Invited Review

Comparative morphology of the primate tongue

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ABSTRACT

To clarify the role of the primate tongue as a means to better understand the evolution of oral function among primates – an example of adaptation within the restricted phylogenetic group - we review the morphological knowledge of the tongues of extant primates in relation to phylogenetic classification. Prosimians tongues are more effective than those of Haplorhini for taking up food with the tongue alone, because they are capable of fine movement when outside the oral cavity. However, the role of the tongue in food uptake has diminished when juxtaposed with progress in hand manipulation of food and tools in Haplorhini, especially with the manipulation of tools by Homininae. This change in the tongue from prosimians to Homininae can be regarded as degeneration in food uptake by the tongue, although the functional role of the tongue within the oral cavity has not diminished. The distribution pattern and form of lingual papillae, except foliate papillae, are very similar among all reported primates species. Although foliate papillae are generally well developed in Haplorhini, most prosimian species have no foliate papillae, or a different type of papillae that substitute for foliate papillae. There are three vallate papillae in prosimian species and the New-World macaques, Platyrrhini. These papillae exhibit an inverted V-shape and are more numerous in Old World macaques, Catarrhini. These differences seem to be the result of phylogenetic origin.

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1. Introduction

The tongue has important roles in food uptake, mastication and swallowing in most tetrapods. A movable tongue of voluntary muscle has developed through adaptation in terrestrial vertebrate evolution and has persisted in almost all extant tetrapods, irrespective of their living environment (Iwasaki, 2002). Recently, Iwasaki et al. (2019) reported significant variations in the role of the tongue in tetrapods. On the one hand, the tongue can be extremely important in food uptake, as in frogs of the Amphibia, chameleons of the Reptilia and humming birds of the Aves. On the other hand, the role of the tongue is significantly diminished in a few species of frogs, turtle species and some bird species. Naturally, in the latter case, the tongue cannot play an important role in food uptake, mastication or swallowing. The degenerative tendency of the tongue illustrated by these examples is a form of evolutionary specialization. However, the mechanism by which this form of degeneration originated during the process of evolution has not been described.

Unlike that of all other vertebrates, the human tongue has an extremely unusual role as the essential organ of spoken language. This function also exemplifies evolutionary specialization of the vertebrate tongue. An important challenge is to clarify the evolutionary process underlying this function. However, we first need to clarify morphological knowledge of the tongues of extant primates in relation to phylogenetic classification. Before describing the evolution of the anthropoid tongue prior to the appearance of humans, the role of the primate tongue should be considered in order to better understand how oral function evolved among primates, an example of adaptation within a restricted phylogenetic group. In particular, among primates the tongue of the human, *Homo sapiens*, has achieved significant specialization in language acquisition. Taken together, these analyses may improve our understanding of the evolutionary role of the human tongue.

In this report, we review the relevant literature in order to clarify the morphological differences and similarities of primate tongues, including the human tongue. We hope that our findings will lead to new hypotheses on the functional role of the primate tongue, including that of humans which combine insights from different fields, thus yielding a more comprehensive understanding of primate evolution.

2. Primate evolution and phylogenetics

The amniotic Synapsids include the original mammalian ancestor and are thought to have diverged from a *Sauropsid* reptile during the late Carboniferous, about 320 to 315 million years ago (Mya), i.e., just a few tens of millions of years after the appearance of the first amniotes in the mid-Carboniferous, around 340 Mya (Carroll, 1992; Steward, 1997; Laurin and Gauthier, 2011). At the end of the Mesozoic, the Cretaceous-Paleogene extinction around 65.5 Mya decisively changed the interrelationship between reptiles and mammals (Alvarez et al., 1980; Schulte et al., 2010). During this event, all non-avian dinosaurs, ammonites, Mosasaurus, Plesiosaurus, and many groups of mammals suddenly disappeared (MacLeod et al., 1997). The consensus is that mammals began to rapidly diversify during the Paleogene period after the Cretaceous-Paleogene extinction (Chambers et al., 1997) and evolved from a few small groups into most of the modern species (Meredith et al., 2011).

Recent molecular phylogenetics indicate that primates originated before or during the Cretaceous-Paleogene extinction (Tavaré et al., 2002; Janečka et al., 2007; Perelman et al., 2011; Springer et al., 2012; Finstermeier et al., 2013; Pozzi et al., 2014). Furthermore, there are, broadly speaking, two perspectives of the Strepsirrhini (ancestor of Lemuriformes) -Haplorhini
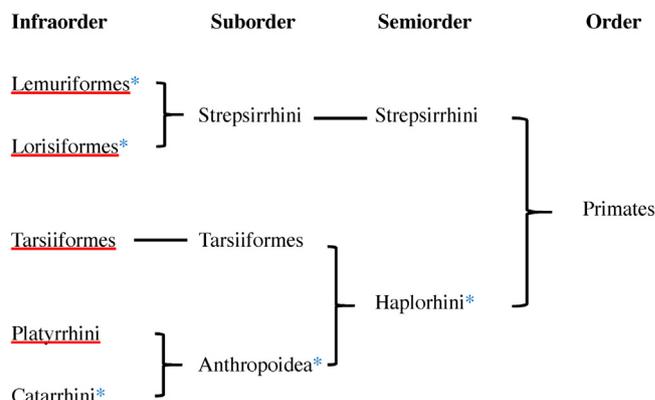
Fig. 1. Classification of extant primate genera from order to infraorder, as compared with the results of molecular phylogenetic analysis. The red underlining shows five groups (infraorder) of the systematic classification. The blue asterisks show the five groups identified by molecular phylogenetic analysis.

split - the first divergence after the appearance of the primates - namely, the estimation before the Cretaceous-Paleogene extinction (Springer et al., 2012; Pozzi et al., 2014), and that after the Cretaceous-Paleogene extinction (Martin 1993; Chatterjee et al., 2009; O'Leary et al., 2013). Strepsirrhini is thought to be the ancestor of all extant prosimians (Whitten and Brockman, 2001). Molecular and fossil evidence (Goodman et al., 1998) suggested that Strepsirrhini divided into Lemuriformes and Loriformes, which is thought to be the ancestor of lemurs, lorises and allies, whereas Haplorhines divided into Tarsiiformes, the putative ancestor of tarsiers, which are classified as prosimians, and Anthropoides, after the Cretaceous-Paleogene extinction. Furthermore, Anthropoides divided into Platyrrhini, which is thought to be the ancestor of New World monkeys, and Catarrhini, the putative ancestor of Old World monkeys. The divergence of the Catarrhini groups Hominoidea and Cercopithecidea is estimated to have occurred 23 to 29 Mya (Raaum et al., 2005; Chatterjee et al., 2009; Steiper and Young, 2009). In addition, the divergence of genus *Homo* and genus *Pan* is estimated to have occurred 6 Mya (Raaum et al., 2005).

In a review of primate phylogenetics, Perelman et al. (2011) estimated the extant number of primate species at 261 to 377, and 67 to 69 primate genera originated from a common ancestor (Goodman et al., 1998; Grove, 2001; Wilson and Reeder, 2005). Data is accumulating on the numbers of primate species and genera. Although there are several different classifications of extant primates (Goodman et al., 1998; Groves, 2001; Miller et al., 2005; Masters et al., 2007; Disotell, 2008; Perelman et al., 2011; Fleagle, 2013; Pozzi et al., 2014), there are five primate infraorders, namely Lemuriformes, Lorisiformes, Tarsiiformes, Platyrrhini and Catarrhini, according to a recent classification, as shown in Fig. 1 (Disotell, 2008; Fleagle, 2013). On the basis of the most recent molecular phylogenetic analysis, Pozzi et al. (2014) reported that extant primates can be divided into five groups; Lorisiformes, Lemuriformes, Haplorhini, Anthropoidea and Catarrhini. However, in a classification of extant primate genera, Haplorhini is a semiorder that includes the suborders Tarsiiformes and Anthropoidea, and the suborder Anthropoidea includes the infraorders Platyrrhini and Catarrhini (Disotell, 2008; Fleagle, 2013). This discrepancy will likely be resolved in future studies.

