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Primate Olfaction: A Phylogenetic Analysis of Cribriform Plate Morphology

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A Phylogenetic Analysis of Cribriform Plate Morphology

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ABSTRACT

Decreased olfaction, or smell, is a diagnostic characteristic of primates. Despite this, olfaction remains important for diet and social behaviors in primates. To assess how morphological changes impact olfactory-based behaviors between the two major clades of primates, Strepsirrhini and Haplorrhini, this study examined the surface area of the cribriform plate, the bony interface between the brain and nasal cavity. Previous work has found several functional associations between cribriform plate morphology and species diet/ ecology, making this structure possibly more reflective of a species reliance on olfaction in its environment. Primate social structure, such as average group size, mating system, and scent-marking behaviors, and activity patterns also have functional implications for cribriform plate morphology.

Data were comprised of micro computed tomography (microCT) scans collected from MorphoSource.org and the Terhune Lab to measure cribriform plate surface area. The sample represents a wide cross-section of primates and included corresponding data on diet, social system, and activity pattern. Descriptive statistics and t-tests were used to analyze cribriform plate surface area across sex and species. To study in-group and between group variances, phylogenetic generalized least squares (PGLS) and phylogenetic analysis of variance (ANOVA) were performed. From the paired t-tests, no sex difference was found between males and females throughout the sample. Additionally, the phylogenetic regressions showed significant correlations between both plate surface area and margin surface area, as well as between cranial length and plate/margin surface area. From the phylogenetic ANOVAs, no results were significant except the influence of clade (or the evolutionary relationships among species). This novel study reveals that primate olfaction is mainly influenced by clade rather than other factors such as diet, social system, or activity pattern.

INTRODUCTION

One major diagnostic characteristic of members of the mammalian order Primates is a general trend towards decreased olfaction (i.e., smell) (Osman 1953; Smith and Rossie 2006; Rossie and Smith 2007; Smith et al. 2007). This trend is significant because it coincides with an increased reliance on vision (another diagnostic characteristic of primates), shown through more forward-facing orbits (i.e., orbital convergence) (Osman 1953; Smith et al. 2007; Smith and Rossie 2007; Garrett et al. 2013). This reduced importance of olfaction is demonstrated in the deterioration of olfactory receptor genes in some primate groups, possibly correlated with the acquisition of trichromatic (three-colored: red, green, and blue) vision (Gilad et al. 2004; Barton 2006; Smith and Rossie 2006; Smith et al. 2007; Nevo and Heymann 2015). Further genetic evidence of reduced olfaction in primates relative to other mammals comes from the high percentage of olfactory pseudogenes (non-functional genes) in primates compared to mice which lack these olfactory pseudogenes (Rouquier et al. 2000; Gilad et al. 2004; Nevo and Heymann 2015).

Olfaction is tightly linked with several important behaviors, including activity patterns, foraging strategies and diet, and social behaviors (Barton 2006; Smith and Rossie 2006; Ankel-Simons 2007; Smith et al. 2007; delBarco-Trillo et al. 2011). In mammals, activity patterns are usually either nocturnal (active during the night) or diurnal (active during the day), with nocturnality being associated with increased olfaction compared to diurnal species (Barton et al. 1995; Nevo and Heymann 2015). Barton et al. (1995) observed that there was an evolutionary trade-off between specialization in olfactory systems and those in visual systems that is partly due to the difference between diurnal and nocturnal activity patterns. Their study also goes on to reveal that olfactory bulbs are larger in nocturnal primate lineages, whereas the striate visual

cortexes (i.e., the variable used to be a proxy for the visual system) were larger in diurnal primate lineages (Barton et al. 1995).

Dietarily, olfaction is considered more important in fruit selection than in foraging for insects or leaves (Nevo and Heymann 2015). For example, Nevo and Heymann (2015) discussed a possible scenario where species with a higher dependence on olfactory cues will have more pressure to amplify olfactory ability in order to have an easier time during foraging. This was to test their goal to examine whether species with different diets or with less visual cues are less available to use their sense of smell more than other primates while foraging, similar to one of the hypotheses being tested in this study (Nevo and Heymann 2015).

There are also many olfactory cues related to social behavior. Several mammalian orders have what is called the vomeronasal system (VNS), which provides accessory olfaction to the main olfactory system and is tied closely with pheromones and social behavior (Ankel-Simons 2007). The VNS receives odorants that are transmitted to the accessory olfactory bulb (AOB) and is linked to visual perception and circadian behaviors (i.e., behaviors associated with activity patterns, which will be discussed later) (Ankel-Simons 2007). One example of sociosexual behaviors linked to the VNS is scent-marking (i.e., a form of olfactory communication that has socioecological functions) (Heymann 2006; Smith and Rossie 2006; delBarco-Trillo et al. 2011). Scent-marking is used by many species of mammals and can either be via urine or glands (non-urine) and these can be associated with whether olfactory communication is related to more overt signaling (like in diurnal species, which often also utilizes a visual component) or covert signaling (like in nocturnal species) (Heymann 2006; Ankel-Simons 2007; Smith et al. 2007; delBarco-Trillo et al. 2011). Given how olfaction is associated with a variety of behaviors, it is clear that smell is integral to the everyday behaviors of mammalian species.

Within primates, the observed trend of decreased olfaction is represented by the separation of primates into two major clades, Haplorrhini (monkeys and apes) and Strepsirrhini (lemurs and lorises). Haplorrhines have a more compact and less complex nasal cavity, which reflects a reduction in olfaction relative to that observed in strepsirrhines (Smith and Rossie 2006; Smith et al. 2007; Garrett et al. 2013). Historically, external differences in nasal anatomy were the most readily apparent and therefore frequently studied (Pocock 1918; Osman 1953; Hofer 1976; Hofer 1980; Maier 1980; Smith and Rossie 2006; Smith et al. 2007). For example, strepsirrhines have more basal (i.e., closer to the base of a clade) traits in the form of a lengthened snout, presence of a rhinarium (a moist patch of skin that surrounds the nostrils), and a comparatively broad distance between the orbits (Smith et al. 2007). Because many strepsirrhine species are nocturnal, this would mean that they might depend on their olfaction more than diurnal primates to perform their feeding behaviors, such as foraging, prey detection, and social behaviors (Dominy et al. 2004; Garrett et al. 2013; Nevo and Heymann 2015; Laska 2017). This has already been demonstrated in comparative analyses of the main olfactory bulb (i.e., a projection of the brain that transmits olfactory data), where nocturnal primates have larger bulbs when compared to diurnal primates (Baron et al. 1983; Barton et al. 1995; Dominy et al. 2004; Barton 2006). Additionally, the VNS is present in strepsirrhines, while this system is only variably present in platyrrhines (New World Monkeys) and tarsiers, and vestigial or lost entirely in catarrhines (Old World Monkeys and apes) (Smith and Rossie 2006; Garrett et al. 2013). This suggests that strepsirrhines have the capability to employ more social cues than haplorrhines because they can detect pheromones via the VNS (Zhang and Wang 2003; Garrett et al. 2013).

While it is clear that haplorrhines and strepsirrhines differ in their olfactory anatomy and abilities, there are numerous internal differences in nasal cavity structure between the two clades that have not been as adequately studied. Some notable differences include the number of turbinals (scroll-like body structures in the nasal cavity), presence of the olfactory recess (a space that is mostly lined with olfactory epithelium) in strepsirrhines, and the olfactory organ itself (e.g., olfactory bulb size, relative function of the vomeronasal organ) (Pihlström et al. 2005; Smith and Rossie 2006; Rossie and Smith 2007; Smith et al. 2007). Notably, while these studies show the numerous differences between the two clades, there have been no studies that analyze the internal bony anatomy associated with the olfactory system of strepsirrhines compared to haplorrhines.

One of the most overlooked internal structures of the olfactory system is the cribriform plate (Figure 1). In mammals, the cribriform plate of the ethmoid bone is the bony border between the nasal cavity and the olfactory bulb (Bird et al. 2014). The cribriform plate can be visualized as a multi-perforated concave structure that provides pathways for olfactory nerves (which are situated in the nasal epithelium of the nasal cavity) to transmit signals to the olfactory bulb and ultimately to the brain (Figure 1) (Smith and Rossie 2006). Since the cribriform plate is important for olfaction, the size and shape of the cribriform plate has been studied to evaluate the olfactory capability of some mammalian species. Olfactory capability can be defined as the extent to which a species can discriminate between two different odorants as well as the species' sensitivity to low concentrations of a certain odorant (Laska 2017). Previous studies have utilized a variety of methods to study olfactory capability, such as analyzing the number of foramina in the cribriform plate, olfactory organ size, cribriform plate surface area (CPSA), foramina cross-sectional area (FXSA), and olfactory bulb area (Bhatnagar and Kallen 1974; Kalmey et al. 1998;

Pihlström et al. 2005; Bird et al. 2014). Of these methods, the strongest correlate to olfactory capability when analyzing the cribriform plate has shown to be cribriform plate surface area (CPSA) (Pihlström et al. 2005; Bird et al. 2014), which suggests that CPSA can serve as a proxy for understanding olfactory capability in primates.

