip on the trochlea. Pitheciids and some of the fossil individuals have long medial epicondyles and very well developed posterolateral trochlear lips, whereas *Xenothrix* has a shorter medial epicondyle and a less well developed posterolateral trochlear lip.

When the three axes are examined together, it is possible to see some degree of phylogenetic patterning. Extant pitheciids form a distinct cluster, as do callitrichines. Atelids are distributed between the two major cebid groups. All of the fossils in the analysis, including *Cebupithecia*, also occupy a discrete area of the morphospace. The hypothetical root of the tree is located between *Antillothrix* (MHD 03a) and the extant pitheciids.

Discussion

UF 114718 functional morphology

UF 114718 has a mosaic of traits. It has a broad, v-shaped insertion for the deltoid, defined by ridges on both the anterior and posterior aspect, as well as a defined ridge for the insertion point of teres major. The broad, flat deltoid insertion gives the appearance that the humerus is bowed. Bowing of the humeral diaphysis increases the moment arms of the deltoid muscle for more powerful flexion, extension and abduction of the arm (Nakatsukasa, 1994) and is characteristic for predominantly quadrupedal primates (MacPhee and Meldrum, 2006). This

1 arrangement of muscular insertions is most similar to *Cebus* and *Saimiri*, which are both arboreal
2 quadrupeds (Boinski, 1989; Fontaine, 1990; Gebo, 1992; Johnson and Shapiro, 1998).

3 UF 114718 has a relatively long and slightly posteriorly flexed medial epicondyle, most
4 similar to *Pithecia* and *Alouatta*. The posterior retroflexion is not as great as in *Cebus* or
5 *Chiropotes* but greater than in *Callithrix*, *Cebuella* and *Ateles*. This can be seen in the
6 intermediate placement of UF 114718 on the second axes of the CVAs in Figures 5 and 6. A
7 long medial epicondyle is related to an increase in the muscle mass of the flexors of the forearm
8 and digits while loss of entepicondylar foramen is thought to be related to buttressing of the
9 medial epicondyle when flexors are employed powerfully and frequently (Sargis, 2002a,b).
10 Medial rotational torques on the distal humeral joints increase when the medial epicondyle is
11 directed directly medially. A posteriorly flexed medial epicondyle will result in more powerful
12 action of the pronators and flexors during pronograde quadrupedalism, while reducing rotational
13 torque (Fleagle and Simons, 1978). Additionally, a posteriorly flexed medial epicondyle helps to
14 strengthen the medial side of the humerus against weight-bearing stress when the arm is
15 regularly pronated (Harrison, 1989), which is important considering the relatively large size of
16 UF 114718 compared to most modern platyrrhines. The morphology of the medial epicondyle of
17 UF 114718 is consistent with a large-bodied, generalized, arboreal quadruped with powerful
18 grasping capabilities.

19 UF 114718 has a defined lateral condyle that projects past the capitulum and is slightly
20 posteriorly rolled. There is disagreement about the functional inferences that can be derived for
21 this feature; it could be indicative of a large muscle mass for the extensors in the forearm, which
22 would complement the more massive forearm flexors during grasp-and-release movement in
23 arboreal, quadrupedal locomotion (Aziz and Dunlap, 1986). Alternatively, it could indicate a

greater reliance on climbing vertical substrates (Conroy, 1976), and in fact Ford (1990) favored the idea that an enlarged lateral condyle is related to climbing, based on the presence of an enlarged lateral condyle in some large-bodied atelids that climb.

In the humeroradial joint, the capitular tail is a distinct proximolateral extension of the anterior capitular surface and functions as a lateral “stop” for the rotation of the radius across the capitulum while the medial gutter is wide depression between the capitulum and trochlea that acts as a medial stop for the rotation of the radius (Rose, 1988). If both a capitular tail and medial gutter are present, they work together to stabilize the radius at the elbow joint during flexion. The medial gutter in particular is most utilized during flexed and abducted postures typically associated with arboreal locomotion to stabilize the joint (Rose, 1993). A bulbous, or anteriorly rounded, capitulum is typically associated with a highly mobile radius, allowing for extensive ability to pronate and supinate, whereas a less bulbous capitulum is associated with more restricted movements at the radial joint (Rose, 1993; Gebo and Sargis, 1994; Nakatsukasa, 1994). UF 114718 has a poorly defined medial gutter in combination with a low, rounded capitulum and poorly defined capitular tail; this combination is not found in any extant genus. In arboreal and terrestrial quadrupeds the capitulum tends to narrow distally to restrict movement in the parasagittal plane while the arms are extended, whereas suspensory primates tend to have rounded distal capitula as mobility is most important in extended arm postures (Harrison, 1989). In the CVA (Figs. 4 and 5), this combination of characters (as well as others from the trochlea – see below) places UF 114718 near *Saguinus* and early anthropoids on CA 1 and 3, which account for variability related to the anterior projection of the capitulum, the mediolateral width of the trochlea and the degree of separation between the capitulum and trochlear (the medial gutter).

1 At the humeroulnar joint, the trochlea of UF 114718 is slightly keeled on the
2 anteromedial aspect and “creased” on the posterolateral aspect. There is some abrasion on the
3 posterior aspect, so it is possible that the trochlea was better developed than it currently appears.
4 This condition is most qualitatively and quantitatively similar to that of *Saguinus*. UF 114718
5 groups near the distribution of *Saguinus* on CA 1 and 3 based partially on the degree of medial
6 keeling in the trochlea. Its trochlea is also proximally extensive on the anterior surface, like
7 *Saguinus*, rather than shorter as in some other platyrrhines, such as *Pithecia* or *Saimiri*, and the
8 same width as the capitulum. An especially narrow trochlea restricts movement at the
9 humeroulnar joint to the anteroposterior plane, common in terrestrial monkeys (MacPhee and
10 Meldrum, 2006). The olecranon fossa in UF 114718 is short, deep and oval shaped, most similar
11 to *Saguinus* and *Callithrix*, and not triangular, as in pitheciines, atelines and cebines. This is also
12 apparent in its position on CA 1 with callitrichines. A triangular olecranon fossa with well-
13 defined borders is indicative of stability in the humeroulnar joint through the entire range of
14 flexion/extension (Harrison, 1989). There are clear depressions of similar size for the coronoid
15 and radial fossae present in UF 114718, separated by a low ridge. Separation of the radial and
16 coronoid fossa is common in quadrupedal primates that hold the arm in habitually flexed
17 positions (Napier and Davis, 1959).

