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Analyzing the sclerocarpy adaptations of the Pitheciidae mandible

Thomas A. Püschel[1] | Jordi Marcé-Nogué[2,3] | Thomas M. Kaiser[2] | Robert J. Brocklehurst[1] | William I. Sellers[1]

[1] School of Earth and Environmental Sciences, University of Mancheste, Manchester, United Kingdom

[2] Center of Natural History (CeNak), Universität Hamburg, Hamburg, Germany

[3] Institut Català de Paleontologia M. Crusafont, Universitat Autònoma de Barcelona, Cerdanyola del Vallès, Barcelona, Spain

Correspondence
Thomas A. Püschel, School of Earth and Environmental Sciences, University of Manchester, Michael Smith Building, Oxford Road, Manchester, M13 9PT, United Kingdom.
Email: thomas.puschel@postgrad.manchester.ac.uk

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Primates are interpreted to be ancestrally adapted to frugivory, although some modern groups show clear adaptations to other diets. Among them, pitheciids stand out for specifically predating seeds. This dietary specialization is known as sclerocarpy and refers to the extraction of seeds from surrounding hard tissues using the anterior dentition followed by the mastication of seeds by the molars. It has been proposed that *Callicebus-Pithecia-Chiropotes-Cacajao* represent a morphocline of increasingly specialized anatomical traits for sclerocarpic foraging. This study addresses whether there is a sclerocarpic specialization gradient in the mandibular morphology of pitheciids. Finite element analysis (FEA) was used to simulate two biting scenarios and the obtained stress values were compared between different pitheciids. Geometric morphometrics (GM) were used to display the morphological variation of this group. No support was found for the morphocline hypothesis from a biomechanical viewpoint since all pitheciins showed similar stress values and on average *Chiropotes* rather than *Cacajao* exhibited the strongest mandible. From a morphological perspective, it was found that there is indeed relative "robusticity" continuum in the pitheciid mandible for some aspects of shape as expected for the morphocline hypothesis, but this gradient could be related to other factors rather than sclerocarpic specialization. The present results are expected to contribute to a better insight regarding the ecomorphological relationship between mandibular morphology and mechanical performance among pitheciids.

KEYWORDS
finite element analysis, geometric morphometrics, lower jaw, pitheciids, seed predation

1 | INTRODUCTION

Primates are often interpreted as morphologically and behaviorally adapted to frugivory, this trait being regarded as the ancestral condition of this order (Fleagle & McGraw, 1999; Kay, 1984). Nearly all primates will eat fruit when available: however it has been argued that it is almost always an ephemeral resource in natural environments (Chapman, Wrangham, Chapman, Kennard, & Zanne, 1999; ter Steege & Persaud, 1991) and fruits provide a variable amount of essential nutrients

(Conklin-Brittain, Wrangham, & Hunt, 1998; Milton, 1998; Norconk & Conklin-Brittain, 2004; Norconk, Wright, Conklin-Brittain, & Vinyard, 2009; Oftedal, Whiten, Southgate, & van Soest, 1991). Many frugivorous primates also add insects and/or leaves to their diets in order to both balance their nutritional intake as well as to supply possible deficiencies in their food (Fleagle, 2013). Besides the main dietary groups of fruit, leaves, and insects, there are also several other incidental food items that can contribute important nutrients or serve as fallback items when required, such as flowers, gum, bark, fungus, lichen, pith, and

seeds (Conklin-Brittain et al., 1998; Grueter et al., 2009; Lambert, 1998; Lambert, Chapman, Wrangham, & Conklin-Brittain, 2004; Marshall, Boyko, Feilen, Boyko, & Leighton, 2009; Norconk et al., 2009; Sayers & Norconk, 2008). Among these different dietary items, seeds are relevant nutritional items for at least 31 primate species that consume seeds either seasonally or regularly (Norconk, Grafton, & McGraw, 2013). Seed predation has been defined as the action of masticating and ingesting seeds or whole fruits that include seeds (Norconk et al., 2013). Due to the fact that seeds are often well protected against predation, seed predators show a broad variety of adaptations to extract them from protecting tissues, and later consume them. Primates typically tend to prefer the soft, outer layers of the fruit (i.e., the pericarp). The soft parts are obtained by swallowing the fruit whole, or by removing the edible portions with teeth and/or hands and then dropping the seeds (Kay, Meldrum, & Takai 2013). Whole seeds ingested together with the soft outer layers can germinate if passed intact through the gastrointestinal tract (Norconk et al., 2013). However, among primates, pitheciines (i.e., *Pithecia*, *Chiropotes*, *Cacajao*) follow a different pattern. They actively extract seeds from the fruit, chewing them before swallowing, and are consequently recognized as seed predators (Rosenberger, 1992). Some other primates from South America are sporadic seed predators, but pitheciines appear to be specialized to varying degrees in seed predation or sclerocarpic foraging (van Roosmalen, Mittermeier, & Fleagle, 1988). Even though this specific dietary strategy is rare among primates, it might have arisen as way to reduce dietary stresses and competition with sympatric taxa during periods of scarcity of other preferred food (Davis, 1996; Norconk et al., 2009). The seeds of unripe fruit seem to represent a particularly unique means of acquiring fundamental nutrients, especially when considering that young seeds are an exceptionally good source of lipids, proteins, and carbohydrates (Kinzey & Norconk, 1993; Norconk & Conklin-Brittain, 2004).

Sclerocarpy refers to the extraction of seeds using the anterior dentition (i.e., incisors, canines, and/or the first premolar in the tooth row) and hands, followed by the mastication of seed by the molars (Kinzey & Norconk, 1990). Interestingly, within the Pitheciidae the pitheciines are the quintessential example of this type of seed predation; in fact the pitheciin fossil record (e.g., *Proteropithecia neuquensis*, *Nuciruptor rubicae*) suggests that the lineage began to fill their hard-object feeding niche around the middle Miocene, thus scleorcarpic foraging is a relatively old trait in this lineage (Kay et al., 1998, 2013; Meldrum & Kay, 1997). Pitheciids comprise two distinctive platyrrhine sub-families: the Callicebinae consisting of the genus *Callicebus* (titi monkeys) and the Pitheciinae comprising *Pithecia* (sakis), *Chiropotes* (bearded sakis), and *Cacajao* (uakaris). All these genera predate hard unripe seeds to a varying degree, although only the Pitheciinae exhibit most marked specializations to this particular diet, showing noticeable modifications of the cranium, mandible, dentition, cranial musculature, and viscera (Kay et al., 2013; Kinzey, 1992; Ledogar, Winchester, St. Clair, & Boyer, 2013; Norconk et al., 2013; Norconk & Veres, 2011). These features are particularly evident and developed in *Cacajao* (Kinzey, 1992); nonetheless, in all three pitheciin genera the most significant food element consumed is seeds. Furthermore, it is been shown that when resources are scarce, *Pithecia*,

Chiropotes, and *Cacajao* further increase their seed consumption (Norconk et al., 2009). Pitheciins are pre-dispersal seed predators (Janzen, 1971), therefore, they eat fruit primarily covered with a hard pericarp that is subsequently opened with their canines and/or incisors (Kinzey & Norconk, 1990). *Callicebus* also share the seed-eating habits of pitheciines but to a lesser degree, although it has been reported that almost a quarter of the diet of *Callicebus personatus* (Müller, 1996), and almost half of that of *Callicebus lugens* may correspond to immature seeds (Palacios, Rodríguez, & Defler, 1997). It has been actually proposed that *Callicebus-Pithecia-Chiropotes-Cacajao* represent a morphocline of increasingly specialized anatomical traits for sclerocarpic foraging (Kay, 1990; Kinzey, 1992; Meldrum & Kay, 1997; Rosenberger, 1992). A pattern of derived traits related to this feeding behavior distinguish the living pitheciids from any other extant platyrrhine (Kay, 1990; Rosenberger, 1992).

