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The Circumorbital Foramina in Primates: A Phylogenetic Perspective

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Abstract

This paper documents the diversity and variation in the circumorbital foramina in extant primates. A qualitative and quantitative analysis of the circumorbital foramina, comprising the supraorbital foramen, the infraorbital foramen, and the malar foramina, was carried out using representative species from nine extant families of primates. The information obtained from the study is used to reconstruct ancestral morphotypes, and to make inferences about evolutionary changes that may have taken place in the major primate lineages. In addition, the analysis provides potentially useful comparative data for interpretation of the phylogenetic significance and paleobiological implications of the circumorbital foramina in fossil primates.

Introduction

The aim of this paper is to examine the phylogenetic implications of the circumorbital foramina in primates. The circumorbital foramina comprise the supraorbital foramen in the frontal bone, the infraorbital foramen in the maxillary bone and the malar foramina (alternatively known as the jugal or zygomatic foramina) in the zygomatic bone. A comparative survey of the circumorbital foramina in extant primates yields new information that is useful in documenting evolutionary changes in facial morphology in the various primate lineages, and provides a comparative framework for interpretation of the significance and paleobiological implications of the circumorbital foramina in fossil primates.

We had already published the main results of our comparative analysis of the primate circumorbital foramina (MSUYA & HARRISON 1994), so only a brief overview is provided below. In this paper we focus in particular on the phylogenetic significance of the circumorbital foramina in primates. The comparative data are used to reconstruct ancestral morphotypes of the major primate groups, and to make inferences about the evolutionary changes that may have taken place in the major primate lineages.

Materials and methods

The crania of 38 species of primates, comprising over 1,200 individual specimens, were examined to provide a comparative series for qualitative and quantitative analyses (Tab. 1). Only adult specimens collected from the wild were included in the sample. The species were selected so as to ad-

equately sample the taxonomic and adaptive diversity within the primates. They include representatives from the following nine families: Indriidae; Lemuridae; Lorisidae; Tarsiidae; Cebidae; Callitrichidae; Cercopithecidae (including Colobinae and Cercopithecinae); and Hylobatidae and Hominidae (including the great apes and humans).

Most of the non-human osteological specimens included in this study are housed in the Department of Mammology, American Museum of Natural History, New York. Additional data on the number of infraorbital foramina in *Pongo* were obtained from the Zoological Reference Collection, National University of Singapore. The sample of human skulls is housed in the Department of Anthropology, New York University.

The following variables were noted for each of the circumorbital foramina: (1) the number of foramina on each side of the face; (2) the size of the main (largest) foramen; (3) the shape and structure of the foramen; and (4) the location of the foramen and its relationship to other major anatomical structures on the face.

Supraorbital foramen

The supraorbital foramen in humans is small in size and oval in shape. As a common variation, the foramen may appear as an incomplete foramen or a notch. By contrast, a distinct supraorbital foramen is less common in apes and when it occurs it is usually relatively much smaller in size. Supraorbital notches are found throughout the Hominoidea as a relatively common variation, although

they occur much less frequently than a true foramen in all species examined, except *Hylobates lar* (Tab. 1).

The supraorbital foramen was found to occur in all species of cercopithecids. They have a higher frequency of occurrence than in hominoids, with an incidence in all species greater than 50% of individuals. In several species of cercopithecids, all or almost all individuals possess a well-defined supraorbital foramen or notch (Tab. 1). Multiple foramina are common and they frequently consist of a full foramen in association with a supraorbital notch. Most of Old World monkeys show some incidence of a supraorbital notch, although this feature is found most commonly among the papionins.

A supraorbital foramen is found to occur in most platyrrhines and is almost always a complete foramen (Tab. 1). A supraorbital foramen or a notch is generally lacking in strepsirhines, although it can be identified in a few specimens as a tiny perforation along the superior orbital margin. It appears to be entirely lacking in *Tarsius*.