3. Comparative morphology of the tongue and lingual papillae in extant primates

The morphology of the primate tongue was broadly described in a wide range (22) of species by Machida et al. (1967). After that report, a large number of studies about the primate tongue have

been published. In this section, we use the classification of Disotell (2008) and Fleagle (2013) to describe the reported morphological features of the primate tongue. However, recent morphological studies of the primate tongue were limited to two infraorders (Platyrrhini and Catarrhini) rather than to all infraorders (i.e., Lorisiformes, Lemuriformes, Tarsiiformes, Platyrrhini and Catarrhini). We identified several reports on tongue morphology in these two infraorders. The results of the published reports have been arranged in relation to species belonging to the same infraorder. All published morphological studies of the tongues of primate species are summarized in Fig. 2.

3.1. Strepsirrhini (Semiorder)

As mentioned above, this semiorder includes two infraorders, Lemuriformes and Lorisiformes. All extant prosimians in Lemu-riformes and Lorisiformes are thought to be derived from the common ancestor of Strepsirrhini (Whitten and Brockman, 2001).

3.1.1. Lemuriformes (Infraorder)

A morphological study of the tongue in infraorder Lemuriformes has been reported only in the family of Lemuridae. The reported species included two genera, Lemur and Eulemur, of the Lemuridae family. The details of these studies are as follows.

3.1.1.1. Lemuridae (Family). In genus Lemur, Machida et al. (1967) describe the tongue of the Mongoose lemur, *Lemur mongoz*. They reported that in most prosimians the lingual apex is narrow and pointed, and the tongue of this species is thought to exhibit the same outline. The cartilaginous sublingua is well developed. The filiform papillae are distributed over the anterior two thirds of the dorsal surface, and the fungiform papillae are scattered among

1. Lemuriformes (Infraorder)
  a. Lemuridae (Family)
    Lemur (Genus)
      Species: Mongoose lemur, *Lemur mongoz* (Machida et al., 1967)
    Eulemur (Genus)
      Species: Rufous lemur, *Eulemur fulvus rufus* (Hofer, 1981; Overdorff, 1992)
        Red-bellied lemur, *Eulemur rubriventer*, (Overdorff, 1992)
        Eulemur sp. (Fleagle, 2013)
2. Lorisiformes (Infraorder)
  a. Lorisidae (Family)
    Arctocebus (Genus)
      Species: Angwantibo, *Arctocebus calabarensis* (Machida et al., 1967)
    Perodicticus (Genus)
      Species: Potto, *Perodicticus potto* (Machida et al., 1967)
    Nycticebus (Genus)
      Species: Slow loris, *Nycticebus coucang* (Machida et al., 1967; Kubota & Iwamoto, 1967; Xie & Zhang, 2017)
        Bengal slow loris, *Nycticebus bengalensis* (Nekaris, 2014)
        Javan slow loris, *Nycticebus javanicus* (Nekaris, 2014)
        Philippine slow loris, *Nycticebus menagensis* (Nekaris, 2014)
        Bornean slow loris, *Nycticebus borneanus* (Nekaris, 2014)
        Kayan slow loris, *Nycticebus kayan* (Nekaris, 2014)
        Sody's slow loris, *Nycticebus.bancanus* (Nekaris, 2014)
        Pygma slow loris, *Nycticebus pygmaeus* (Xie & Zhang, 2017)
    Loris (Genus)
      Species: Slender loris, *Loris tardigradus* (Machida et al., 1967)
  b. Galagidae (Family)
    Galago (Genus)
      Species: Pygmy bushbaby, *Galago demidovii* (Machida et al., 1967)
        Lesser bushbaby, *Galago senegalensis* (Machida et al., 1967)
        Galago sp. (Fleagle, 2013)
    Otolemur (Genus)
      Species: Brown greater galago, *Otolemur crassicaudatus* (Machida et al., 1967; Hofer et al., 1990a)
3. Tarsiiformes (Infraorder)
  a. Tarsiidae (Family)
    Carlito (Genus)
      Species: Philippine tarsier, *Carlito syrichta* (Machida et al., 1967)
4. Platyrrhini (Infraorder)
  a. Atelidae (Family)
    Alouatta (Genus)
      Species: Black howler, *Alouatta caraya* (Machida et al., 1967; Nitta et al., 2013)
    Lagothrix (Genus)
      Species: Woolly monkey, *Lagothrix lagotricha* (Machida et al., 1967)
  b. Cebidae (Family)
    Cebus (Genus)
      Species: Tufted capuchin, *Cebus apella = Sapajus apella* (Muchilinski et al., 2011)
    Saimiri (Genus)
      Species: Squirrel monkey, *Saimiri sciureus* (Machida et al., 1967; Kubota et al., 1966; Iwasaki et al., 1988; Branco et al., 2011)
    Callithrix (Genus)
      Species: Common marmoset, *Callithrix jacchus* (Kubota & Hayama, 1966)
        Black-tufted marmoset, *Callithrix penicillata* (Branco et al., 2012; Nitta et al., 2013; Fleagle, 2013)

Fig. 2. Morphological studies of the tongues of primate species, to date.

Cebuella (Genus)
  Species: Pygmy marmoset, *Cebuella pygmaea* (Kubota & Hayama, 1966)
Leontopithecus (Genus)
  Species: Golden lion tamarin, *Leontopithecus rosalia* (Burity et al., 2009)
Saguinus (Genus)
  Species: Schwarzer tamarin, *Saguinus ursula* (Kobayashi et al., 2004)
    Black-mantled tamarin, *Saguinus nigricollis* (Machida et al., 1967)
5. Catarrhini (Infraorder)
  a. Cercopithecidae (Family)
    Cercopithecus (Genus)
      Species: Blue monkey, *Cercopithecus mitis* (Machida et al., 1967)
        Grivet, *Cercopithecus aethiops* (Machida et al., 1967; Emura et al., 2002)
    Papio (Genus)
      Species: Yellow baboon, *Papio cynocephalus* (Machida et al., 1967)
        Olive baboon, *Papio anubis* (Machida et al., 1967)
    Mandrillus (Genus)
      Species: Mandrill, *Mandrillus sphinx* (Kobayashi et al., 2004)
    Macaca (Genus)
      Species: Rhesus macaque, *Macaca mulatta* (Machida et al., 1967)
        Southern pig-tailed macaque, *Macaca nemestrina* (Machida et al., 1967)
        Celebes crested macaque, *Macaca nigra* (Machida et al., 1967)
        Crab-eating macaque, *Macaca irus* (Arvidson, 1976; Iwasaki, 1992a; Kobayashi et al., 2004)
        Japanese macaque, *Macaca fuscata* (Iwasaki et al., 1992b; Emura et al., 2002)
    Colobus (Genus)
      Species: Abyssinian black-and-white colobus, *Colobus guereza* (Yoshimura et al., 2018)
  b. Hylobatidae (Family)
    Hylobates (Genus)
      Species: Lar gibbon, *Hylobates lar* (Fleagle, 2013)
  c. Hominidae (Family)
    Gorilla (Genus)
      Species: Gorilla, *Gorilla gorilla* (Machida et al., 1967)
    Pan (Genus)
      Species: Common chimpanzee, *Pan troglodytes* (Hofer et al., 1990b; Hladik & Simmen, 1997)
    Homo (Genus)
      Species: Human, *Homo sapiens* (Machida et al., 1967; Arvidson, 1976; Provenza, 1986; Hladik & Simmen, 1997; Kobayashi et al., 2004)

Fig. 2. (*Continued*)

them. There are three vallate papillae, which are located on the dorsal surface of the border between the lingual body and radix. One is located in the posterior center, and two are on either side of the anterior region of the border, thus exhibiting an inverted V-shaped pattern. The vallate papillae are flat and dish-like. In this species, the foliate papillae are particularly recognizable among prosimians (Machida et al., 1967).

In genus Eulemur, the rufous lemur, *Eulemur fulvus rufus* (Hofer, 1981; Overdorff, 1992), and red-bellied lemur, *Eulemur rubriventer* (Overdorff, 1992), are flower feeders. However, the red-bellied lemur licks nectar from flowers while rufous lemurs eat all flower parts from the same flower species. In accordance with these species-specific patterns of flower feeding, red-bellied lemurs have a feathered, brush-like tongue tip, which lemurs lack (Overdorff, 1992). In both species, the tongues are elongated and have a rounded apex, the width of which is somewhat narrower than that of the posterior part. The dorsal surface has three types of papillae: filiform, fungiform and vallate papillae (Hofer, 1981; Overdorff, 1992; Fleagle, 2013). However, details of the form of the four lingual papillae were not reported.