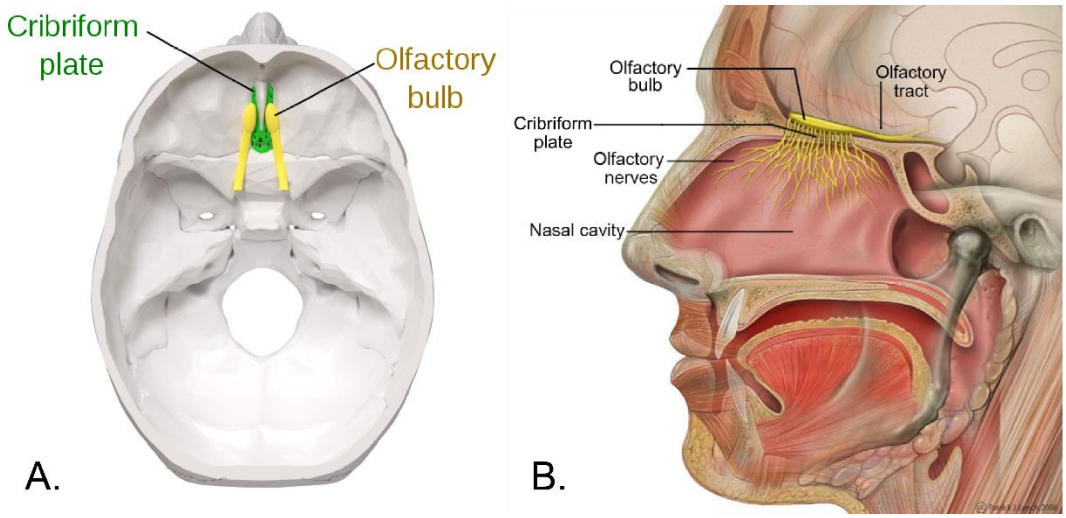

Figure 1. **A: Human skull in the superior view, with the calvaria (top of the skull) removed to reveal the cribriform plate and olfactory bulb (sourced from DBCLS [2019]). B: Human skull hemi-sectioned into the left lateral view, visualizing the cribriform plate and the olfactory bulb and nerves transmitting into the nasal cavity (sourced from Lynch [2006]).**

Research Goals

The goal of this research is to evaluate the extent of cribriform plate variation across primates and assess how this variation may be related to primate social and dietary behaviors. Since strepsirrhines typically present with more complex nasal cavities and have more olfactory behaviors through the presence of a functional VNS (Dominy et al. 2004; Heymann 2006; delBarco-Trillo et al. 2011; Garrett et al. 2013), I anticipate that, when compared to haplorrhines (Smith and Rossie 2006), cribriform plate surface area will be larger in strepsirrhines. Further, the degree to which the cribriform plate is larger and more complex in different primate groups is

likely dependent on factors such as whether the primate is nocturnal or diurnal, its dietary pattern (i.e., frugivore/folivore/insectivore), and social behaviors that utilize olfaction. These patterns can be summarized by the following (non-mutually exclusive) hypotheses:

H_1: Strepsirrhines will have relatively larger cribriform plates than haplorrhines.

H_2: Because frugivores require higher olfactory capability to forage for and identify ripe fruits than folivores or omnivores, frugivorous primates should present with larger cribriform plates than either folivorous or insectivorous primates. This will be true both when compared within and across strepsirrhines vs. haplorrhines. For example, strepsirrhine/haplorrhine frugivores will have larger cribriform plates than folivorous or insectivorous members of that clade, and strepsirrhine frugivores will have relatively larger cribriform plates than haplorrhine frugivores comparatively.

H_3: Primates that typically live in larger groups or form multi-male/multi-female social systems should utilize more olfactory cues and therefore will also present with larger cribriform plates.

H_4: Nocturnal primates will have larger cribriform plates compared to primates that perform foraging behaviors diurnally. For example, nocturnal strepsirrhines should have larger cribriform plates than diurnal strepsirrhines, and nocturnal haplorrhines should have larger cribriform plates than diurnal haplorrhines.

MATERIALS AND METHODS

Samples for this analysis were drawn from across the primate family tree, with at least two species for each of the sixteen primate families, and at least one male and one female from each species. Several phylogenetic outgroups were employed to compare to the primate sample, including common brown rats (*Rattus norvegicus*), tree shrews (*Tupaia belangeri*), and rock hyraxes (*Procavia capensis*). This represented a total sample size of 58 individuals (Figure 2; Table 1).

Table 1. **List of the variables that were tested, separated by whether they are haplorrhines, strepsirrhines, or an outgroup (Outgr).**

	Species	Diet-DeCasien	Diet-Handbook	Social System	Activity Pattern	Clade
Haplorrhines	*Alouatta caraya*	Folivore	Folivore	Polygynandry	Diurnal	Platyrrhini
	Aotus trivirgatus	Frugivore	Frugivore	Pair	Nocturnal	Platyrrhini
	Carlito syrichta	Omnivore	Omnivore	Solitary	Nocturnal	Tarsiiformes
	Cercocebus agilis	Frugivore	Frugivore	Polygynandry	Diurnal	Cercopithecoidea
	Colobus polykomos	Folivore	Folivore	Polygynandry	Diurnal	Cercopithecoidea
	Gorilla gorilla	Folivore	Frugivore	Polygyny	Diurnal	Hominoidea
	Homo sapiens	Omnivore	Omnivore	Polygynandry	Diurnal	Hominoidea
	Hylobates lar	Frugivore	Frugivore	Pair	Diurnal	Hominoidea
	Lagothrix lagotricha	Omnivore	Frugivore	Polygynandry	Diurnal	Platyrrhini
	Macaca fascicularis	Frugivore	Frugivore	Polygynandry	Diurnal	Cercopithecoidea
	Mandrillus sphinx	Frugivore	Frugivore	Polygynandry	Diurnal	Cercopithecoidea
	Miopithecus talapoin	Omnivore	Frugivore	Polygynandry	Diurnal	Cercopithecoidea
	Nasalis larvartus	Folivore	Folivore	Polygynandry	Diurnal	Cercopithecoidea
	Pan paniscus	Frugivore	Frugivore	Polygynandry	Diurnal	Hominoidea
	Papio anubis	Frugivore	Omnivore	Polygynandry	Diurnal	Cercopithecoidea
	Pithecia pithecia	Frugivore	Granivore	Polygynandry	Diurnal	Platyrrhini
	Pongo pygmaeus	Frugivore	Frugivore	Solitary	Diurnal	Hominoidea
	Presbytis melalophos	Frugivore	Frugivore	Polygynandry	Diurnal	Cercopithecoidea
	Saguinus oedipus	Omnivore	Frugivore	Pair	Diurnal	Platyrrhini
	Saimiri sciureus	Omnivore	Frugivore	Polygynandry	Diurnal	Platyrrhini
Strepsirrhine	*Daubentonia madagascariensis*	Omnivore	Omnivore	Solitary	Nocturnal	Lemuriformes
	Eulemur albifrons	Frugivore	Frugivore	Polygynandry	Cathemeral	Lemuriformes
	Galago senegalensis	Omnivore	Omnivore	Solitary	Nocturnal	Lorisiformes
	Microcebus murinus	Omnivore	Omnivore	Solitary	Nocturnal	Lemuriformes
	Perodicticus potto	Omnivore	Omnivore	Solitary	Nocturnal	Lorisiformes
	Propithecus verreauxi	Folivore	Omnivore	Polygynandry	Diurnal	Lemuriformes
Outg	*Procavia capensis*	Folivore	Folivore	Polygyny	Diurnal	Procaviidae
	Rattus norvegicus	Omnivore	Omnivore	Polygynandry	Nocturnal	Muridae
	Tupaia belangeri	Omnivore	Omnivore	Pair	Diurnal	Tupaiidae

Micro computed tomography (microCT) scans were utilized to measure cribriform plate surface area. All microCT scans for this project were either freely accessible via the online database MorphoSource.org or were made available by researchers (C. Yoakum and C. Terhune) in the Terhune Lab.