Infraorbital foramen

In humans, the infraorbital foramen perforates the facial surface of the maxilla just above the canine fossa. A single foramen occurs in 83.6% of humans (Le DOUBLE 1906; SCHULTZ 1954; RIESENFELD 1956; MSUYA & HARRISON 1994). Le DOUBLE (1906) reported that two and three foramina occur in only 11.0% and 0.6% of humans respectively. Four foramina occur very rarely, being found in only 0.1% of cases examined by both Le DOUBLE (1906) & RIESENFELD (1956), while a single case of a human with five foramina was reported by GRÜBER (1874).

A single foramen is the modal condition in *Hylobates lar*, although other hylobatids commonly have two infraorbital foramina. Two foramina is also the modal pattern in the African apes (ASHTON & ZUCKERMAN 1958). In *Pongo pygmaeus*, the modal number is four foramina, but up to six foramina may occur in some individuals (Tab. 1).

In Old World monkeys, the most common modal number is three foramina. The highest number of foramina occurs in *Papio* and *Mandrillus* which have a modal frequency of eight foramina (SCHAEFER 1954; HILL 1966, 1970; MSUYA & HARRISON 1994).

Among platyrrhines, a single infraorbital foramen is found in callitrichids and the more generalized cebids, such as *Aotus* and *Callicebus*. However, the most common modal number in New World monkeys is two foramina, although several species have a modal number of three or even four infraorbital foramina. The modal number in strepsirhines and in *Tarsius* ranges from one to three (Tab. 1; OPPENHEIM 1911; SCHAEFER 1954; HERSHKOVITZ 1977; MSUYA & HARRISON 1994).

Malar foramen

In humans, several malar foramina perforate the zygomatic bone – the zygomaticofacial foramen, the zygomatico-orbital foramen and the zygomaticotemporal foramen. Only those foramina that open directly onto the anterior aspect of the face (i.e., the zygomaticofacial foramina) were included in this study. The modal number of malar foramina in humans is two, although up to four perforations may be found in some individuals (Tab. 1). The size of the main malar foramen varies considerably in size, although it is always much smaller than the infraorbital foramen (MSUYA & HARRISON 1994).

Most apes have a modal number of two malar foramina. However, three foramina occur as the modal number in *Symphalangus* and *Pan*, while the highest incidence occurs in *Hylobates lar*, which has a modal frequency of four foramina (Tab. 1). In most apes, the main malar foramen is much smaller than the infraorbital foramen. The foramen is particularly small in *Gorilla* and *Homo*, and tends to be somewhat larger in hylobatids. Among the hominoids, *Pongo* is exceptional in having a relatively large malar foramen, one which approaches the infraorbital foramen in size.

In cercopithecids, the modal pattern is two or three malar foramina, which are usually smaller than the infraorbital foramen. Among platyrrhines, modal frequencies range from two to five, but the most common number is two foramina. The malar foramen in these primates is generally relatively larger in size than the infraorbital foramen, especially in *Alouatta*, *Ateles*, *Brachyteles*, *Lagothrix*, *Callicebus* and *Pithecia*. However, it remains relatively small in *Callithrix*, *Cebus*, *Aotus*, *Cacajao*, *Chiropotes* and *Saimiri*.

Usually only a single malar foramen is present in strepsirhines, although two foramina may occur in some species (MSUYA & HARRISON 1994). In general, the malar foramen in strepsirhines is smaller in size than the infraorbital foramen, although in *Lemur catta* the former is slightly larger. In *Tarsius* the malar foramen is absent.

Discussion

Some significant differences in the configuration of the circumorbital foramina occur between the major groups of primates. It is suggested that these differences may reflect important adaptive changes in the structure of the facial region of the cranium, and that they may be of some value in interpreting evolutionary changes among extant and fossil primates (MSUYA & HARRISON 1994). The evolutionary changes in the circumorbital foramina in primates can best be assessed by defining the nodal characteristics of a consensus cladogram derived from a set of a well-established relationships between the major groups of extant pri-