3.1.2. Lorisiformes (Infraorder)

The tongue morphology of this infraorder has been reported in the families Lorisidae and Galagidae.

3.1.2.1. Lorisidae (Family). In Lorisidae, tongue morphology has been reported in four genera; Arctocebus, Perodicticus, Nycticebus and Loris.

In genus Arctocebus, a morphological study of the tongue investigated only one species, the Angwantibo, *Arctocebus calabarensis*. The lingual apex is narrow and pointed, and the cartilaginous sublingua is well developed. The filiform papillae are distributed over the anterior two thirds of the dorsal surface, and the fungiform

papillae are scattered among them. There are three vallate papillae on the border between the lingual body and radix. One is located in the posterior center, and one is present on each side of the anterior region of the border. These three vallate papillae form an inverted V-shaped pattern. The vallate papillae are flat and dish-like. In this species, no foliate papillae are present, as is the case in most prosimians (Machida et al., 1967).

In genus Perodicticus, a morphological study of the tongue investigated only one species, the Potto, *Perodicticus potto*. The lingual apex is narrow and pointed, and the cartilaginous sublingua is well developed. The filiform papillae are distributed over the anterior two thirds of the dorsal surface, and fungiform papillae are scattered among them. There are three vallate papillae on the border between the lingual body and radix. One is located in the posterior center, and one is present on each side of the anterior region of the border. These three vallate papillae form an inverted V-shaped pattern. The vallate papillae are flat and dish-like. In this species, no foliate papillae are present, as is the case in most prosimians (Machida et al., 1967).

In genus Nycticebus, morphological studies of the tongue have investigated eight species, namely, the slow loris, *Nycticebus coucang* (Machida et al., 1967; Kubota and Iwamoto, 1967; Xie and Zhang, 2017); the Bengal slow loris, *N. bengalensis*; the Javan slow loris, *N. javanicus*; the Philippine slow loris, *N. menagensis*; the Bornean slow loris, *N. boneanus*; the Kayan slow loris, *N. kayan*; Sody's slow loris, *N. bancanus* (Nekaris, 2014); and the Pygmy slow loris, *N. pygmaeus* (Xie and Zhang, 2017). Machida et al. (1967) reported that the features of the tongue of *N. coucang* are similar to those of other prosimians. The lingual apex is narrow and pointed, and the cartilaginous sublingua is well developed. The filiform papillae are distributed over the anterior two thirds of the dorsal surface, and the fungiform papillae are scattered among them. There are three vallate papillae, which are located near the

border between the lingual body and radix. One is located in the posterior center, and one is located on each side of the anterior region of the border. These three vallate papillae are arrange in an inverted pattern of V-shape (Kubota and Iwamoto, 1967; Machida et al., 1967; Xie and Zhang, 2017). The form of vallate papillae is flat and dish-like. In this species, no foliate papillae is recognizable as same as in most prosimians (Machida et al., 1967).

In *N. pygmaeus,* three types of lingual papillae are present on the dorsal surface of the tongue: filiform, fungiform and vallate papillae. Filiform papillae are conical or branched and consist of one thick main process and several slender accessory processes, located on the apex and body. The three vallate papillae are arranged in an inverted V-shaped pattern, between the anterior and posterior regions of the tongue (Kubota and Iwamoto, 1967; Xie and Zhang, 2017).

According to a report by Xie and Zhang (2017), the tongue of *N. coucang* is about 24 mm in length and about 18 mm in width; the tongue of *N. pygmaeus* is about 17 mm and 6 mm. In the former, the length of the tongue is about 1.3 times longer than the width, while in the latter, the length of the tongue is about 3 times longer than the width. The ratio of the length to the width of the tongue is relatively different within the same genus. The feeding habitat is not thought to be so different between these two species. Namely, both species feed on a mixed diet, with the majority of the food items consisting of fruits, vegetables, insects, honey, fresh leaves and berries (Xie and Zhang, 2017).

Furthermore, in several species of Nycticebus, *N. pygmaeus*, *N. coucang*, *N. javanicus* (Javan slow loris), *N. menagensis* (Philippine slow loris), *N. borneanus* (Bornean slow loris), *N. kayan* (Kayan slowloris) and *N. bancanus* (Sody's slow loris), have some of the longest tongues of any primate, along with a short, broad sublingual structure bedecked with six to nine denticles. The loris can insert its tongue and sublingual structure into many varieties of flowers and lap up the nectar (Nekaris, 2014).

3.1.2.2. Galagidae (Family). In genus Galago, tongue morphology has been reported for the lesser bushbaby, *Galago senegalensis*, and Prince Demidoff's bushbaby, *Galago demidovii*, by Machida et al. (1967). The fundamental features of tongue morphology in these two species are almost identical to those in other prosimians. Namely, the lingual apex is narrow and pointed, and the cartilaginous sublingua is well developed. The filiform papillae are distributed over the anterior two thirds of the dorsal surface, and the fungiform papillae are scattered among them. There are three vallate papillae near the border between the lingual body and radix. One is located in the posterior center, and one each is located on either sides of the anterior region of the border. These three vallate papillae form an inverted V-shaped pattern. The vallate papillae are flat and dish-like. In these species, no foliate papillae present, as is the case for most prosimians (Machida et al., 1967).

In an illustration of the tongue of *Galago* sp., by Fleagle (2013), a dorsal view shows a longitudinal triangular tongue with a somewhat pointed apex. The filiform papillae are compactly distributed over the entire dorsal surface, and the fungiform papillae are scattered among the filiform papillae. Three circumvallate papillae one central papilla and one on each side of the central one are located on the posterior end of the dorsal surface, as reported by Machida et al. (1967). There is no detailed information on the form of filiform, fungiform or circumvallate papillae in Galagidae.

In genus Otolemur, the morphology of the tongue of the brown greater galago, *Otolemur crassicaudatus*, was reported by Machida et al. (1967). The fundamental features are almost identical to those in other prosimians. The lingual apex is narrow and pointed, and the cartilaginous sublingua is well developed. The filiform papillae are distributed over the anterior two thirds of the dorsal surface, and the fungiform papillae are scattered among them. There are

three vallate papillae located on the border between the lingual body and radix. One is located in the posterior center, and one is located on each side of the anterior region of the border. These three vallate papillae are arranged in an inverted V-shaped pattern. The vallate papillae are flat and dish-like. No foliate papillae are present (Machida et al., 1967; Hofer, 1975; Hofer et al., 1990a).

3.2. Haplorhini (Semiorder)

As mentioned above, this semiorder comprises two suborders; Tarsiiformes and Anthropoidea. Furthermore, Anthropoidea is divided into two infraorder; Platyrrhini and Catrrhini (Whitten and Brockman, 2001).

3.2.1. Tarsiiformes (Infraorder)
Infraorder Tarsiiformes includes only the family Tarsiidae, which consists of three genera; Carlito, Tarsius and Cephalopachus (Fleagle, 2013). The morphology of the tongue has been reported for only one species of this infraorder the Philippine tarsier, *Carlito syrichta* (Machida et al., 1967). Although this species is classified in the Haplorhini, the fundamental tongue morphological features are almost identical to those of the prosimians, Strepsirrhini. The lingual apex is narrow and pointed, and the cartilaginous sublingua is well developed. The filiform papillae are distributed over the anterior two thirds of the dorsal surface, and the fungiform papillae are scattered among them. There are three vallate papillae, which are located on the border between the lingual body and radix, as is the case in the prosimians. One is located in the posterior center, and one is located on each side of the anterior region of the border. These three vallate papillae are arranged in an inverted V-shaped pattern. No foliate papillae are presented in these species (Machida et al., 1967).

