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Shape and Sexual Dimorphism of Canines in New World Monkeys

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Abstract

The outline of the upper and lower canines and their sexual dimorphism were compared for many extant New World monkeys. The shape of the upper canines in male New World monkeys consisted of two main shape types. The first was dagger-shaped. The second type was hook-shaped, which was primarily found in leaf-eating monkeys, such as *Alouatta* and *Brachyteles*. The dagger-shaped comprised three subtypes. One was common and ideal for eating ripe fruit, such as *Ateles*. Another was the chisel-shaped canines of *Pithecia*, or the trigonal pyramid-shaped canines of *Chiropotes*, perfect for crushing hard seeds. The third had rounded, slanted tips suited to extracting gum like *Callicebus* and *Callithrix*. Similar sexual dimorphism in terms of size and shape was observed in canine teeth of both polygamous and monogamous species. However, this relationship was not observed in the following six species: *Plecturocebus moloch*, *Callithrix jacchus*, *Sapajus apella*, *Saimiri sciureus*, *Saimiri boliviensis* and *Ateles geoffroyi*. The outline of the lower canines in males varied from a distorted triangle to a distorted hexagon, depending on the position of the mesial tubercle and the degree of development of the heel-shaped protrusions. The differences in canine shape were minor. The female canine teeth and deciduous canine teeth were also discussed.

Keywords: Canine outline, Shape dimorphism, Social structure, Food nature, New World monkeys

Introduction

The morphology of teeth is strongly influenced by genetics and closely reflects phylogenetic ancestry. In particular, the role of canines in primate evolution is clear, in regards to both phylogeny and sexual dimorphism [1]. In general, male canines have been significantly larger than female canines and have played an important part in sex determination in paleontology, and there have been numerous reports on canine size [2-9]. However, few studies have examined canine shape or outline [10-12]. This is probably because canine teeth are conical and little characteristics that can be used to describe their morphology. It is also difficult to express changes in their outline and it has been believed that there is little variation in shape.

Nevertheless, a detailed examination of canine morphology revealed subtle differences that cannot be distinguished by conventional quantitative analyses such as mesiodistal and buccolingual crown diameters [1, 11-13]. For example, there were reports of several primates whose canines have changed in response to their lifestyle [3, 14-16]. The saki in the Pitheciidae has a chisel-shaped tooth, the gibbon in the Hominoidea has a sabre-shaped tooth, and the great apes in the Hominidae have a wide-based, tall, triangular tooth [3, 14-19]. The shape of the canines of primates is thought to be closely related to their evolutionary history [3]. However, it is not easy to describe the outline or degree of their differentiation. One possible method of analysing sexual dimorphism in canine shape is to classify degrees of similarity into four categories: none, slight, moderate or strong. However, this method is subjective and lacks objectivity.

The aim of this study is to confirm the shape of canines using real examples, to investigate the factors that influence their shape, and to clarify their relationship with diet, social structure, lineage, and canine shape and sex dimorphism.

Materials and Methods

The materials used in this study consisted of five families: Pitheciidae, Atelidae, Cebidae, Callitrichidae, and Aotidae. The skull specimens were housed in the collections of the Japan Monkey

Centre (JMC), Department of Natural Anthropology, Faculty of Science, Kyoto University, and Center for the Evolutionary Origins of Human Behavior, Kyoto University (EHUB). The canines were photographed from the lingual aspect with the camera set so that its optical axis was perpendicular to the canine coronal axis. After taking impressions with silicone dental impression material (Provil: Heraeus Kulzer GmbH), plaster models were made and photographed using the same method.

The mesiodistal crown diameter (MD) of the upper canine teeth is a measurement of the distance between the most mesial and the most distal points on a line drawn parallel to the crown axis. The labiolingual tooth diameter (LL) is the greatest measurement between labial and lingual aspects of the tooth crown on a line perpendicular to mesiodistal diameter. In lower canines, the maximum distance along the long axis in the crown cross-section was defined as the mesiodistal diameter or crown length, and the maximum distance along the short axis at a line perpendicular to mesiodistal diameter as the labiolingual diameter or crown width. The size of the canines was expressed as the canine area which was calculated (MD×LL). The size dimorphism was exhibited using the average value in males divided by the average value in females. These values were then divided into four categories: 1. None: 1.00–1.09; 2. Small: 1.10–1.19; 3. Moderate: 1.20–1.29; and 4. Large: 1.30 or higher. The average values for the canines of New World monkeys (MD and LL) were taken from the data sources [1, 13, 20-21]. The area values were classified as follows: The size is categorised as follows: less than 10.0 mm^2 is small, between 10.0 and 20.0 mm^2 is medium, and greater than 20.0 mm^2 is large. The dimorphism of the outline was determined in detail by observing photographs of individuals of both sexes. The categories were as follows: none, slight, moderate, and strong.

The lingual outline of the upper canine consists of five components: the mesial and distal crests, the mesial and distal marginal ridges, and the cervical ridge [22]. The shape of the crown was estimated based on these components. Previous studies have examined the outline of the crown from the occlusal surface using the crown index, a simple ratio of MD to LL [1, 6-7, 10, 23]. However, this ratio value only indicates whether the crown outline is longer vertically or horizontally; it does not reflect actual shape.

When it comes to shape analysis, measuring objects in three dimensions is one way to examine them in detail. But this method takes a long time when investigating a large number of individuals. The current approach to shape analysis allows for detailed descriptions based on observation. Unfortunately, however, this approach is subjective and lacks objectivity. To avoid this problem, the shape of the teeth was described as accurately as possible using specific examples. Concrete expressions such as “chisel-like shape”, “dagger-like shape”, “hook shape”, “half spindle shape” and “spatula shape” were used.