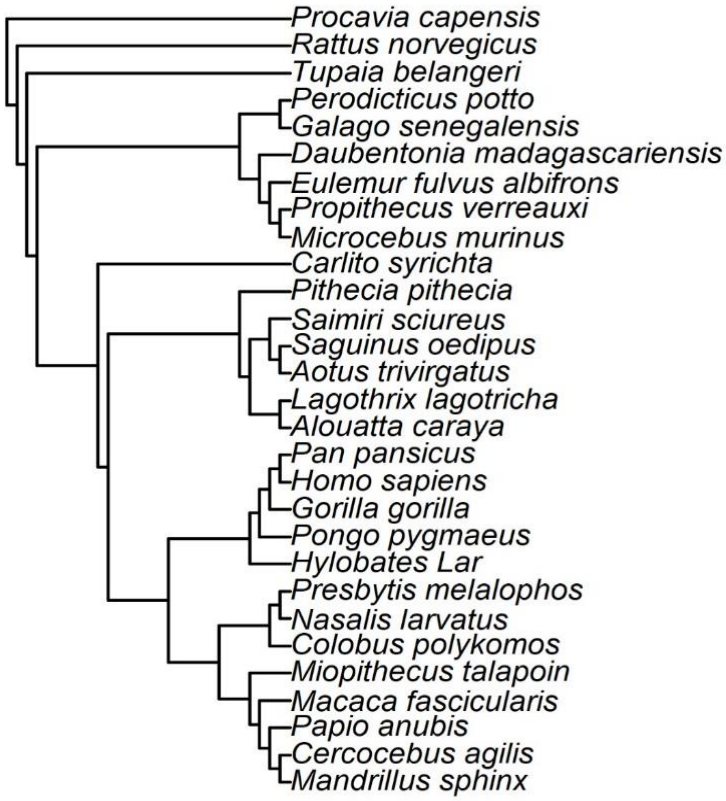

Figure 2. **Phylogenetic tree generated via 10K Trees (Arnold et al. 2014) listing the relationships between all of the sample species, with outgroups included.**

The process of data collection for each specimen was as follows: first, I segmented (i.e., digitally sectioned out and removed from the rest of the ethmoid bone to easily measure) each specimen's cribriform plate, utilizing a similar methodology to Bird and Amirkhanian (2014) (Figure 3). Then, a threshold was established to delineate bone from nonbone in the microCT scan. In the program Avizo Lite (Thermo Fisher Scientific 2007), the cribriform plate and the most posterior ethmoturbinals was segmented until the ethmoid foramen was reached, since this foramen houses the nasociliary branch of the trigeminal nerve (CN V) (Bird and Amirkhanian

2014). This protocol ensured that the ethmoid foramen, which is comparatively larger than the olfactory foramina of the cribriform plate, does not interfere with surface area measurements. The olfactory foramina were also filled in Avizo, utilizing the "point wrap function" feature and smoothed using the "smooth surface" feature (to minimize rough edges and points that could disrupt the surface area measurements). This continuous surface was then exported as a .ply file into Geomagic Studio (3D Systems 2013), where the function "Mesh Doctor" was run on all the specimens to minimize extreme points that could disrupt the surface area measurements. Some specimens had larger foramina that could not be filled in Avizo and were filled in Geomagic Studio utilizing the "fill hole" function, where the excess bone surrounding the cribriform plate proper was cropped away. With the cribriform plate isolated, the margin and plate surface area could be measured (in mm^2). Surface area was measured in two ways: from the walls of the cribriform base, or what was called the margin surface area; and from the base of the cribriform plate, or what was called the plate surface area (Figure 3C & 3D).

Skull length was used as a proxy for body size. Skull length was defined as the linear distance between glabella (the anterior-most point above the brow ridge) to inion (the most projecting point on the occipital bone). Dividing the square root of cribriform plate and margin surface, respectively, by skull length measurement ensured correct scaling and allowed for comparison of individuals that vary considerably in overall size (Mosimann 1970; Jungers et al. 1995).

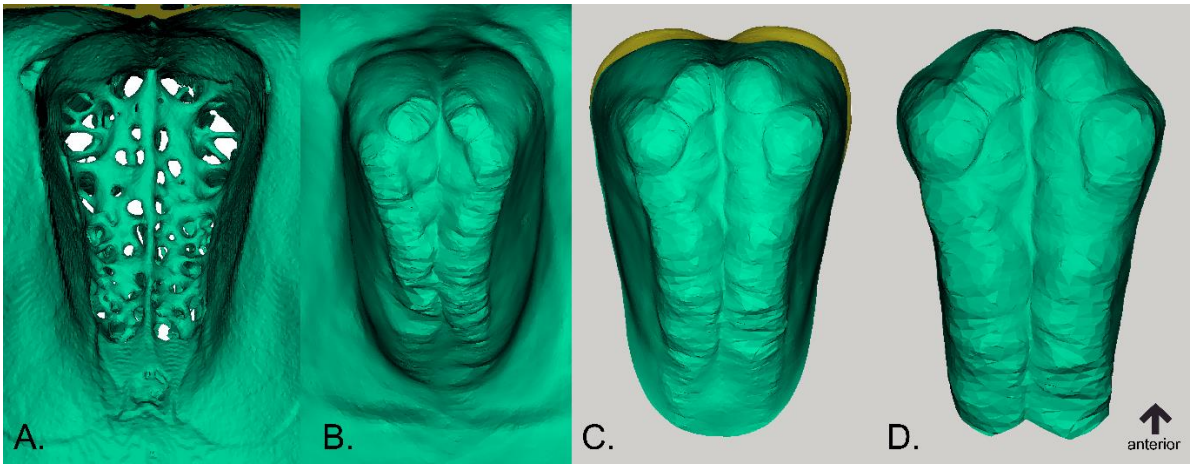

Figure 3. **Superior view of the cribriform plate (CP) in *Galago senegalensis* (Senegal bushbaby) showing the original surface model without holes filled (A); the continuous surface created by wrapping the cribriform plate foramina (B); the CP margin sectioned out from surrounding cranium to calculate the margin CPSA (C); and the CP after further cropping to exclude the margin and isolate the plate to calculate the plate CPSA (D).**

Data on diet, social structure, and activity patterns were derived from the literature (Tables 1 and 2). Because different authors quantify diet differently, two different sources were used: the Handbook of the Mammals of the World, Primate edition (Mittermeier et al. 2013) and previously aggregated data presented by DeCasien et al. (2017). Both Mittermeier et al. (2013) and DeCasien et al. (2017) use categorical variables to identify the primary diet based on a three-category scheme that includes folivore, frugivore and omnivore; however, Mittermeier et al. (2013) also includes the category granivore (Tables 1 and 2). Importantly, these sources conflict on their categorization for some primate species, so to compensate for this, tests were run using both sources.

Data on social structure was also pulled from DeCasien et al. (2017), which was originally sourced from reference literature compiled from observational studies. Here, these categories included solitary, pair-living, polygyny, and polygynandry (Tables 1 and 2). Data on activity patterns came from Mittermeier et al. (2013). In this instance, species were defined as either diurnal, nocturnal, or cathemeral (Tables 1 and 2).

Table 2. **Definitions of the variables tested and the categories utilized to characterize species. Definitions of social systems and activity pattern cited from Swedell (2012).**

Variables	***Categories***	***Definition***
Diet (DeCasien)	Folivore	Primarily eats leaves
	Frugivore	Primarily eats fruits
	Omnivore	Eats both plant and animal matter
Diet (Handbook/ Mittermeier)	Folivore	See above definition
	Frugivore	See above definition
	Omnivore	See above definition
	Granivore	Adapted to eat seeds and pits inside fruits
Activity Patterns	Diurnal	Primarily active in the daytime
	Nocturnal	Primarily active in the nighttime
	Cathemeral	Active at any point in the day or night
Social System	Solitary	An adult male's territory overlaps with one or more female's territory, but forage alone and socialize with vocalizations
	Pair-Living	One male and one female form a bond and defend territory from other pairs
	Polygyny	Single male mates with multiple females and excludes other adult males from the mating
	Polygynandry	Both males and females are polygamous and mate with multiple members of the opposite sex

Data analysis first included calculating descriptive statistics (mean, standard deviation) for the plate and margin of each species. Then, data for sexes within species were compared using a paired t-test in the program SPSS (IBM Corp 2015); no significant difference between males and females were found (plate SA $p = 0.840$; margin SA $p = 0.533$), thus patterns were analyzed by species average rather than species and sex average. For all analyses, the alpha value was 0.05 to indicate significance. Phylogenetic codependence of data points was accounted for using phylogenetic comparative methods such as phylogenetic generalized least squares (PGLS) regression and phylogenetic ANOVA (Garland et al. 1993; Butler and King 2004). The relationship between size (i.e., skull length, the independent variable) and how that affected the plate and margin CPSA (i.e., the dependent variables) were examined using PGLS regression analysis. The phylogenetic ANOVAs compared how the categorical variables (listed in Table 2) affected the average plate and margin CPSA respectively. Therefore, a total of 10 phylogenetic

ANOVAs were conducted to test each independent variable (the tested categories from Table 2) affected the average plate CPSA mean and the average margin CPSA mean.

In addition to the plate and margin CPSA averages being divided by skull length to control for size (Jungers et al. 1995), the averages were also natural log transformed to ensure normality of the data. Further, a Tukey's Honestly Significant Difference (HSD) was employed to examine differences in plate and margin CPSA between clade for each tested variable. These tests were run using the averages of the data, separated into several groups such as: haplorrhine, strepsirrhine, all primates, and all species. All these tests were conducted in RStudio utilizing the packages "stats", "caper", and "phytools" respectively. A phylogenetic tree of all species included here was downloaded from the website "10K Trees" (Arnold et al. 2014) (Figure 2).