18 The full suite of traits in the humeroulnar and humeroradial joints of UF 114718
19 pointstowards a lack of real specialization at this joint. The humeroulnar joint is not especially
20 restricted as seen in committed arboreal and terrestrial quadrupeds, but nor are there adaptations
21 towards extreme mobility in the humeroradial joint as seen in more suspensory, acrobatic taxa.
22 The overall morphology of the humerus of UF 114718 is indicative of a primate that practices a
23 less acrobatic form of generalized, arboreal quadrupedalism, with the possibility of some limited

1 climbing and clambering. The relatively enlarged attachment areas for the forearm flexor and
2 extensor muscle masses might indicate powerful grasping capabilities, which would be useful in
3 climbing in arboreal substrates. This locomotor reconstruction is largely consistent with that of
4 UF 114717, a femur recovered in the same region of Haiti (Cooke and Tallman, 2012).

6 *Taxonomic attribution of UF 114718*

7 Taxonomically, we suggest that UF 114718 is not a representative of *Antillothrix*
8 *bernensis*, known from the eastern portion of Hispaniola. A conspecific relationship with
9 *Antillothrix* can be excluded based on qualitative comparison with MHD 03a. These differences
10 clearly relate to functional differences in the locomotor repertoires of these two taxa, as outlined
11 above. Additionally, UF 114718 is also distinct from other Antillean primate humeri, as
12 previously described. Qualitatively, among all fossil taxa, UF 114718 most closely resembles
13 *Cebupithecia* based on shared traits such as shorter olecranon fossae, more medially directed
14 medial epicondyles, and less keeled trochleae that are mediolaterally wider than seen in the other
15 Antillean primates. Since UF 114718 is not associated with cranio-dental remains, it cannot be
16 definitively attributed to *Insulacebus toussaintiana*, but its location on the eastern portion of the
17 Tiburon Peninsula, approximately 5 km from Trouing Jérémie #5, the *Insulacebus* type site,
18 indicates that this humerus came from a primate that was at least sympatric with if not the same
19 species as *Insulacebus*.

20 The presence of a two endemic Hispaniolan primates is unsurprising considering the
21 biogeography of the island. Today, Hispaniola is made up of two former paleoislands, which
22 collided and sutured together during the Miocene (Heubeck and Mann, 1991; Iturralde-Vinent

and MacPhee 1999; Iturralde-Vinent, 2006). The southern paleoisland is composed of the Tiburon Peninsula, and the portion of Hispaniola south of the Enriquillo Graben was a seaway until the late Pleistocene (Maurrasse et al., 1982; Iturralde-Vinent and MacPhee, 1999; Iturralde-Vinent, 2006), effectively filtering faunal exchange between the two portions of Hispaniola. The peninsula itself is divided by the Jacmel-Fauché Depression into the Massif de la Hotte to the west and the Massif de la Selle and Sierra Baoruco to the east (Fig. 10). The southern portion of Hispaniola still harbors a significant amount of endemism in herpetofauna (Powell et al., 1999; Thomas, 2000; Thomas and Hedges, 2006) and avifauna (Rimmer et al., 2006; Townsend et al., 2007; Rimmer et al., 2010). Amongst the extinct Hispaniolan mammalian fauna, there is some evidence that unique rodent fauna were once present only on the southern paleoisland (Woods, 1989).

The ancestral platyrrhine morphotype

Using our morphometric data, we posit an ancestral platyrrhine humeral morphotype that has a moderately long medial epicondyle that is slightly retroflexed, a posteriorly large lateral epicondyle, a relatively developed medial trochlear keel, a shallow, poorly developed medial gutter, and a gently rounded capitulum with a poorly developed capitular tail. The deepest point of the olecranon fossa would be close to the trochlea, likely indicating a proximodistally short, ovoid olecranon fossa. There are some known difficulties in constructing ancestral states using squared-change parsimony, most notably that there is no inherent measure of accuracy, the model works best under assumed conditions of Brownian evolution, and the probability of calculating the correct ancestral type decreases as time depth increases (Martins, 1999). In addition, low bootstrap values near the root of the parsimony tree indicate that ancestral state reconstructions derived from those trees should be interpreted with extreme caution.

1 Nevertheless, our shape reconstruction is also supported by qualitative characters from
2 the cladistic analyses. Using Mesquite to do a character transformation analysis with the
3 parsimony criterion, we reconstruct the ancestral platyrrhine to have had an entepicondylar
4 foramen, a feature which has been lost multiple times in the platyrrhine lineage, most notably
5 among all atelids and some callitrichines. Amongst the Caribbean forms, it is absent in both
6 specimens of *Antillothrix bernensis* and UF 114718, present in *Xenothrix*, and variably present in
7 *Paralouatta varonai*. In reference to this feature, the most parsimonious tree suggests an
8 entepicondylar foramen positioned above the anterior trochlea as seen in the Fayum taxa and in
9 the Caribbean forms which possess a foramen. The ancestral platyrrhine also possessed an
10 angled distal trochlea relative to the diaphysis that was medially flared, a waisted trochlea, a
11 dorsoepitrochlear fossa, a deep olecranon fossa, a broad brachioradialis flange, a shallow
12 bicipital groove, and a prominent deltopectoral crest. The brachioradialis flange is the attachment
13 site of the brachialis and brachioradialis, important for rotation and flexion of the elbow. While
14 likely as wide in the basal platyrrhine, it may have reversed back to this condition in some of the
15 cebids and pitheciids.

16 In sum, the data presented here mostly agree with the ancestral platyrrhine morphotype
17 suggested by Ford (1988), which adds further support to our model. Ford (1988) characterized
18 the ancestral platyrrhine as having a wide bicipital groove, an entepicondylar foramen, a non-
19 cylindrical trochlea that is cone-shaped on the anterior aspect and spool-shaped on the posterior
20 aspect, a rounded, but distinctly present trochleocapitular ridge, and a wide supinator and
21 brachioradialis flange, all of which agree with the data presented here. However, our
22 reconstruction differs in that we hypothesize that the ancestral morphotype had a relatively wide
23 lateral condyle, a more rounded capitulum than postulated by Ford (1988) although not spherical

1 as in most atelids, a more dorsally oriented medial epicondyle, an entepicondylar foramen
2 located over the anterior trochlea, a more strongly keeled trochlea, and a ventral trochlea equal to
3 or slightly longer than the ventral capitulum. The overall morphological pattern that emerges is
4 one that suggests a generalized, arboreal quadruped as the ancestral platyrrhine, as previously
5 suggested by Ford (1988), with differences in the characterization of the ancestral platyrrhine
6 morphotype here (versus Ford, 1988) likely functionally related to increased pronation ability
7 (Fleagle and Simons, 1978; Harrison, 1989; Rose, 1993; Gebo and Sargis, 1994; Nakatsukasa,
8 1994) and potentially climbing ability (Conroy, 1976; Ford 1990. This locomotor reconstruction
9 is also in line with that of the Haitian primate femur, UF 118717 (Cooke and Tallman, 2012),
10 and UF 118718, described here.

