Title: Stem members of Platyrrhini are distinct from catarrhines in at least one derived cranial feature

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Abstract

The pterion, on the lateral aspect of the cranium, is where the zygomatic, frontal, sphenoid, squamosal, and parietal bones approach and contact. The configuration of these bones distinguishes New and Old World anthropoids: most extant platyrrhines exhibit contact between the parietal and zygomatic bones, while all known catarrhines exhibit frontal-alisphenoid contact. However, it is thought that early stem-platyrrhines retained the apparently primitive catarrhine condition. Here we re-evaluate the condition of key fossil taxa using μ CT imaging. The single known specimen of *Tremacebus* and an adult cranium of *Antillothrix* exhibit the typical platyrrhine condition of parietal-zygomatic contact. The same is true of one specimen of *Homunculus*, while a second specimen has the ‘catarrhine’ condition. When these new data are incorporated into an ancestral state reconstruction, they support the conclusion that pterion frontal-alisphenoid contact characterized the last common ancestor of crown anthropoids and that contact between the parietal and zygomatic is a synapomorphy of Platyrrhini.

Keywords: New World Monkeys, Pterion, *Homunculus*, *Tremacebus*, microCT

Introduction

New World monkeys (Platyrrhini) appear to have originated in Africa and rafted to South America in the later Eocene (Ciochon and Chiarelli, 1980; Lavocat, 1980; Fleagle, 1986; Hartwig, 1994; Fleagle and Kay, 1997; Houle, 1998, 1999; Bond et al., 2015; Kay, 2015a, 2015b). Several families of late Eocene African anthropoids have been allied with platyrrhines, but determining whether any of these families might be the

platyrrhine sister group is complicated by a dearth of platyrrhine synapomorphies (Hartwig, 1994; Bond et al., 2015; Kay, 2015b). Platyrrhines are distinguished from catarrhines primarily by the apparent retention of characters thought primitive for anthropoids, including three premolars and a ring-shaped extrabullar (phaneric) ectotympanic (Herskovitz, 1977). A zygomatic-parietal pattern of sutural contact among the bones comprising the pterion region on the lateral wall of the braincase (the medial wall of the temporal fossa) stands as the most important putative synapomorphy of the bones of the cranium (Herskovitz, 1977; Horovitz and MacPhee, 1999). In catarrhines, tarsiers, and strepsirrhine primates, the frontal and alisphenoid bones (the greater wing of the sphenoid in human anatomy) directly contact on the medial wall of the temporal fossa. In most platyrrhines, the zygomatic and parietal form a direct external suture excluding the frontal and alisphenoid (Figure 1). This difference in sutural configuration is often taken to have phylogenetic valence (Ashley-Montagu, 1933; Le Gros Clark, 1959; Herskovitz, 1977; Rosenberger, 1977; Fleagle and Kay, 1987; Horovitz and MacPhee, 1999) especially as variation in suture pattern appears to be at least partly heritable (Wang et al., 2006). Confident deployment of the pterion as a character distinguishing platyrrhines from non-platyrrhine anthropoids is, however, contingent upon understanding first the pattern and potential causes of intraspecific variation in pterion configuration in extant platyrrhines, the character polarity of the pterion in anthropoids, and the pterion configuration of the earliest known fossil platyrrhines.

It has long been appreciated that the pattern of pterion contact is variable in extant platyrrhines, especially among the atelids. The ‘catarrhine’ condition occurs in 55% of *Alouatta* specimens, and 38% of *Ateles* specimens. Fourteen per cent of *Brachyteles*

skulls have the ‘catarrhine’ condition, as do 1.5% of *Lagothrix* individuals (Ashley-Montagu, 1933). Hershkovitz (1977) defines seven variant pterion patterns in platyrrhines in addition to the typical broad parietal-zygomatic contact, most of which are expressed in the large-bodied Atelidae. Some of these variants preserve parietal-zygomatic contact, such as Hershkovitz’s Type II (Hershkovitz, 1977), wherein the parietal and zygomatic share a narrow contact near an emissary foramen, but others resemble more closely the catarrhine condition with an external frontal-alisphenoid suture. This variability in the large-bodied atelids has led some to question the phylogenetic utility of the feature and to suggest that a higher incidence of frontal-alisphenoid contact may be a function of the generally larger body sizes of catarrhines (Fleagle and Kay, 1987).