RESULTS

Visually, there is a stark difference between haplorrhine and strepsirrhine species, though this visual difference does not always extend to being statistically significant. Generally, strepsirrhine CPs more closely resemble other mammal CPs, being more mediolaterally wide than anteroposteriorly long or superoinferiorly tall, while haplorrhine CPs are the opposite (Figure 4). Interestingly, some species of haplorrhines, such as mandrills, macaques (Figure 4B, 4E, & 4H), and *Cercocebus*, have deeper recessed CPs, being more 'U'-shaped (i.e., the CP sits in a deep concavity formed by the frontal bone, which means that models of the CP margin in these taxa are superoinferiorly very tall).

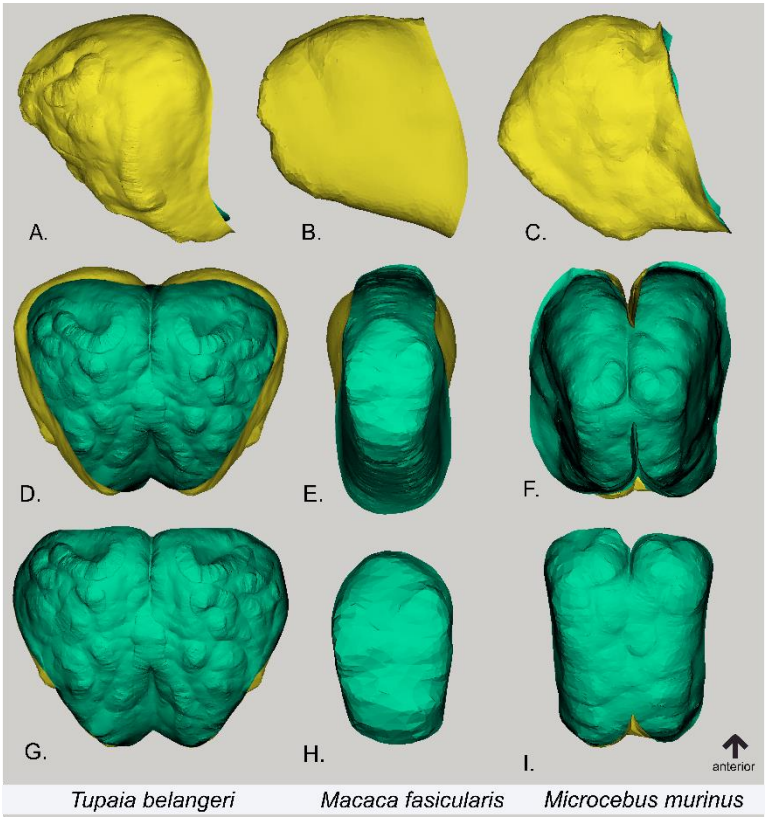

Figure 4. **Example of mammal outgroup (A, D, & G), haplorrhine (B, E, & H), and strepsirrhine (C, F, & I) cribriform plates (CP) showing the CP margin in the right lateral view (top row), the CP margin in the superior view (middle row), and CP plate also in the superior view (bottom row) for *Tupaia belangeri* (A, D, & G), *Macaca fasicularis* (B, E, & H), and *Microcebus murinus* (C, F, & I).**

Summary statistics for the raw (non-corrected for body size) cribriform plate measurements are shown in Table 3. Hominoids (apes) had the largest averages, which is consistent with them having the largest body sizes; however, the comparatively small-bodied lemurs and lorises had the second largest values of the primates. One lemur, *Daubentonia madagascariensis* (also known as aye-ayes), had extraordinarily large CP averages for both the margin (avg.= 454.683mm) and plate (avg.= 409.646mm).

Table 3. Descriptive statistics of each group of primates separated by clade. SD = standard deviation; CP = cribriform plate; N = number of individuals. Scaled values are where the raw variables have been divided by skull length.

	Clade	***N***	***CP Plate Mean and SD (mm^2)***	***Scaled CP Plate***	***CP Margin Mean and SD (mm^2)***	***Scaled CP Margin***	***Skull Length Mean and SD (mm)***
Haplorrhines	*Cercopithecoidea*	16	41.80 (28.01)	0.29	140.33 (85.54)	0.96	146.31 (6.79)
	Hominoidea	10	245.98 (164.11)	1.72	377.38 (282.78)	2.65	142.66 (16.43)
	Platyrrhine	12	41.16 (35.54)	0.72	77.35 (39.43)	1.36	56.93 (1.90)
	Tarsiiformes	2	3.76 (0.14)	0.15	15.66 (4.78)	0.63	24.88 (0.64)
Strepsirrhines	*Lemuriformes*	8	190.51 (153.94)	3.81	262.07 (153.39)	5.16	50.81 (1.58)
	Lorisiformes	4	122.57 (43.25)	3.90	122.57 (69.85)	3.90	31.39 (4.68)
Mammal Outgroups	*Muridae*	2	60.25 (1.33)	2.29	126.81 (5.49)	4.83	26.27 (0.39)
	Procaviidae	2	170.57 (81.36)	4.15	246.91 (86.78)	6.00	41.11 (5.07)
	Tupaiidae	2	93.49 (0.003)	3.19	148.04 (5.48)	5.05	29.30 (0.60)

When scaled by skull length, some interesting trends appear, such that the lemurs and lorises more closely align with the mammal outgroups than the haplorrhines. Lemuriformes even surpasses *Muridae* (i.e., Norway rat) and *Tupaiidae* (i.e., tree shrews) for scaled plate and margin CPSA mean (Table 3). Somewhat expectedly (given their large eye-to-body size ratio), Tarsiiformes have the smallest plate and margin CPSA mean when scaled by body size (Table 3).

Relationship between the Margin CPSA and the Plate CPSA

Phylogenetic generalized least squares (PGLS) regressions indicate that the margin and plate CPSA are significantly related to one another ($p = <0.00001$, $r^2 = 0.713 – 0.996$; Table 4). This indicates there is a significant relationship between the margin and plate CPSA for the entire sample (including the outgroups), primates only (excluding the outgroups), strepsirrhines only, and haplorrhines only.

Table 4. **Phylogenetic generalized least squares (PGLS) regression results for analyses comparing the two different measures of cribriform plate surface area (CPSA), plate surface area and margin surface area, and comparisons of these measures to cranial length.**

		R^2	P-value	Slope
Plate vs. Margin	All Species	0.885	<0.00001	1.320
	All Primates	0.845	<0.00001	1.264
	Strepsirrhine	0.996	<0.00001	1.525
	Haplorrhine	0.813	<0.00001	1.196
Plate vs. Cranial Length	All Species	0.762	<0.00001	1.233
	All Primates	0.730	<0.00001	1.283
	Strepsirrhine	0.957	0.0007	1.262
	Haplorrhine	0.813	<0.00001	1.269
Margin vs. Cranial Length	All Species	0.740	<0.00001	0.852
	All Primates	0.713	<0.00001	0.897
	Strepsirrhine	0.946	0.001	0.822
	Haplorrhine	0.900	<0.00001	0.885

Influence of size on CPSA

Utilizing PGLS regressions, both the plate and margin CPSA were compared with cranial length measurements for all species (Table 4). There is a significant relationship between both plate ($r^2 = 0.762$, $p = <0.00001$; Figure 5) and margin ($r^2 = 0.740$, $p = <0.00001$; Figure 6) with cranial length (Table 4) when the entire sample is analyzed. This significant relationship held

when strepsirrhines ($r^2 = 0.914$, $p = 0.003$; Figure 7) and haplorrhines ($r^2 = 0.457$, $p = <0.00001$; Figure 8) were examined separately (Table 4).

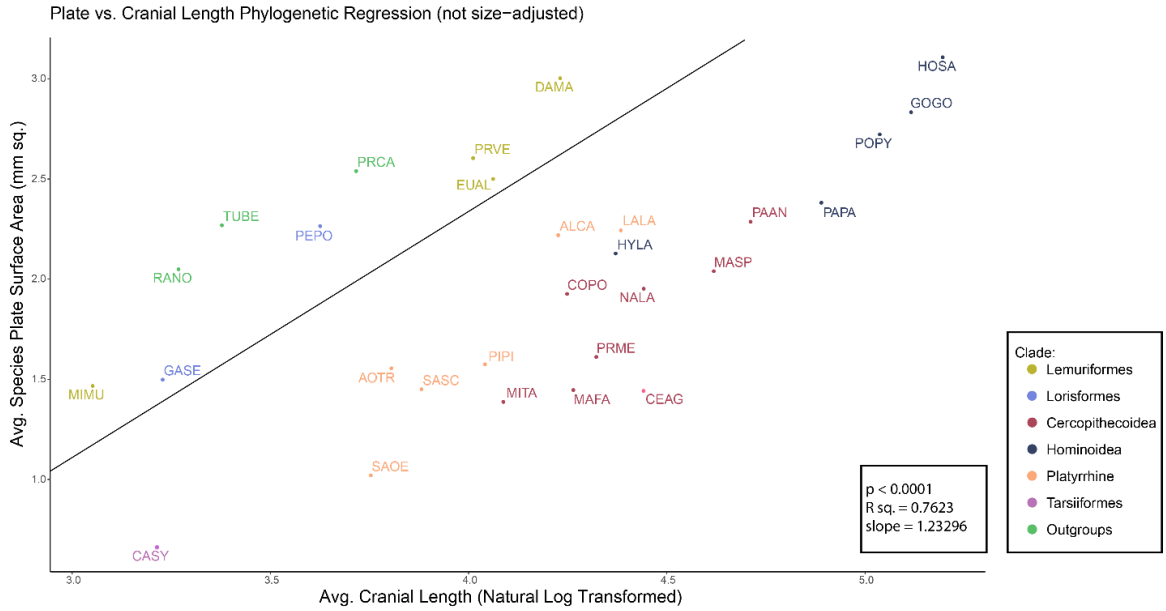

Figure 5. **Bivariate plot showing the relationship between the average cranial length of all the species (including outgroups) that was natural log transformed and the average plate CPSA of all species (including outgroups). The regression line shown was produced from the PGLS regression model. Abbreviations of species are named from the first two letters of the genus and species of each specimen.**