The primate classification was based on the JMC and the EHUB [24], as well as Fleagle (2013) [25]. Sex identification was determined using records from the research institution. The social structure of New World monkeys was based on the previous research [25-27].

Results

Upper canines

Pitheciidae

Pithecia

The upper canine teeth of the male *Pithecia monachus* (Figure 1-A) had well-developed labial, mesial, and lingual ridges, giving them an overall chisel-like shape. The distal crest was as sharp and pointed as a knife blade. From a lingual view, the mesial groove was interrupted by the marginal ridge, and the cervical ridge was moderately swollen. The mesial tubercle, also known as the style or shoulder, was slightly projected, and the distal tubercle was slightly developed. The canines were large in size. The female (Figure 2-A) was very similar in shape to the male. However, the cervical ridge was more well-developed than in the male. The cross-section was orbicular. Shape dimorphism in canines was slight.

Chiropotes

As a whole, the canines of the male *Chiropotes satanas* had a trigonal pyramid-shaped canines. The crown was curved only a little distally. The distal crest was as sharp and pointed as a knife blade (Figure 1-B). The distal crest was concave. The cervical ridge was moderately developed and surrounded the cervical region. The cross-section was elliptical. The canines were large in size. The female canines (Figure 2-B) were almost identical to those of the males. There was no shape dimorphism.

Callitrichidae

Plecturoccebus

The male *Plecturocebus moloch* (Figure 1-C) had dagger-shaped canines with rounded tips that sloped distally, as well as a loosely concave distal crest. The mesial and distal tubercles both projected slightly outward. The distal tubercle was located further apically. The basal cross-section was elliptical in the mesiodistal direction. It was small size for a canine. The female (Figure 2-C) had dagger-shaped teeth and a slender appearance. The mesial tubercle projected strongly outward. The cervical ridge was well developed and swollen. The cross-section was almost circular. There was slight shape dimorphism.

Cheracebus

The canines of the male *Cheracebus torquatus* (Figure 1-D) were dagger-shaped, with a concave distal crest. The mesial groove was interrupted by the mesial marginal ridge. The width of the cervical ridge was about one-third of the crown height. The distal tubercles were mildly elevated. The cross-section was elliptical in a labiolingual direction. The canines were small in size.

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Callithrix

The outline of the male *Callithrix jacchus* (Figure 1-E) was dagger-shaped. The tips of the canines were curved distally and the distal crests were moderately concave. The deep mesial groove was interrupted by the marginal ridge. The lingual ridge was well-developed. The distostyle was nodular and piercing, and located more apically than the mesial one. The cross-section was triangular. The canines were small in size. Females (Figure 2-E) had a similar shape to males but were rounder overall. The distostyle was slightly smaller than in the male. The cervical ridge was more prominent. The cross-section was triangular. Moderate sexual dimorphism was present in shape.

Callimico

The *Callimico goeldii* (Figure 1-F) had a dagger-shaped tooth with a crown that sloped distally. The mesial and distal crests were straight. The mesial and distal tubercles were moderately nodular. The distal tubercle was positioned closer to the apex than the mesial one. The size of the canines was small. The female (Figure 2-F) was fairly similar in shape to the male. Sexual dimorphism in shape was rarely observed.

Saguinus

The outline of the male *Saguinus labiatus* was a broad and dagger-shaped (Figure 1-G). The mesial crest was loosely convex, while the distal was straight. The lingual ridge was well-developed. The distal tubercle was nodular and projected moderately, being located more apically than the mesial. It was small in canine size. Females had a similar shape to males but were rounder overall (Figure 2-G). There was no sexual dimorphism in the outline.

Leontocebus

The canines of both sexes of the *Leontocebus fuscicollis* (Figures 1,2-H) were found to be very similar in size and shape to those of *Saguinus labiatus*. The female had a slender shape and a more prominent distal tubercle than the male. The canine was small in size. There was no sexual dimorphism in the outline.

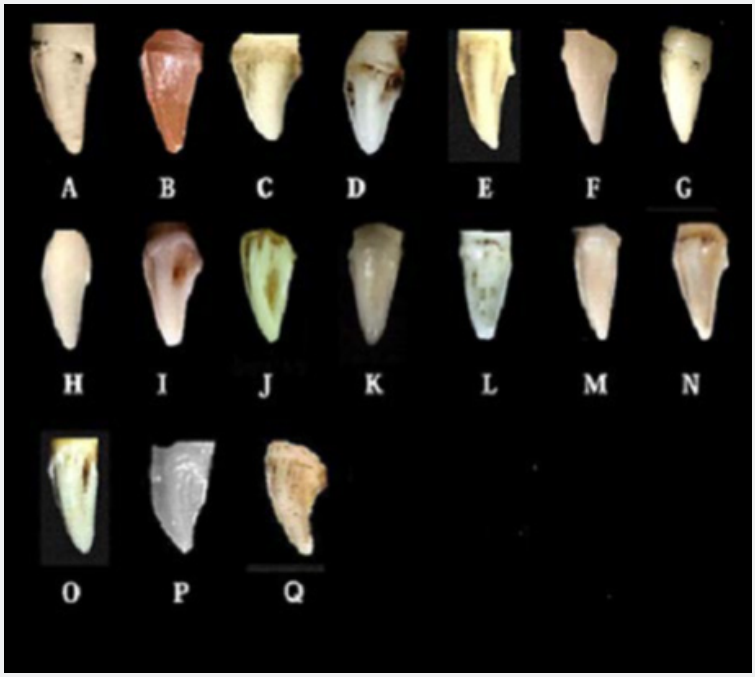

Figure 1: Lingual views of upper male canines in New World monkeys. All drawn to approximately same size.
Uppercase letters: A: *Pithecia monachus*, B: *Chiropotes satanas*, C: *Plecturocebus moloch*, D: *Cheracebus torquatus*, E: *Callithrix jacchus*, F: *Callimico goeldii*, G: *Saguinus labiatus*, H: *Leontocebus fuscicollis*, I: *Aotus trivirgatus*, J: *Cebus albifrons*, K: *Cebus capucinus*, L: *Sapajus apella*, M: *Saimiri sciureus*, N: *Ateles geoffroyi*, O: *Lagothrix lagothricha*, P: *Brachyteles arachnoides*, Q: *Alouatta seniculus*.