Parsimony suggests that the catarrhine condition of alisphenoid-frontal contact is primitive for the clade, as it is also present in the anthropoid outgroup Tarsiidae and in primates without postorbital closure (Le Gros Clark, 1959; Hershkovitz, 1977; Rosenberger, 1977; Horovitz and MacPhee, 1999). Ashley-Montagu (1933), however, in the first major contribution on the topic, considered frontal-alisphenoid contact to be derived, based on an inferred evolutionary gradient linking tree shrew-like insectivores to living humans. He believed that the initial closure of the postorbital septum involved the posterior extension of the zygomatic until it came to contact the parietal. The zygomatic was then pushed forward again by the alisphenoid as the orbits of catarrhines decreased in size and increased in frontation. Intraspecific variation in extant atelids holds the potential to test this hypothesis. Halenar (2015), analyzing a large sample of *Alouatta*, found no such relationship between frontation and pterion pattern. The fossil record presents the obvious recourse for resolving questions of polarity.

Among Old World Paleogene fossil anthropoids, the Parapithecidae – from the Late Eocene and Early Oligocene of North Africa (Fleagle and Kay, 1987; Simons, 1995, 2001, 2004; Seiffert et al., 2005, 2009; Seiffert, 2012) – are represented by a handful of specimens preserving evidence of a postorbital septum and the pterion region.

Understanding the form of the sutural arrangement expressed in these taxa would be especially interesting, regardless of their ultimate phylogenetic affinities. If these taxa represent stem anthropoids, the configuration of their pterion would bear on the likely ancestral state for Anthropoidea. If, instead, they are best interpreted as crown anthropoids, it might link them uniquely to platyrrhines. Fleagle and Kay (1987) suggested that the roughened surface of the temporal process of an isolated frontal of *Apidium phiomense* is consistent with an internal alisphenoid-frontal suture overlain by parietal-zygomatic contact. A more complete cranium of *A. phiomense* was subsequently described, but contact in the pterion cannot be determined owing to breakage and fusion of the bones (Simons, 1995). Simons described the pterion region of another parapithecoid, *Simonsius* (= *Parapithecus*) *grangeri*, as tentatively exhibiting frontal-alisphenoid contact (Simons, 2001, 2004). Finally, it is uncertain when parietal-zygomatic pterion contact evolved among South American primates. Because parietal-zygomatic contact is present in at least some proportion of individuals of all living platyrrhine species, as well as the recently extinct taxa *Paralouatta varonai* (Rivero and Arredondo, 1991) and one figured individual of *Antillothrix bernensis* (Rosenberger et al., 2011) – the only Antillean taxa in which the pterion region is preserved adequately for assessment (MacPhee and Horovitz, 2004; Cooke et al., 2011) – zygomatic-parietal contact is most parsimoniously inferred to have characterized the last common ancestor

of crown platyrrhines. However, the stem platyrrhines *Homunculus patagonicus* and *Tremacebus harringtoni*, both from the Miocene of Argentina (Tauber, 1991; Kay et al., 2008; Kay and Fleagle, 2010; Kay, 2015a), reportedly exhibit an external frontal-alisphenoid suture, resembling that of catarrhines (Tauber, 1991; Kay et al., 2008). This implies that the shift to zygomatic-parietal dominant pterion patterns occurred on the South American continent some time before the origin of the crown group and diminishes the importance to systematics of the pterion pattern of early Old World anthropoids (Kay et al., 2008, 2011).

To help clarify the interpretation of the fossil evidence, we reassess pterion pattern in the fossil platyrrhines *Dolichocebus*, *Homunculus*, *Tremacebus*, and *Antillothrix* and the North African anthropoids *Simonsius* and *Proteopithecus* through the use of μ CT (micro-computed tomography) scans of crania from each taxon. μ CT has proven useful in detecting differences in texture and internal structure in fossil material that may not be visible through external examination (Ketcham and Carlson, 2001; Tafforeau et al., 2006; Scherf, 2013; Weber, 2015), including in the tracing of sutural boundaries and evaluation of suture patency in primates (Reinholt et al., 2009; Curtis et al., 2014). This technique may allow more reliable determination of the pattern of pterion contact in these important taxa. We incorporate new information provided by this approach into a phylogenetic analysis of platyrrhine relationships and an ancestral state reconstruction of the pterion configuration at the last common ancestors of platyrrhines and haplorhines, respectively.