11 The Platyrrhini is assumed to be a monophyletic group that has its origin in the Eocene of
12 Africa (Ciochon and Chiarelli, 1980; Houle, 1999). Most of the fossil evidence from this time
13 period in Africa derives from the Fayum of Egypt, which can be divided into a propliopithecid
14 group, containing *Aegyptopithecus zeuxis* and *Propiopithecus chirobates*, an oligopithecid group
15 containing *Catopithecus browni* (Fleagle and Simons, 1982a,b; Seiffert et al., 2000), and a
16 parapithecoid group, containing *Parapithecus grangeri*, *Apidium phiomense*, and possibly
17 *Proteopithecus sylviae* (Simons, 1959; Fleagle and Simons, 1995; Seiffert et al., 2000; Simons,
18 2004). Of these taxa, *Apidium* or another member of the Parapithecidae has been suggested to be
19 the best representation of the original platyrrhine morphotype (Simons, 1967; Hoffstetter, 1980;
20 Ford, 1990a; Fleagle and Kay, 1994; Takai 2000). In these analyses, the early anthropoids were
21 closely linked to the Caribbean fossil primates in both the parsimony and neighbor-joining trees
22 and the phylomorphospace plot. Thus, while these may not be perfect models for the ancestral
23 platyrrhine morphotype, the data presented here further add to the evidence that an early African

anthropoid is probably the best estimation of the platyrrhine ancestral “stock” in the fossil record.

Caribbean platyrrhine phylogeny

The data presented here lend support to the idea that at least UF 114718 and *Antillothrix* form a monophyletic group, with the positions of *Paralouatta* and *Xenothrix* changing in the parsimony and neighbor-joining analyses. In addition, UF 114718, *Antillothrix*, and *Xenothrix* also occupied an area of the phylomorphospace that was distinct from any of the extant groups. This finding is largely in line with that of the cladistic analyses of Horowitz and MacPhee (1999) based on craniodental characters; however, we remain circumspect in allocating the Caribbean group to a particular platyrrhine family (in contrast to Horowitz and MacPhee [1999] who place it within Pitheciidae) at this juncture and remain open to the possibility that it could be placed either as a basal pitheciid or as a stem platyrrhine lineage.

There has been disagreement in the literature about the number of families represented by the Caribbean forms, and to which family each of the fossils belongs, largely due to the unique combinations of primitive and autapomorphic characters. Depending on the element being examined and the type of analysis conducted, each Caribbean form has been tied to multiple families (Table 10) (e.g., MacPhee and Woods, 1982; MacPhee et al., 1995; Rosenberger et al., 2011; Rosenberger et al., 2013).

Ford (1986, 1990) and Ford and Morgan (1986) have suggested that some of the Greater Antillean primates are cebids, and specifically descendants of callitrichines based on phenetic similarity in their tibiae (putative *Antillothrix*, USNM 254682[Ford, 1986]) and femora

(Jamaican Coco Ree femur, UF 40097, not currently attributed to any extant taxon [Ford and Morgan, 1986]) and have cited the Antillean fossils as evidence for island gigantism in primates. While CVAs in this study seem to support that idea, a closer inspection of the Mahalanobis distances reveal that while UF 114718, MHD 03 and MNHNCu 76.1010 were all classified at some point as callitrichines, the distance from each of those individuals to its classified group centroid was greater than the maximum distance between any individual in any group and its group centroid, indicating that their morphology is not truly represented by any extant group. In addition, callitrichines were united by the only qualitative character with a CI of 1 in the cladistic analyses: a low medial and lateral trochlear keel (although it was variable in both *Callithrix* and *Saguinus*), a trait absent in all of the Antillean primates.

Recently, in a large-scale analysis of almost all platyrrhine fossil species and living genera, Kay (2015) proposed that the Caribbean platyrrhines are basal to the living families with *Xenothrix* branching first, followed by a clade containing *Antillothrix* and *Paralouatta*. The position of *Insulacebus*, which he notes is morphologically very similar to *Antillothrix*, is not addressed. As we used portions of this craniodental character matrix, it is unsurprising that our results are broadly consistent with those of Kay (2015), however, there were some differences. Our results differ in the relationships among the Caribbean taxa. We found support for a *Paralouatta*, *Antillothrix*, UF 114718 group in our parsimony analyses and their placement in relation to the extant forms is consistent with that of Kay (2015). However, in our analysis, *Xenothrix* was basal to this group while in the analysis of Kay (2015) it was sister to extant platyrrhines.

Other researchers have suggested that the Caribbean forms are pitheciids (MacPhee et al., 1995; Horowitz and MacPhee, 1999; Cooke et al., 2011; Rosenberger et al., 2013). While the

1 results presented here do not specifically support this idea, the bootstrap support for the position
2 of Caribbean primates is weak and it is certainly possible that they were positioned as stem
3 platyrrhines due to the persistence of plesiomorphic characters. In fact, all fossil taxa including
4 *Cebupithecia*, which is agreed to be a definitive pitheciid (Stirton, 1951; Setoguchi et al., 1988;
5 Meldrum and Lemelin, 1991), fell as basal platyrrhines, which underlines that fact that even in
6 forms showing relatively modern craniodental morphology, the postcranium, as represented by
7 the distal humerus, remained primitive in many features. This result is supported by the results
8 of the phylomorphospace analysis, where all of the fossil forms, including *Cebupithecia* and
9 fossil Fayum forms, shared a common portion of the morphospace. It is possible that including
10 other portions of the postcranium in cladistic analyses would affect the placement of
11 *Cebupithecia*; for instance, a phenetic analysis utilizing two-dimensional measures of the medial
12 facet of the talus found *Cebupithecia* to be basal to all pitheciids (Boyer et al., 2015). However,
13 results from 3D GM analyses of the proximal femur found *Cebupithecia* to be most similar to
14 either *Cebus* or *Callicebus*, depending on the analysis, and it was never phenetically grouped
15 with the other members of the pitheciid family (Cooke and Tallman, 2012). Similarly, phenetic
16 analyses of distance data based on 3D GM data of the calcaneum placed *Cebupithecia* either as
17 sister to atelids or sister to all extant platyrrhines (Gladman et al., 2013). Thus, it is also possible
18 that the generally primitive pattern seen here in the humerus would be supported by analysis of
19 other parts of the postcranium in fossil platyrrhines.