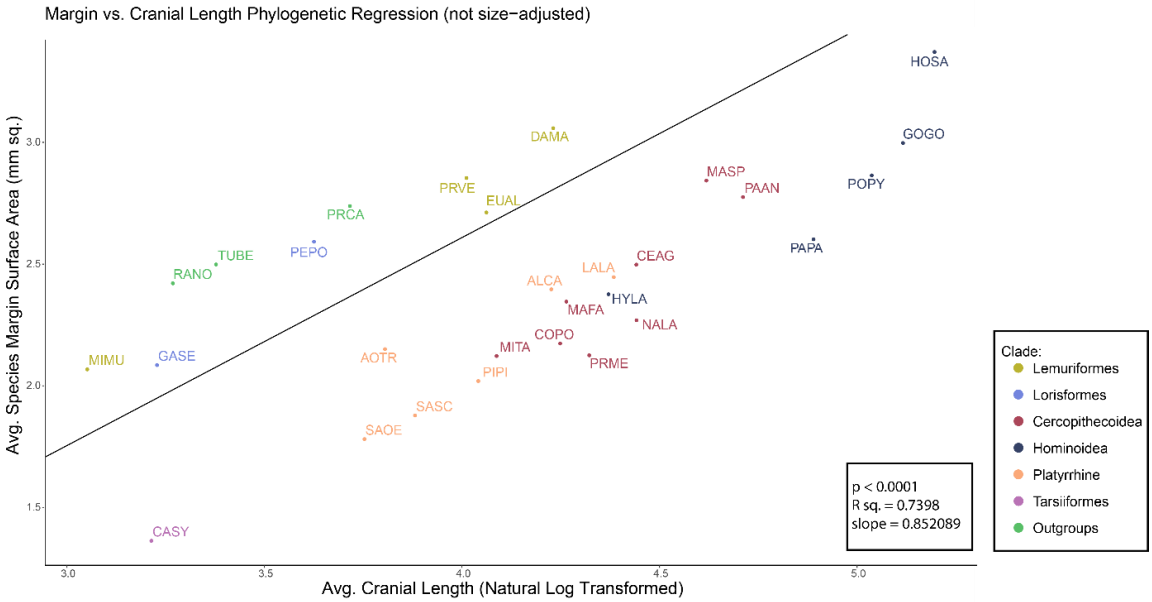

Figure 6. **Bivariate plot showing the relationship between the average cranial length of all the species (including outgroups) that was natural log transformed and the average margin CPSA of all species (including outgroups). The regression line shown was produced from the PGLS regression model. Abbreviations of species are named from the first two letters of the genus and species of each specimen.**

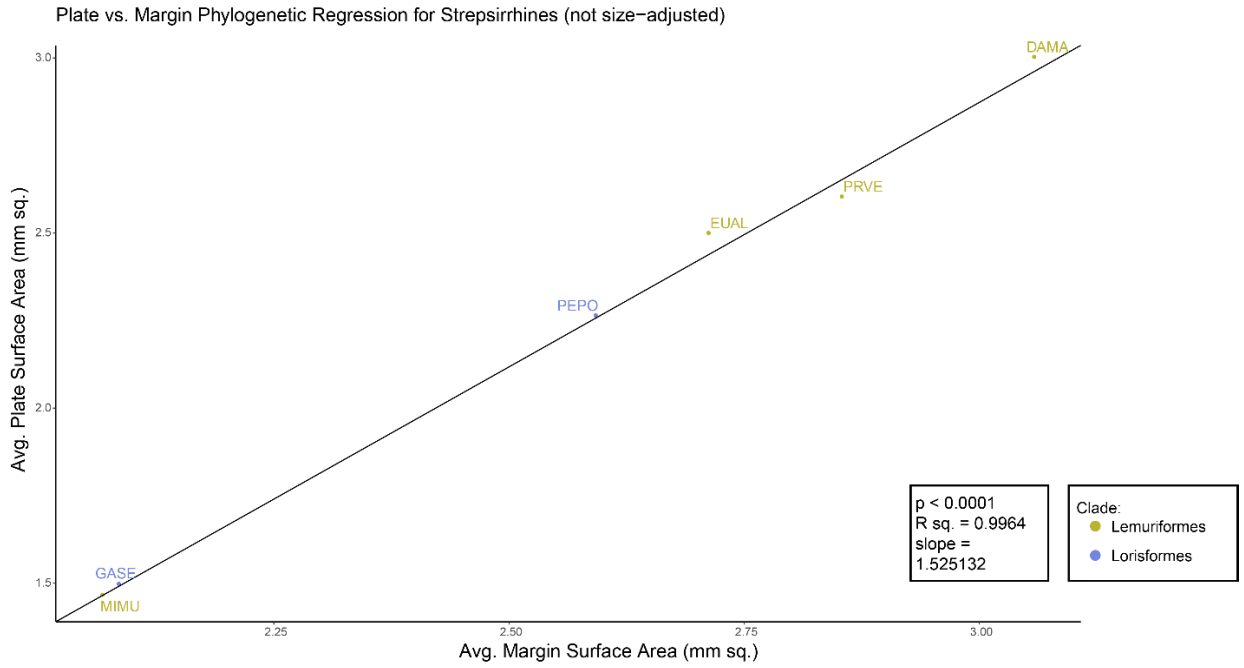

Figure 7. **Phylogenetic Linear Regression comparing the average plate CPSA, natural log transformed with the average margin CPSA, natural log transformed of only strepsirrhines. Abbreviations of species are named from the first two letters of the genus and species of each specimen.**

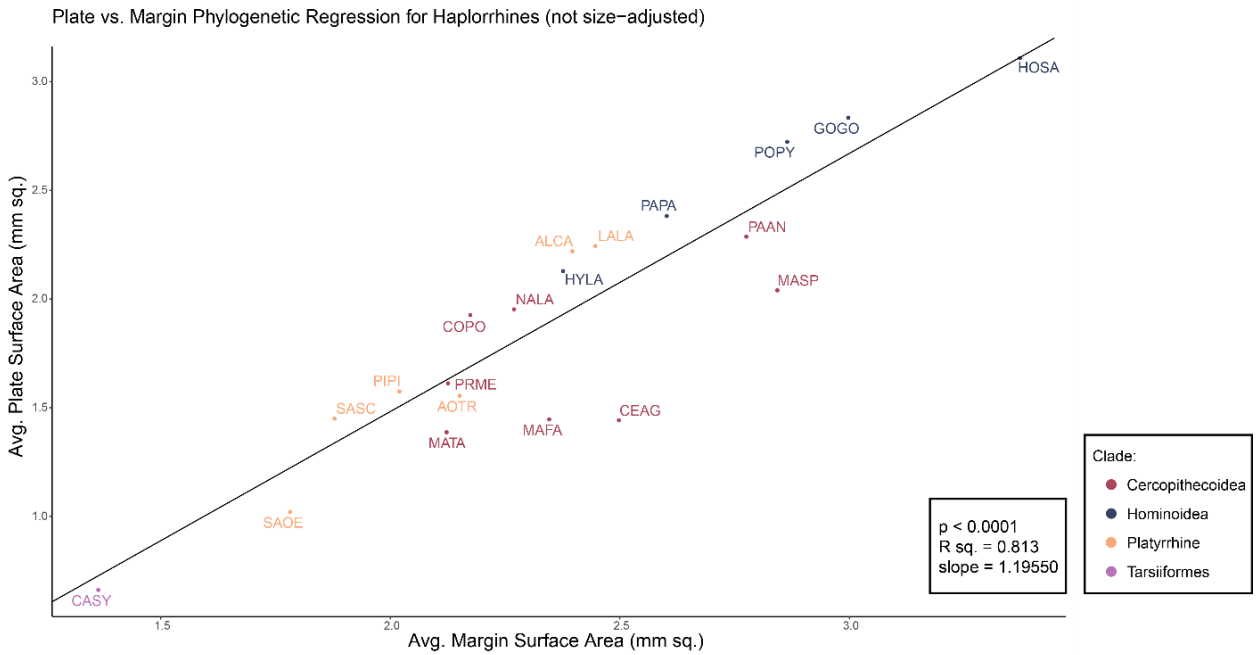

Figure 8. **Phylogenetic Linear Regression comparing the average plate CPSA, natural log transformed with the average margin CPSA, natural log transformed of only haplorrhines. Abbreviations of species are named from the first two letters of the genus and species of each specimen.**

Hypothesis Testing

Clade-level variation in CPSA (H_1)

When scaled relative to skull length, both plate and margin measurements are significantly different between strepsirrhines and haplorrhines (plate CPSA p = 0.006 and margin CPSA p = 0.007; Table 5; Figure 9). Though, this significance does not extend to the superfamily level average measures (Table 5), there is one measure, plate CPSA (p = 0.062) that approaches significance and may warrant future study.