In this sclerocarpy specialization gradient, *Callicebus* would represent the least specialized genus for seed predation among the pitheciids, because it lacks some of the dental, and mandibular associated with sclerocarpy, such as enlarged canines, molarized premolars, and flatter molars with poorly developed crests (Kinzey, 1992). Nonetheless, *Callicebus* does show some seed predation features, like a posterior deepening of the mandible, as well as narrow, and elongated incisors (Kinzey, 1992). On the other hand, *Pithecia*, *Chiropotes*, and *Cacajao* would exhibit adaptations for sclerocarpy in an increasing manner (Kay et al., 2013). All of these genera exhibit an incisor–canine complex that enables a specialized puncturing and prying mechanism (Kay et al., 2013). The lower incisors are narrow, styliform, and particularly procumbent, which creates a gouge (Kay et al., 2013). The canines are enlarged, laterally splayed, and have a sharp lingual crest (i.e., entocristid), producing a triangular cross-section (Rosenberger & Tejedor, 2013). This specialized large-seed scraping and splitting mechanism is powered by extremely hypertrophied mastication musculature with associated posterior jaw deepening (Rosenberger & Tejedor, 2013). The first lower molars are also enlarged (Kinzey, 1992; Norconk et al., 2013), and they show molarized last premolars with high complexity and low relief, shear, and curvature of molar occlusal surfaces (Ledogar et al., 2013; Winchester et al., 2014). Interestingly, it has been shown that the molar enamel of pitheciins is relatively thin and often crenulated, although it exhibits extremely well-defined Hunter-Schreger bands, a trait that seems to strengthen the enamel and prevent cracks from propagating through the tooth (Rensberger, 1993; von Koenigswald & Pfretzschner, 1987). On the other hand, *Callicebus* exhibits relatively thin, and radial enamel with no evident Hunter-Schreger bands, indicative of a softer diet (Martin, Olejniczak, & Maas, 2003). This relatively thin molar enamel exhibited by the pitheciins could be related to the fact that although they are sclerocarpic foragers that open hard husks with their canines and/or anterior incisors, the seeds that they then chew can be comparatively soft and pliable when compared to the ones consumed by other primates (although they can still be tough/hard). A recent study comparing the microwear of molars belonging to different pitheciid genera found that they slightly differ in their dental microwear textures thus is still challenging to discriminate seed-based

diets in pitheciids using molar microwear pattern (Ragni, Teaford, & Ungar, 2017). In contrast, the other platyrrhine that often consumes hard objects (i.e. *Cebus*) has probably the thickest molar enamel of all primates (Dumont, 1995; Martin et al., 2003). This is possibly an adaptation that slows wear, thus prolonging the life of the tooth, in particular their relief, and cusps. Taking into account the extreme hardness of the items ingested by *Cebus*, such adaptation might be of crucial benefit. However, it is important to keep in mind that even though the seeds consumed by the pitheciines are comparatively soft, the sclerotized pericarp that protects them is still extremely hard. For example, the maximum hardness of the pericarp ingested by *Pithecia pithecia* is approximately five times that of fruits ingested by *Ateles*, while the maximum hardness recorded for fruits ingested by *Chiropotes satanas* was 27 times that of the hardest fruit opened by *Ateles* (Kinzey & Norconk, 1990).

Even though several studies report on some specific phenotypic aspects related to the sclerocarpic behavior of the pitheciids, there are only few quantitative analyses focusing on the sclerocarpy adaptations of the mandibular morphology. For instance, Wright (2005) compared the mechanical advantage (MA) of the jaw-closing muscles at different biting positions across ten platyrrhine species, focusing especially on *Cebus* spp. due to their known durophagic behavior. He found that *Cebus* showed the highest MA for the jaw-closing muscles (excepting the medial pterygoid), while *Chiropotes satanas* exhibited the next highest MA followed by *Pithecia pithecia*, *Lagothrix lagotricha*, and *Ateles paniscus* (Wright, 2005). On the other hand *Alouatta seniculus*, *Callicebus* spp., and *Aotus trivirgatus* exhibited the least MA among the analyzed species (Wright, 2005). In another study, Anapol and Lee (1994) estimated the temporalis and masseter lever arms for eight platyrrhine species, focusing mostly on variation among lever arm lengths. They noticed that the temporalis lever arm showed relatively more variation than the masseter lever arm (Norconk et al., 2009). They measured moment arms for the temporalis, masseter, and medial pterygoid in 22 platyrrhine species, in a similar fashion to Wright (2005). Subsequently, Anapol and Lee (1994) scaled these measurements by the proportion of the total jaw-adductor muscle weight each muscle represents based on the few platyrrhine data provided by (Turnbull, 1970). It was found that individual moment arms and average moment arm scale close to or slightly below isometry relative to incisor, canine, and molar biting moment arms (Norconk et al., 2009). They also found that relative MA among platyrrhines seemed to trend toward a size-related decrease in biting leverage, especially for biting along the post-canine dentition (i.e. smaller platyrrhines seemed to have greater MA on average than larger species for biting at M1) (Norconk et al., 2009). They also found that among the non-callitrichines, *Cebus apella* exhibited the highest leverage for biting, while *Chiropotes satanas*, and *Cacajao melanocephalus* have the next highest advantage followed by *Pithecia pithecia* and *Cebus albifrons*. Consequently, they proposed that these results support previous observations suggesting that "hard-object" feeders have relatively greater MAs, predominantly during anterior tooth use (Anapol & Lee, 1994; Wright, 2005). In addition to these MA estimations, Norconk et al. (2009) also attempted to summarize morphological variation in

load bearing ability across platyrrhine species by carrying out a principal component analysis (PCA) of various ratios calculated from a set of mandibular measurements. They interpreted their PC1 as a general jaw robusticity factor, where *Chiropotes satanas*, and *Cacajao melanocephalus* had the largest scores followed by *Cebus*, thus suggesting these taxa must have relatively robust mandibles, likely due to their ingestion of mechanically challenging seeds (Anapol & Lee, 1994; Bouvier, 1986; Kinzey, 1992).

In spite of all these valuable studies, most of these investigations have been restricted to morphological comparisons, and simple biomechanical comparisons (i.e., comparing lever arms and MA), with fewer studies using modern virtual functional morphology techniques or experimental approaches applied to analyze platyrrhine mandibles (Ross et al., 2013; Ross, Iriarte-Diaz, Reed, Stewart, & Taylor, 2016). Only recently, one study analyzed feeding biomechanics in pitheciine monkeys, by applying finite element analysis (FEA) to assess cranial biting mechanics (Ledogar et al., 2018). They found that pitheciines have higher biting leverage and are generally more resistant to masticatory strain as compared to *Callicebus*. However, they found limited support for the morphocline hypothesis since *Cacajao* showed higher strain magnitudes in various facial regions when compared with the other analyzed taxa (Ledogar et al., 2018). This study also found that biting leverage in *Cacajao* was slightly less than in *Chiropotes*, and that strain values during canine biting (i.e., one of the main mechanisms to open unripe fruits) followed a strength trend described as *Cacajao–Chiropotes–Pithecia*, rather than the proposed morphocline hypothesis (Kinzey, 1992). However, it is important to notice that this study exclusively analyzed the pitheciid cranium, which is an anatomical structure involved in diverse functions, thus probably exhibiting a mixed signal. In fact, Ledogar et al. (2018) noted that cranial shape reflects a compromise between many functions (e.g., phonation, cognition, feeding, respiration), which could mask a strong dietary signal.

Therefore, in the present study we chose to focus on the mandible rather than the whole cranium, because as stated above this latter structure exhibits a morphology associated with multiple, and diverse functions, while the lower jaw is primarily involved in food acquisition and consumption, and consequently it would be expected that its morphology better reflects dietary adaptations (Agrawal, Lucas, Bruce, & Prinz, 1998; Chew, Lucas, Tay, Keng, & Ow, 1988; Gröning, Fagan, & O'Higgins, 2012; Hiiemae, 1978; Hiiemae & Kay, 1972; Hylander, Johnson,& Crompton, 1987; Marcé-Nogué, Püschel, & Kaiser, 2017; Vinyard, Wall, Williams, & Hylander, 2003). In fact it has been stated that understanding the biomechanical behavior of the primate mandible seems to be essential to gain insight about primate dietary adaptations, and thus about their evolution (Perry, Hartstone-Rose, & Logan, 2011; Wroe, Ferrara, McHenry, Curnoe, & Chamoli, 2010). This study investigates the biomechanical performance of four different pitheciid species representing the seed predation specialization gradient using FEA. This technique reconstructs stress, strain, and deformation in material structures that has become a standard part of the biomechanical toolkit (Rayfield, 2007). The application of FEA to analyze primate mandibular morphology is particularly relevant, due to

the limited number of studies where ecological data on primate diet is used to explicitly test biomechanical hypotheses. It was expected that those species that rely more on seed consumption should exhibit stronger jaws (i.e., lower stress values) due to morphological adaptations to this particular diet, when compared to those species that eat fewer seeds. In addition, by using geometric morphometrics (GM) it was decided to display the morphological variation of the group under analysis to examine if there was an evident morphological trend that could be linked to the morphocline hypothesis. GM refers to the quantitative analysis of Cartesian coordinates representing form (i.e., shape and size) and how it covaries with respect to other factors (e.g., biomechanics, development, ecology, genetics, etc.) (Adams, Rohlf, & Slice, 2013). The following hypotheses were tested:

H1: The strength of the mandible obtained from the FEA simulations reflect the sclerocarpy specialization gradient described for pitheciids. Consequently, the results observed in the mandible should show a gradient from weaker to stronger mandibles following the seed predation specialization observed in this group (i.e. *Callicebus–Pithecia–Chiropotes–Cacajao*).