Materials and methods

Specimens examined

μ CT scans of two specimens of *Alouatta palliata* (DU-BAA-19, DU-BAA-24) from the collections of the Duke University Department of Evolutionary Anthropology were used to evaluate the use of μ CT to identify suture boundaries in the pterion. These scans were produced at the Shared Materials Instrumentation Facility (SMiF) at Duke University (Nikon XTH 225 ST scanner) by Allen (2014). DU-BAA-19 clearly demonstrates the ‘platyrrhine’ condition while DU-BAA-24 demonstrates the ‘catarrhine’ condition.

μ CT scans were obtained of cranial specimens of *H. patagonicus* (MPM-PV 3501, MPM-PV 3502, MPM-PV 3503), *T. harringtoni* (FML 619), *Antillothrix bernensis* (PN-09-01), *Dolichocebus gaimensis* (MACN 14128), *S. (=P.) grangeri* (DPC 18651), and *Proteopithecus sylviae* (DPC 14095). Scans of *Homunculus*, *Simonsius*, and *Proteopithecus* were produced at SMiF, scans of *Tremacebus* and *Dolichocebus* at the High-Resolution X-ray Computed Tomography Facility at the University of Texas (Kay et al., 2004a; Coleman et al., 2010), and the scan of *Antillothrix* at the Center for Quantitative Imaging at Pennsylvania State University (Kay et al., 2011). MPM-PV 3502 was recovered from the Santa Cruz Formation, Santacrucian SALMA (South American Land Mammal Age; ~16.8 Ma), at the Kilik Aike Norte locality, Santa Cruz Province, Argentina. MPM-PV 3501 and MPM-PV 3503 were recovered from the Santa Cruz Formation, at the Puesto Estancia La Costa locality (~17.9 Ma), Santa Cruz Province, Argentina. The *T. harringtoni* type, Museum of the Fundacion Miguel Lillo specimen no. 619, was recovered from the Sarmiento Formation, Colhuehuapian SALMA (~21 Ma) of the Sacanana locality, Chubut Province, Argentina (Rusconi, 1935; Fleagle and Bown,

1983). MACN 14128 is also Colheuhupian, from the Gaiman locality in Chubut Province (Kay et al., 2008). PN-09-01 was recovered from the Holocene cave deposit of Padre Nuestro in the Dominican Republic. DPC 18651 and DPC 14095 are from the Oligocene and Eocene deposits of the Jebel Qatrani Formation of the Fayum region of Egypt, respectively (Simons, 1997, 2001). All scans are available through the MorphoSource webpage (Boyer et al., 2014). Information on each scan is presented in Table 1.

Visualization techniques

The CT images were viewed in coronal, transverse, sagittal, and various oblique planes. On each slice (= two-dimensional [2D] cross section through the scan volume), regions of bone separated by apparent sutural boundaries were inferred to represent distinct cranial elements and segmented accordingly with the labeling tool in the program Avizo (Version 8.0). Our objective in this process was to identify continuous surfaces of bone. Similar approaches have been taken in investigations of the cranial osteology in fossils in the past (Curtis et al., 2014; Krause et al., 2014). At least three orthogonal views were taken as necessary to distinguish between postmortem breaks and actual sutures. Cracks were ‘bridged’ (marked on either side as regions of the same bone) when they could be distinguished from sutures based on texture, continuity across slices, and external appearance.

Cladistic analysis

Revised character states for *Homunculus* and *Tremacebus* were incorporated to update the character-taxon matrix of Kay (2015a; the character-taxon matrix used in the present study is provided as Supplementary Online Material [SOM]). The only changes

made in the present study concern the rescoring of the pterion of *Homunculus* and *Tremacebus* (see Results) and the addition of the newly described Paleogene taxon *Perupithecus* (Bond et al., 2015; Kay, 2015b) (Table 2).