Aotidae

Aotus

The male *Aotus trivirgatus* had a dagger-shaped canines (Figure 1-I). The distal crest was slightly concave. The distal tubercle was moderately swollen and positioned further apically than mesial. The deep mesial groove was interrupted by the marginal ridge. The cervical ridge was quite swollen. It was small in canine size. The females were also very similar in shape to the males (Figure 2-I). The cervical ridge was more developed than in males. There was no sexual dimorphism in shape.

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Figure 2: Lingual views of upper female canines in New World monkeys. All drawn to approximately same size. N.d.: No data. Capital letters are the same as in Figure 1.
Uppercase letters: A: *Pithecia monachus*, B: *Chiropotes satanas*, C: *Plecturocebus moloch*, D: *Cheracebus torquatus*, E:*Callithrix jacchus*, F: *Callimico goeldii*, G: *Saguinus labiatus*, H: *Leontocebus fuscicollis*, I: *Aotus trivirgatus*, J: *Cebus albifrons*, K: *Cebus capucinus*, L: *Sapajus apella*, M: *Saimiri sciureus*, N: *Ateles geoffroyi*, O: *Lagothrix lagothricha*, P: *Brachyteles arachnoides*, Q: *Alouatta seniculus*

Cebidae

Cebus

The male *Cebus albifrons* had a dagger-shaped tooth (Figure 1-J). The distal tubercle was slightly developed. Both the mesial and distal crests were slightly convex. The deep mesial groove was interrupted by the mesial marginal ridge. The cervical ridge showed little bulging and was thin. The canine tooth was large. The female (Figure 2-J) was shaped like a distorted rhombus or pentagon. It had a deep mesial groove. The distal tubercle was moderately developed and located more apically. The cervical ridge was more pronounced, with moderate sexual dimorphism observed in the outline.

Sapajus

The outline of the canines of the male *Sapajus apella* was dagger-shaped (Figure 1-L). The mesial and distal crests were slightly convex. The cross-section was triangular. The distal tubercle bulged mildly and was located more apically. The canines were large. The female canines were similar in shape to those of *Cebus albifrons*, and rounded overall (Figure 2-L). Moderate dimorphism in shape was observed.

Saimiri

The male *Saimiri sciureus* had dagger-shaped canines with gently curved crowns. The mesial and distal tubercles were not particularly pronounced. The cervical ridge developed mildly. The canine was of medium size. The deep mesial groove was not interrupted by the marginal ridge. The cross-section was heart-shaped (Figure 1-M). The female was either a distorted pentagon or a distorted rhombus with a slightly concave distal crest (Figure 2-M). The distal tubercle protruded strongly. There was strong sexual dimorphism in shape. The basal cross-section was elliptical in the mesiodistal direction.

Atelidae

Ateles

Ateles geoffroyi (Figure 1-N) had a dagger-shaped outline with a loosely concave distal crest. The distal tubercle was moderately projected and located more apically than the mesial. The cross-section was triangular. The canines were large in size. The female (Figure 2-N) was slightly equilateral triangle in shape. The cervical ridge sloped downwards at an angle. The cross-section was triangular. Overall, the morphology was rounded. The

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distal tubercle projected strongly and a wedge-shaped notch was observed between the distal marginal ridge and the cervical ridge. There was strong sexual dimorphism in shape.

Lagothrix

The male *Lagothrix lagothricha* (Figure 1-O) was tall and sturdy with a dagger-like shape. Its mesial groove was deep and interrupted by the marginal ridge. The lingual ridge was wide and well-developed. The distal tubercle was slightly swollen. The basal cross-section was elliptical in a mesiodistal direction. The canines were large. The female (Figure 2-O) was short and stout, resembling an equilateral triangle. It had a more developed cervical ridge than the male. The basal cross-section was elliptical labiolingually. There was moderate sexual dimorphism.

Brachyteles

The outline of the male *Brachyteles arachnoides* resembled a hook-shaped (Fig. 1-P), with a convex mesial crest and a moderately concave distal crest. Its mesial groove was not interrupted by the marginal ridge. The cervical ridge was well developed. The distal tubercle bulged slightly. The canine tooth was large. The cross-section was triangular. The female (Figure 2-P) had a similar shape to the male, with a particularly well-developed cervical ridge that sloped downwards at an angle. The cross-section was triangular. The distal tubercle was well developed and projected strongly. There was slight sexual dimorphism in outline.

Alouatta

The outline of the male *Alouatta seniculus* (Figure 1-Q) was hook-shaped. It had a markedly convex mesial crest and a distinctly concave distal crest. The distal tubercle was noticeably swollen. The cross-section was heart-shaped. The canines were large. The female (Figure 2-Q) had a distorted hexagonal outline with a strongly concave distal crest. The basal cross-section was elliptical mesiodistally. The canine exhibited strong sexual dimorphism in shape (Figure 3).