20 In addition, there were some aspects of shape that united pitheciids, early anthropoids and
21 some Caribbean taxa. Pitheciids were the first group to diverge from the ancestral platyrrhine
22 (Perelmen *et al.*, 2011) and basal pitheciids may not have been substantially different from stem
23 platyrrhines, although the reconstructed root of the pitheciid clade falls away from the

1 reconstructed root of the platyrrhine in our phylomorphospace analysis. Placing the Caribbean
2 forms as basal pitheciids also does not necessarily negate the idea that some fossil Patagonian
3 and Caribbean primates form a monophyletic clade as there is dental evidence, particularly in the
4 incisor morphology that some early Patagonian forms, such as *Soriacebus ameghinorum*
5 (Fleagle et al., 1987) may be basal pitheciids.

6 The strongest evidence in favor of any Caribbean form belonging to the Atelidae comes
7 from the cranial material of *Paralouatta*. In their initial description of the cranium, Rivero and
8 Arredondo (1991) suggested that *Paralouatta* was an atelid, and specifically an alouattin, based
9 on cranial characters, such as a prognathic, airohynchus face, and a small brain. However,
10 *Paralouatta* lacks the derived dental characteristics of modern *Alouatta* (Horowitz and MacPhee,
11 1999; Cooke, 2011), and many of the derived postcranial characteristics relating to suspension
12 present in modern *Alouatta* (MacPhee and Meldrum, 2006). The data presented here contribute
13 to the uncertainty surrounding the phylogenetic position of *Paralouatta*. In neither of the
14 analyses does *Paralouatta* group with the other Caribbean forms, and it is alternately basal to the
15 Caribbean clade plus the extant platyrrhines and *Cebupithecia* or is basal to the extant
16 platyrrhines and *Cebupithecia*. In CVA, *Paralouatta* was classified as *Saguinus* or an atelid.
17 However, in these analyses, the distribution of *Ateles* and *Brachyteles* overlapped with that of
18 callitrichines on CA 1 and 2 based on having a straight medial epicondyle and less keeled
19 trochlea; however these traits likely evolved in parallel as neither is present in the reconstructed
20 ancestral platyrrhine.

21 Ultimately, in considering the placement of the Caribbean primate taxa, the role that
22 mosaicism played in early platyrrhine evolution must not be discounted. Our cladistic and
23 phylogenetic shape analyses illustrated many instances of convergence of characteristics of the

distal humerus in disparate lineages. For instance, cebines and pitheciids have a similar morphology to each other, partially due to the presence of shapes that have not changed from the ancestral morphotype and partially due to the presence of traits that evolved in parallel in these two lineages. As an example, the highly posteriorly flexed medial epicondyle in *Cebus* and *Chiropotes* likely evolved in parallel from the slightly posteriorly flexed medial epicondyle of the common ancestor, whereas the degree of trochlear keeling seen in the cebines and pitheciids, as well as the shallow bicipital groove, are similar to that seen in the reconstructed ancestral morphotype. Something else to note is that most of the standard qualitative characters were highly variable within a single species or genus with several characters (e.g., trochleocapitular ridge, length of trochlea relative to capitulum, position of entepicondylar foramen) exhibiting three character states within a single species. While other studies have found cladistic postcranial characters to reproduce a valid phylogeny (e.g., Young, 2003), homoplasy in this particular dataset was high for the humeral characters.

Conclusions

In conclusion, we reconstruct UF 114718 to be a generalized, arboreal quadruped attributed to the species *Insulacebus toussaintiana* with a close phylogenetic relationship with *Antillothrix bernensis* from the Dominican Republic. Several of the Greater Antillean fossil taxa potentially form a monophyletic clade that is sister to all extant platyrrhine taxa. This lends support to the idea that the Greater Antillean primates could be stem platyrrhines. Based on the distal humeral data, we reconstruct the earliest ancestral platyrrhine to be a generalized, arboreal quadruped that potentially emphasized pronated arm postures during locomotion and may have engaged in some limited climbing. This reconstructed root of the platyrrhine clade was similar in the aspects of shape that vary most among the sample to both early anthropoids and fossil

1 platyrrhines. However, as aspects of shape and qualitative characters relating to the distal
2 humerus seem to be variable within a single genus, and prone to both homoplasy and reversals,
3 these results must be interpreted cautiously and (where possible) within the context provided by
4 other parts of the skeleton.

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Figure Legends

FIGURE 1. Image showing anterior (top) and posterior (bottom) views of a sample of platyrrhine primate humeri. A) *Cebus albifrons* (AMNH 211563); B) *Saimiri boliviensis* (AMNH 209933); C) *Saguinus midas* (AMNH 266481); D) *Aotus azarae* (AMNH 211460); E) *Callicebus domacophilus* (AMNH 211490); F) *Pithecia pithecia* (AMNH 149149); G) *Chiropotes satanas* (AMNH 95760); H) *Alouatta seniculus* (AMNH 211527); I) *Lagothrix lagotricha* (AMNH 188156); J) *Ateles belzebuth* (AMNH 259); and UF 114718 in K) anterior L) posterior M) medial N) lateral views.

FIGURE 2. Linear measures collected on the distal humerus of UF114718. Measures include: A) proximodistal (PD) capitulum height, 9.3 mm; B) mediolateral (ML) capitulum maximum breadth, 8.8 mm; C) PD lateral trochlear height, 9.0 mm; D) PD medial trochlear height, 7.4 mm; E) ML trochlear breadth excluding capitulum, 7.0 mm; F) biepicondylar breadth, 25.8 mm; G) posterior trochlear breadth, 7.7 mm; H) PD width of olecranon fossa, 6.0 mm; I) ML height of olecranon fossa, 14.2 mm; J) ML width of brachioradialis flange, 3.8 mm.

FIGURE 3. Landmarks collected on the distal humerus. Gray landmarks were removed in all analyses including the taxon *Paralouatta varoni* (MNHNCu 76.1010).