Parietal contact at pterion (cranial character 46 in Kay et al., [2004]) is coded as an ordered three-state character: 0= zygomatic-parietal contact; 1= polymorphic and occurs >25% of cases; 2= alisphenoid-frontal contact. We used maximum parsimony implemented in PAUP (version 4.0a145, Beta) to analyze the data (Swofford, 2001). In all analyses, heuristic analyses were performed as follows: the tree-bisection-reconnection (TBR) branch-swapping algorithms of PAUP were selected; for each set of comparisons, starting trees were obtained via stepwise addition with a random-addition sequence with one tree held at each step; each analysis was replicated 1000 times.

The joint analyses of extant and extinct taxa use a ‘molecular scaffold’ phylogeny as implemented using the ‘Constraints Backbone’ option of PAUP (Springer et al., 2001) (Figure 2). This approach allows the tree search algorithm to place fossils on the basis of their morphological characters but constrains the topology of the final tree to be consistent with information on primate relationships gleaned from molecular systematics. Thanks to enormous effort combining molecular sequence and molecular marker data, the extant platyrrhine tree is fully resolved at the level of the genus. Hitherto, a major uncertainty related to the placement of *Aotus* within Cebidae. Earlier work recovered *Aotus* (*Saimiri* + *Cebus*) with callitrichines as the outgroup (Opazo et al., 2006). However, that grouping was supported by low bootstrap percentages and posterior probabilities. More comprehensive studies have resolved this branching sequence as *Saimiri*+*Cebus* in a basal split, with *Aotus* linked with callitrichines (Perelman et al.,

2011; Kiesling et al., 2015). This relationship was therefore enforced in the molecular scaffold.

Ancestral state reconstruction

A consensus molecular tree of 208 haplorhine taxa was retrieved from the 10k Trees project website (Arnold et al., 2010). *Aegyptopithecus*, *Homunculus*, *Tremacebus*, and *Antillothrix* were added to this tree using functions in the R package “ape” (Paradis et al., 2004), with branch lengths corresponding to the approximate first occurrence of each genus in the fossil record (30 Ma [Seiffert, 2006], 17.5 Ma [Fleagle et al., 2012], 21 Ma [Dunn et al., 2013], and 1.32 Ma [Rosenberger et al., 2015], respectively).

Aegyptopithecus was placed in a polytomy with the last common ancestor (LCA) of crown catarrhines and *Homunculus*, *Tremacebus*, and *Antillothrix* were placed in a polytomy with the LCA of crown platyrrhines (SOM Figure S1). All extant tarsiers and catarrhines were coded with frontal-alisphenoid contact (state “0”). All species of *Alouatta* and *Ateles* were coded as polymorphic (“0” and “1”) and all other platyrrhines as possessing zygomatic-parietal contact (state “1”). For the extinct taxa, *Tremacebus* and *Antillothrix* were coded as “1,” *Aegyptopithecus* as “0,” and *Homunculus* as polymorphic (see results). This coding differs from that used in the cladistic analysis in that it does not use an intermediate polymorphic state, but instead codes polymorphic taxa as expressing both states. This allows the more straightforward calculation of relative support for reconstructions of each pterion state at internal nodes.

All analyses were performed using Bayesian methods in the program Multistate implemented in BayesTraits V2 (Meade and Pagel, 2014) and accessed using the R package “btw,” which was also used to perform significance tests (Griffin, 2015). First,

models of evolution with symmetric and asymmetric transition rates between states “0” and “1” were tested using Bayes factors (Kass and Raftery, 1995). Symmetric rates were preferred by both parsimony and Bayes factor ($BF = 3.56$). To test for the most likely state at the LCA of platyrrhines (including the extinct taxa), this node was ‘fossilized’ to states “0” and “1” the two models compared using Bayes factors. This procedure was repeated to test for the most likely state at the LCA of anthropoids. Because of controversy over the homology of post-orbital closure in anthropoids and tarsiers, and hence of the frontal-alisphenoid pterion pattern present in both (Smith et al., 2013), a second test of the state at the LCA of anthropoids was run with tarsiers coded as “no data” instead of “0.” Bayes factors greater than two were considered to offer positive evidence for a model, those between five and 10 strong evidence, and those greater than 10 very strong evidence (Kass and Raftery, 1995; Meade and Pagel, 2014).