Figure 3: Lingual views of upper deciduous canines in New World monkeys. All drawn to approximately same size.
Lowercase letters: a: *Pithecia pithecia*, b: *Sapajus apella*, c: *Saimiri boliviensis*, d: *Lagothrix lagothricha*, e: *Aotus trivirgatus*, f: *Callithrix jacchus*, g: *Alouatta palliata*, h: *Alouatta caraya*

Deciduous canines

The *Pithecia pithecia* was a slightly elongated isosceles triangle. The mesial and distal crests were straight. The cervical ridge was well-developed, surrounding the neck of the tooth. The lingual views of the deciduous canines of other species were all similar to equilateral triangles and had well-developed cervical ridges (Figure 3).

Lower canines

In general, the crown morphology of the lower canines in New World monkeys were conical in the anterior region and had a nodule-like "heel" in the posterior region.

Pitheciidae

Pithecia

The outline of the male *Pithecia monachus* (Figure 4-A) had a trigonal pyramid-shaped canines as a whole. From the lingual aspect, tall isosceles triangle was observed with a swollen structure resembling a heel. The distal crest was as sharp and pointed as a knife blade. Its cross-section was triangular. The cervical ridge was mildly swollen. Females (Figure 5-A) were similar in form to males.

Chiropotes

The male *Chiropotes satanas* had trigonal, pyramid-shaped canines. The distal crest was shaped like a knife blade, being both sharp and pointed (Figure 4B). These were relatively similar to those of Pithecia (Figure 4B). The lingual mesial and distal crests were straight. The mesial groove was interrupted by the marginal ridge. The heel-shaped elevation was poorly developed. The cervical ridge was moderately bulging and the mesial and distal tubercles were located near the cervical region. The female canines (Figure 5B) were similar in shape to those of the males.

Callitrichidae

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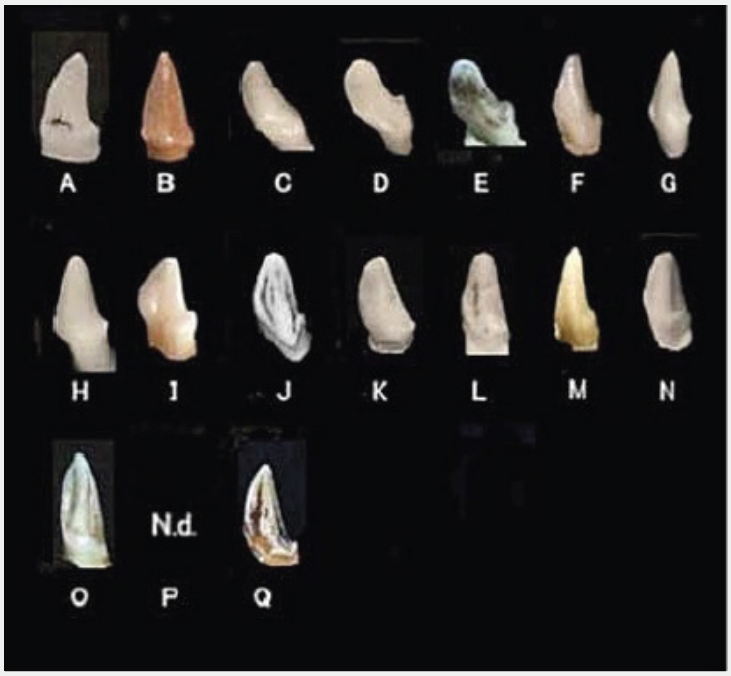

Figure 4: Lingual views of lower male canines in New World monkeys. All drawn to approximately same size. N.d.: No data. Capital letters are the same as in Figure 1.
Uppercase letters: A: *Pithecia monachus*, B: *Chiropotes satanas*, C: *Plecturocebus moloch*, D: *Cheracebus torquatus*, E: *Callithrix jacchus*, F: *Callimico goeldii*, G: *Saguinus labiatus*, H: *Leontocebus fuscicollis*, I: *Aotus trivirgatus*, J: *Cebus albifrons*, K: *Cebus capucinus*, L: *Sapajus apella*, M: *Saimiri sciureus*, N: *Ateles Paniscus*, O: *Lagothrix lagothricha*, P: *Brachyteles arachnoides*, Q: *Alouatta seniculus*

Plecturocebus

The presence of distorted, pentagonal, spatula-shaped lower canines was observed on the male *Plecturocebus moloch* (Figure 4-C). The mesial crest was slightly convex and the distal crest concave. The crown inclined forwards. There were poorly developed, heel-shaped protrusions on the distal base. The cross-section was elliptical. The outline of the female canine was almost identical to that of the male (Figure 5-C). The cross-section was elliptical along the long tooth axis. However, the cervical ridge was more pronounced in the female tooth.

Cheracebus

The outline of the male *Cheracebus torquatus* canines was a distorted hexagon, with a convex mesial crest and a straight distal crest (Figure 4-D). They appeared comparatively similar to those of *Plecturocebus*. The heel-shaped swelling was moderate.

Callithrix

The outline of the male *Callithrix jacchus* had a distorted, hexagonal shape (Figure 4-E). A strongly developed, heel-shaped protrusion was observed at the distal base. The mesial tubercle was located approximately half the height of the tooth crown from the cervical line. The cross-section was elliptical along the long tooth axis. The outline of the female (Figure 5-E) was similar to that of the male.