FIGURE 4. Comparison of the distal humeri of fossil platyrrhines taken from screenshots of laser surface scans. UF 114718, MHD 03a, MNHNCu 76.1010 and AMNH 266008 were scanned with the Breukmann white light scanner. UCMP 38762 and MCL 06 were scanned using a NextEngine portable surface scanner. All have been scaled using Adobe Photoshop CS5 to the same biepicondylar width. MHD 03a has been reflected for ease of comparison.

FIGURE 5. Results of CVA including all 18 landmarks on the distal humerus. Three dimensional models represent the maximum and minimum of each axis and were made by warping a scan of *Saguinus* to each maximum and minimum landmark configuration using Landmark Editor (Wiley et al., 2005). Models are show in anterior (right), posterior (left) and distal (bottom) views. Lines represent convex hulls around each extant group. Fossils are labeled in the graph.

FIGURE 6. Results of CVA for the partial landmark configuration. Three dimensional models represent the maximum and minimum of each axis and were made by warping a scan of *Saguinus* to each maximum and minimum landmark configuration using Landmark Editor (Wiley et al., 2005). Models are show in anterior (right), posterior (left) and distal (bottom) views. Lines represent convex hulls around each extant group. Fossils are labeled in the graph.

FIGURE 7. Parsimony tree generated from a branch and bound search shown with bootstrap support values.

FIGURE 8. Platyrrhine phylogenetic tree (taken from Perelman et al., 2011) with models representing extant taxon means for the OTUs and reconstructed HTUs. Landmark

configurations for the HTUs were reconstructed using MorphoJ (Klingenberg, 2011) via weighted squared change parsimony. Branch lengths for the weights were taken from Perelmen et al. (2011). Three dimensional models were made by warping a scan of *Saguinus* to each OTU and HTU landmark configuration using Landmark Editor (Wiley et al., 2005). Models are shown for each OTU in distal (left), anterior (middle) and posterior (right) views. Models are shown for each HTU in distal (bottom), anterior (left) and posterior (right) views. OTU blocks are colored based on family level relationships with Cebidae in green, Pitheciidae in blue and Atelidae in red.

FIGURE 9. Principal components analysis (axes 1, 2 and 3) of the extant taxa and fossils in phylomorphospace based on the results of the neighbor-joining tree analysis. The colors are based on family attribution. Solid lines represent the branches of the neighbor-joining tree and all taxa are labeled in the graph. All humeri are depicted in anterior view on the left, posterior view on the right and distal view at the bottom.

FIGURE 10. Map of Hispaniola, illustrating the locations of fossil primate finds. The dark stippled area indicates the portions of modern day Hispaniola which would have formed the southern paleoisland which is itself separated into two sections by the Jacmel-Fauché Depression.

Table Legends

TABLE 1. List of comparative sample.

TABLE 2. Description of landmarks collected on the distal humerus.

TABLE 3. Characters used for phylogenetic analyses

- 1 TABLE 4. Code distribution for phylogenetic analyses
- 2 TABLE 5. Classification data from the discriminant analyses of the full and partial landmark
- 3 sets. Probability refers to the posterior probability of belonging to that group among all
- 4 possible groups.
- 5 TABLE 6. Minimum, maximum and average Mahalanobis distances between group members
- 6 and their centroid, using genus as the grouping criterion.
- 7 TABLE 7. Maximum, minimum and average Mahalanobis distances between individuals within
- 8 each group to their group centroid, using family/subfamily as the grouping criterion.
- 9 TABLE 8. Character list with Consistency Index.
- 10 TABLE 9. Ancestral node codes.
- 11 TABLE 10. A summary of the current suggestions on the phylogenetic placement of fossil
- 12 Caribbean platyrrhines.
- 13

Table 1 List of comparative samples for morphometric and phylogenetic analyses.

	males	females	unknown
<i>Alouatta seniculus</i> (n=24)	3	10	11
<i>Aotus</i> (n=22)			
<i>Aotus azarae</i>	5	6	1
<i>Aotus trivirgatus</i>	3	6	1
<i>Ateles</i> (n=7)			
<i>Ateles belzebuth</i>	1	1	0
<i>Ateles fusciceps</i>	1	0	0
<i>Ateles geoffroyi</i>	2	1	0
<i>Ateles paniscus</i>	0	1	0
<i>Callicebus</i> (n=8)			
<i>Callicebus cupreus</i>	0	1	0
<i>Callicebus donaphilus</i>	1	1	0
<i>Callicebus moloch</i>	4	0	1
<i>Callithrix</i> (n=7)			
<i>Callithrix argentata</i>	1	0	0
<i>Callithrix jacchus</i>	1	2	2
<i>Callithrix santaremensis</i>	0	0	1
<i>Cebuella pygmaea</i> (n=2)	1	0	1
<i>Cebus apella</i> (n=20)	13	7	0
<i>Chiropotes satanas</i> (n=2)	2	0	0
<i>Lagothrix lagotricha</i> (n=4)	2	2	0
<i>Pithecia</i> (n=3)			
<i>Pithecia monachus</i>	0	0	1
<i>Pithecia irrorato</i>	1	0	0
<i>Pithecia pithecia</i>	1	0	0
<i>Saimiri boliviensis</i> (n=21)	12	9	0
<i>Saguinus</i> (n=10)			
<i>Saguinus fuscicollis</i>	0	1	0
<i>Saguinus midas</i>	0	1	1
<i>Saguinus mystax</i>	3	2	2
Early anthropoids (n=4)			
DPC 1275 [cast] (<i>Aegyptopithecus zeuxis</i>)			1
DPC 1033 [cast] (<i>Propliopithecus chirobates</i>)			1
DPC 3101 [cast] (<i>Apidium phiomense</i>)			1
DPC 8710 [cast] (<i>Parapithecus grangeri</i>)			1
Fossil platyrrhines (n=11)			
AMNH 268002 (<i>Xenothrix macgregori</i>)			1
AMNH 268005 (<i>Xenothrix macgregori</i>)			1
AMNH 266008 (<i>Xenothrix macgregori</i>)			1

AMNH 259905 (<i>Xenothrix macgregori</i>)	1
MHD 03a (<i>Antillothrix bernensis</i>)	1
MHD 16 (<i>Antillothrix bernensis</i>)	1
MNHNCu 76.1010 (<i>Paralouatta varonai</i>)	1
MNHNCu 76.1011 (<i>Paralouatta varonai</i>)	1
MNHNCu 76.1013 (<i>Paralouatta varonai</i>)	1
MNHNCu 76.1035 (<i>Paralouatta varonai</i>)	1
UCMP 38762 [cast] (<i>Cebupitheciasarmientoi</i>)	1

TABLE 2 Description of landmarks collected on the distal humerus.