H2: The main aspect of mandibular shape variation (i.e. PC1) follows a trend consistent with the morphocline hypothesis (i.e. *Callicebus–Pithecia–Chiropotes–Cacajao*).

2 | METHODS

This research met the animal research requirements of the UK, and adhered to the American Society of Primatologists principles for the ethical treatment of primates.

2.1 | Sample

The CT-scan data of four pitheciid genera were obtained from the Morphosource database (http://morphosource.org/) (Table 1; Figure 1) (Copes, Lucas, Thostenson, Hoekstra, & Boyer, 2016). The genera under study are *Cacajao*, *Callicebus*, *Chiropotes*, and *Pithecia*.
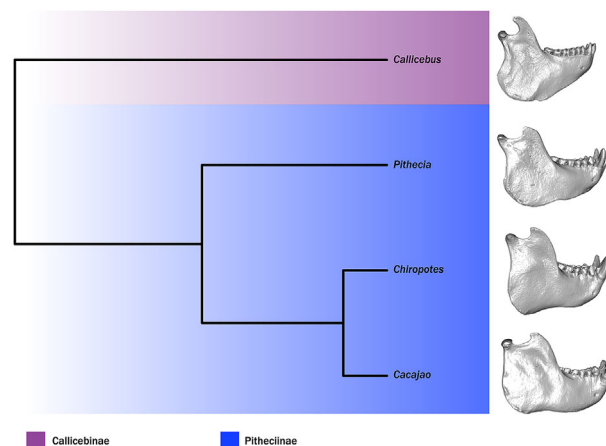

FIGURE 1 Analyzed pitheciid mandibles plotted next to a consensus phylogenetic tree computed from 10,000 phylogenies downloaded from the 10kTrees dataset (http://10ktrees.fas.harvard.edu/Primates/index.html)

This sample was selected to consider two specimens of every genus within Pitheciidae, in order to represent the proposed sclerocarpy specialization gradient exhibited by this group. All specimens were adult with no reported or evident pathologies associated with their mandibular anatomy. Most individuals were male according to the information available from the museum records. In order to avoid any bias, this sample was randomly selected from the available scans if they met the abovementioned criteria (i.e., adults, non-pathological, preferably male). Unfortunately, there was no information regarding the sex of some of the analyzed individuals. Nonetheless, it is well known that black-bearded sakis (i.e., *Chiropotes satanas*) are only slightly sexually dimorphic (Hershkovitz, 1985; Smith & Jungers, 1997), and that *Pithecia* also shows minor sexual dimorphism in their skull morphology, the males being on average only slightly larger (in all measurements) when compared to females (Hershkovitz, 1987a). *Cacajao calvus* is also described as exhibiting only slight sexual dimorphism (Fleagle, 2013; Hershkovitz, 1987b). Therefore, this uncertainty should not affect our results, particularly when considering that the FEA represents simplified loading scenarios. Further details regarding the scanning process can be found in http://morphosource.org/.

TABLE 1 Sample

Accession number	Species	Scan resolution [mm]	Sex	ID
MCZ-27870	*Cacajao calvus*	0.08	Male	*Cacajao 1*
MCZ-BOM-1957	*Cacajao calvus*	0.08	?	*Cacajao 2*
MCZ-20186	*Callicebus moloch*	0.05	Male	*Callicebus 1*
MCZ-30566	*Callicebus moloch*	0.05	Male	*Callicebus 2*
MCZ-BOM-6028	*Chiropotes satanas*	0.05	?	*Chiropotes 1*
USNM-388166	*Chiropotes satanas*	0.05	Male	*Chiropotes 2*
MCZ-27124	*Pithecia monachus*	0.05	?	*Pithecia 1*
USNM-374754	*Pithecia pithecia*	0.05	Male	*Pithecia 2*

2.2 | Image segmentation

The CT-scans of the different pitheciid genera were segmented in the following manner. DICOM files were imported into AVIZO® (VSG, version 9.1) where each specimen was segmented by applying a combination of manual painting techniques and case-specific thresholding. The segmented models were then converted to CAD models (Marcé-Nogué, Fortuny, Gil, & Sánchez, 2015). During this step, surface irregularities from model generation were repaired using the refinement and smoothing tools from Rhinoceros® (McNeel & associates, version 5.0, Seattle, WA). The models were all oriented with respect to the same occlusal plane to facilitate the comparison between them. This occlusal plane was defined as an imaginary surface that "touched" the incisal edges of the incisors and the tips of the occluding surfaces of the posterior teeth.

2.3 | Finite element analysis

2.4 | Model properties

A structural static analysis to evaluate the biomechanical behavior of the eight different jaws during biting was performed using ANSYS® (Ansys Inc., version 17.1, Canonsburg, PA) on a Dell Precision™ Workstation T5500 (Dell, Round Rock, TX). It is important to bear in mind that the objective of this study was to develop a FEA structural comparative analysis; therefore, we were not interested in the in vivo value of load forces or resulting stresses (Püschel & Sellers, 2016). The aim was to analyze mandibular strength under equivalent loads and comparable loading scenarios. Consequently, in this work FEA was used in a comparative fashion rather than being used to validate the models against experimental data. FEA was applied as a structural comparative technique, the idea being to compare a general measure of mechanical performance. This means that any simplification performed in our models is present in all the eight jaws and is therefore not affecting our macroscopic comparisons because the same simplifications were applied to all the models.

In this study, we obtained the von Mises stress distribution in the jaw under the chosen loading conditions, which reflect different feeding scenarios. Among the different criteria to compute equivalent stresses (for a detailed definition of different available criteria to compute equivalent stresses see Reddy, 2007), von Mises is the most accurate value when isotropic material properties are used in cortical bone (Doblaré, García, & Gómez, 2004). Elastic, linear, and homogeneous material properties were assumed for the bone using the following values from *Macaca*: Young Modulus $E = 21$ GPa and Poisson's ratio $v = 0.3$ for the mandible (Strait et al., 2005), while for the teeth the values for the enamel were $E = 99.4$ GPa and $v = 0.3$ (Constantino et al., 2012). Strait et al. (2005) have shown that the Young's Modulus of bone in the primate skull varies depending on the analyzed anatomical locations, ranging from 12.5 GPa (posterior portion of the zygomatic arch) to 20.8 GPa (anterior zygomatic). However, the use of these values is not crucial for the development of the analyses proposed here because these values do not affect the

results when a relative comparison of stress results between models is performed (Gil, Marcé-Nogué, & Sánchez, 2015). The models were segmented as solid models without including trabecular bone properties because it has been shown that the exclusion of trabecular bone does not affect the general results of a comparative FEA (Fitton, Prôa, Rowland, Toro-Ibacache, & O'Higgins, 2015) and because it been also shown that simplified models can reproduce the overall stress distribution patterns in ex vivo validation experiments (Bright & Rayfield, 2011; Dumont, Piccirillo, & Grosse, 2005; Ross et al., 2011). Additionally, we decided not to segment the periodontal ligament (PDL) because there is some debate in the literature regarding the importance or not of modeling the PDL in FEA (Bright, 2014). Some modeling studies of the primate mandible have suggested that the presence or absence of the PDL might affect the obtained results substantially throughout the whole structure (e.g., Gröning, Fagan, & O'Higgins, 2011; Marinescu, Daegling, & Rapoff, 2005), while other researchers found that it is only important in the areas immediately adjacent to the teeth (e.g., Panagiotopoulou, Kupczik, & Cobb, 2011). Likewise, models of the crania of *Cebus* (Wood, Strait, Dumont, Ross, & Grosse, 2011) found that the PDL had exclusively local effects when performing FEA. Therefore, we decided not to include this extra variable in our models until its role is better understood, because it can introduce further uncertainties in our models that might confuse our result interpretation. Finally, the jaws were meshed using an adaptive mesh of hexahedral elements also using ANSYS® (Marcé-Nogué et al., 2015). The model meshes ranged between 200,000–860,000 elements depending on the particular specimen and biting case.