Callimico

The shape of *Callimico goeldii* was a distorted hexagonal, with a heel-shaped protrusion that developed at the distal base (Figure 4-F). Its cervical ridge was thick and broad. The mesial and distal crests were straight. The mesial tubercle was observed at approximately half the height of the crown. The distal tubercle was well developed and bulging. Females had a similar outline to males (Figure 5-F).

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Saguinus

The male *Saguinus labiatus* had an outline that was distorted into a pentagon or hexagon (Figure 4-G). The mesial and distal crests were straight. The mesial tubercle was positioned one-third of the crown height from the cervical line. The distal tubercle was small. The mesial and distal tubercles were located near the cervical region. The females were similar in shape to the males (Figure 5-G). The mesial tubercles were located approximately at the quarter point of the crown from the cervical line.

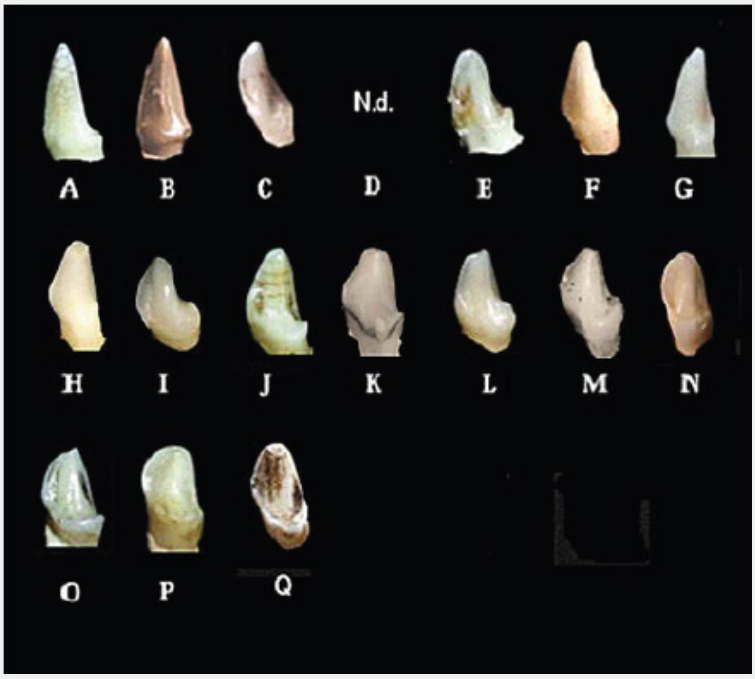

Figure 5: Lingual views of lower female canines in New World monkeys. All drawn to approximately same size. N.d.: No data. Capital letters are the same as in Figure 1.
Uppercase letters: A: *Pithecia monachus*, B: *Chiropotes satanas*, C: *Plecturocebus moloch*, D: *Cheracebus torquatus*, E: *Callithrix jacchus*, F: *Callimico goeldii*, G: *Saguinus labiatus*, H: *Leontocebus fuscicollis*, I: *Aotus trivirgatus*, J: *Cebus albifrons*, K: *Cebus capucinus*, L: *Sapajus apella*, M: *Saimiri sciureus*, N: *Ateles geoffroyi*, O: *Lagothrix lagothricha*, P: *Brachyteles arachnoides*, Q: *Alouatta seniculus*

Leontocebus

The outline of the male Leontocebus fuscicollis was a strongly symmetrical distorted hexagon (Figure 4-H). The mesial and distal crests were straight, and the mesial and distal tubercles were located approximately one quarter of the height of the crown from the cervical line. The female canines were quite similar in shape to the male ones (Figure 5-H). The mesial tubercle was located closer to the crown apex than in males.

Aotidae

Aotus

The male *Aotus trivirgatus* had a distorted hexagonal outline with a heel-shaped protrusion that developed distally (Figure 4-I). The mesial tubercle was well developed and positioned approximately one-half of the crown height. The female outline was similar to the male (Figure 5-I). Both sexes exhibited strong flexion around the mesial tubercle. However, the heel-shaped protrusion was weaker in females than in males.

Cebidae

Cebus

The outline of the lower canines of the male *Cebus albifrons* was a distorted hexagon with straight incisal crests mesially and distally (Figure 4-J). The mesial tubercle was located

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approximately halfway up the crown and the distal tubercle was situated one-third of the way from the cervical line. The female had a similar distorted hexagonal outline with straight mesial and distal crests (Figure 5-J). The mesial tubercle was located approximately halfway from the cervical line. There was a steeper degree of flexion around the mesial tubercle. The dimorphism in shape was moderate.

Figure 6: Lingual views of upper deciduous canines in New World monkeys. All drawn to approximately same size. Lowercase letters are the same as in Figure 3.
Lowercase letters: a: *Pithecia monachus*, b: *Alouatta seniculus*, c: *Lagothrix lagothricha*, d: *Sapajus apella*, e: *Saimiri sciureus*, f: *Aotus trivirgatus*, g: *Callimico goeldii*

The male *Cebus capucinus* had a distorted hexagonal outline (Figure 4-K). The mesial tubercle was positioned approximately two-thirds of the crown height. The female outline formed a distorted quadrilateral (Figure 5-K). Strong flexure was observed around the mesial cusp of the female. However, the heel-like protrusion was weak.

Sapajus

The male *Sapajus apella* had an outline that was distorted and quadrangular (Figure 4-L). It had a poorly developed heel. The cross-section was eliptical. The mesial tubercle was located at approximately half the height of the tooth crown. The female (Figure 5-L) had a more distorted, hexagonal shape than the male, resulting in a stronger degree of flexion around the mesial tubercle. The heel-like bulge at the distal base and the cervical ridge were more pronounced than in males. The cross-section was elliptical.