Results

Morphological observations

The poor state of preservation in the available specimens of *Dolichocebus* and *Proteopithecus* prevented determination of sutural patterns. Though it is possible that investigation of these taxa could produce unequivocal results, the breakage and/or advanced state of fusion of the sutures in these specimens was severe enough that we did not feel comfortable attempting to infer contact patterns given the scan resolution and analytical techniques available to us. DPC 14095 (*Proteopithecus*) is too crushed for the pterion region to be visible, but an attempt to segment fragments of bone in the region of the pterion is presented for MACN 14128 (*Dolichocebus*) in the (SOM Figure S2). Past

detailed investigation of the cranial anatomy of *Catopithecus* specimens housed at Duke University (DPC 8701, DPC 12367, DPC 42214) found these specimens too crushed for definitive evaluation (Allen, personal communication). Examination of *Simonsius*, however, is at least consistent with the identification of frontal-alisphenoid contact noted by Simons (Simons, 2001, 2004). The right side of the cranium is extensively fractured in the region of the pterion, and the zygomatic and parietal are not well preserved on the left. A continuous strip of bone extends from the inferior of the left side of the cranium to contact the frontal, however, which may represent the alisphenoid (SOM Fig. S3).

In the type specimen of *T. harringtoni* (Museum of the Fundacion Miguel Lillo specimen no. 619), an apparently continuous surface of bone could be traced from the anterior zygomatic arch to the parietal on both sides, which we identify as the zygomatic (Figs. 3A-D). Another, half-moon shaped region of bone on the margin of the orbit is most likely a broken part of the zygomatic as it does not participate significantly in the formation of the post-orbital septum or in the ‘cheek’ on the left side (Fig. 4: bones highlighted in orange and green). The bone identified as the main body of the zygomatic is in direct contact with the parietal posteriorly, which indicates that *Tremacebus* exhibited the crown platyrrhine pterion condition.

MPM-PV 3502, the first examined specimen of *H. patagonicus*, is more damaged than the type of *T. harringtoni*, making sutures more difficult to trace and distinguish from cracks. However, continuous surfaces of bone extending from the neurocranium to the region of the pterion show a narrow extension of the parietal anteriorly (Figs 4A-C). This bony process is in direct contact with a bone constituting much of the zygomatic arch, which is comprised of the zygomatic bone. This specimen appears to resemble

Herskovitz's Type II pterion pattern more closely than the Type I pattern of broad zygomatic/parietal contact modal for many smaller bodied platyrrhines (Herskovitz, 1977).

Two other specimens of *H. patagonicus*, MPM-PV 3501 and 3503, were also examined using μ CT, but results were ambiguous, indicating what was probably, at most, a very narrow contact between the zygomatic and parietal prior to postmortem deformation. MPM-PV 3501 preserves the pterion region in good condition, but sutures in the region of potential contact between the parietal and zygomatic have become fused, and this region is difficult to assign definitively to either the frontal or the zygomatic (SOM Fig. S4A). MPM-PV 3503 appears to preserve a very inferiorly extending frontal that would be consistent with exclusive contact with the alisphenoid, but the critical region where this contact might have occurred is broken, and an extension of the parietal to the zygomatic cannot be ruled out (SOM Fig. S4B). In addition to these specimens, a fourth cranium of *H. patagonicus* known from Puesto Estancia La Costa (CORD-1130) was visually examined by RFK and interpreted to show a catarrhine-like sutural pattern in the pterion (see SOM Fig. S5). Interestingly, both MPM-PV 3501 and MPM-PV 3502, as well as CORD-1130, have an emissary foramen in the region of the pterion, similar to the structure mentioned by Herskovitz (1977) as variably present in some extant platyrrhines.

The PN-09-01 specimen of *A. bernensis* exhibits a narrow contact between the parietal and zygomatic on the right side and a broader contact between the zygomatic and the parietal on the left (Figure 5), at variance with the initial published description (Kay et al., 2011). The presence of zygomatic-parietal contact in this species is also supported

by the published figure of a juvenile *A. bernensis* cranium (MHD-01) from Rosenberger et al. (2011) which shows broad parietal-zygomatic contact. The states of these two specimens suggest that *Antillothrix* should be understood to possess crown platyrrhine-like zygomatic-parietal contact.