2.5 | Boundary conditions and applied loadings

The available literature on sclerocarpic foraging was reviewed in order to define sensible loading conditions (Norconk et al., 2013; van Roosmalen et al., 1988). Based on the available descriptions of sclerocarpic foraging behavior, it was possible to establish commonalities regarding the way in which the pitheciines extract seeds. They basically apply two different bites, either using their procumbent incisors or their wedge-shaped canines (Figure 2a), seemingly depending on the hardness of the fruit (Norconk et al., 2013). For instance, it has been reported that *Chiropotes* bites a hole into the fruit at the edge of the operculum when dealing with *Eschweilera* fruits from the Brazil nut family (Lecythidaceae) (van Roosmalen et al., 1988). Then it uses its incisors like a can opener to pop the operculum off and gain access to the seeds inside. When feeding on the very hard seedpods of larger Lecythidaceae such as *Lecythis davisii*, sakis use their powerful wedge-shaped canines rather than their incisors (van Roosmalen et al., 1988).

Boundary conditions were defined to represent the loads and fixed displacements that the mandibles experience during two biting scenarios (Figure 2b). The first boundary condition restrained the condyle at the level of the contact points with the mandibular fossa of the cranium in order to represent the immobilization of the mandible constraining the translation of the jaw in all the directions (condyles were fixed using multiple nodes). The analysis simulated an
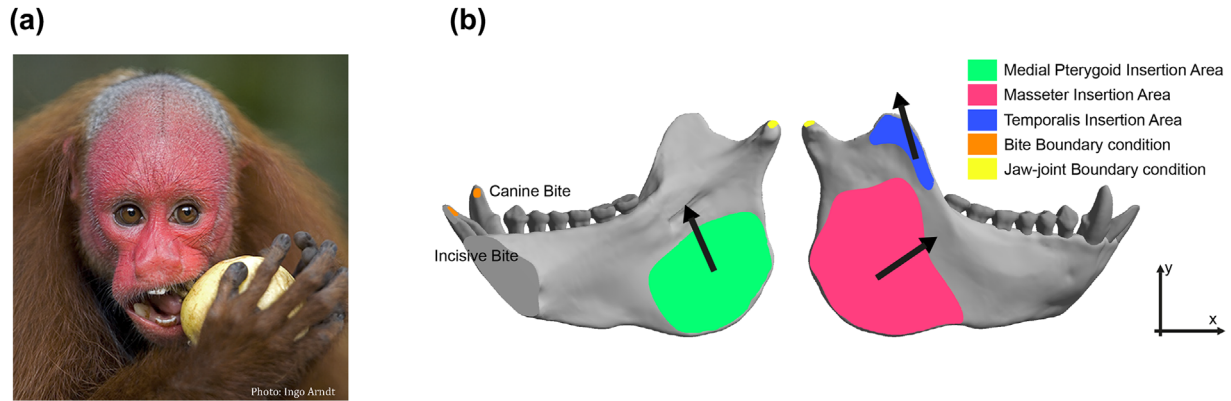
(a)   **(b)**

FIGURE 2 (a) *Cacajao calvus* individual biting a hole into a fruit using its wedge-shaped canines; (b) Free-body diagram of the applied biomechanical cases showing boundary conditions, muscular forces and insertion areas, as well as dental positions used to simulate incisive, and canine biting scenarios

instantaneous event at static equilibrium, in order to examine overall patterns of stress distribution in the mandible. In order to simulate biting, a fixed displacement boundary condition in the y-axis was applied in two different dental positions: 1) Incisive bite: at the occlusal edge of the central incisor and 2) Canine bite: at the tip of the canine (Figure 2b).

The muscular insertion areas of the masseter, medial pterygoid and temporalis were defined in the model in order to apply the forces of muscular contraction during the bite in the jaw. The directions of the forces were defined by lines joining the centroid of the insertion area on the skull with the centroid of the insertion areas on the mandible (Supplementary material S1). The reduced Physiological Cross-Section Areas (PCSA) of *P. monachus* were obtained from (Anapol, Shahnoor, & Ross, 2008) for the temporalis (163 mm^2), masseter (133 mm^2) and the medial pterygoid (84 mm^2). Assuming a value of 0.3 MPa as muscular contraction pressure (Alexander, 1992), the muscle force was obtained for *P. monachus*, which was used again as a reference model (Table 2).

2.6 | Scaling

One relevant concern to be considered when analyzing different individuals using FEA is how to compare models that differ in shape

and size (Dumont, Grosse, & Slater, 2009). In this study, the values of muscular forces applied in the models were calculated according to the methodology developed by Marcé-Nogué et al. (2013) and rearranged for 3D models by Fortuny et al. (2015) based on scaling the forces via the volume ratio (Equation 1). VB is the volume of the reference model and VA is the volume of the scaled model. The muscular force (F) of both models A and B were related with the variation of the volume (V) of the skull as stated in equation 1 (Table 2). *P. monachus* was used as the reference model B in Equation (1), scaling the values of these forces in the other models to enable an appropriate comparison.

$$F_A = \left(\sqrt[3]{\frac{V_A}{V_B}}\right)^2 F_B \tag{1}$$

2.7 | Analysis of the FEA results

In order to facilitate the comparison between models, quantitative measurements of the relative strength of the different jaws were used to summarize the FEA results. The von Mises stress distributions of the different mandibles were evaluated using their average values and presented using box-plots to display their stress

TABLE 2 Muscle forces and volumes of the models

Model	Volume of the jaw (mm^3)	Pterygoid force (N)	Masseter force (N)	Temporalis force (N)
Callicebus 1	3,288.3	22.92	36.28	44.47
Callicebus 2	1,651.2	14.48	22.92	28.09
Pithecia 1	3,792	25.20	39.90	48.90
Pithecia 2	2,907.4	21.11	33.42	40.96
Chiropotes 1	6,923.9	37.65	59.61	73.05
Chiropotes 2	7,806.4	40.78	64.57	79.13
Cacajao 1	6,641.8	36.62	57.98	71.05
Cacajao 2	11,554	52.96	83.86	102.77

distributions following the proposal by Farke (2008), who recommends plotting stress distributions as quantitative data. However, the use of box-plots for the stress and statistics derived from them (e.g. percentiles or whiskers) requires the use of a quasi-ideal mesh (QIM), thus involving corrections for mesh non-uniformity. In the present paper we used QIM for our models—a mesh where all the elements have practically the same size—thus allowing the display the obtained stress values as boxplots (Marcé-Nogué, De Esteban-Trivigno, Escrig, & Gil, 2016). Due to the fact that a QIM is a non-uniform mesh (i.e. different elements have dissimilar sizes, although nearly identical in a QIM), new statistics that take into account this non-uniformity were estimated, such as the mesh-weighted arithmetic mean (MWAM), and the mesh-weighted median (MWM). For the MWAM some data points contribute more than others depending on the size of the element (i.e., the sum of the value of the von Mises stress for each element multiplied by its own volume and divided by the total volume), while the MWM is defined as the division of the median of the product of stress and volume by the median of the volume (Marcé-Nogué et al., 2016). These values (i.e., MWAM and MWM), are required to estimate the percentage error of the arithmetic mean (PEofAM) and percentage error of the median (PEofM), which are statistics used to ensure that our models were good QIMs as described in Marcé-Nogué et al. (2016).