Number	Type	Description
<i>Medial</i>		
<i>Epicondyle</i>		
1	II	Most lateral point on the lateral epicondyle
2	II	Most medial point on the medial epicondyle
3	II	Most posterior point on the adductor tubercle
<i>Trochlea</i>		
4	II	Proximoanterior extreme of medial margin of trochlea
5	II	Distal extreme of medial margin of trochlea
6	II	Proximoposterior extreme of medial margin of trochlea
7	II	Proximoanterior extreme of trochlear groove
8	II	Distal extreme of trochlear groove
9	II	Proximoposterior extreme of trochlear groove
10	II	Proximoanterior extreme of lateral margin of trochlea
11	II	Distal extreme of lateral margin of trochlea
12	II	Proximoposterior extreme of lateral margin of trochlea
<i>Capitulum</i>		
13	II	Most anterior point of the capitulum
14	III	Most proximal point in line with the most anterior point of the capitulum
15	III	Most distal point in line with the most anterior point of the capitulum
16	III	Most lateral point in line with the most anterior point of the capitulum
17	II	Most proximolateral point of the capitulum
<i>Olecranon</i>		
<i>Fossa</i>		
18	II	Deepest point on olecranon fossa

Table 3. Traits used for phylogenetic analyses.

	Trait	Character States		References
A	Shape of the trochlea	0	distal edge perpendicular to diaphysis	Fleagle and Kay, 1987; Dagosto and Gebo, 1994; Ford, 1994; Ross et al., 1998
		1	polymorphic between states 0 & 2	
		2	distal edge slightly angled to diaphysis	
		3	polymorphic between states 2 & 4	
		4	distal edge very angle to diaphysis	
B	Relative height of medial vs. lateral trochlear margins	0	equal	Ross et al., 1998
		1	polymorphic	
		2	medial more greatly flared	
C	Trochleocapitular ridge	0	absent	Ford, 1994; Ross et al. 1998
		1	polymorphic between states 0 & 2	
		2	slight	
		3	polymorphic between states 2 & 4	
		4	intermediate	
		5	polymorphic between states 4 & 6	
		6	very distinct	
D	Length of trochlea relative to capitulum	0	capitulum wider than trochlea	Modified from Ford, 1994; Ross et al. 1998
		1	polymorphic between states 0 & 2	
		2	equal	
		3	polymorphic between states 4 & 6	
		4	trocheal wider than capitulum	
E	Trochlear waisting	0	minimum and maximum distal trochlear width appear equal	Ford, 1994; Ross et al. 1998
		1	polymorphic between states 0 & 2	
		2	minimum distal trochlear width slightly smaller than maximum	

		3	Polymorphic between states 2 & 4	
		4	minimum distal trochlear width much smaller than maximum	
F	Entepicondylar foramen	0	present	Ford, 1986; Ross et al., 1998
		1	asymmetrically present / polymorphic	
		2	absent	
G	Position of entepicondylar foramen	0	over medial epicondyle	Ford, 1986; Ross et al., 1998
		1	polymorphic between states 0 & 2	
		2	above anterior trochlea	
		3	polymorphic between states 2 & 4	
		4	above posterior trochlea	
H	Medial epicondyle size	0	small	Fleagle and Kay, 1987; Ross et al., 1998
		1	large	
I	Dorsal placement of medial epicondyle	0	parallel to distal epiphysis	Ford, 1994; Ross et al. 1998
		1	polymorphic between states 0 & 2	
		2	slight posterior angle	
		3	polymorphic between states 2 & 4	
		4	large posterior angle	
J	Posterior trochlear shape	0	flat; edges flush with diaphysis	Fleagle, 1995; Ross et al. 1998
		1	both medial and lateral edges pronounced	
		2	polymorphic between states 1 & 3	
		3	lateral edge very pronounced	
K	Dorsoepitrochlear fossa	0	present	Fleagle, 1995; Ross et al. 1998
		1	polymorphic	
		2	absent	

L	Olecranon fossa depth	0	shallow	Fleagle, 1995; Ross et al. 1998
		1	polymorphic between states 0 & 2	
		2	intermediate	
		3	polymorphic between states 2 & 4	
		4	deep	
M	Olecranon fossa shape	0	oval	
		1	polymorphic between states 0 & 2	
		2	triangle	
N	Supinator crest	0	prominent	Fleagle and Kay, 1987; Ross et al., 1998
		1	polymorphic between states 0 & 2	
		2	low	
O	Brachioradialis flange	0	broad	Ross et al., 1998
		1	polymorphic between states 0 & 2	
		2	intermediate	
		3	polymorphic between states 2 & 4	
		4	narrow	
P	Bicipital groove morphology	0	shallow	Fleagle and Kay, 1987; Ross et al., 1998
		1	deep	
Q	Deltopectoral crest	0	prominent	Fleagle and Kay, 1987; Ross et al., 1998
		1	polymorphic between states 0 & 2	
		2	low	
R	Deltotriceps crest	0	low	Fleagle and Kay, 1987; Ross et al., 1998
		1	polymorphic between states 0 & 2	
		2	prominent	

Table 4a.Code distribution for cladistic character analyses of extant taxa.