Cladistic Analysis

The new morphological information described above indicates that character states used in Kay (2015a) need to be modified for *Homunculus* and *Tremacebus*.

Homunculus is now coded as polymorphic for the catarrhine and platyrrhine condition (instead of as monomorphic for the catarrhine condition). *Tremacebus* is now coded as monomorphic for the platyrrhine condition. We repeated the phylogenetic analysis using the dataset of Kay (2015a) substituting this revised coding. Using the molecular scaffold approach (see Materials and methods and Figure 2), Kay (2015a) found two most parsimonious trees, each of which place Miocene *Tremacebus* and *Homunculus* as stem members of the Platyrrhini and Pleistocene-Recent Antillean *Paralouatta* and *Antillothrix* as stem platyrrhines but closer to the LCA of crown platyrrhines.

Using our revised matrix, we find two most parsimonious trees, with the strict consensus presented in Figure 6. The trees are the same as those of Kay (2015a). Frontal-alisphenoid contact is still reconstructed as a symplesiomorphy of stem anthropoids and perhaps even a *Tarsius*-anthropoid clade. Now, however, a zygomatic-parietal contact becomes a synapomorphy of stem Platyrrhini. Frontal-alisphenoid contact (the ‘catarrhine’ condition) occurs as a variant in *Homunculus* and some extant platyrrhines but these instances of polymorphism are reconstructed as homoplasies.

Ancestral state reconstruction

When revised character states for the fossil taxa are included, a Bayes factor test strongly prefers zygomatic-parietal contact as the most likely state in the LCA of stem platyrrhines (BF = 40.91). Tests with (BF = 4.07) and without (BF = 0.536) tarsiers coded as showing frontal-alisphenoid contact prefer this state as the most likely for the LCA of stem anthropoids as well, although without considering tarsiers, the Bayes factor fails to reach the threshold of confidence, and a reconstruction of the catarrhine state at the anthropoid LCA is preferred only 59% to 41%, which might indicate evidence for polymorphism. However, by the available fossil and extant evidence, parietal-zygomatic contact is best interpreted as a synapomorphy not just of crown platyrrhines but also of the LCA of platyrrhines as a whole.

Discussion

The patterns of pterion contact we report for *T. harringtoni* and *A. bernensis* differ from earlier interpretations. In the case of *H. patagonicus*, the pattern in MPM-PV 3502 is different from that reported for CORD-1130, suggesting a variable condition for this species. The ambiguous character states present in MPM-PV 3501 and 3503 may support this conclusion, as zygomatic-parietal contact must be very narrow in these specimens if it existed at all. In the light of the demonstrated potential of μ CT to resolve the identity of cranial sutures, it will be important to re-evaluate the condition in CORD-1130 if it ever becomes accessible for digitization.

We argue that zygomatic-parietal contact is present in at least some individuals of every fossil platyrrhine taxon available to us and for which the feature can be assessed by current methods – including known stem members of the clade. For further corroboration,

it will be important to assess this character in *Chilecebus*, a ~20 million-year old stem platyrrhine that was unavailable to us (Flynn et al., 1995). We also interpret our results to suggest that platyrrhine taxa variably exhibiting the catarrhine condition likely arrive at this state through a convergent process. Although the incorporation of this new information into the character matrix of Kay (2015a) does not alter the placement of *Tremacebus* and *Homunculus* on the platyrrhine stem, when paired with phylogenetic ancestral state reconstruction it alters our understanding of the most likely character states at the LCA of Platyrrhini and Anthropoidea. Bayes factor tests of alternate character reconstructions at these nodes suggest that frontal-alisphenoid contact is primitive for crown anthropoids and that zygomatic-parietal contact is a synapomorphy of Platyrrhini, as previously indicated by maximum parsimony citing the common possession of frontal-alisphenoid contact in catarrhines and tarsiers (Le Gros Clark, 1959; Hershkovitz, 1977; Rosenberger, 1977; Horovitz and MacPhee, 1999) and the appearance of frontal-alisphenoid contact in the earliest catarrhines for which the feature can be assessed (Simons et al., 2007).