2.8 | Geometric morphometrics

Shape variables were obtained using GM methods (Slice, 2007; Zelditch, Swiderski, & Sheets, 2012). Landmark acquisition was carried out in Landmark Editor (IDAV, version 3.6, Davis, CA) by collecting 22 homologous and well-defined 3D points (Figure 3). GM and statistical analysis were carried out in R (R Core Team, version 3.4.0, Vienna, Austria; https://www.r-project.org/) using the "geomorph" package (Adams & Otárola-Castillo, 2013). A generalized Procrustes analysis was applied to extract the shape variables from the raw landmark data, by removing all the differences due to translation, rotation, and scale (Bookstein, 1991). This generalized Procrustes analysis took into account object symmetry; therefore two separate matrices were generated, representing the symmetric, and asymmetric components of shape variation respectively, (Klingenberg, Barluenga, & Meyer, 2002). The symmetric component represents shape variation among individuals in what could be regarded as a left-right average, while the asymmetric component represents the differences between the original, and mirrored configurations (Klingenberg et al., 2002). For the following analyses, only the symmetric component was analyzed. A PCA of the symmetric component was carried out to visualize the main axes of variation in mandibular shape to examine if there was a morphocline trend (i.e., if specimens were located along PC1 following the Callicebus–Pithecia–Chiropotes-Cacajao order). In addition, a regression of the symmetric component of shape on centroid size was performed to estimate size-adjusted shape coordinates to subsequently use these variables to perform another PCA taking into account allometry. This PCA using the size-adjusted shape

coordinates was carried out to assess the existence or not of the morphocline trend once the allometric effects were removed.

3 | RESULTS

3.1 | Finite element analysis

The visual representation of the von Mises stress distributions for each mandible is a useful proxy for qualitative comparisons regarding their biomechanical behavior because these stress patterns can be interpreted as a sign of relative strength independent of orientation (e.g., specimens exhibiting higher stress would be weaker) (Figure 4). All the models in Figure 4 showed higher stresses in the ramus than in the corpus of the mandible. In general when comparing the different models, Callicebus showed a greater area of higher stress, whereas Chiropotes showed the lowest stress levels, with the corpus being the area exhibiting more noticeable higher stresses. However, most of analyzed pitheciines exhibited similar stress patterns.

Figure 5 shows the stress distribution of the QIM in boxplots. These boxplots show that the stress values in the mandible of Callicebus 1 exhibit a wider range, including higher stresses than the other models. Callicebus 2 show values similar to Pithecia 1, but they were still comparatively higher with respect to the other analyzed pitheciines. The boxplots also show that Chiropotes and Cacajao have a more restricted range of stress values. When averaging the obtained results by genus the following pattern arises from lowest to higher stresses (for both MWAM and MWM): Chiropotes-Cacajao-Pithecia-Callicebus. In terms of biting force, the average value by genus shows the following trend from highest to lowest values in both biting scenarios: Callicebus-Pithecia-Chiropotes/Cacajao (these last two genera showed extremely similar values). The MA values (i.e., bite force/muscle force) were relatively similar for all the analyzed genera ranging from lowest to highest in the following way: Incisive bite Pithecia-Callicebus/Cacajao-Chiropotes; Canine bite: Pithecia/Callicebus-Cacajao-Chiropotes. The MWAM, MWM, the stress quartile values of the boxplots, the estimated bite forces, and the MA can be found in Table 3, as well as their averages values computed by genus. All the values were calculated for the two loading cases. The percentage error of the arithmetic mean (PEofAM) and the percentage error of the median (PEofM) used to ensure QIM are also provided in the same table.

3.2 | Geometric morphometrics

The PCA of the symmetric component shows the morphological differences between the analyzed genera (Figure 6a). The first two PCs accounted for 76.7% of the total shape variation, thus providing a reasonable approximation of the total amount of shape variation. PC1 seems to represent the robusticty morphocline described for this platyrrhine family (i.e., Callicebus–Pithecia–Chiropotes–Cacajao). The warped model on the left of the plot is characterized by less pronounced coronoid processes and a more "robust" ramus, while on the right of the graph the warped lower jaw exhibited a more "gracile" mandibular body and higher coronoid processes. In other
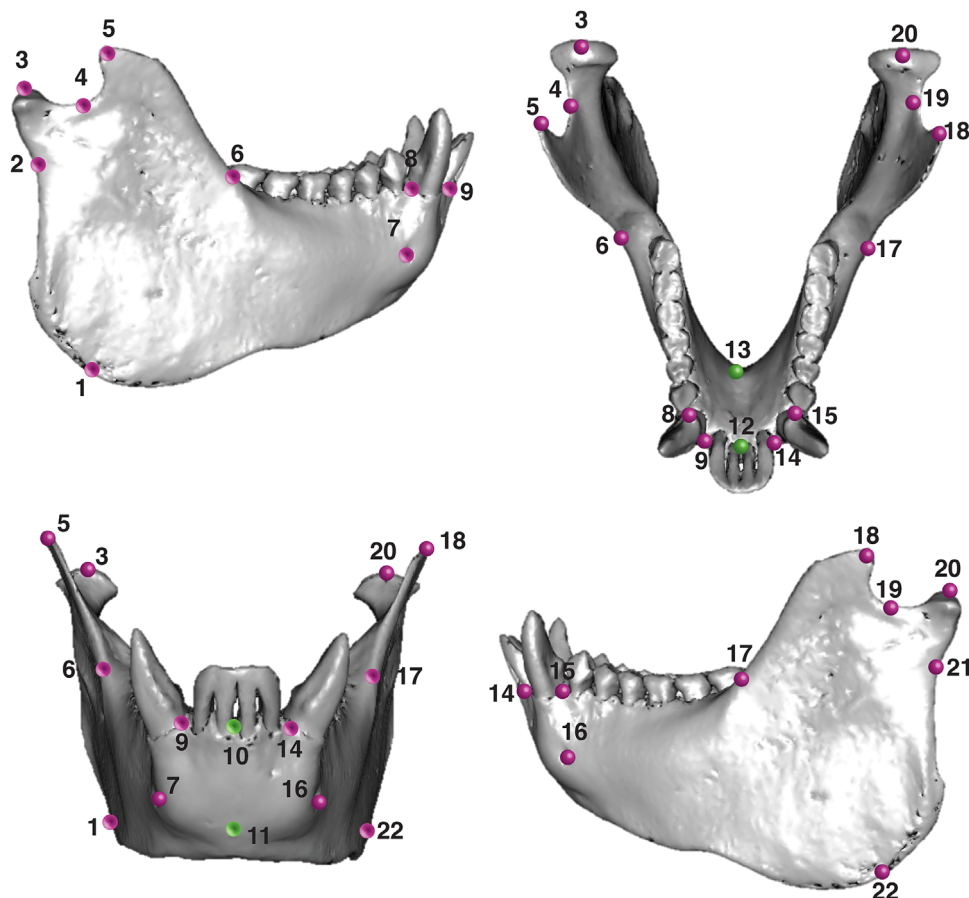
FIGURE 3 3D landmarks used to perform GM analyses. Green spheres represent the median landmarks, while the purple ones correspond to bilateral coordinates
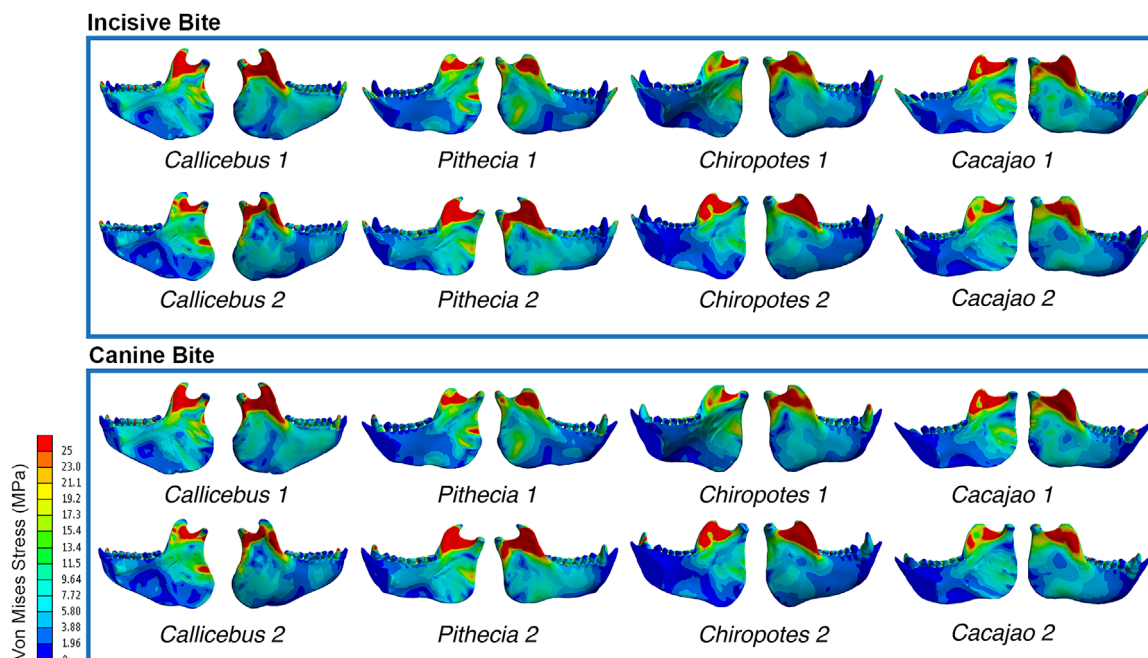