	A			B		C				D			E			F			G			H		I			J			K		L			M		N			O			P		Q		R	
	0	2	4	0	2	0	2	4	6	0	2	4	0	1	2	0	1	2	0	2	4	0	1	0	2	4	0	1	3	0	2	0	2	4	0	2	0	2	4	0	1	0	2	0	2			
<i>Alouattapalliat</i> <i>a</i>			4		4	4				1	2	1		4				4	4			4		1	3			3	1	4		4				4	3	1	3	1		4		4		4		
<i>Alouattasenicu</i> <i>lus</i>			4		4	2	2				2	2		3	1			4	4			4		4				3	1	4		4			4		1	3		3	1	4		1	3	4		
<i>Atelespaniscus</i>			2		2		2			2			2					2	2				2	2				2		2			2			2			2		2		2		2	2		
<i>Atelesfusiceps</i>		5	1		6		5	1		5		1	6					6	6				6	6				4	2	6			4	2		6		6			6		6	1	5	6		
<i>Lagothrixlagot</i> <i>richa</i>		3	1		4		1	3			4			4				4	4				4	1	3			3	1	2	2			4		4	2	2			4		4	1	3	4		
<i>Lagothrixcana</i>			4		4			4			1	3		4				4	4				4		3	1			4	2	2			4		4	1	3			4		4		4	4		
<i>Callicebustorq</i> <i>uatus</i>		2			2		2			2			2		2				2				2		2			2		1	1		2		2			2			2	2			2	2		
<i>C.</i> <i>donacophilus</i>			5		5	3	2				3	2		5				5	5				5	2	2	1		5		2	3	5			5			5			5	5			3	2	3	2
<i>Pitheciamonac</i> <i>hus</i>			5		5		4	1				5			5	5					5		5		5			5		4	1	1	4		5			5			5	5			5	5		
<i>Pitheciapitheci</i> <i>a</i>		3			3		1	2			3			3		3					3		3		3			3			3		3		2	1		3		1	2	3		1	2	3		
<i>Chiropotessata</i> <i>nas</i>			5		5		5				5				5	5				5			5			5		5		5			5			5	5		5			5		5	5			
<i>Aotuslemurinu</i> <i>s</i>		2	6		8	1	6	1		1	5	1		7	1			8	8				8	3	5			8		2	6	5	2		5	3		8			8	8		6	2	4	4	
<i>Cebuscapucinu</i> <i>s</i>		4	4		8	1	5	2			8			3	5	8				8			8			8			8		7	1		8		6	2	8		8			8		5	3	3	5
<i>Saimiri</i> <i>sciureus</i>		4	2		6	2	4				2	4		6		6				6		6		6				3	3	4	2		6		2	4	6		6			6			6	6		
<i>Saguinusoedip</i> <i>us</i>	7	1		5	3			8				8	7	1		6	2		1	6	1		8	4	4			4	4	3	5		8		8		6	2		1	7	8		6	2	2	6	
<i>Callithrixjacch</i> <i>us</i>		8		6	2			2	6		8		7	1			1	7	7	1			8	8				8			8		8		8		6	2		8		8		7	1	2	6	
<i>Cebuella</i> <i>pygmaea</i>	8			8					8	2	5		8					8	8				8	8				8			8		8		8	7	1	5	3		7	1	8		5	3	4	4

Table 4b. Code distribution for cladistic character analyses of extinct taxa.

	A			B		C				D			E			F			G			H		I			J			K		L			M		N		O			P		Q		R		
	0	2	4	0	2	0	2	4	6	0	2	4	0	1	2	0	1	2	0	2	4	0	1	0	2	4	0	1	3	0	2	0	2	4	0	2	0	2	0	2	4	0	1	0	2	0	2	
<i>Xenothrix</i> <i>AMNH</i> 268008, 268005, 268002, 25??05			1		1		1				1				1	2				2		1				1		1	1	1			2		2	1		1			3		2			2		
<i>Antillothrix</i> <i>MHD</i> 3, 16			2		2		2			1				1	1			2	2			1	1		1	1		1	1	2				2	1	1	1	1	1	1	1		1		1			1
UF 114718			1		1		1			1					1	1						1		1				1	1				1	1			1	1			?		1				1	
<i>Paralouatta</i> <i>M</i> <i>HNH</i> <i>Cu</i> 76.103, 76.1010, 76.1013, 76.1011		1	2		3	1	2				1		2	2	1	2		1	1	2		2	1			3		2		3				2	1	1		2			2	1		1			1	
<i>Cebupithecia</i> (UCMP 38762)		1			1				1		1			1		1			1			1		1			1		1			1			1			1	1			1			1			
<i>Aegyptopithec</i> <i>us</i> (DPC 1275)		1			1	?				?			?			1				1			1	?			?			1		?			1		1			1	1		1			1		
<i>Propliolithe</i> <i>us</i> (DPC 1033)			1		1		1					1			1	1			?				1		1			1		1				1	1		1			?		?		?				
<i>Parapithecus</i> (DPC 8710)			1				1				1			1		1		?				1			1		1		1				1	1		1			?		1			1				
<i>Apidium</i> (DPC 3101)			1		1	1					1				1	1				1			1			1		1				1		1		1			?		?			?				

TABLE 5 Classification data from the discriminant analysis of the full and partial landmark sets.^a

Full Landmark Set						
	Groups by genus (72.3%)			Groups by subfamily (79.2%)		
	Predicted Group	Probability	D ²	Predicted Group	Probability	D ²
UF 114718	<i>Saguinus</i>	0.99	29.4	Callitrichinae	0.99	4.7
AMNH 266008 (<i>Xenothrix macgregori</i>)	Early Anthropoids	0.89	45.5	Early Anthropoids	0.50	16.9
MCL 06 (<i>Cartelles coimbrafilhoi</i>)	<i>Ateles</i>	1	41.0	Callitrichinae	0.94	20.7
MHD 03a (<i>Antillothrix bernensis</i>)	<i>Chiropotes</i>	0.83	42.8	Pitheciinae	1	4.5
UCMP 38762 (<i>Cebupithecia sarmientoi</i>)	<i>Saguinus</i>	0.81	26.9	Callitrichinae	0.99	5.8
Partial Landmark Set						
	Groups by genus (76.2%)			Groups by subfamily (81.8%)		
	Predicted Group	Probability	D ²	Predicted Group	Probability	D ²
UF 114718	<i>Saguinus</i>	0.76	22.4	Callitrichinae	0.99	4.9
AMNH 266009 (<i>Xenothrix macgregori</i>)	Early Anthropoids	1	26.5	Pitheciinae	0.98	9.3
MCL 06 (<i>Cartelles coimbrafilhoi</i>)	<i>Callithrix</i>	0.95	36.8	Callitrichinae	0.99	13.2
MHD 03a (<i>Antillothrix bernensis</i>)	<i>Chiropotes</i>	0.99	15.6	Pitheciinae	0.99	2.8
MNHNCU 76.1010 (<i>Paralouatta varonai</i>)	<i>Saguinus</i>	0.72	44.3	Atelinae	0.96	7.5
UCMP 38762 (<i>Cebupithecia sarmientoi</i>)	<i>Callithrix</i>	0.67	18.2	Callitrichinae	0.93	6.5

^aProbability refers to the posterior probability of belonging to that group among all possible groups. D² refers to the squared Mahalanobis distance between that individual and the predicted group centroid. Percentage number indicates the percent of individuals correctly classified on cross-validation.

Table 6 Maximum, minimum and mean Mahalanobis distances between individuals within each group to their group centroid using genus as the grouping criterion.