	Sample size ^a	Supraorbital foramen			Infraorbital foramen ^b		Malar foramina	
		% notch	% complete foramen	% occurrence of foramen and/or notch	Number of foramina	Modal Number	Number of foramina	Modal Number
<i>Propithecus</i> spp.	20 (10, 9)	0	5.0	5.0	1-4	3	1-4	1
<i>Lemur fulvous</i>	40 (10, 29)	0	2.5	2.5	1-3	1	1-4	2
<i>Lemur catta</i>	16 (4, 6)	0	0	0	2-3	2	1-4	1
<i>Loris tardigradus</i>	33 (16, 10)	0	0	0	2-4	3	1-2	1
<i>Nycticebus coucang</i>	33 (17, 12)	0	0	0	1-4	2	1-3	1
<i>Galago crassicaudatus</i>	40 (23, 14)	0	15.0	15.0	2-4	3	0-1	1
<i>Tarsius spectrum</i>	40 (16, 19)	0	0	0	1-3	1	0	0
<i>Callithrix jacchus</i>	20 (9, 9)	45.0	10.0	55.0	1-2	1	1-5	2
<i>Saquinus fuscicollis</i>	40 (20, 18)	0	12.5	12.5	1-4	1	2-5	2
<i>Alouatta seniculus</i>	40 (15, 14)	0	42.5	42.5	1-4	2	2-7	3
<i>Aotus trivirgatus</i>	20 (5, 10)	5.0	5.0	5.0	1-2	1	1-6	2
<i>Ateles goeffroyi</i>	40 (13, 25)	0	10.0	1.0	2-5	3	1-6	3
<i>Ateles paniscus</i>	15 (3, 9)	0	0	0	2-6	3	3-9	5
<i>Brachyteles arachnoides</i>	2 (0,1)	0	0	0	2-3	2	3-5	5
<i>Lagothrix lagothricha</i>	40 (17, 23)	0	5.0	5.0	1-5	2	2-4	2
<i>Callicebus torquatus</i>	4 (18, 20)	0	25.0	25.0	1-4	1	1-5	2
<i>Cebus apella</i>	40 (26, 14)	0	25.0	25.0	1-3	2	1-4	2
<i>Cebus nigrivittatus</i>	40 (25, 15)	0	40.0	40.0	2-6	4	2-5	3
<i>Cacajao calvus</i>	20 (12,6)	0	80.0	80.0	2-6	3	2-8	2
<i>Chiropotes satanus</i>	40 (18, 18)	0	62.5	62.5	2-4	2	2-7	3
<i>Pithecia pithecia</i>	40 (23, 14)	0	25.0	25.0	2-52-5	2	1-4	2
<i>Saimiri sciureus</i>	40 (18, 21)	45.0	47.5	82.5	1-5	2	1-4	1
<i>Cercocebus albigena</i>	40 (19, 17)	87.5	70.0	100.0	3-10	5	1-7	3
<i>Cercopithecus mitis</i>	40 (20, 18)	35.0	40.0	55.0	2-7	3	2-6	3
<i>Cercopithecus ascanius</i>	40 (27, 13)	20.0	67.5	70.0	1-7	3	1-4	2
<i>Macaca fascicularis</i>	40 (19, 17)	80.0	55.0	87.5	2-5	3	1-4	2
<i>Mandrillus sphinx</i>	9 (6, 3)	44.4	66.7	77.7	3-8	8	1-5	2
<i>Papio anubis</i>	39 (27, 5)	84.6	69.2	94.9	5-12	8	1-3	2
<i>Colobus badius</i>	40 (29, 19)	75.0	87.5	100.0	2-7	3	1-5	3
<i>Nasalis larvatus</i>	20 (9, 9)	40.0	75.0	85.0	2-8	4	1-5	2
<i>Presbytis cristata</i>	40 (20, 20)	0	52.5	52.5	2-5	3	1-5	2
<i>Hylobates lar</i>	18 (7, 10)	44.4	5.5	44.4	1-2	1	2-8	4
<i>Hylobates hoolock</i>	40 (25, 13)	15.0	35.0	42.5	1-3	2	1-5	2
<i>Symphalangus syndactylus</i>	16 (6, 9)	12.5	43.8	50.0	1-4	2	1-5	3
<i>Pongo pygmaeus</i>	23 (8, 7)	0	12.5	12.5	1-6	3	2-7	2
<i>Gorilla gorilla</i>	38 (21, 10)	15.7	84.2	86.8	1-3	2	1-5	2
<i>Pan troglodytes</i>	40 (8, 10)	7.5	37.5	40.0	1-3	2	2-6	3
<i>Homo sapiens</i>	27 (0, 0)	63.0	66.7	85.2	1-2	1	1-4	2