FIGURE 4 von Mises stress distribution for the analyzed genera under the boundary conditions defined for the two analyzed biting scenarios
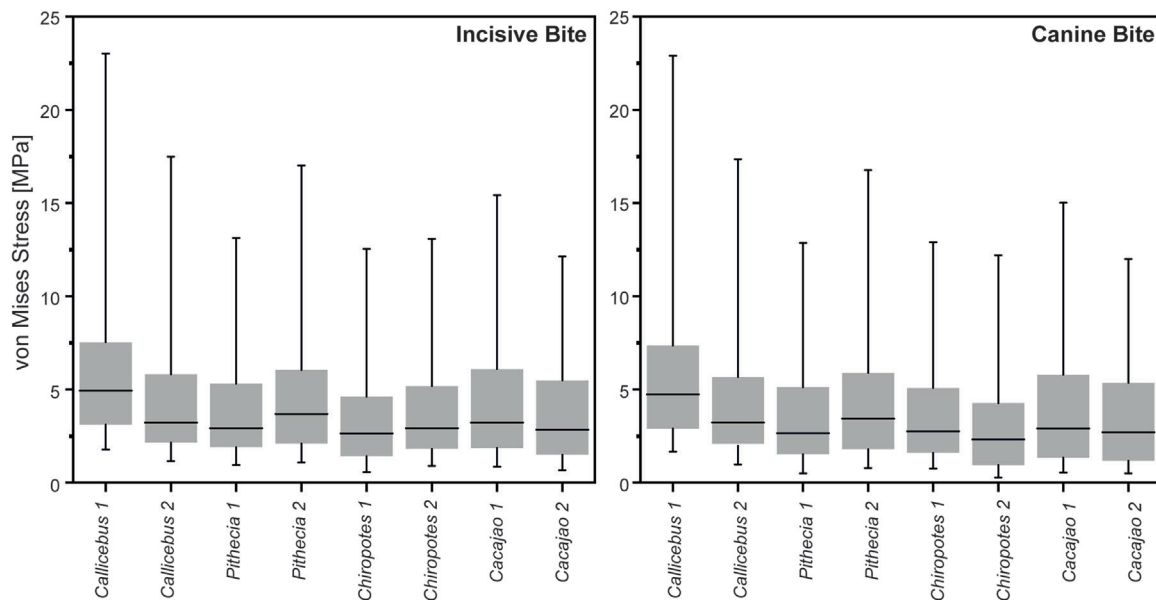
FIGURE 5 Box-plots of the von Mises stress values for the analyzed genera for the two loading scenarios

words, the positive side of the axis describes more "gracile" mandibles showing elongated mandibular corpus along with a narrower gonial angle, while the negative side shows more "robust" mandibles exhibiting a shorten mandibular ramus and less projecting coronoid process. On the other hand, PC2 distinguishes *Pithecia* from the rest of the sample. The warped model on the top of the plot shows a slightly antero-posteriorly thinner mandibular ramus when compared to the model at the bottom of the graph, which is more "robust" with a shorter and broader ramus. The regression of the symmetric shape component on centroid size showed a moderate relationship ($R^2 = 0.55$, $F = 7.28$, $Z = 3$, $p = 0.0009$; 9,999 permutations). The residuals from this regression were used to perform a size-corrected PCA. This PCA (Figure 6b) shows a different pattern, where PC1 distinguishes between *Pithecia* and the rest of the analyzed sample, while PC2 mostly differentiates between *Chiropotes*, and the other pitheciid genera. By correcting for the allometric effects, *Cacajao*, and *Callicebus* occupy the relatively same location of the morphospace defined by first two PCs. Warped models were also plotted in the size-corrected PCA to visualize shape changes.

4 | DISCUSSION

The sclerocarpic biomechanics of the pitheciid mandible were analyzed using FEA, while mandibular shape was assessed using GM. These analyses were carried out in order to get insight about some of the mandibular adaptations of this primate clade to their particular diet specialization. We first tested the hypothesis (H1) that *Callicebus–Pithecia–Chiropotes–Cacajao* correspond to a morphocline of increasing sclerocarpic specialization with respect mandibular strength. We expected that the stress results observed in the mandible should show a gradient from weaker to stronger mandibles following the seed predation specialization observed in this group. In addition, a

complementary hypothesis (H2) was also assessed to test if the mandibular shape variation of this group followed a trend consistent with the morphocline hypothesis. It was expected that the analyzed genera would be located in PC1 (i.e., main aspect of mandibular shape variation) following the proposed morphocline trend.

Regarding H1, we did not find a strong biomechanical support for the morphocline hypothesis. The obtained results do not demonstrate the expected trend in mandibular strength for the analyzed species. All the pitheciin genera (i.e., *Chiropotes*, *Cacajao*, and *Pithecia*) showed similar stress values, and in both biting scenarios *Chiropotes* displayed lower values than *Cacajao*. Nevertheless, *Callicebus* showed higher stress values when compared to the pitheciine genera, thus supporting the argument that among the analyzed taxa, this species represents the less robust member of this seed-eating clade (Anapol & Lee, 1994; Kinzey, 1992). A relatively similar result was obtained in a recent study that analyzed the same genera but focused on craniofacial biomechanics (Ledogar et al., 2018). Our averaged results in Table 3 showed a *Chiropotes-Cacajao-Pithecia-Callicebus* mandibular stress trend from lowest to higher values, thus differing from the expected morphocline (i.e. *Cacajao-Chiropotes-Pithecia-Callicebus*). However, it is important to notice that most analyzed pitheciine specimens showed similar values, without exhibiting striking differences (Figure 5).

Although this result could be regarded as intriguing, previous studies have found similar results applying other techniques. For instance, when analyzing robusticity using shape ratios of mandibular condyle, corpus, and symphysis by using a PCA, Norconk et al. (2009) found that *Chiropotes* followed by *Cacajao* and then *Cebus* have the largest scores along PC1, thus suggesting these taxa have relatively robust mandibles probably due to their consumption of mechanically challenging seeds (e.g., Anapol & Lee, 1994; Bouvier, 1986; Kinzey, 1992). Additionally, they also devised a biomechanical robusticity index for platyrrhines by combining several measures of the masticatory apparatus (Norconk et al., 2009). They averaged z-scores