Table 5. **Phylogenetic ANOVA results for plate and margin cribriform plate surface area (CPSA), scaled by skull length, relative to the categorical variables tested here.**

		Plate		***Margin***	
		F-Stat	P-value	F-Stat	P-value
Clade	Superfamily	20.999	0.062	8.121	0.387
	Strep vs. Hap	73.899	0.006	73.899	0.007
Diet- DeCasien	Strepsirrhine	0.116	0.866	0.234	0.779
	Haplorrhine	1.500	0.276	0.436	0.677
Diet- Handbook	Strepsirrhine	0.215	0.656	0.027	0.871
	Haplorrhine	0.882	0.539	0.514	0.727
Social System	Strepsirrhine	0.004	0.961	0.216	0.715
	Haplorrhine	0.202	0.951	0.676	0.731
Activity Pattern	Strepsirrhine	0.116	0.872	0.234	0.795
	Haplorrhine	0.778	0.86	1.456	0.456

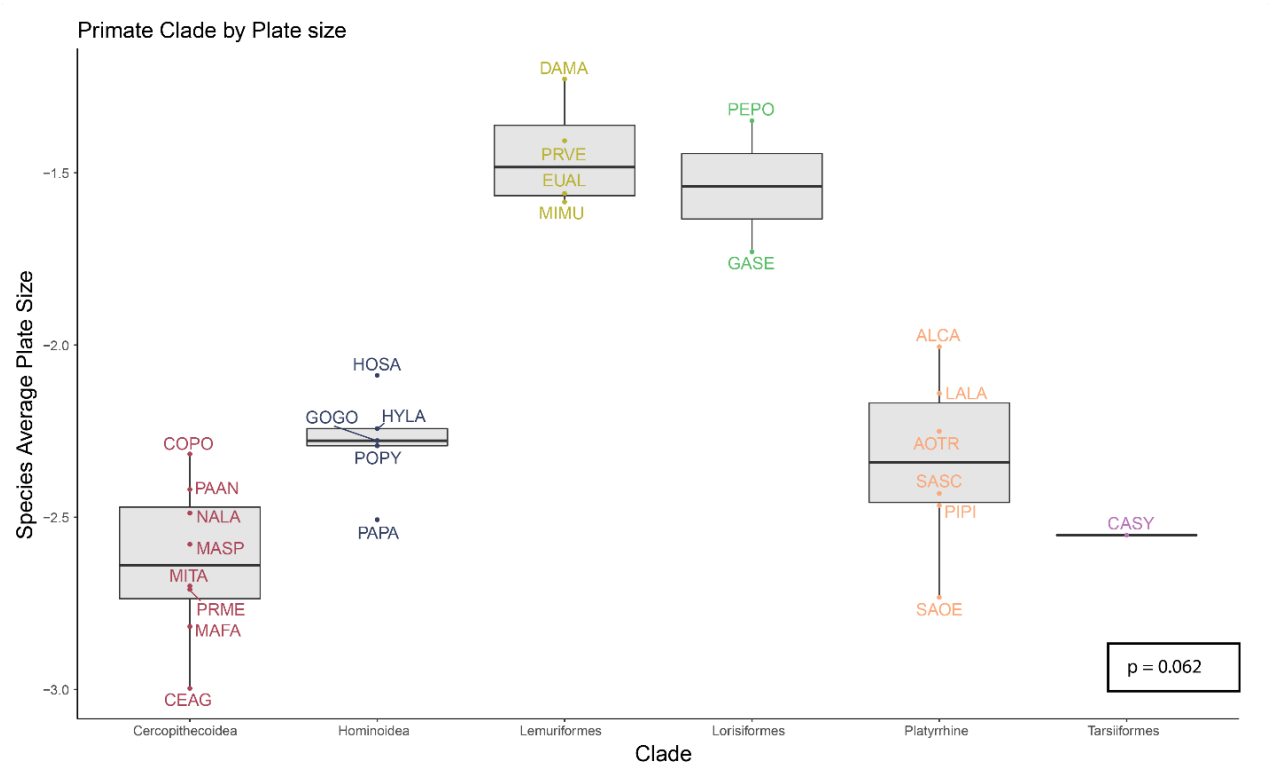

Figure 9. **Boxplot comparing the primate clades against the average species plate CPSA, scaled by skull length. Abbreviations of species are named from the first two letters of the genus and species of each specimen.**

CPSA variation relative to diet (H_2)

The phylogenetic ANOVA indicated that both margin and plate CPSA do not differ significantly by diet for all diet categories ($p > 0.05$; Table 5; Figures 10-11). However, frugivores do have visually smaller CPSAs on average, for both the plate and margin, relative to other dietary categories, though not to a significant degree.

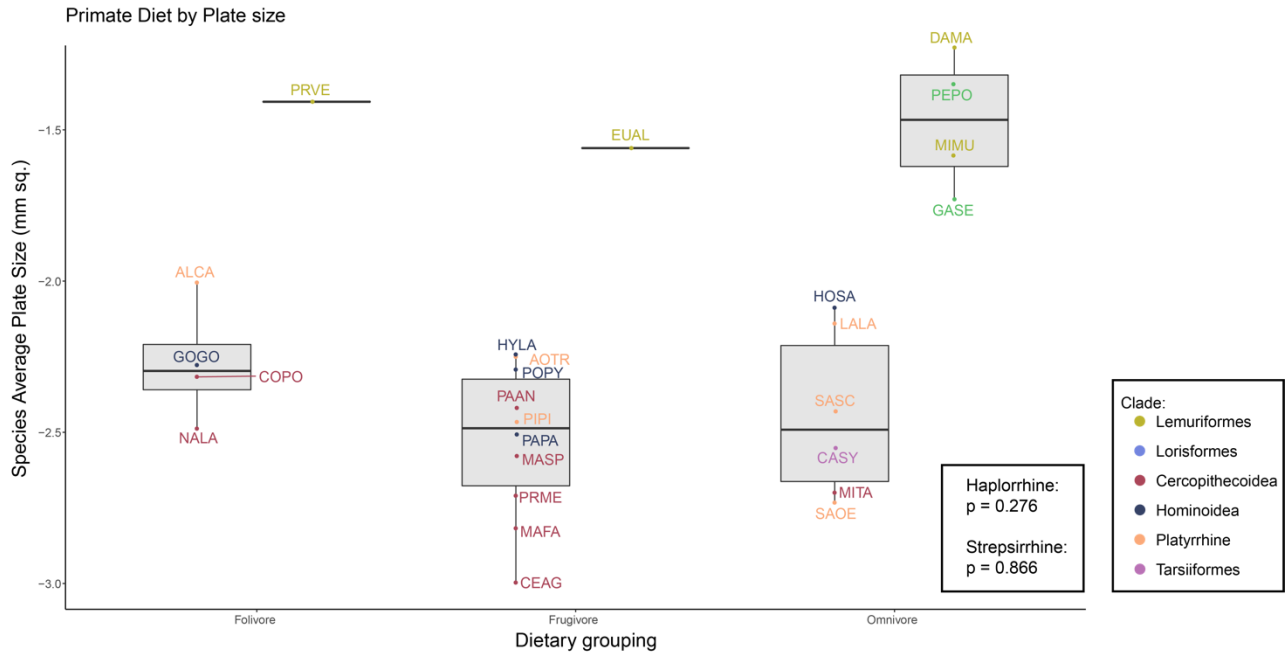

Figure 10. **Boxplot comparing the primate diet (DeCasien) against the average species plate CPSA, scaled by skull length. Since there were no significant differences found in either plate or margin CPSA, only plate CPSA is represented. P-values are separated by strepsirrhine and haplorrhine groups, in order to show variation between the groups. Abbreviations of species are named from the first two letters of the genus and species of each specimen.**