Our results support the use of parietal-zygomatic contact as a potential indicator of platyrrhine affinities in any Old World Paleogene anthropoid taxa in which it might be found in the future, with considerable implications for understanding the biogeographic, temporal, and adaptive origins of the group. Parapithecids and proteopithecids seem particularly promising in this regard. Descriptions of the pteria of these taxa include the conflicting identification of catarrhine-like frontal-alisphenoid contact in the cranium of *S. grangeri* made by Simons (2001, 2004), and the designation of the roughened temporal process of the frontal of the parapithecoid *A. phiomense* as indicating a ‘platyrrhine-like’

condition by Fleagle and Kay (1987). None of the parapithecoid specimens on which pterion interpretations are based directly preserves the pterion region in a complete or unambiguous fashion, although our investigation of *S. grangeri* is consistent with the observation of Simons (2001, 2004). On the other hand, we find corroborating evidence that an externally roughened frontal process is a correlate of the platyrrhine pterion condition as suggested by Fleagle and Kay (1987), in the form of an inferior extension of the temporal process of the frontal bone internal to the parietal-zygomatic suture in the MPM-VP 3502 specimen of *Homunculus* as well as the DU-BAA-19 specimen of *A. palliata* (Figure 5C, Figure 7).

Conclusion

Our understanding of anthropoid evolutionary and biogeographic history continues to be impeded by a lack of evidence for the presence of the platyrrhine lineage in Africa. Because of the primitive nature of the platyrrhine skeleton, platyrrhine affinities for various fossil anthropoids have been difficult to establish. The current study suggests that the platyrrhine skull may hold more phylogenetic information than previously believed. We were able to revise our understanding of the contact pattern of cranial bones in the pterion region of the skull in two of the earliest fossil New World monkeys. We find them to share the zygomatic-parietal pterion pattern reported in at least some individuals of all species of crown platyrrhines, which ancestral state reconstruction supports as derived. These findings support the treatment of pterion contact as a synapomorphy of both stem and crown platyrrhines. This newly revealed, more inclusive distribution of the derived pterion condition holds promise for identifying members of the New World monkey lineage among early anthropoid primates in Africa or elsewhere.

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Figure Legends

Figure 1- Primate crania demonstrating the “platyrrhine” and “catarrhine” pterion states, respectively. A) *Cebus albifrons* (DKY 2325) showing “platyrrhine-like” zygomatic-parietal contact; B) *Miopithecus talapoin* (ILF 0137) showing “catarrhine-like” frontal-alsphenoid contact, excluding the parietal and zygomatic. Images from the Mammalian Cranial Photographic Archive, Kyoto University (Takahashi et al., 2006).

Figure 2 – Phylogeny of extant taxa used as a molecular scaffold in the phylogenetic analysis, based on trees of Perelman et al. (2011) and Kiesling et al. (2015). *Aotus* is placed with callitrichines within Cebidae.

Figure 3 – Segmented cranium of *Tremacebus harringtoni* (Museum of the Fundacion Miguel Lillo specimen no. 619). Frontal – yellow, zygomatic – blue, parietal – red, orbital bone fragments – green (left) and orange (right). A) Left lateral view; B) Right lateral view; C) Sagittal slice showing internal suture boundaries; D) Transverse slice showing internal suture boundaries.

Figure 4 – Segmented cranium of *Homunculus patagonicus* (MPM-PV 3502). Frontal – yellow, zygomatic – blue, parietal – red. A) Left lateral view; B) Sagittal slice showing internal suture boundaries; C) Transverse slice showing internal suture boundaries.

Figure 5 – Segmented cranium of *Antillothrix bernensis* (PN-09-01). Frontal – yellow, right zygomatic – blue, likely left zygomatic – orange, parietal – red, A) Right lateral view; B) Left lateral view; C) Transverse slice showing internal suture boundaries.

Figure 6 - Strict consensus of two maximum-parsimony trees using the modified character-taxon matrix of Kay (2015a) with changes made to the coding of the pterion region, as indicated in the text, and with the addition of the taxon *Perupithecus*. The tree length = 110590 (1105.90 when characters are scaled with base weight of 1 rather than 100); consistency index (CI) = 0.304; Rescaled consistency index (RC) = 0.156; retention index = 0.513.