Saimir

The male *Saimir sciureus* had a vertically distorted, pentagonal shape with a small tubercle at its distal base (Figure 4-M). The mesial crest was straight, while the distal crest was slightly concave. The cross-section was elliptical along the long tooth axis. The mesial and distal tubercles were located in the cervical region. The outline of the female (Figure 5-M) was a distorted hexagon and the mesial tubercle was located approximately two-thirds of the crown from the cervical line. The degree of flexion around the mesial tubercle was stronger in the female. The heel-shaped bulge was more pronounced than in males. The cross-section was elliptical along the long tooth axis. There was a strong shape sexual dimorphisn.

Atelidae

Ateles

The male *Ateles geoffroyi* had a distorted, pentagonal shape, with straight mesial and distal crests (Figure 4-N). There was minimal bulging at the distal base. The mesial groove was interrupted by the marginal ridge. The cervical ridge was moderate. The cross-section was elliptical along the long tooth axis. The shape of the female (Figure 5-N) was similar to that of the male, but the mesial tubercle was positioned closer to the crown apex than in the male. The cervical ridge was strongly developed. The cross-section was elliptical along the long tooth axis.

Lagothrix

The outline of the *Lagothrix lagothricha* canine was a distorted triangle (Figure 4-O). The mesial and distal crests were convexly curved. The mesial groove was interrupted by the marginal ridge. The lingual ridge was broad and well-developed. The cervical ridge was well-developed and slanted downwards at an angle. The cross-section was elliptical along the long tooth axis. The canines of the females were distorted and hexagonal in shape (Figure 5-O). The mesial tubercle was located closer to the crown apex, resulting in a stronger degree of flexion around the mesial tubercle than in males. The heel-like protrusion was much more pronounced in females. The cross-section was elliptical along the long tooth axis.

Brachyteles

The female *Brachyteles arachnoides* had a distorted, hexagonal outline (Figure 5-P). The mesial tubercle was developed and positioned approximately one half of the crown height. The cervical ridge was moderately swollen with a slight heel-shaped bulge present at the distal base. The cross-section was elliptical along the long tooth axis.

Alouatta

The *Alouatta seniculus* had a distorted, pentagonal shape (Figure 4-Q). The cervical ridge was notably well developed. The protrusions at the distal base were highly developed. The cross-section was elliptical along the long tooth axis. In females (Figure 5-Q), the shape was more distorted and pentagonal, with the mesial tubercle located closer to the crown apex than in

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males, resulting in a stronger degree of flexion around the mesial tubercle than in males. The heel-shaped protrusions were weakly developed. The cross-section was elliptical along the long tooth axis. There was a strong shape sexual dimorphism (Figure 6).

Deciduous canines

The deciduous lower canines of *Pithecia monachus* were elongated isosceles triangles. They were surrounded by a moderately developed cervical ridge. No dimorphism in the shape of the crown was observed. The deciduous lower canines of other species commonly appeared as distorted hexagons. The degree of flexion around the mesial tubercle was stronger than in the permanent lower canines (Figure 6).

Discussion

Primates are omnivorous and eat a variety of foods, including leaves, fruit, bark, tree sap, insects, and so on. The large canines of male primates are used as weapons of aggression against predators and other males, both within and between troops. They are also involved in sexual selection [3, 21]. However, some scholars argue that, although large canines are designed for piercing and cutting prey, they are rarely used for feeding purposes, such as folivorous and frugivore and are therefore not closely linked to feeding behaviour [3, 28]. However, it is well known that diet significantly affects canine form [10]. New World saki monkeys, for instance, have chisel-like canines that they use to open hard fruits, and their teeth are specially adapted for this activity [19].

The size of the canines of monkeys belonging to the Cercopithecoidea is generally a reliable indicator of their sex. This is because the canines of males are larger than those of females. However, in some Platyrrhini species, it is not possible to distinguish between the sexes based on tooth size alone. Even if the size of the canines is the same in both sexes, sexual dimorphism in shape still exists if their shape differs. Although changes in the shape of canine teeth are significant, reports on the shape of canines in primates are scarce, and studies on sexual dimorphism in this respect are rare [3, 21, 29]. Plavcan and van Schaik [3] stated that the shape of the canines also strongly correlated with phylogeny and could serve as a means of classification, emphasizing its necessity.

The shape of the canines is most closely related to the nature of the food consumed. The first factor to consider in this relationship is the hardness, softness or toughness of the food, followed by determining whether the species is herbivorous, frugivorous or omnivorous [10, 30]. Hershkovitz (1977) [22] described the upper canines of all other living platyrrhines as follows: "The canine tooth is a subtriangular cross-section with sharp mesial and distal edges, anterior and posterior cingula always present and distal and/or mesial tubercles often preserved."

New World monkeys are omnivorous and mainly eat plant matter. Saki monkeys primarily consume seeds, but they are also adaptable frugivores that eat hard, unripe fruit earlier than other monkeys [21, 25, 31-33]. The *Plecturocebus* diet consists of more than 70% fruit. The remainder of their diet consists of leaves, insects, and seeds [1, 14]. *Callithrix* use their claws to cling to tree trunks and drill holes in which to lick or scrape out sap. Nearly 70% of their diet consists of sap, and they also enjoy eating fruit and insects. The diet of the *Aotus* species consists primarily of fruit, with consumption of berries, flowers, leaves, nectar, insects and spiders also being a feature [21-22]. The Cebidae are highly omnivorous, primarily feeding on fruit and insects. They also hunt and eat small animals, such as mice, bats and squirrels. They have been observed using their canines and stones to crack open hard fruits [34]. *Ateles* mostly eat fruit, especially ripe fruit [35]. *Lagothrix* also eat fruit, but their diet includes tree leaves, seeds, and other plant matter. *Brachyteles* tend to eat leaves [25]. *Alouatta* primarily feed on leaves, particularly young ones, as well as flowers and fruits, making them mainly folivorous. They also selectively consume certain insects and small vertebrates.