Table 1: The frequency of circumorbital foramina in extant primates (from MSUYA & HARRISON 1994). a: The numbers in parentheses indicates the number of male and female specimens included in the sample respectively. The remaining specimens were of unknown sex. b: Individuals with multiple supraorbital foramina comprising a combination of notches and complete foramina were included in the columns for both notch and complete foramen. Hence, in some cases the total of these two columns exceeds 100%.

mates (Fig. 1). The circumorbital foramina do not themselves provide a sufficiently robust set of characteristics to be used as a basis for establishing or redefining the primary cladogram, but, when

used in conjunction with a consensus cladogram, they may offer new insights into the evolutionary transformation and palaeobiological implications of the circumorbital foramina (MSUYA & HARRISON

Node 1 – Ancestral primate morphotype

1. Supraorbital foramen: (a) absent or occurring as a very rare variant
(b) notches absent
2. Infraorbital foramen: (a) modal number = 1 (or possibly 2); range = 1–4
3. Malar foramen: (a) modal number = 1
(b) malar foramen very much smaller than infraorbital foramen

Node 2 – Ancestral haplorhine morphotype

Same as Node 1

Node 2a – Ancestral tarsiid morphotype

3. Malar foramen: (a) absent

Node 3 – Ancestral anthropoid morphotype

1. Supraorbital foramen: (a) more common variant (but less than 30% of individuals)
3. Malar foramen: (a) modal number = 2
(b) malar foramen slightly smaller than infraorbital foramen

Node 31 – Ancestral cebid morphotype

3. Malar foramen: (b) malar foramen relatively large

Node 4 – Ancestral catarrhine morphotype

1. Supraorbital foramen: (a) common variant (greater than 40% of individuals)
(b) notches occur as a variant

Node 4a – Ancestral cercopithecoid morphotype

1. Supraorbital foramen: (a) very common variant (greater than 50% individuals)
2. Infraorbital foramen: (a) multiple foramina; modal number = probably 3; range = 1–7

Node 5 – Ancestral hominoid morphotype

3. Malar foramen: (b) malar foramen much smaller than infraorbital foramen

Node 6 – Ancestral hominid morphotype

Same as Node 5

Node 6a – Ancestral pongine morphotype

2. Infraorbital foramina: (a) multiple foramina; modal number = 3; range 1–5
3. Malar foramen: (b) malar foramen relatively large

Node 7 – Ancestral hominine morphotype

3. Malar foramen: (b) malar foramen further reduced in size

Table 2: Summary of inferred phylogenetic changes in the circumorbital foramina of primates (see Fig. 2 for location of nodes) (from MSUYA & HARRISON 1994).

1994). The main conclusions of this analysis are presented below.