3.2.2. Platyrrhini (Infraorder)
Infraorder Platyrrhini includes three families; Pitheciidae, Atelidae and Cebidae (Fleagle, 2013). No morphological study has investigated the tongues of Pitheciidae, and only one study has examined tongue morphology in *Alouatta caraya*, family Atelidae. Several studies have described tongue morphology of species belonging to the family Cebidae, such as the black howler, *Alouatta caraya* (Nitta et al. 2013); *Aotus trivirgatus* (Hofer, 1977); tufted capuchin, *Cebus apella* or *Sapajus apella* (Muchlinski et al., 2011; Fleagle, 2013); squirrel monkey, *Saimiri sciureus* (Kubota et al., 1966; Iwasaki et al., 1988; Branco et al., 2011); black-tufted marmoset, *Callithrix penicillata* (Branco et al., 2012; Nitta et al., 2013, Fleagle, 2013); golden lion tamarin, *Leontopithecus rosalia* (Burity et al., 2009); and tamarin, *Saguinas ursula* (Kobayashi et al., 2004).

3.2.2.1. Atelidae (Family). In the black howler, *Alouatta caraya*, the tongues are elongated and have a rounded apex. The width of the tongue is wider than that of prosimians. The dorsal and lateral tongue surfaces have filiform, fungiform, vallate and foliate papillae. The form of the filiform papillae varies according to tongue region, such as crown-shaped in the anterior, spear-shaped in the middle and filamentous in the posterior dorsal surface of the lingual body. The fungiform papillae are distributed among the filiform papillae. There are three vallate papillae; one median and two laterals which are tall and conical. The foliate papillae are well developed (Machida et al., 1967; Nitta et al., 2013). *Alouatta palliata* has a plica sublingualis, which is part of the mucous membranes of the mouth floor (Hofer, 1977).

3.2.2.2. Cebidae (Family). This family includes three subfamilies; Aotinae, Cebinae and Callitrichinae (Fleagle, 2013). Tongue morphology was investigated in several species of this family. However, most studies focused on the subfamilies Cebinae and Callitrichinae

(Kubota et al., 1966; Machida et al., 1967; Hofer, 1977; Iwasaki et al., 1988; Matsukawa and Okada, 1994; Kobayashi et al., 2004; Burity et al., 2009; Muchlinski et al., 2011; Branco et al., 2011; Nitta et al., 2013; Fleagle, 2013).

No study has examined tongue morphology in the subfamily Aotinae. However, in the three-striped night monkey, *Aotus trivirgatus*, only the plica sublingualis, part of the mucous membranes of the mouth floor was similar to that of the *Alouatta palliata* (Hofer, 1977).

The subfamily Cebinae includes two genera; Cebus and Saimiri (Fleagle, 2013). In genus Cebus, tongue morphology was reported in one species, the tufted capuchin, *Cebus apella*. The crown-shaped filiform papillae have several branched processes and are compactly distributed over the entire dorsal surface of the anterior two thirds of the tongue. The dome-shaped fungiform papillae are scattered among filiform papillae, with taste pores (Muchlinski et al., 2011). An illustration of the tongue of *Cebus sp.* by Fleagle (2013) shown that the tongue is long antero-posteriorly and wide from the apex to the radix. The filiform papillae are compactly distributed on the anterior two thirds of dorsal surface, and the fungiform papillae are scattered among them. Three vallate papillae are present on the marginal end of the lingual body. The central vallate papilla and one vallate papilla on each side are located at the border between the body and radix and exhibit an inverted V-shaped pattern (Fleagle, 2013).

In genus Saimiri, some studies have examined the tongue morphology of the common squirrel monkey, *Saimiri sciureus*. In this species, the tongue is elongated and has a rounded apex. The dorsal surface has filiform, fungiform, vallate and foliate papillae. Filiform papillae are distributed over the entire dorsal surface of the tongue, except in the lingual radix zone. A flattened circular area in the center of the filiform papillae is surrounded by several pointed processes. The structure of the filiform papillae is almost identical in any area of the dorsal and lateral surfaces of the tongue. Dome-shaped, fungiform papillae are scattered among the filiform papillae on the dorsal and lateral surfaces. Three vallate papillae are present on the marginal end of the lingual body and exhibit a V-shaped pattern (Kubota et al., 1966; Machida et al., 1967; Iwasaki et al., 1988; Matsukawa and Okada, 1994; Branco et al., 2011). In addition, Kubota et al. (1966) reported that the foliate papillae, which comprise five ridges, are anterior to the attachment of the glossopalatine fold.

In the subfamily Callitrichinae, the tongue morphology has been reported for the common marmoset, *Callithrix jacchus* (Kubota and Hayama, 1966; Matsukawa and Okada, 1994), and black-tufted marmoset, *Callithrix penicillata* (Branco et al., 2011; Nitta et al., 2013), of genus Callithrix for the pigmy marmoset, *Cebuella pygmaea*, of genus Cebuella (Kubota and Hayama, 1966), for the golden lion tamarin, *Leontopithecus rosalia*, of genus Leontopithecus (Burity et al., 2009) and for the black-mantled tamarin, *Saguinus nigricollis* (Machida et al., 1967), and Schwarzer tamarin, *Saguinus ursula* (Kobayashi et al., 2004), of genus Saguinus.

In genus Callithrix, tongue morphology has been reported for two species; *Callithrix penicillate* and *Callithrix jacchus*. In *Callithrix penicillata,* their tongues are small and elongated and have a rounded apex. The dorsal surface has filiform, fungiform, vallate and foliate papillae. Filiform papillae are distributed over the entire dorsal surface of the tongue, except in the lingual radix zone. The form of the filiform papillae varies somewhat according to the region of the tongue: they are conical with a few protrusions in the anterior region and crown-shaped in the posterior of the body. The fungiform papillae are distributed among the filiform papillae. The vallate papillae comprise one median and two lateral papillae and exhibit an inverted V-shaped pattern. The foliate papillae are well developed (Branco et al., 2011; Nitta et al., 2013). In *Callithrix jacchus*, Kubota and Hayama (1966) reported that the adult tongue is

about 21 mm in length and 8 mm in width. The filiform papillae are compactly distributed on the dorsal tongue surface. The fungiform papillae are distributed among the filiform papillae. The median vallate papilla has an oval-shape, and the lateral vallate papillae on both sides are located in the border between the body and radix and exhibit an inverted V-shaped pattern. In addition, the foliate papillae are well developed and clearly visible bilaterally between the body and radix (Kubota and Hayama, 1966; Matsukawa and Okada, 1994).

In genus Cebuella, tongue morphology has been reported for only one species, *Cebuella pygmaea*. The adult tongue is about 17 mm in length and 6 mm in width and is somewhat smaller than that of *Callithrix jacchus*. The filiform papillae are compactly distributed on the dorsal surface of the tongue, except in the lingual radix zone. The fungiform papillae are distributed among the filiform papillae. The median vallate papilla has an oval-shape, and the lateral vallate papillae are located bilaterally on the border between the body and radix and exhibit an inverted V-shaped pattern. In addition, the foliate papillae are well developed and clearly visible bilaterally between the body and radix (Kubota and Hayama, 1966).

In genus Leontopithecus, tongue morphology has been reported in only one species, *Leontopithecus rosalia*. Their tongues are elongated and have a rounded flat apex. The dorsal surface has four types of papillae: filiform, fungiform, vallate and foliate. The filiform papillae are compactly distributed on the dorsal surface of the tongue, except in the lingual radix zone. The filiform papillae are crown-shaped or finger-like papillae and have a flat center and longer and more numerous prolongations pointing towards the posterior region and a lesser number of shorter prolongations pointing toward the opposite margin. The fungiform papillae are present among filiform papillae. The vallate papillae comprise one median and two lateral papillae, and the foliate papillae have very few folds (Burity et al., 2009).

In genus Saguinus, tongue morphology has been reported in two species; *Saguinus ursula* and *Saguinus nigricollis*. In *Saguinus ursula*, their tongues are elongated and flat and have a rounded apex. The dorsal surface has filiform, fungiform, vallate and foliate papillae. The filiform papillae are compactly distributed on the dorsal surface of the tongue, except in the lingual radix zone. The filiform papillae comprise of small spine-like protrusions in a U-shaped arrangement that resembles those of other members in Platyrrhini. The fungiform papillae are distributed among the filiform papillae. The vallate papillae comprise one median and two lateral papillae, and the well-developed foliate papillae consist of approximately five slits (Kobayashi et al., 2004). In *Saguinus nigricollis*, their tongues are elongated, have a rounded apex and are wide and flat. The dorsal and lateral surfaces of the tongue have four types of papillae: filiform, fungiform, vallate and foliate. The fungiform papillae are distributed among the filiform papillae. There are three vallate papillae: one median and two lateral papillae. These papillae are tall and conical and form an inverted V-shaped pattern. The foliate papillae are well developed (Machida et al., 1967).