Upper canines

The shape of the upper canines of male New World monkeys could be categorised into two main types, depending on their diet. One type involved teeth shaped like daggers. This type was further divided into three subtypes. One of these was adapted for eating ripe fruit and included the following species: *Cheracebus torquatus*, *Callimico goeldii*, *Saguinus labiatus*, *Leontocebus fuscicollis*, *Aotus trivirgatus*, *Cebus albifrons*, *Cebus capucinus*, *Sapajus apella*, *Sapajus nigritus*, *Saimiri sciureus*, *Ateles geoffroyi* and *Ateles paniscus*. A second subtype had either chisel-like canines, like those of *Pithecia monachus*, or trigonal, pyramid-shaped canines, like those of *Chiropotes satanas*. These canines were used for crushing hard seeds. A third subtype had rounded, slanted teeth for extracting resin and included *Plecturocebus moloch* and *Callithrix jacchus*. Another main shape type was observed in folivorous primates with hook-like canines and included *Alouatta seniculus*, *Alouatta caraya* and *Brachyteles arachnoides*.

Table 1 shows the morphology and sexual dimorphism in shape and size for males of several species of New World monkey. As with Old World monkeys, New World monkeys also exhibit diverse social structures. According to Kay et al. [26], the greater the dimorphism of canine size, the higher the level of competition between males. Those species with monogamous and polyandrous social structures exhibit the lowest canine dimorphism, while species with male dominance hierarchies show the highest. Species with fission-fusion social structures and transitory intermale breeding-season competition fall between these extremes.

This study found that pair-living primates among New World monkeys was more diverse than among Old World monkeys [27]. The saki monkey is monogamous, much like the *Plecturocebus* and *Aotus* groups [25, 27]. By contrast, *Callithrix* exhibit a variety of social structures, including monogamous pairs and polygynous, polyandrous, and polygynandrous groups [21, 25, 27]. The *Cebus*

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and *Sapajus* species exhibit a promiscuous, dominance hierachy, and multimale/multifemale mating system [25-26], whereas the *Saimiri* have a multimale/multifemale society in which females are dominant throughout the year and intense competition between males occurs during the short mating season [25-27]. *Ateles* form promiscuous multimale/multifemale groups [26]. These groups live in fission-fusion societies that are similar to those of chimpanzees [25, 35-38]. The social structure of *Alouatta* is characterised primarily by multimale/multifemale fission-fusion promiscuity [25-27].

Table 1: Morphology of male upper canines and sexual dimorphism.

Family	Subfamily	Genus	species	Social structure	Canine shape	Shape dimorphism	Size dimorphism	Area
Pitheciidae	Pitheciinae	*Pithecia*	*P. monachus*	Multimale/multifemale low competition[#1] Monogamy[#2]	Chisel-shaped	Slight	Slight[*1]	Large[*1]
		Chiropotes	*C. satanas*	Monogamy[#1]	trigonal pyramid-shaped	None	None[*1]	Large[*1]
Callitrichidae	Callicebinae[#3]	*Plecturocebus*	*P. moloch*	Monogamy[#1]	Dagger-shaped with apical curvature distally	Slight	None[*2]	Small[*2]
		Cheracebus	*C. torquatus*	Monogamy[#1]	Dagger-shaped	N.d.	None[*1]	Small[*1]
	Callitrichinae[#3]	*Callithrix*	*C. jacchus*	Monogamy/polyandry[#1, #3]	Dagger-shaped with apical curvature distally	Moderate	None[*2]	Small[*2]
		Callimico	*C. goeldii*	Multimale/multifemale[#2, #3]	Dagger-shaped, crown inclination distally	None	None	Small
		Saguinus	*S. niger*	Polyandry[#1] multimale/multifemale[#3]	Dagger-shaped	None	None	Small
			S. labiatus		Dagger-shaped	None	None[*1]	Small[*1]
		Leontocebus	*L. fuscicollis*	Polyandry[#1]	Dagger-shaped	None	None[*2]	Small[*2]
Aotidae	Aotinae[#3]	*Aotus*	*A. trivirgatus*	Monogamy[#1, #2]	Dagger-shaped,	None	None[*2]	Small[*2]
			A. nigriceps		Dagger-shaped	None	None[*1]	Small[*1]
			A. lemurinus		Dagger-shaped	None	None[*2]	Small[*2]
Cebidae	Cebinae	*Cebus*	*C. albiforns*	Mating season competition[#1] Multimale/multifemale[#3]	Dagger-shaped	Moderate	Moderate[*1]	Large[*1]
			C. capucinus		Dagger-shaped	Moderate	Moderate[*2]	Large[*2]
		Sapajus	*S. apella*	Dominance rank competition[#1]	Dagger-shaped,	Moderate	Strong[*2]	Large[*2]
	Saimiriinae	*Saimiri*	*S. oerstedii*	Mating season competition [#1] Multimale/multifemale [#3]	Dagger-shaped	Strong	Strong[*3]	Medium[*3]
			S. sciureus		Dagger-shaped	Strong	Moderate[*3]	Medium[*3]
			S. bolivienses		Dagger-shaped	Strong	Moderate[*2]	Medium[*2]
Atelidae	Atelinae	*Ateles*	*A. geoffroyi*	Fission/fusion [#1] Multimale/multifemale [#3]	Dagger-shaped	Strong	Moderate[*2]	Large[*2]
			A. paniscus		Dagger-shaped	Slight	Slight[*1]	Large[*1]
		Brachyteles	*B. arachnoides*	Multimale/multifemale low competition Fission/Fusion [#1]	Hook-shaped	Moderate	Moderate[*2]	Large[*2]
		Lagothrix	*L. lagothricha*	Multimale/multifemale [#3]	Dagger-shaped	Moderate	Moderate[*2]	Large[*1]
	Alouattinae	*Alouatta*	*A. seniculus*	Dominance rank competition[#1] Multimale/multifemale[#3]	Hook-shaped	Strong	Strong[*2]	Large[*2]
			A. caraya		Hook-shaped	Strong	Strong[*2]	Large[*2]