TABLE 3 Finite element analysis results

Specimens	Elements	MWAM	MWM	M (25%)	M (50%)	M (75%)	M (95%)	Bite Force (N)	MA	PEofAM	PEofM
CASE 1: Incisive bite											
Callicebus 1	423408	7.3543	4.7463	3.1165	4.9367	7.5291	23.032	43.7	0.42	0.8217	4.012
Callicebus 2	857956	5.2101	3.1468	2.0371	3.2181	5.6862	17.367	30.65	0.47	0.5021	2.2647
Averaged *Callicebus*		**6.2822**	**3.9466**	**2.5768**	**4.0774**	**6.6077**	**20.1995**	**37.18**	**0.45**		
Pithecia 1	424913	4.4244	2.8784	1.8974	2.9216	5.3096	13.1379	47.44	0.42	0.7901	1.5005
Pithecia 2	326561	5.8678	3.6154	2.2269	3.6833	6.1622	17.1405	39.99	0.42	1.781	1.8783
Averaged *Pithecia*		**5.1461**	**3.2469**	**2.06215**	**3.30245**	**5.7359**	**15.1392**	**43.72**	**0.42**		
Chiropotes 1	201335	4.2943	2.8548	1.8191	2.9127	5.1822	13.067	76.88	0.45	0.4136	2.028
Chiropotes 2	506157	4.231	2.581	1.4278	2.6401	4.6077	12.5307	99.7	0.54	0.8258	2.2891
Averaged *Chiropotes*		**4.2627**	**2.71791**	**1.62345**	**2.7764**	**4.89495**	**12.79885**	**88.29**	**0.5**		
Cacajao 1	744420	5.2553	3.1718	1.8551	3.2143	6.0965	15.429	76.79	0.46	0.7689	1.3399
Cacajao 2	414016	4.1775	2.7807	1.4877	2.8424	5.4829	12.123	99.27	0.41	0.6106	2.2193
Averaged *Cacajao*		4.7164	2.97624	1.6714	3.02835	5.7897	13.776	88.03	0.44		
CASE 2: CANINE BITE											
Callicebus 1	423375	7.1881	4.557	2.9043	4.7315	7.3541	22.9088	46.12	0.44	0.8296	3.8302
Callicebus 2	857956	5.1035	3.0321	1.9675	3.098	5.5391	17.24	32.46	0.5	0.4991	2.1734
Averaged *Callicebus*		**6.1458**	**3.7945**	**2.4359**	**3.9148**	**6.4466**	**20.0744**	**39.29**	**0.47**		
Pithecia 1	424989	4.1249	2.6054	1.5303	2.654	5.1185	12.8501	52.09	0.46	0.839	1.8658
Pithecia 2	326715	5.6454	3.4634	1.9094	3.5609	6.0068	16.8858	44.64	0.47	1.8596	2.8152
Averaged *Pithecia*		**4.88515**	**3.03439**	**1.71985**	**3.10745**	**5.56265**	**14.86795**	**48.37**	**0.47**		
Chiropotes 1	201308	4.1359	2.6817	1.6021	2.7542	5.0715	12.8931	81.6	0.48	0.3881	2.7032
Chiropotes 2	506116	3.8775	2.2758	0.9371	2.3179	4.2627	12.203	114.17	0.62	0.8785	1.8499
Averaged *Chiropotes*		**4.0067**	**2.47875**	**1.2696**	**2.53605**	**4.6671**	**12.54805**	**97.89**	**0.55**		
Cacajao 1	744399	4.8772	2.8415	1.3321	2.8954	5.7935	15.011	90.73	0.55	0.7738	1.897
Cacajao 2	336121	3.9948	2.6305	1.1794	2.6936	5.3559	11.998	106.15	0.44	0.6034	2.4007
Averaged *Cacajao*		**4.436**	**2.73597**	**1.25575**	**2.7945**	**5.5747**	**13.5045**	**98.44**	**0.5**		

Key, MWAM; mesh-weighted average mean, MWM; mesh-weighted median, M(25%); 25% percentile, M(50%); 50% percentile, M(75%); 75% percentile, M(95%); 95% percentile, PEofAM; percentage error of the arithmetic mean, PEofM; percentage error of the median.
Values in bold correspond to FEA metrics averaged by species.

for 10 relative measures of the masticatory apparatus associated with load bearing, dental function and bite force production and found again that *Chiropotes* followed by *Cacajao* and then by *Cebus* exhibit the largest average scores for this masticatory apparatus index. These previous results already indicated that the morphocline hypothesis as proposed by Kinzey (1992), was not as clear as initially suggested. We obtained the same trend when averaging stress values by genus, where *Chiropotes* exhibited the strongest mandible followed by *Cacajao* and then by *Pithecia* and *Callicebus*. However, it is important to notice that the results from our work showed that in the mandible and at least for the analyzed biomechanical scenarios there are not major differences between all the analyzed pitheciin species, so, apparently all these mandibular phenotypes seem adjusted for sclerocarpy. Nonetheless, we did find that pitheciines experienced lower stress values than *Callicebus*, and that this latter genus showed the highest stress values of the entire sample.
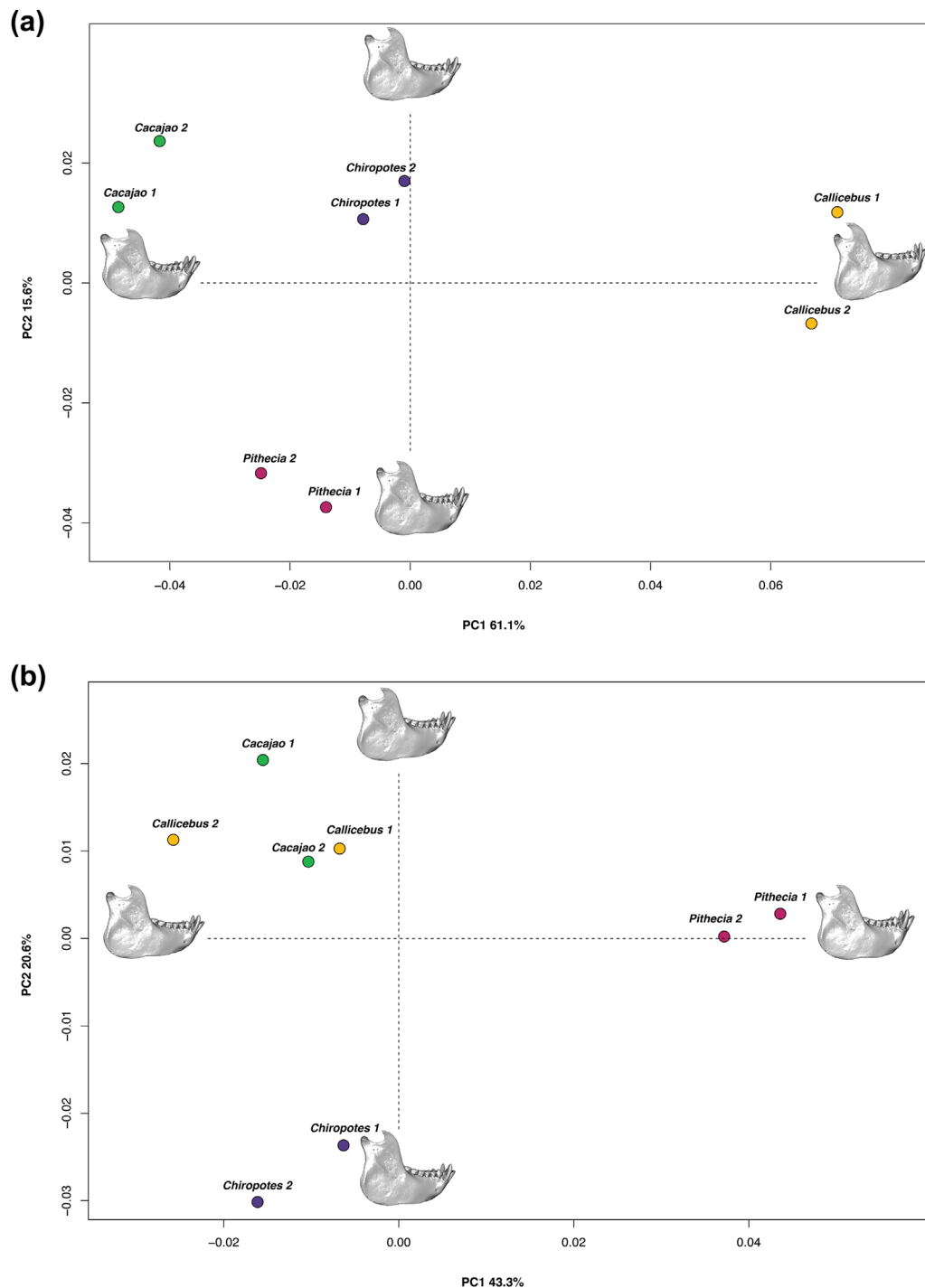
FIGURE 6 PCAs of (a) pitheciid mandibular variation and (b) when correcting for allometric effects. The mandible models were used to depict the morphological variation along the first two PC axes in both morphospaces. The model closest to the mean shape was warped to match the multivariate mean using the thin-plate spline method (Bookstein, 1991). Then the obtained average model was warped to represent the variation along the two plotted PC axes in both analyses

Regarding MA, we found the following patterns from lower to higher: Incisive bite *Pithecia-Callicebus/Cacajao-Chiropotes*; Canine bite: *Pithecia/Callicebus-Cacajao-Chiropotes*. The higher values for *Chiropotes* and *Cacajao* are consistent with other studies that also showed that these two genera have greater MA (Ledogar et al., 2018; Norconk et al., 2009). When analyzing craniofacial biomechanics Ledogar et al. (2018) found that the mechanical efficiency of

canine biting increased from *Callicebus* to *Pithecia* to *Chiropotes*, although *Cacajao* displayed the same efficiency as *Chiropotes*. They also analyzed second molar biting were they found a higher MA in *Chiropotes* as compared to *Cacajao* (Ledogar et al., 2018), which seems consistent with our mandibular results. When comparing the MA of the platyrrhine masticatory apparatus, Norconk et al. (2009) found that among the non-callitrichines, the durophagus *Cebus*

possesses the highest leverage for biting at the canines, and incisors followed by *Chiropotes* and then by *Cacajao*, which is also coherent with the results obtained in the present study. These consistent results support previous observations that predominant seed feeders seem to exhibit relatively greater mechanical advantage, especially during anterior tooth use (Anapol & Lee, 1994; Wright, 2005). However, the low MA value obtained for *Pithecia* in the present study is intriguing. One possible explanation for the observed disagreement might be related to the different MA estimation techniques applied in each study. Norconk et al. (2009) estimated MA as the ratio of the perpendicular distance from the line of action of the jaw-closing muscle to the temporomandibular joint divided by the distance from the joint to the incisal bite point, whereas we computed MA as the ratio of bite force to total input muscle force. In this sense, Norconk et al. (2009) used a simpler approach assuming one vertical vector for all the jaw closing muscles, while our estimation differs because it considered three separate muscles, and their respective vector orientations. However, it is not impossible to discard the possibility that the reduced sample size used in our work could have influenced the obtained results. Future studies addressing MA should consider more individuals to better assess this issue.