3.2.3. Catarrhini (Infraorder)

The infraorder Catarrhini includes three families: Cercopithecidae, Hylobatidae and Hominidae (Muchlinski et al., 2011; Fleagle, 2013). The family Cercopithecidae is composed of two subfamilies, Cercopithecinae and Colobinae, and each family includes over ten genera. The family Hylobatidae includes four genera. The family Hominidae consists of two subfamilies, Ponginae and Homininae. Ponginae has only one genus, Pongo, while Homininae has three genera, Gorilla, Pan and Homo.

In family Cercopithecidae, several morphological studies have investigated the tongue in species belonging to the subfamily Cercopithecinae, such as the Savanna monkey, *Cercopithecus mitis* (Machida et al., 1967), and *Cercopithecus aethiops* (Machida et al.,

1967; Emura et al., 2002) of genus Cercopithecus; yellow baboon, *Papio cynocephalus*, and olive baboon, *Papio Anubis*, of genus Papio (Machida et al., 1967); the Mandrill, *Mandrillus sphinx*, of genus Mandrillus (Kobayashi et al., 2004); and the rhesus macaque, *Macaca mulatta*, southern pig-tailed macaque, *Macaca nemestrina*, Celebes crested macaque, *Macaca nigra* (Machida et al., 1967), crab-eating macaque, *Macaca irus* (Arvidson, 1976; Iwasaki, 1992a, b; Kobayashi et al., 2004) and Japanese macaque, *Macaca fuscata* (Iwasaki et al., 1992; Emura et al., 2002), of genus Macaca. Recently, only one study has reported the morphology of the tongue in subfamily Colobinae; Abyssinian black-and-white colobus, *Colobus guereza* (Yoshimura et al., 2019).

In the family Hylobatidae, the tongue of the Lar gibbon, *Hylobates lar*, was illustrated by Fleagle (2013).

The family Hominidae includes two subfamilies Ponginae and Homininae and the subfamily Homininae includes three genera namely Gorilla, Pan and Homo. In the subfamily Ponginae, there is no report on tongue morphology. In the subfamily Homininae, tongue morphology was examined in three species: the gorilla, *Gorilla gorilla*, of genus Gorilla (Machida et al., 1967), common chimpanzee, *Pan troglodytes*, of genus Pan (Hofer et al., 1990b; Hladic and Simmen, 1997) and Human, *Homo sapiens*, of genus Homo (Provenza, 1986; Kobayashi et al., 2004).

3.2.3.1. Cercopithecidae (Family). Several studies have investigated tongue morphology in the Subfamily Cercopithecinae and, in contrast, only one study of tongue morphology has reported in the subfamily Colobinae. In the subfamily Cercopithecinae, tongue morphology of eight species of four genera has been examined. In *Cercopithecus mitis*, the tongues are elongated, have a rounded apex and are wide and flat. The dorsal and lateral surfaces of the tongue have filiform, fungiform, vallate and foliate papillae. The filiform papillae are compactly distributed on the dorsal surface of the tongue, except in the lingual radix zone. The fungiform papillae are distributed among the filiform papillae. There are three vallate papillae one median and two laterals and these tall and conical papillae exhibit an inverted V-shaped pattern. The foliate papillae are well developed (Machida et al., 1967). In *Cercopithecus aethiops*, the tongues are elongated, have a rounded apex and are wide and flat. The filiform papillae are distributed over the entire dorsal surface of the lingual body. Most filiform papillae have several pointed processes; however, those of the lingual apex have a conical shape. Dome-shaped fungiform papillae are scattered among these filiform papillae, especially at the lingual apex. The foliate papillae have ridges separated by deep grooves. (Machida et al., 1967; Emura et al., 2002). Machida et al. (1967) reported that this species has four vallate papillae, while Emura et al. (2002) reported a triangular arrangement of the vallate papillae, which are surrounded by a groove. The number of vallate papillae may thus vary among individuals.

In *Papio cynocephalus*, the tongues are elongated, have a rounded apex and are wide and flat. The dorsal and lateral tongue surfaces have filiform, fungiform, vallate and foliate papillae. The filiform papillae are compactly distributed on the dorsal surface of the tongue, except in the lingual radix zone. The fungiform papillae are distributed among the filiform papillae. The foliate papillae are well developed. There are five tall and conical vallate papillae, which are arranged horizontally between the lingual body and lingual radix (Machida et al., 1967). In *Papio anubis*, the morphological features of the tongue are almost identical to those of *Papio cynocephalus*. However, Machida et al. (1967) reported that the number of vallate papillae is four rather than the five observed in *Papio cynocephalus*.

In *Mandrillus sphinx*, their tongues are flat and fairly slender. The dorsal surface has filiform, fungiform, vallate and foliate papillae. The filiform papillae are compactly distributed on the dorsal surface of the tongue, except in the lingual radix zone. The filiform papillae

consist of a thick main process with several slender accessory processes extending from the anterior base. The fungiform papillae are distributed among the filiform papillae. The vallate papillae comprise one median and two lateral papillae, and the foliate papillae consist of several ridges and slits (Kobayashi et al. 2004).

Machida et al. (1967) described the morphology of the tongue in three species of genus Macaca: *Macaca mulatta*, *Macaca nemestrina* and *Macaca nigra*. Their tongues of these species are elongated, have a rounded apex and are wide and flat. The dorsal and lateral surfaces of the tongue have filiform, fungiform, vallate and foliate papillae. The filiform papillae are compactly distributed on the dorsal surface of the tongue, except in the lingual radix zone. The fungiform papillae are distributed among the filiform ones. The foliate papillae are well-developed. There are four vallate papillae in *Macaca mulatta* and five in *Macaca nemestrina* and *Macaca nigra*. The tall and conical vallate papillae are arranged horizontally between the lingual body and lingual radix (Machida et al., 1967). The difference in the number of vallate papillae is likely attributed to inter-individuals variability rather to species differences, as very few or only one member of each species was studies. The number of vallate papillae might vary among individuals of the same species.

In *Macaca irus*, macroscopically the tongue is somewhat elongated antero-posteriorly, has a round tip when viewed dorsally and is flat when viewed from the side. Filiform papillae are densely distributed over the entire dorsal surface of the tongue, except in the narrow lingual-radix zone. Dome-shaped fungiform papillae are scattered among these filiform papillae. Each filiform papilla is crown-shaped and has a central round concavity and several or many branches surrounding it from the rear. These branches adhere together around the basal quarter of each papilla and resemble a fence opened only on the anterior side. The structure of filiform papillae is almost identical throughout the dorsal surface of the tongue. There are four to six vallate papillae, which are located at the end of the lingual body (Iwasaki, 1992a, b; Kobayashi et al., 2004). The foliate papillae comprise several ridges and slits arranged vertically on the posterolateral tongue margin (Kobayashi et al., 2004).

In *Macaca fuscata*, the structural features of the tongue are similar to those of *Macaca irus*. Namely, macroscopically the tongue is somewhat elongated antero-posteriorly, has a round tip when viewed dorsally and is flat when viewed laterally. Filiform papillae are densely distributed over the entire dorsal tongue surface, except for the radix zone. Dome-shaped fungiform papillae are scattered among the filiform papillae. The filiform papillae are crown-shaped and have a central round concavity and several branches surround each papilla posteriorly. The structure of the filiform papillae is fundamentally identical in all areas of the dorsal tongue surface (Iwasaki et al., 1992; Emura et al., 2002). Iwasaki et al. (1992) and Emura et al. (2002) disagree regarding the distribution of vallate papillae: the former reported that four vallate papillae are located on the dorsal surface at the end of the body, the latter group observed three vallate papillae, with the apex of the triangle directed posteriorly. The distribution pattern of vallate papillae may therefore vary in this species, as in *Macaca irus*. The foliate papillae have ridges separated by deep grooves and are present on the dorsolateral aspect of the posterior tongue (Emura et al., 2002).