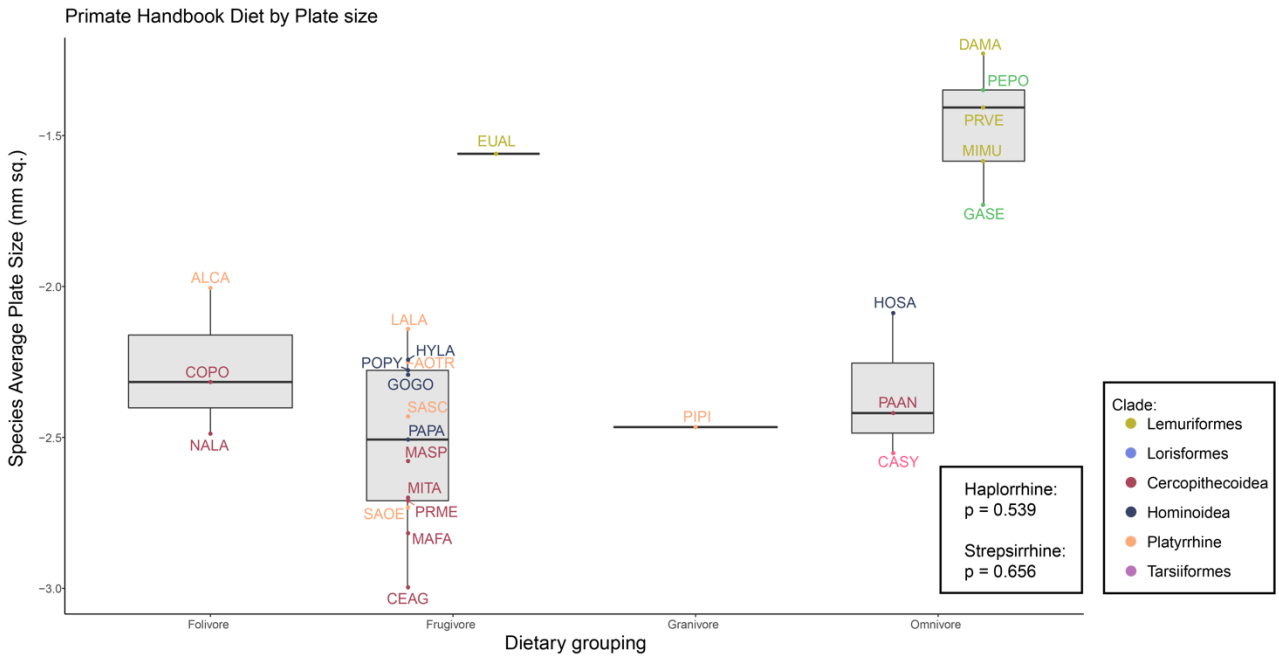

Figure 11. **Boxplot comparing the primate diet (Handbook) against the average species plate CPSA, scaled by skull length. Since there were no significant differences found in either plate or margin CPSA, plate CPSA is only represented. P-values are separated by strepsirrhine and haplorrhine groups, in order to show variation between the groups. Abbreviations of species are named from the first two letters of the genus and species of each specimen.**

CPSA variation relative to social system (H_3)

CPSA and primate social system also showed no significant differences (haplorrhine plate CPSA p = 0.539, margin CPSA p = 0.731; strepsirrhine plate CPSA p = 0.656, margin CPSA p = 0.715) (Figure 12; Table 5). Like the other variables that are not significant, there is still a stark visual difference between strepsirrhines and haplorrhines.

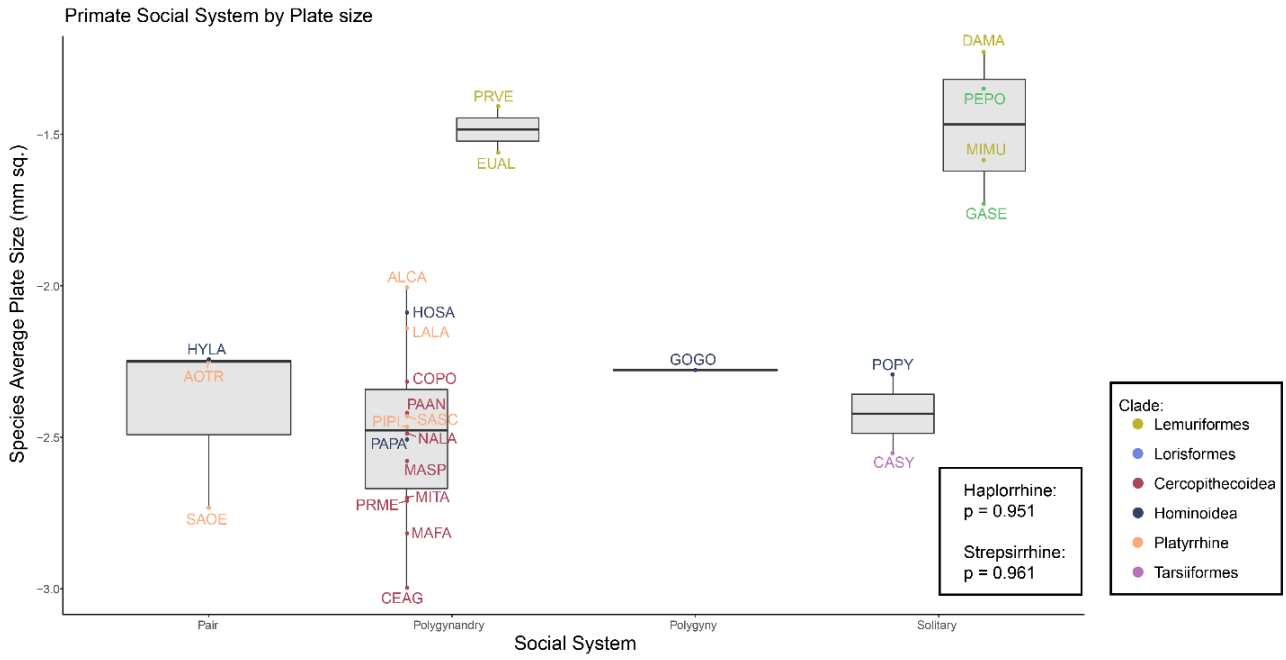

Figure 12. **Boxplot comparing the primate social systems against the average species plate CPSA, scaled by skull length. Since there were no significant differences found in either plate or margin CPSA, plate CPSA is only represented. P-values are separated by strepsirrhine and haplorrhine groups, in order to show variation between the groups. Abbreviations of species are named from the first two letters of the genus and species of each specimen.**

CPSA variation relative to activity pattern (H_4)

No significant differences were found for activity pattern (haplorrhine plate CPSA p = 0.951, margin CPSA p = 0.456; strepsirrhine plate CPSA p = 0.961, margin CPSA p = 0.795) (Figure 13; Table 5). Within the polygynandry social system, there seems to be a large variation of CPSA means, though this still does not come close to the measures for the strepsirrhines, thus maintaining that visual difference between the clades.

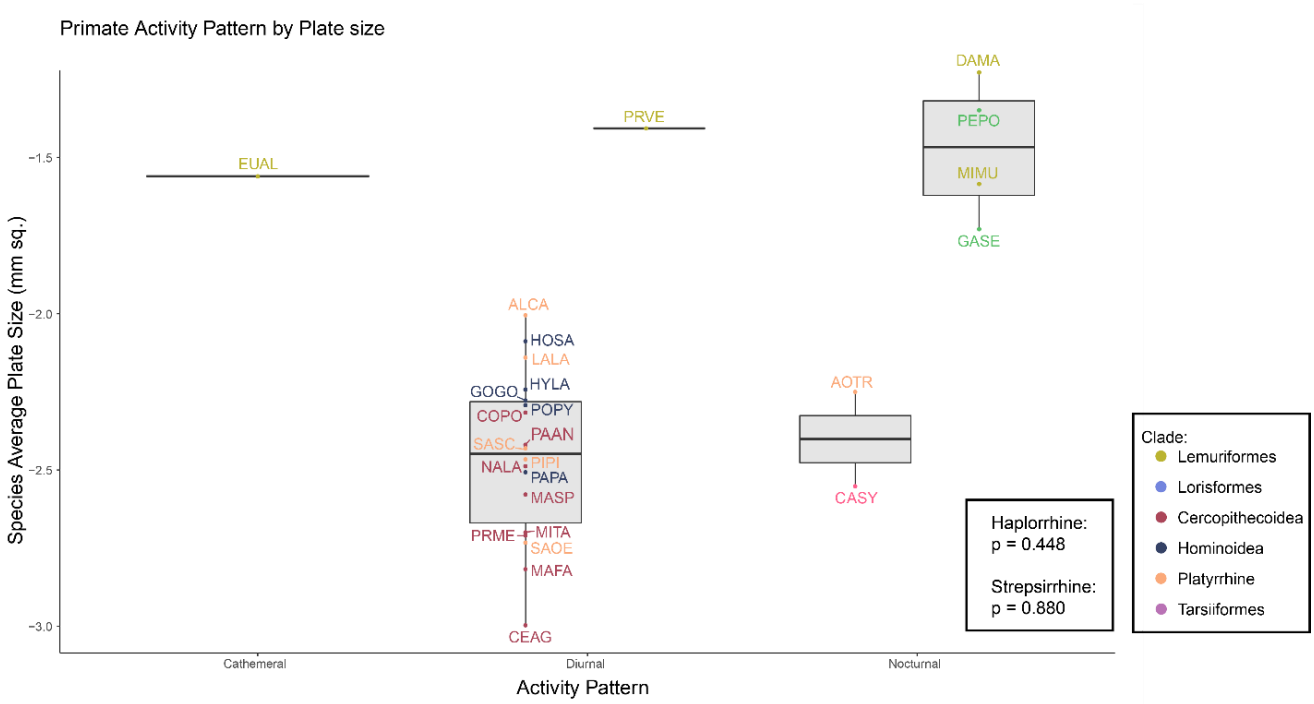

Figure 13. **Boxplot comparing the primate activity pattern against the average species plate CPSA, scaled by skull length. P-values are separated by strepsirrhine and haplorrhine groups, in order to show variation between the groups. Abbreviations of species are named from the first two letters of the genus and species of each specimen.**