*1: Tejedor (13); *2: Plavcan and Ruff (21); *3: Swindler (20); #1: Kay et al. (26); #2: Fleagle (25); #3: Izawa (27), N.d.: No data

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The size of the canines of the Cebidae and Atelidae families was sexually dimorphic in New World monkeys [2, 3, 25-26, 36-37]. Generally, groups with monogamous social structures exhibit little dimorphism, whereas those with polygamous structures tend to display strong dimorphism [3, 39]. Intense competition among males for females is likely to cause the canines in males to enlarge, thereby increasing the degree of dimorphism [26].

The same trend was observed in canine shape dimorphism. Species with monogamous social structures exhibited less shape dimorphism, which is a key feature of such structures. By contrast, species with polygynous social structures exhibited pronounced sexual dimorphism in shape. Furthermore, species with small canines displayed less sexual dimorphism in shape than those with large canines.

In many species of New World monkey, tooth size dimorphism was associated with shape dimorphism, though this was not always consistent across all species. According to the survey data used here, six species showed a mismatch between size and shape dimorphism in the upper canines: *Plecturocebus moloch*, *Callithrix jacchus*, *Sapajus apella*, *Saimiri sciureus*, *Saimiri boliviensis* and *Ateles geoffroyi*.

In general, female anthropoids have smaller canines than males. It is thought that this is because female canines have little evolutionary value as weapons [19]. The outlines of female canines in species with little shape dimorphism were similar to those of males, but the outlines of females showing marked shape dimorphism were pentagonal or distorted rhombic. In addition, the cervical ridge was more prominent than in males, giving the overall appearance a rounded shape.

Deciduous teeth exhibit more conservative characteristics than permanent teeth [40-41]. Lucas et al. (1986) [42] reported that the size and shape of deciduous canines in anthropoids (Ceboidea, Cercopithecoidea and Hominoidea) resembled those of permanent canines in females but differed greatly from those in males. The deciduous canines of New World monkeys were shaped like equilateral triangles. In contrast, only the canines of *Pithecia monachus* were elongated isosceles triangle. There was little variation in the shape of deciduous canines throughout phylogenetic groups, and no sexual dimorphism was observed. This similarity suggests that this shape is primitive.

Lower canines

In general, lower permanent canines were simpler in shape throughout phylogenetic groups than the upper canines [43]. The outline of the tooth crown varied from a distorted triangle to a distorted hexagon across all classified species. This variation depended on the position and degree of flexion of the mesial tubercle, and on the degree of development of the heel-shaped tubercle at the distal base. If the distal tubercle was underdeveloped, the shape became distorted and looked like a triangle. If it was well developed, the shape was more likely to be a distorted hexagon. Unlike the upper canines, diet was not a factor altering canine tooth morphology in the lower canine [44-47].

The shape of the female lower canines was similar to that of the male ones, but the mesial tubercle was located further apically and the degree of flexion around the mesial tubercle was stronger than in the permanent lower canines.

In Deciduous canines, all species had well-developed mesial and distal tubercles. Many species exhibited a distorted hexagonal shape. Unlike these species, *Pithecia* had a distorted isosceles triangle shape.

Conclusion

The crown outlines and sexual dimorphism were examined in the context of their phylogenetic relationships. The outline of the upper canines of males could be categorised into two main shape types, depending on their diet. The first type was dagger-shaped, while the second type was hook-shaped, which was predominantly observed in leaf-eating primates. The dagger-shaped group can be divided into three subtypes. One of these had adapted canines for eating ripe fruit. Another species had chisel-like canines (*Pithecia monachus*) or trigonal pyramid-shaped canines (*Chiropotes satanas*) for crushing hard seeds. A third subtype had rounded, slanted teeth for extracting resin. Species with little shape dimorphism tended to be monogamous or polyandrous, and had small canines and ate tree sap, fruit and insects. In contrast, species with pronounced shape sexual dimorphism tended to be polygamous or multimale/multifemale. They had a strong male hierarchy and large canines. Their diet mainly consisted of ripe fruit and leaves. Dimorphism in the size and shape of the upper canines was similar in many species of New World monkey, though not always consistent. Six species exhibited discrepancies between size and shape dimorphism. In species with little shape dimorphism, the shape of the female canine resembled that of the male. In contrast, species exhibiting significant shape dimorphism had unique female canine shapes, such as short pentagons or distorted rhombi. The shape of the deciduous canines resembled an equilateral triangle, among the New World monkeys except for *Pithecia monachus*.

The shape of the lower canines in males varied from a distorted triangle to a distorted hexagon. Only slight differences between species were observed. The female lower canines were similar in shape to those of the males. The deciduous lower canines were distorted and hexagonal in shape, except for those of the *Pithecia monachus* which were isosceles triangular.

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