In the subfamily Colobinae, only one study of tongue morphology has reported in *Colobus guereza*. Macroscopically the tongue is somewhat elongated antero-posteriorly, has a round tip when viewed dorsally and is flat when viewed laterally. The filiform papillae are compactly distributed on the lingual body, except in the lingual radix zone. The fungiform papillae are scattered among them. There are three vallate papillae: one median and two lateral papillae. These papillae are tall and conical and form an inverted V-shaped pattern. The foliate papillae comprise several

ridges and slits arranged vertically on the posterolateral tongue margin (Yoshimura et al., 2019).

3.2.3.2. Hylobatidae (Family). Fleagle (2013) illustrated the lingual dorsal surface of *Hylobates lar* of the family Hylobatidae. The anteroposterior length of the tongue is about twice the width of its central portion, when viewed dorsally, and the apex is rounded. On the basis of the distribution of lingual papillae, the dorsal surface can be divided into the anterior two thirds (the lingual body) and posterior one third (the lingual radix). Namely, the filiform papillae are compactly distributed on the lingual body, and fungiform papillae are scattered among them. No filiform or fungiform papillae are present on the lingual radix. The vallate papillae are located on the border between the lingual body and radix and, exhibit a Y-shape. One large vallate papilla is located on the central part of the radix, and a small papilla is present on each side of the border area. Foliate papillae are present bilaterally on the sides of the border area. The lingual papillae have not been extensively studies in this species.

3.2.3.3. Hominidae (Family). Machida et al. (1967) reported morphological observation of the tongue of *Gorilla gorilla* in genus Gorilla. The tongue of this species is elongated, has a rounded apex and is wide and flat. The dorsal and lateral surfaces of the tongue have filiform, fungiform, vallate and foliate papillae. The filiform papillae are compactly distributed on the dorsal surface of the tongue, except in the lingual radix zone. The fungiform papillae are distributed among the filiform papillae. The foliate papillae are well developed. There are six to seven vallate papillae, and the number varies among individuals. The tall and conical vallate papillae are arranged horizontally between the lingual body and lingual radix (Machida et al., 1967).

The morphology of the tongue of genus Pan was studied in the common chimpanzee, *Pan troglodytes*, by Hofer et al. (1990b) and Hladik and Simmen (1997). The tongue of *Pan troglodytes* is macroscopically elongated, oval-shaped and of moderate thickness. The body and radix are separated by the distribution of vallate papillae, and the dorsal surface of the body is divided longitudinally by a slight median sulcus in the anterior half. Filiform papillae are densely distributed over the entire dorsal tongue surface, including the radix. The fungiform papillae are scattered among these filiform papillae. Filiform and fungiform papillae are plentiful at the lingual apex. However, the form of individual filiform papillae is unclear. The structure of the fungiform papillae is mushroom-shaped with a dome shaped upper surface and a narrow base. The foliate papillae consist of about ten ridges and slits arranged vertically on the posterolateral margin of the tongue. The vallate papillae vary in number from six to nine and are located at the boundary between the body and radix (Hofer et al., 1990b).

The tongue of *Homo sapiens* is macroscopically oval-shaped and of moderate thickness. The body and radix are clearly separated by a V-shaped depression, the *sulcus terminalis*, and the dorsal surface of the body is divided longitudinally by a median sulcus. Filiform papillae are densely distributed over the entire dorsal surface of the tongue except for the radix. The fungiform papillae are scattered among the filiform papillae. Each filiform papilla has a basal column with numerous slender protrusions from the upper periphery. The fungiform papillae are mushroom-shaped, with a dome-shaped upper surface and a narrow base. The vallate papillae vary in number from four to twelve and are located at the boundary between the body and radix. The foliate papillae consist of three to eight ridges and slits arranged vertically on the posterolateral margin of the tongue (Provenza, 1986; Kobayashi et al., 2004).

4. Comparative morphology of the tongue and lingual papillae among species

The comments of the specialized feature of the tongue of the extant primates are summarized in Table 1.

Dorsal and lateral views of the outline of the tongue are very similar for all species of suborders Platyrrhini and Catarrhini, although tongue size varies in relation to the length of the body. Filiform papillae have the same fundamental structure in all species reported: namely, filiform papillae are crown-shaped and have a central round concavity. There are several or many branches that surround each papilla posteriorly. The distribution pattern of the filiform papillae does not significantly differ among the species reported. These features of filiform papillae can be regarded as common to the primate tongue. The form and distribution pattern of fungiform and foliate papillae do not significantly differ among species of Platyrrhini and Catarrhin. However, the distribution pattern of vallate papillae does differ somewhat between these suborders. In all species of the infraorder Platyrrhini, three vallate papillae are located on the marginal end of the lingual body and exhibit a V-shaped pattern.

In contrast, in species of infraorder Catarrhini, the distribution pattern of the vallate papillae seems to differ among species. In *Cercopithecus aethiops* and *Mandrillus sphinx*, the vallate papillae consist of one median and two lateral papillae, as in almost all species of the Platyrrhini. In *Macaca fuscata*, both three and four vallate papillae have been reported. In *Macaca irus* and *Homo sapiens*, more than three vallate papillae are located at the end of the lingual body; *Macaca irus* has four to six vallate papillae, and *Homo sapiens* has four to twelve, which are located at the boundary between the body and radix. However, the form of vallate papillae is similar among all observed species. At minimum, the distribution pattern of vallate papillae may be specific to *Macaca irus* and *Homo sapiens*. However, to test this hypothesis, further information on the distribution pattern of vallate papillae should be obtained from a wide range of species, including members of the infraorders Lorisiformes, Lemuriformes and Tarsiiformes. If it is true, explanation of functional differences in the distribution pattern of vallate papillae will require a better understanding of the evolutionary background of differences between the distribution of vallate papillae in these two species and the distribution in other species of infraorder Catarrhini.

5. The tongue musculature in extant primates

In almost all tetrapods the tongue can be regarded morphologically as a mass of voluntary muscle covered by a mucosal sheath (Iwasaki et al., 2019). Considering the special function of the human tongue in speech, it is very important to identify how changes occurred in lingual muscle in primate evolution. However, the musculature of the primate tongue has rarely been studied even to this day.

The tongue muscles of *Homo sapiens* are also divided into extrinsic and intrinsic muscles according to their origin. Extrinsic muscles arise from external organs and are inserted into the tongue, whereas intrinsic muscles have their origin and terminations within the tongue (Barnwell, 1976). In the tongue of the chimpanzee, *Pan troglodytes*, Takemoto (2008) identified four extrinsic muscles (the genioglossus muscle, hypoglossus muscle, styloglossus muscle and palatoglossus muscle) and four intrinsic muscles (the transverse muscle, vertical muscle, superior longitudinal muscle and inferior longitudinal muscle), and indicated that the tongue consists of inner and outer regions. The external shape of the tongue of *Pan troglodytes* is flatter than that of *Homo sapiens*, although the tongue musculature of these species is similar.

Table 1
Summarized features of the tongue of primates reported.