	Full Configuration			Partial Configuration		
	Minimum	Maximum	Mean	Minimum	Maximum	Mean
Early Anthropoids	7.32	19.57	12.48	8.37	19.46	13.04
<i>Callithrix</i>	4.84	20.78	11.37	5.06	16.63	8.62
<i>Saguinus</i>	4.92	13.02	9.58	3.35	13.97	8.60
<i>Aotus</i>	1.94	24.91	12.80	3.94	22.89	12.49
<i>Callicebus</i>	5.54	13.39	10.07	7.83	17.41	12.45
<i>Pithecia</i>	3.55	11.29	7.74	5.02	12.81	8.98
<i>Alouatta</i>	5.06	13.79	9.85	2.80	19.18	10.31
<i>Lagothrix</i>	2.79	11.01	7.85	3.20	14.67	8.72
<i>Saimiri</i>	3.05	18.42	11.61	4.09	19.38	11.50
<i>Ateles/Brachyteles</i>	5.75	12.20	8.79	8.50	16.14	11.73
<i>Cebus</i>	7.35	20.69	11.52	5.40	18.75	11.67

Table 7 Maximum, minimum and average Mahalanobis distances between individuals within each group to their group centroid, using family/subfamily as the grouping criterion.

	Full Configuration			Partial Configuration		
	Minimum	Maximum	Average	Minimum	Maximum	Average
Early Anthropoids	0.720	2.016	2.787	3.391	35.473	9.290
Pitheciinae	1.050	6.367	3.984	0.498	11.264	4.789
Atelinae	.325	7.811	3.416	0.278	10.066	2.410
Callitrichinae	0.384	10.367	2.818	0.641	10.037	3.020
Cebinae	0.408	15.334	4.390	0.169	12.506	3.908

Table 8. Character list with Consistency Index (CI).

Character		CI
A	Shape of the trochlea	0.364
B	Relative height of medial vs. lateral trochlear margins	1.000
C	Trochleocapitular ridge	0.300
D	Length of trochlea relative to capitulum	0.286
E	Trochlear waisting	0.250
F	Entepicondylar foramen	0.222
G	Position of entepicondylar foramen	0.308
H	Medial epicondyle size	0.500
I	Dorsal placement of medial epicondyle	0.267
J	Posterior trochlear shape	0.250
K	Dorsoepitrochlear fossa	0.222
L	Olecranon fossa depth	0.286
M	Olecranon fossa shape	0.200
N	Supinator crest	0.200
O	Brachioradialis flange	0.190
P	Bicipital groove morphology	0.500
Q	Deltopectoral crest	0.500
R	Deltotriceps crest	0.250

Table 9. Ancestral states for the basal platyrrhine.

Character	Basal platyrrhine		Base of the crown radiation
	Parsimony Tree	NJ Tree	
A Shape of the trochlea	(4) distal edge very angled to diaphysis	(4) distal edge very angled to diaphysis	(4) distal edge very angled to diaphysis
B Relative height of medial vs. lateral trochlear margins	(2) medial more greatly flared	(2) medial more greatly flared	(2) medial more greatly flared
C Trochleocapitular ridge	(2) slight	(2) slight	(2 3) slight, polymorphic
D Length of trochlea relative to capitulum	(0 2 4) capitulum wider than trochlea, equal, trochlea wider than capitulum	(0) capitulum wider than trochlea	(2 3) equal, polymorphic
E Trochlear waisting	(2 4) minimum distal trochlear width slightly smaller than maximum, minimum distal trochlear width much smaller than maximum	(2) minimum distal trochlear width slightly smaller than maximum	(2) minimum distal trochlear width slightly smaller than maximum,
F Entepicondylar foramen	(0) present	(0) present	(0 2) present, absent
G Position of entepicondylar foramen	(2) above anterior trochlea	(2) above anterior trochlea	(2) above anterior trochlea
H Medial epicondyle size	(2) large	(2) large	(2) large
I Dorsal placement of medial epicondyle	(2 4) slight posterior angle, large posterior angle	(2 4) slight posterior angle, large posterior angle	(2 4) slight posterior angle, large posterior angle
J Posterior trochlear shape	(0 2) both edges pronounced or lateral edge very pronounced	(2) lateral edge very pronounced	(0) both medial and lateral edges pronounced
K Dorsoepitrochlear fossa	(0) present	(0) present	(0) present
L Olecranon fossa depth	(4) deep	(4) deep	(2) intermediate
M Olecranon fossa shape	(0) oval	(0) oval	(0 1 2) oval, polymorphic, triangle

N	Supinator crest	(0) prominent	(0 2) prominent or low	(1 2) polymorphic, low
O	Brachioradialis flange	(0) broad	(0) broad	(4) narrow
P	Bicipital groove morphology	(0) shallow	(0) shallow	(0) shallow
Q	Deltopectoral crest	(0) prominent	(0) prominent	(1) polymorphic
R	Deltotriceps crest	(0 2) low or prominent	(0 1) low or prominent	(0) low

Table 10. Table showing all phylogenetic affinities for each of the Caribbean species proposed.

	Platyrrhine family to which a Caribbean species or specimen (in brackets) has been assigned			
	Pitheciidae	Cebidae	Atelidae	Stem platyrrhine
<i>Xenothrix mcgregori</i> , Williams and Koopman, 1952	Rosenberger, 1977; MacPhee et al., 1995 et seq.; Horovitz and MacPhee, 1999; MacPhee and Horovitz, 2004	Williams and Koopman, 1952; Ford, 1986, 1990		
	Cooke et al., 2011			
<i>Antillothrix bernensis</i> , Rimoli, 1977	MacPhee et al., 1995 et seq.; Rosenberger et al., 2013 [MHD 01 mandible]	Rimoli, 1977; MacPhee and Woods, 1982 [UF 28038]; Ford, 1986 [USNM 254682] Rosenberger et al., 2011 [MHD 01 cranium]		Kay et al., 2011
<i>Paralouatta varonai</i> , Rivero and Arredondo, 1991	MacPhee et al., 1995; Horovitz and MacPhee, 1999; MacPhee and Horovitz, 2004		Rivero and Arredondo, 1991; Cooke, 2011; Rosenberger et al., 2011	
<i>Insulacebus toussaintiana</i> , Cooke et al., 2011		Ford, 1990		
	Cooke et al., 2011			

Figure 1

Figure 2

Figure3

Figure4

Figure 5

Figure 6

Figure 7

Figure 8

Figure 9

Figure 10