Figure 7 – Segmented cranium of *Alouatta palliata* (BAA-19). Frontal – yellow, zygomatic – blue, parietal – red. A) Left lateral view; B) Transverse slice showing internal suture boundaries.

Tables

Table 1 – Specimen scans examined in study.^a

Species	Specimen	Resolution	Voltage	Amperage	Facility	Morphosource links
<i>Alouatta palliata</i>	DU-BAA-19	0.055 mm	200 kV	190 µa	Duke SMif	http://morphosource.org/index.php/Detail/SpecimenDetail/Show/specimen_id/1112
<i>Alouatta palliata</i>	DU-BAA-24	0.051 mm	185 kV	190 µa	Duke SMif	http://morphosource.org/index.php/Detail/SpecimenDetail/Show/specimen_id/1114
<i>Homunculus patagonicus</i>	MPM-PV-3501	0.040 mm	165 kV	130 µa	Duke SMif	http://dx.doi:10.17602/M2/M9341
<i>Homunculus patagonicus</i>	MPM-PV-3502	0.039 mm	165 kV	140 µa	Duke SMif	http://dx.doi:10.17602/M2/M9469
<i>Homunculus patagonicus</i>	MPM-PV-3503	0.044 mm	165 kV	140 µa	Duke SMif	http://dx.doi:10.17602/M2/M9345
<i>Tremacebus harringtoni</i>	FMI 619	0.056 mm	150 kV	160 µa	University of Texas	http://dx.doi:10.17602/M2/M9470
<i>Dolichocebus gaimanensis</i>	MACN 14128	0.047 mm	150 kV	160 µa	University of Texas	http://dx.doi:10.17602/M2/M9347
<i>Antillothrix bernensis</i>	PN-09-01	0.059 mm	180 kV	250 µa	Penn State University	http://dx.doi:10.17602/M2/M9472
<i>Simonsius (=Parapithecus) grangeri</i>	DPC 18651	0.035 mm	200 kV	140 µa	Duke SMif	http://dx.doi:10.17602/M2/M9339
<i>Proteopithecus sylviae</i>	DPC 42214	0.029 mm	150 kv	97 µa	Duke SMif	http://dx.doi:10.17602/M2/M9340

^a Institutional abbreviations: DPC – Division of Fossil Primates, Duke Lemur Center; DU-BAA – Department of Evolutionary Anthropology, Duke University; MACN - Museo Argentino de Ciencias

Naturales; FMI - Museo de Fundacion Miguel Lillo; MPM-PV – Museo Regional Provincial Padre Manuel Jesus Molina; PN - Parque Nacional Del Este-Padre Nuestro Park.

Table 2 - Changes in the scoring of pterion condition based on the work presented in this study.^a

Taxon	Kay (2015)	This study
<i>Aegyptopithecus zeuxis</i>	2	2
<i>Alouatta</i>	Polymorphic	Polymorphic
<i>Antillothrix</i>	0	0
<i>Aotus</i>	0	0
<i>Apidium phiomense</i>	?	?
<i>Ateles</i>	0	1
<i>Brachyteles</i>	1	0
<i>Cacajao</i>	0	0
<i>Callicebus</i>	0	0
<i>Callimico</i>	0	0
<i>Callithrix</i>	0	0
<i>Catopithecus browni</i>	?	?
<i>Cebuella</i>	0	0
<i>Cebus</i>	0	0
<i>Chiropotes</i>	0	0
<i>Homunculus patagonicus</i>	2	0
<i>Hylobates</i>	2	2
<i>Lagothrix</i>	0	0
<i>Leontopithecus</i>	0	0
<i>Miopithecus talapoin</i>	2	2
<i>Paralouatta</i>	0	0
<i>Pithecia</i>	0	0
<i>Presbytis melalophos</i>	2	2
<i>Proteopithecus sylviae</i>	?	?
<i>Saguinus</i>	0	0
<i>Saimiri</i>	0	0
<i>Simonsius grangeri</i>	?	?
<i>Tremaceubs harringtoni</i>	2	1

^aScoring is 0 = zygomatic-parietal contact; 1 = polymorphic; 2 = frontal-alisphenoid contact.

Figureg
Figure 1

Figure 2

Figure 3

Figure 4

A

B

C

Figure 5

A

B

C

Figure 6

Figure 7

A

B