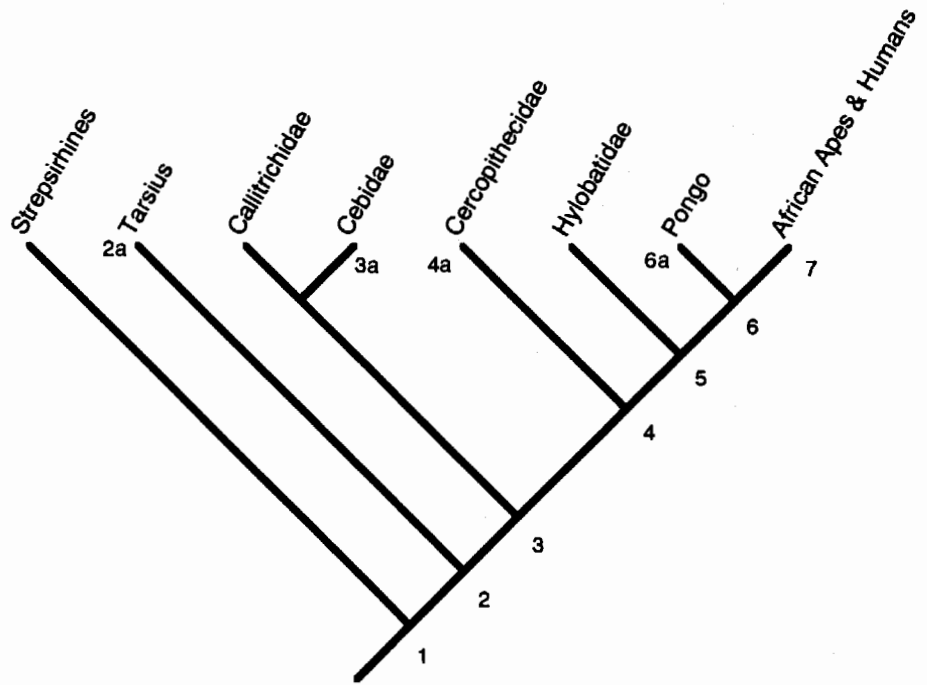
Supraorbital foramen

Strepsirhine primates almost universally lack a distinct supraorbital foramen (present in only 4.4% of the specimens sampled). We may conclude from this evidence that the primitive condition for the strepsirhine primates is the lack of a supraorbital foramen in which it occurs only as a very infrequent variant. If this is the case, then it follows that either (a) the lack of a supraorbital foramen is primitive for primates, or (b) the supraorbital foramen was present in primitive primates, and that its absence in modern strepsirhines is an autapomorphic development. Some support for the second of these alternatives comes from comparisons with primitive eutherian mammals, such as *Leptictis*, in which one or two small foramina perforate the frontal, just dorsal to the posterior end of the supraorbital process

(NOVACEK 1986). However, NOVACEK (1986) has noted that these perforations may have been developed independently in several eutherian lineages and that they may not represent a plesiomorphic trait in mammals. Furthermore, the absence of a supraorbital foramen in *Tarsius* would tend to support the inference that the lack of a supraorbital foramen is the primitive condition for all modern primates.

Among extant anthropoids, the supraorbital foramen occurs as a common variant. Most platyrrhine species have a low incidence of supraorbital foramina (less than 30% of individuals). Only two species, *Ateles paniscus* and *Brachyteles arachnoides*, were recorded as entirely lacking a foramen, but this may be an artifact of the small sample sizes for these taxa, rather than due to their being specialized cases. Several platyrrhines exhibit higher frequencies of supraorbital foramina, especially *Chiropotes satanus* (62.5%), *Cacajao calvus* (80.0%) and *Saimiri sciureus* (82.5%) (see Tab. 1). In almost

Fig. 1: Cladogram showing the relationships between the major groups of extant primates. For characteristics defining the numbered nodes refer to Tab. 2 (from MSUYA & HARRISON 1994).



all species the supraorbital foramen, when it occurred, formed a complete aperture, although supraorbital notches were identified as common variants in *Callithrix* and *Saimiri*. Although platyrrhines display considerable diversity in the expression of the supraorbital foramen, it seems reasonable to conclude that anthropoids, when compared with primitive primates, show an increased tendency to develop a supraorbital foramen. The evidence indicates that the primitive anthropoid condition is characterized by the occurrence of a supraorbital foramen which appears as a common variant (up to 30% of individuals).

Among extant catarrhines, all species exhibit the variable presence of a supraorbital foramen (all taxa have an incidence which exceeds 40% of individuals). Most species typically have a complete foramen, although a supraorbital notch may occur as a common variation (Tab. 1). However, in *Hylobates lar* and in several species of cercopithecids, especially the papionins, a supraorbital notch is found more frequently than a complete foramen. The highest incidence of a supraorbital foramen occurs in cercopithecoid monkeys, in which all species have more than 50% of individuals with a distinct foramen, and in many cases almost all of the individuals examined possess a supraorbital foramen or notch (Tab. 1, MSUYA & HARRISON 1994).

The comparative evidence suggests that there is a progressive increase in the incidence of supra-

orbital foramina from the strepsirrhines and *Tarsius* (3.6%), through the platyrrhines (33.5%) and hominoids (56.7%), to cercopithecids (85.7%). Although the factors that may underlie this progressive tendency in primates are not clearly understood, the increased incidence of supraorbital foramina in anthropoids, and especially in catarrhines, may be related to the development of distinct supraorbital tori in these primates. There appears to be a direct correlation between the development of a thickened torus in most species with the need for a well-developed means of neural and vascular communication through the bone itself. However, exceptions to this general tendency would indicate that the development and structural/functional relationships are complex and multifactorial.