Semiorder	Strepsirrhini			
Suborder	Strepsirrhini			
Infraorder	Lemiriformes		Lorisiformes	
Family	Lemuridae		Lorisidae	
Genus	Lemur	Eulemur	Arctociebus	Perodicticus
Species reported	*Lemur mongoz*	*Eulemur fulvus rufus* *Eulemur rubriventer* *Eulmur sp.*	*Arctocebus calabarensis*	*Prodicticus potto*
Shape of the tongue	The lingual apex is narrow and pointed. The cartilaginous sublingua is well developed.	The tongues are elongated and have a rounded apex, the width of which is somewhat narrower than that of the posterior part. Red-bellied lemurs have a feathered, brush-like tongue tip which lemurs lack.	The lingual apex is narrow and pointed, and the cartilaginous sublingua is well developed.	The lingual apex is narrow and pointed, and the cartilaginous sublingua is wesll developed.
Filiform and fungiform papillae	The filiform papillae are distributed over the anterior two thirds of the dorsal surface, and the fungiform papillae are scattered among them.	The dorsal surface has three types of papillae: filiform, fungiform and vallate papillae.	The filiform papillae are distributed over the anterior two thirds of the dorsal surface, and the fungiform papillae are scattered among them.	The filiform papillae are distributed over the anterior two thirds of the dorsal surface, and fungiform papillae are scattered among them.
Vallate and foliate papillae	Three vallate papillae are located on the dorsal surface of the border between the lingual body and radix. One is located in the posterior center, and two are on either side of the anterior region of the boder, thus exhibiting an inverted V-shaped pattern. The foliate papillae are particularlly recognizable.	No detail information of vallate papillae. No foliate papillae is recognizable.	There are three vallate papillae on the border between the lingual body and radix. One is located in the posterior center, and one is present on each side of anterior region of the border. These three vallate papillae form an inverted V-shaped pattern. No foliate papillae is recognizable.	There are three vallate papillae on the border between the lingual body and radix. One is located in the posterior center, and one is present on each side of anterior region of the border. These three vallate papillae form an inverted V-shaped pattern. No foliate papillae is recognizable.
Semiorder	Strepsirrhini			Haplorhini
Suborder	Strepsirrhini			Tarsiiformes
Infraorder	Lorisiformes			Tarsiiformes
Family	Lorisidae	Galagidae		Tarsiidae
Genus	Nycticebus	Galago	Otolemur	Carlito
Species reported	*Nycticebus coucang* *Nycticebus bengalensis* *Nycticebus javanicus* *Nycticebus menagensis* *Nycticebus boneanus* *Nycticebus kayan* *Nycticebus bancanus* *Nycticebus pygmaes*	*Galago demidovii* *Galago senegalensis* *Galago sp.*	*Otolemur crassicaudatus*	*Carlito syrichta*
Shape of the tongue	The lingual apex is narrow and pointed, and cartilaginous sublingua is well developed.	The lingual apex is narrow and pointed, and cartilaginous sublingua is well developed.	The lingual apex is narrow and pointed, and the cartilaginous sublingua is well developed.	The lingual apex is narrow and pointed, and the cartilaginous sublingua is well developed.
Filiform and fungiform papillae	The filiform papillae are distributed over the anterior two thirds of the dorsal surface, and the fungiform papillae are scattered among them.	The filiform papillae are distributed over the anterior two thirds of the dorsal surface, and the fungiform papillae are scattered among them.	The filiform papillae are distributed over the anterior two thirds of the dorsal surface, and the fungiform papillae are scattered among them.	The filiform papillae are distributed over the anterior two thirds of the dorsal surface, and the fungiform papillae are scattered among them.
Vallate and foliate papillae	There are three vallate papillae, which are located near the border between the lingual body and radix. One is located in the posterior center, and one is located on each side of anterior region of the border. These three vallate papillae are arrange in an inverted pattern of V-shape. No foliate papillae is recognizable.	There are three vallate papillae near the border between the lingual body and radix. One is located in the posterior center, and one each is located on either sides of the anterior region of the border. These three vallate papillae form an inverted V-shape pattern. No foliate papillae is recognizable.	There are three vallate papillae located on the border between the lingual body and radix. One is located in the posterior center, and one is located on each side of anterior region of the border. These three vallate papillae are arrange in an inverted V-shaped pattern.	There are three vallate papillae, which are located on the border between the lingual body and radix. One is located in the posterior center, and one is located on each side of anterior region of the border. These three vallate papillae are arrange in an inverted V-shaped pattern. No foliate papillae is recognizable.
Semiorder	Haplorhini			
Suborder	Anthropoidea			
Infraorder	Platyrrhini			
Family	Atelidae	Cebidae		
Genus	Alouatta	Cebus	Saimiri	Callithrix
Species reported	*Alouatta caraya*	*Cebus apella*	*Saimiri aciureus*	*Callithrix jacchus* *Callithrix penicillata*
Shape of the tongue	The tongues are elongated and have a rounded apex. The plica sublingualis is observed.	The tongue is antero-posterior long and wide from the apex to the radix.	The tongue is elongated and has a rounded apex.	The tongues are small and elongated and have a rounded apex.

Table 1 (*Continued*)

Filiform and fungiform papillae	The form of the filiform papillae varies according to the tongue region, such as crown-shaped in the anterior, spear-shaped in the middle and filamentous in the posterior dorsal surface of the lingual body. The fungiform papillae are distributed among the filiform papillae.	The crow-shaped filiform papillae have several branched processes and are compactly distributed over the entire dorsal surface of the anterior two thirds of the tongue.The dome-shaped fungiform papillae are scattered among filiform papillae, with taste pores.	Filiform papillae are distributed over the entire dorsal surface of the tongue, except in the lingual radix zone. A flattened circular area in the center of the filiform papillae is surrounded by several pointed processes. Dome-shaped, fungiform papillae are scattered among the filiform papillae on the dorsal and lateral surfaces.	Filiform papillae are distributed over the entire dorsal surface of the tongue, except in the radix zone. The form of the filiform papillae varies somewhat according to the region of the tongue: they are conical with a few protrusions in the anterior region and crown-shaped in the posterior of the body. The fungiform papillae are distributed among the filiform papillae.
Vallate and fpliate papillae	There aree three vallate papillae; one median and two laterals which are tall and conical.	Three vallate papillae are present on the marginal end of the lingual body. The central vallate papilla and one vallate papilla on each side are located at the border between the body and radix and exhibit an inverted V-shaped pattern.	Three vallate papillae are present on the marginal end of the lingual body and exhibit a V-shaped pattern.	The vallate papillae comprise one median and two laterals papillae and exhibit an inverted V-shaped pattern.
	The foliate papillae are well developed.	No detail information of foliate papillae.	The foliate papillae, which comprise five ridges, are anterior to the attachment of the glossopalatine fold.	The foliate papillae are well developed and clearly visible bilaterally between the body and radix.
Semiorder	Haplorhini			
Suborder	Anthropoidea			
Infraorder	Platyrrhini			Catarrhini
Family	Cebidae			Cercopithecidae
Genus	Cebuella	Leontopithecus	Saguinus	Cercopithecus
Species reported	*Cebuella pygmaea*	*Leontopithecus rosalia*	*Saguinus ursula* *Saguinus nigricollis*	*Cercopithecus mitis* *Cercopithecus aethiops*
Shape of the tongue	The length of the tongue of the adult is about three times longer than the width.	The tongues are elongated and have a rounded flat apex.	The tongues are elongated and flat and have a rounded apex.	The tongues are elongated, have a rounded apex and are wide and flat.
Filiform and fungiform papillae	The filiform papillae are compactly distributed on the dorsal surface of the tongue, except in the lingual radix zone. The fungiform papillae are distributed among the filiform papillae.	The filiform papillae are compactly distributed on the dorsal surface of the tongue, except in the lingual radix zone. The filiform papillae are crown-shaped or finger-like papillae and have a flat center and longer and more numerous prolongations. The fungiform papillae are present among filiform papillae.	The filiform papillae are compactly distributed on the dorsal surface of the tongue, except in the lingual radix zone. The filiform papillae comprise of small spine-like protrusions in a U-shaped arrangement. The fungiform papillae are distributed among the filiform papillae.	The filiform papillae are compactly distributed on the dorsal surface of the tongue, except in the lingual radix zone. The fungiform papillae are distributed among the filiform papillae.
Vallate and foliate papillae	The median vallate papilla has an oral-shape, and the lateral vallate papillae are located bilaterally on the border between the body and radix and exhibit an inverted V-shaped pattern.	The vallate papillae consist of one median and two lateral papillae.	The vallate papillae comprise one median and two lateral papillae. These papillae are tall and conical and form an inverted V-shaped pattern.	There are three vallate papillae one median and two laterals and these tall and conical papillae exhibit an inverted V-shaped pattern.
	The foliate papillae are well developed and clearly visible bilaterally between the body and radix.	The foliate papillae have very few folds.	The well-developed foliate papillae consist of approximately five slits.	The foliate papillae are well developed.
Semiorder	Haplorhini			
Suborder	Anthropoidea			
Infraorder	Catarrhini			
Family	Cercopithecidae			
Genus	Papio	Mandrillus	Macaca	Colobus
Species reported	*Papio cynocephalus* *Papio anubis*	*Mandrillus sphinx*	*Macaca mulatta* *Macaca nemestrina* *Macaca nigra* *Macaca irus* *Macaca fuscata*	*Colobus guereza*
Shape of the tongue	The tongues are elongated, have a rounded apex and are wide and flat.	The tongues are flat and fairly slender.	The tongue are are elongated, have a rounded apex and are wide and flat.	The tongue is somewhat elongated antero-posteriorly, has a round tip when viewed dorsally and is flat when viewed laterally.
Filiform and fungiform papillae	The filiform papillae are compactly distributed on the dorsal surface of the tongue, except in the lingual radix zone. The fungiform papillae are distributed among the filiform papillae.	The filiform papillae are compactly distributed on the dorsal surface of the tongue, except in the lingual radix zone. The filiform papillae consist of a thick main process with several slender accessory processes extending from the anterior base. The fungiform papillae are distributed among the filiform papillae.	The filiform papillae are compactly distributed on the dorsal surface of the tongue, except in the lingual radix zone. Each filiform papilla is crown-shaped and has a central round concavity and several or many branches surrounding it from the rear. The fungiform papillae are distributed among the filiform ones.	The filiform papillae are compactly distributed on the lingual body, except in the lingual radix zone. The fungiform papillae are scattered among them.