We also found that pitheciines generate higher bite forces than *Callicebus*. All three pitheciine taxa exhibited higher bite forces than the titi monkeys. However, *Chiropotes* displayed similar estimated bite forces as *Cacajao*, thus contradicting again the morphocline hypothesis. It is important to keep in mind that bite forces are associated with size (i.e. bite forces increased with increasing model size); therefore, caution is required when interpreting this result because *Cacajao* corresponds to the larger analyzed genus. This result could imply that larger species (e.g., *Cacajao*) could access hardest-husked fruits simply because they are larger, and not necessarily because they show a greater sclerocarpy specialization. In fact PCSA values reported for *Cacajao* seem to be really similar to those described for *Chiropotes*, perhaps explaining the similar obtained bite forces in these two genera in spite of the size differences (Anapol et al., 2008; Taylor, Yuan, Ross, & Vinyard, 2015).

It is also important to consider that *Cacajao* might not be such a hard-fruit feeder after all (Barnett, Boyle, & Thompson, 2016). A recent study has shown that *Cacajao ouakary* is not randomly biting on the surface of fruits, but that on the contrary they focused on those areas needing less force to penetrate in order to gain access to the seeds (Barnett et al., 2016). This behavior was interpreted as being an energy saving mechanism, and/or be performed to reduce the risk of damaging the teeth used in food acquisition (Barnett et al., 2016). This probably also implies that related species might show a similar behavior and that consequently pitheciine should not be simply regarded as nut-cracking primates exclusively applying brute force to break fruit's pericarps (Barnett et al., 2016). Nonetheless, it is relevant to also notice that even though they are selecting the weakest areas of the pericarp, getting access to the seeds still requires substantial force and that this behavior could be repeated several hundred times per day (Ayres, 1989).

Regarding H2, we found that there is a gradient of relative morphological "robusticity" represented by PC1, which accounts for 61.6% of the variance in the sample. As expected more gracile shapes (i.e., *Callicebus*) are located opposite to more robust morphologies (i.e., *Cacajao*). On the other hand, PC2 distinguishes *Pithecia*, which seem to be characterized by vertically elongated, and slightly slender condyles and a robust mandibular body, from the rest of the analyzed pitheciids. Although, the observed pattern for PC1 in the first analysis (Figure 6a) could be indicative a of support for H2 (i.e. we found the expected pattern), we obtained an interesting result once the allometric effect was corrected by using size-adjusted shape coordinates that cast some doubts on this preliminary conclusion. The second PCA (Figure 6b) located *Cacajao* and *Callicebus* occupying a similar position of the morphospace (i.e., upper left). This could mean that many of the observed morphological differences between these two genera that separate them in the first PCA might be accounted by merely size differences. This evidence further complements our biomechanical results that seem to indicate that *Cacajao* is not the epitome of sclerocarpic specialization. In addition, it is important to keep in mind that a more "robust" mandible might not be necessarily indicative of increased sclerocarpy, but that it could be related to other factors such as forceful mastication, allometric effects, or other factors.

The platyrrhine masticatory apparatus experiences significant internal loads in the mandibular condyles, corpora and symphyses during biting and mastication (Hylander, 1979a, 1979b; Hylander 1984, 1985; Hylander et al., 1987). One possible solution to bear these loadings is to either increase in size as observed in the pitheciid lineage and/or change in shape in a certain direction that could improve load bearing ability, which could explain why *Chiropotes* is on average stronger in the two tested biting scenarios than the other analyzed genera. However, as stated before the differences between the different pitheciine genera are not that prominent, so future studies assessing the morphocline hypothesis would benefit greatly from larger sample sizes. Most comparative FEA studies include a single specimen per species (Dumont, Davis, Grosse, & Burrows, 2011; Marcé-Nogué et al., 2017; Wroe et al., 2010) due to the time-consuming process associated with model construction and simulation. Nonetheless, we are optimistic that the increasing availability in 3D models and access to FEA software would probably allow the generation of numerous models in a reasonably inexpensive way in the following years, which would certainly help in comparative studies (Cunningham, Rahman, Lautenschlager, Rayfield, & Donoghue, 2014; Davies et al., 2017).

The ecological implications of the obtained results are the subject of some speculation. The geographic ranges of *Chiropotes* and *Cacajao* are completely allopatric, excepting a possible zone of sympatry in the northern Amazon basin (Boubli, 2002). This geographic distribution might explain the broad ecomorphological similarities between these two genera, which could perhaps imply that they are too competitive to coexist in the same habitat (Ayres & Prance, 2013). As previously discussed, both uakaris and bearded sakis are highly specialized morphologically for the consumption of immature seeds (Kinzey, 1992; Rosenberger, 1992). These similarities are even more striking when

considering that some studies have shown that seed consumption in bearded sakis can reach levels similar or higher than uakaris in some observation sites. *Cacajao's* seed consumption is about 66.9% (Norconk et al., 2009), while *Chiropotes satanas* has reported percentages of 63% (Port-Carvalho & Ferrari, 2004) or even a striking 91% (Kinzey, 1992; Kinzey & Norconk, 1990), while other species such as *Chiropotes sagulatus* have reported values of 86% (Kinzey & Norconk, 1990). Since *Cacajao* is not broadly sympatric with either *Pithecia* or *Chiropotes*, they might not be restricted to eating the hardest-husked fruits, due to relaxed feeding competition with the other pitheciine species (Ledogar et al., 2018). It is possible that this relaxed feeding competition allows *Cacajao* to choose from fruits at diverse ripeness levels, which in turn might have led to reduction in the selection for morphological features associated with sclerocarpy. This could also explain why *Chiropotes* showed the lowest stress values on average among all the analyzed pitheciids. Ledogar et al. (2018) also found that feeding craniofacial biomechanics in sympatric *Chiropotes* and *Pithecia* are coherent with dietary niche separation, with the former being better suited for penetrating hard fruits and the latter better adjusted for crushing hard seeds with their molars. Our results are consistent with this showing that *Chiropotes* exhibits high bite forces and MA, as well as lower stress values.

Summarizing, we did not found biomechanical support for H1 (i.e., the morphocline hypothesis), at least when analyzing the biomechanical metrics measured here. All pitheciine species showed a similar stress pattern that on average could be described from lower to higher values as following a *Chiropotes-Cacajao-Pithecia-Callicebus* trend rather than the proposed morphocline hypothesis. MA and bite force followed a similar tendency, where on average *Chiropotes* showed higher values (although *Cacajao* displayed almost identical bite forces). Regarding H2 (i.e., the expectation that the main aspects of mandibular shape variation would follow a trend consistent with the morphocline hypothesis), we found the expected pattern, but only when we did not account for allometric effects. Consequently, the observed robusticity trend could be related to other factors rather than sclerocarpic specialization, such as for instance size. The present results are expected to contribute in our understanding of feeding biomechanics in pitheciids, as well as in the application of virtual biomechanical techniques to study ecomorphological questions in living primates.

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ORCID

Thomas A. Püschel iD http://orcid.org/0000-0002-2231-2297
Jordi Marcé-Nogué iD http://orcid.org/0000-0001-9852-7027
Thomas M. Kaiser iD http://orcid.org/0000-0002-8154-1751

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