Infraorbital foramen

The infraorbital foramen in primitive eutherian mammals is represented by a single, relatively large aperture, situated quite close to the inferior margin of the orbit. A single foramen is also the modal number for several non-anthropoid primates, such as *Lemur* and *Tarsius*, and this may represent the retention of the primitive mammalian condition. However, there is some diversity among the extant strepsirrhines, and multiple infraorbital foramina are quite common (Tab. 1, MSUYA & HARRISON 1994). Although a single foramen may be retained by primates from the ances-

tral eutherian morphotype, it appears to have undergone a reduction in its relative size. This has been linked to a corresponding reduction in the development of the facial vibrissae in primates (KAY & CARTMILL 1977).

Most platyrrhines and hominoids retain a pattern that approximates the primitive primate condition, with a single (or possibly two) relatively small infraorbital foramen located quite close to the orbital margin. Only *Ateles*, *Cacajao* and *Cebus nigrivittatus* among the New World monkeys, and *Pongo* among the apes, have developed a derived pattern in which the modal number of infraorbital foramina exceeds two (Tab. 1). The cercopithecids, by contrast, are characterized by the presence of multiple infraorbital foramina, and this appears to be a component of their ancestral morphotype (HARRISON 1987). Most cercopithecids have a modal number of three infraorbital foramina, and this is likely to represent the primitive condition for Old World monkeys (Tab. 1). However, it is evident that the large-bodied, long-faced cercopithecines have taken this specialization to an extreme, with some individuals possessing up to 12 foramina on each side of the face.

Malar foramen

Although strepsirhine primates exhibit some degree of variation in the number of malar foramina, with up to four foramina occurring in several isolated individuals, the modal number for the majority of species is a single foramen (MSUYA & HARRISON 1994). Only *Lemur fulvus* deviates from this pattern, with the majority of individuals possessing two discrete foramina (Tab. 1). Based on comparisons with other mammals, it seems reasonable to conclude that a single small foramen represents the primitive mammalian and primate conditions. In strepsirhine primates, which lack a postorbital septum, a single aperture is required to transmit the terminal branches of the malar nerve, while the distal branches which carry the small groups of genal vibrissae are routed laterally around the postorbital bar (ASHTON & OXNARD 1958).

Tarsius is unique among the primates in lacking entirely a malar foramen. This autapomorphic condition is almost certainly a structural specialization associated with the extraordinary hypertrophy of the eyes and orbits in this taxon.

Among anthropoid primates, the minimum modal number of malar foramina is two, although some individual specimens retain only a single foramen (Tab. 1). This increase in number of malar foramina with respect to the primitive primate condition is likely to be associated with the development of a postorbital septum in higher primates (MSUYA & HARRISON 1994). The almost complete separation between the orbit and the temporal

fossa by a bony plate apparently necessitates the development of alternative pathways for the transmission of nerves and blood vessels. In addition, anthropoids show a slight relative increase in size of the main malar foramen in relation to the infraorbital foramen (it is smaller than or subequal in size to the infraorbital foramen) when compared with the condition in strepsirhine primates. Some platyrrhines are specialized in developing relatively large malar foramina (ANTHONY 1946). This condition is especially pronounced in *Alouatta*, *Lagothrix*, *Ateles*, *Brachyteles*, *Callicebus* and *Pithecia*. Among the hominoids the hylobatids have a small malar foramen, which may be interpreted as the retention of the primitive anthropoid and catarrhine conditions. If this interpretation is correct, then *Pongo*, with a malar foramen that approximates in size the infraorbital foramen, may be derived in this respect. The African apes and humans, however, exhibit a contrasting specialization. In these primates, the malar foramen is extremely small, and is possibly a specialization that defines that clade (MSUYA & HARRISON 1994).

The main results of this analysis are summarized in Table 2. The information presented here provides a useful comparative framework for the interpretation of the evolutionary significance and palaeobiological implications of the circumorbital foramina in primates.

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