DISCUSSION

The goal of this research was to assess how cribriform plate variation impacts olfactory-based behaviors, such as diet, activity pattern, and social system in the two major clades of primates, Strepsirrhini and Haplorrhini. Results indicated that only clade was a significant factor in the variation observed in both plate and margin CPSA; this suggests that perhaps CP plate size is not strongly driven by olfactory-based behaviors. The first hypothesis was supported with a significant difference in CP size between the strepsirrhine and haplorrhine clades (plate $p = 0.006$ and margin $p = 0.007$). However, when examined at the level of superfamily this signal was only marginally significant ($p = 0.062$), despite large differences in behaviors across these groups. All the other results related to diet, social system, and activity pattern failed to support the hypotheses (H_2, H_3, and H_4, respectively) with $p > 0.05$, indicating that these olfactory-based behaviors do not significantly impact cribriform plate morphology.

Comparisons to Prior Research

The findings here that these olfactory-based behaviors do not significantly impact CP morphology is a somewhat interesting result since it has been established through the literature that CPSA correlates to olfactory capability across mammalian species (Pihlström et al. 2005; Bird et al. 2014). This result could suggest that CPSA is more related to how strepsirrhines are better at smelling in general than haplorrhines, rather than the olfactory-based behaviors themselves.

Dietarily, prior research has been clear that olfaction is more important for frugivores than folivores in primates (Nevo and Heymann 2015), yet the results of this study do not align with these prior findings. This could be because Nevo and Heymann (2015) measured the

surface area of the olfactory epithelium and the size of the main olfactory bulb (MOB), which is a more direct correlate to olfactory capability. Additionally, for activity patterns, nocturnality is associated with increased olfaction in primates when analyzing the main olfactory bulb size relative to body size (Barton et al. 1995; Nevo and Heymann 2015), though when measuring both the plate and margin CPSA analyzed here, there was no significant relationships between CP size and activity pattern. The same is true for social systems, which have been linked to olfaction via the VNS system and the complex behaviors of scent-marking to communicate olfactorily (Heymann 2006; Smith and Rossie 2006; delBarco-Trillo et al. 2011). This prior work has suggested that urine scent-marking was an ancestral state, with glandular scent-marking being more derived, so as some primate species transitioned to diurnality, there was a reduced investment in these methods (delBarco-Trillo et al. 2011). Therefore, there seems to be a link between activity pattern and social behaviors, which contribute to the reduced olfaction in haplorrhines compared to strepsirrhines, as a greater number of haplorrhines are diurnal compared to strepsirrhines. The results presented here did not include social behaviors like scent-marking, which might have contributed to the non-significance of the social system results.

Since it has already been established that CPSA is the strongest correlate to olfactory capability when looking at the cribriform plate in mammals (though not in primates specifically) (Pihlström et al. 2005; Bird et al. 2014), the general findings here of a lack of relationship between CP size and diet, social systems, and activity patterns indicate that there is a more complex system that contributes to strepsirrhines having larger CPs (and olfactory capabilities) than haplorrhines, such as the presence of a rhinarium, which is indirectly associated with the accessory olfactory (VNS) system and the vomeronasal organ (VNO) (though not the main olfactory system) (Smith and Rossie 2006). Since there was an evolutionary trade-off in

haplorrhines, where they emphasized vision rather than olfaction (Osman 1953; Smith et al. 2007; Smith and Rossie 2007; Garrett et al. 2013), the loss of the rhinarium could have been one of the effects of this reduced emphasis on olfaction. Further, since the VNO is largely vestigial or lost in catarrhines (Cercopithecoidea and Hominoidea), where the VNO has been retained in haplorrhines, these species still lack other crucial behavioral features like the flehmen response (i.e., a behavior where an animal curls back its upper lip when inhaling), which help direct olfactory signals into the VNO (Smith and Rossie 2006).

Limitations and Future Research Questions

This research is the first to examine cribriform plate variation in primates. This included analyzing at least two species per extant primate family, with one male and one female per species. However, one reason these analyses may not have found significant patterns could be related to sample sizes. More research should be conducted on this topic utilizing a greater sample size, since I was only able to analyze one specimen per sex. My limitation of a small sample size was compounded by the fact that within each superfamily of primates there is such wide variation, that it would be difficult to extend this research to other primates that were not included in the research. Bird et al. (2014) mention that olfactory function could be more rigorously tested in smaller sample sizes if cross-sectional surface area of the cribriform plate (FXSA) was combined with CPSA. Utilizing both CPSA and FXSA might have yielded different results; however, measuring FXSA is an incredibly time- and labor-intensive process and therefore was excluded in this study.

Additionally, it would have been beneficial to have a more diverse set of variables for social behaviors instead of just social system, such as mating system (which can be quite

different than social system) and average group size. Further, while most strepsirrhines are nocturnal, more diurnal strepsirrhines would have been beneficial to analyze against the numerous diurnal haplorrhines that were part of the sample. Another limitation was the arbitrary nature of delineating where the plate began and the margin ended on the CP for some specimens, primarily the strepsirrhine and outgroups, who had such broad concave CPs, there almost did not seem to be much of a margin at all.

From this research, several more questions were raised that merit further research. If CPSA might not be directly linked to these olfactory-based behaviors like research suggests (Barton et al. 1995; Pihlström et al. 2005; Heymann 2006; Smith and Rossie 2006; delBarco-Trillo et al. 2011; Nevo and Heymann 2015; Bird et al. 2014), could it be more due to olfactory chemical processing in the brain? Is it just that the olfactory bulb alone is a better indicator of olfactory capability, like some research suggests (Baron et al. 1983; Barton et al. 1995; Dominy et al. 2004; Barton 2006), or could FXSA be combined with CPSA to have a more direct correlation to olfactory bulb, and by extension olfactory capability, as Bird et al. (2014) and Bhatnagar and Kallen (1974) suggest? Do the higher walls of the margin CP in some haplorrhine primates (such as macaques and tarsiers) have any significant impact on olfactory capability or any special anatomical function related to olfaction or is this simply a way to compensate for the more compact haplorrhine nose (Smith and Rossie 2006; Smith et al. 2007; Garrett et al. 2013)? This would be interesting to test by measuring how the flatness of the face is compared to the length of the margin CP walls to see if there is a correlation between these measures.

CONCLUSION

Though there has been previous work that has demonstrated that the cribriform plate can be used to infer olfactory capability (Bhatnagar and Kallen 1974; Kalmey et al. 1998; Pihlström et al. 2005; Smith and Rossie 2006; Bird et al. 2014; Bird et al. 2018), this study was the first to examine this structure within primates. This work found that there is a significant relationship between CPSA and clade across primates, but CP size is not linked to other behavioral factors (diet, activity pattern, and social system). Though the variables of diet, activity pattern, and social system were not significantly related to CPSA, the large visual difference between strepsirrhines and haplorrhines reveal that strepsirrhines still emphasize olfaction more than haplorrhines.

If this study could be replicated on a larger scale, utilize FXSA as an additional measurement, and include more species per sex and superfamily, it could be the first to directly link cribriform plate morphology to olfactory function and behavior in primates. This research is valuable because it will hopefully allow researchers to better analyze how the internal bony anatomy of the olfactory system might translate to functional differences in primates and how that relates to differences in behaviors. This in turn, could be utilized to correlate some morphological differences with potential behaviors of extinct primates by studying their CPSA, which has already been done with other species (Joeckel et al. 1997; Hoch 2009; Kielan-Jaworowska 2004; Garcia et al. 2007; Godfrey et al. 2013).

Further, these results demonstrate how the important evolutionary relationships (i.e., clade) is on determining olfactory capability. With this information, it can be stated that haplorrhines have less olfactory capability (at least as represented by cribriform plate size) than strepsirrhines, but that does not mean that smell is not still incredibly important for haplorrhine

primates to navigate their environments. For example, humans generally do not rely extensively on or have very robust olfactory capabilities compared to other mammals. As a result, olfaction is mostly overlooked when people perform their daily routines. However, olfaction is incredibly important for how humans and other species interact with their environment, from knowing when to eat ripe fruit to avoiding a male during mating season. These links demonstrate how important olfaction is because the more systems that olfaction is tied to, the more important smell is in performing these behaviors.

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