Table 1 (*Continued*)

Vallate and foloiate papillae	There are five tall and conical vallate papillae, which are arranged horizontally between the lingual body and lingual radix.	The vallate papillae comprise one median and two lateral papillae.	There are four to six vallate papillae, which are located at the end of the lingual body, and their shape is tall and conical.	There are three vallate papillae: one median and two lateral papillae. These papillae form an inverted V-shaped pattern.
	The foliate papillae are well developed.	The foliate papillae consist of several ridges and slits.	The foliate papillae are well-developed, and comprise several ridges and slits on the posterolateral tongue margin.	The foliate papillae comprise several ridges and slits arranged vertically on the posterolateral tongue margin.
Semiorder	Haplorhini			
Suborder	Anthropoidea			
Infraorder	Catarrhini			
Family	Hylobatidae	Hominidae		
Genus	Hylobates	Gorilla	Pan	Homo
Species reported	*Hylobates lar*	*Gorilla gorilla*	*Pan troglodytes*	*Homo sapiens*
Shape of the tongue	The anteroposterior length of the tongue is about twice the width of its central portion, when viewed dorsally, and the apex is rounded.	The tongue of this species is elongated, has a rounded apex and is wide and flat.	The tongue is elongated, oval-shaped and of moderate thickness. The dorsal surface of the body is divided longitudinally by a slight median sulcus in the anterior half.	The tongue is oval-shaped and of moderate thickness. The body and radix are clearly separated by a V-shaped depression, and the dorsal surface of the body is divided longitudinally by a median sulcus.
Filiform and fungiform papillae	The filiform papillae are compactly distributed on the lingual body, and fungiform papillae are scattered among them. No filiform or fungiform papillae are present on the lingual radix.	The filiform papillae are compactly distributed on the dorsal surface of the tongue, except in the lingual radix zone. The fungiform papillae are distributed among the filiform papillae.	Filiform papillae are densely distributed over the entire dorsal tongue surface, including the radix. The fungiform papillae are scattered among these filiform papillae. The structure of the fungiform papillae is mushroom-shaped.	Filiform papillae are densely distributed over the entire dorsal surface of the tongue except for the radix. Each filiform papilla has a basal column with numerous slender protrusions from the upper periphery. The mushroom-shaped fungiform papillae are scattered among the filiform papillae.
Vallate and foliate papillae	The vallate papillae are located on the border between the lingual body and radix and, exhibit a Y-shape. One large vallate papilla is located on the central part of the radix, and a small papilla is present on each side of the border area.	There are six to seven vallate papillae, and the number varies among individuals. The tall and conical vallate papillae are arranged horizontally between the lingual body and lingual radix.	The vallate papillae vary in number from six to nine and are located at the boundary between the body and radix.	The vallate papillae vary in number from four to twelve and are located at the boundary between the body and radix.
	Foliate papillae are present bilaterally on the sides of the border area.	The foliate papillae are well developed.	The foliate papillae consist of about ten ridges and slits arranged vertically on the posterolateral margin of the tongue.	The foliate papillae consist of three to eight ridges and slits arranged vertically on the posterolateral margin of the tongue

6. Functional role of the tongue in primate evolution

The food habits of primates in Strepsirrhini and Haplorhini are species dependent. Daily, seasonal and yearly variation in food choice is one of the greatest differences among living primates. Primate diets are generally divided into three categories: fruit, leaves, and fauna. In addition, feeding on foods such as gums, seeds or nectar is an important aspect of primate dietary behavior (Fleagle, 2013). However, Machida et al. (1967), reported that tongue shape significantly differs among prosimians, Strepsirrhini, and New World and Old World monkeys, Haplorhini. The lingual apex of prosimians is narrow and pointed, and the outline is elongated antero-posteriorly. These features are shown in a comparative illustration by Fleagle (2013). In addition, the cartilaginous sublingual is well developed only in prosimians. In contrast, almost all tongues of primates of Haplorhini are wide and oval with a rounded tip. These features of prosimian tongues are effective for taking up foods with the tongue alone, because the tongue is capable of fine movement when outside the oral cavity, more so than those of Haplorhini.

In contrast, primates that use their hands to manipulate food (such as mountain gorillas, capuchins and macaques in Haplorhini) or tools (humans) have well-developed opposable thumbs (Fleagle, 2013). Anakel-Simons (2007) reported that Old World monkeys, great apes, and humans have opposable thumbs, while all prosimians have pseudo-opposable thumbs.

These findings suggest that in Haplorhini the role of the tongue in food uptake has diminished with progress in the manipulation of food by hand, especially with the use of tools by hand in Homininae. In a sense, we can regard this change from prosimians to Homininae as the degeneration of food uptake by the tongue, although the functional role of the tongue within the oral cavity has not diminished.

Relatively few myologic studies of the tongue have been performed, except for analysis of the human tongue. Therefore, we have not discussed the myologic features of the tongue in this report. However, as mentioned above, the features of prosimian tongue are effective for taking up food with the tongue alone. This suggests that extrinsic muscles are better developed in prosimian tongues than in Haplorhini species. However, muscles supporting the intraoral tongue movement principally the intrinsic muscles of the tongue might be better developed in Haplorhini, especially Hominidae, than in Strepsirrhini.

Although there is no comprehensive comparison of the distribution and form of lingual papillae in all Strepsirrhini and Haplorhini species, the distribution pattern and form of lingual papillae, excluding foliate papillae, are very similar in reported primate species. Most of prosimian species have no foliate papillae or have a different type of papilla that substitutes for foliate papillae; however, foliate papillae are generally well developed in Haplorhini. In addition, prosimians and New World macaques, Platyrrhini, have three vallate papillae, which exhibit an inverted

V-shaped pattern, but vallate papillae are more numerous in Old World macaques, Catarrhini. All these differences seem to be attributable to phylogenetic origin rather than to functional role or food habits.

7. Conclusions

To clarify the role of the primate tongue as a means to better understand the evolution of oral function among primates (an example of adaptation within a restricted phylogenetic group), we reviewed the literature on the morphology of the tongues of extant primates in relation to phylogenetic classification.

We noted that prosimian tongues are effective for taking up food with the tongue alone, as they are more capable of fine movements when outside the oral cavity than those of Haplorhini. In contrast, the role of the tongue in food uptake has diminished in conjunction with progress in manual manipulation of food in Haplorhini, especially tool use in Homininae. This change from prosimians to Homininae can be regarded as degeneration of the role of the tongue in food uptake, although the functional role of the tongue within the oral cavity has not diminished.

The distribution pattern and form of the lingual papillae, excluding foliate papillae, are very similar among all reported primate species. Most species of prosimians have no foliate papillae or a different type of papillae that substitutes for foliate papillae; however, foliate papillae are generally well developed in Haplorhini. Prosimians and New World macaques, Platyrrhini, have three vallate papillae in an inverted V-shaped pattern, whereas, Old World macaques, Catarrhini, have a large number of vallate papillae. All these differences appear to result from phylogenetic origin rather than from functional role or food habits.

Ethical Statement Not Applicable for this article.

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