



Nasolacrimal anatomy and haplorhine origins

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ARTICLE INFO

Article history:

Received 6 July 2017

Accepted 15 November 2017

Keywords:

Fossil primates
Anthropoid
Omomyiformes
Rhinarium
Schizoscheilism
Syncheilism

ABSTRACT

Computed tomography X-ray imaging of the internal face in well-preserved primate fossil crania permits reconstruction of the nature of their nasal anatomy, including some soft-tissue features. These features are diagnostic of the primate suborder Haplorhini, and allow reevaluation of the phylogenetic status of several purported early members of the group. Here we examine the nasolacrimal morphology of a broad sample of extant primates, as well as a number of Paleogene fossils. The extant sample confirms the distinctiveness of the two suborders. Of the fossils studied, only *Shoshonius cooperi* from the late-early Eocene exhibits evidence of a haplorhine nose. This suggests that the haplorhine oronasal complex may have evolved before the postorbital septum, and strengthens the claim that *Shoshonius* is a close relative of tarsiers and anthropoids. These results indicate that Omomyiformes is not a monophyletic group, and that few of its members possessed the derived oronasal morphology that characterizes crown haplorhines.

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1. Introduction

Taxa assigned to the Paleogene ‘Omomyiformes’ have long been regarded as the earliest haplorhines (Stehlin, 1916; Simons and Russell, 1960), but the precise composition of the group, as well as their relationship to either tarsiers or anthropoids, remains a subject of debate (Szalay, 1976; Cartmill and Kay, 1978; Cartmill, 1980; Rosenberger, 1985; MacPhee and Cartmill, 1986; Beard et al., 1991; Beard and MacPhee, 1994; Ross, 1994; Kay et al., 1997). The principal reason for this ambiguity is the scarcity of diagnostic haplorhine features that are capable of fossilization. The few that are known (e.g., lack of a stapedia artery, anterior accessory chamber of the middle ear, and some degree of postorbital closure) have so far been found lacking in omomyiforms (MacPhee and Cartmill, 1986; Ross, 1994; Kay et al., 1997; Godinot, 2015), implying either that they are actually convergences, or that some or

all omomyiforms are stem haplorhines (i.e., taxa preceding the tarsier-anthropoid divergence).

Among the many soft tissue synapomorphies of haplorhines is the unique suite of nasal morphology that inspired their name (Pocock, 1918): haploûs = simple, rhinos = nose. In haplorhines, the hairless rhinarium, frenulum, and philtrum typically found in mammals have been lost (Pocock, 1918; Hill, 1955; Schilling, 1970; Hofer, 1980; Maier, 1980; Martin, 1990). These changes are far from superficial, and involve significant functional changes to the external nose, vomeronasal organ (VNO), and upper lip (Hill, 1955; Schilling, 1970; Hofer, 1980; Maier, 1980; Beard, 1988; Martin, 1990). There seemed little hope of detecting these characteristics in fossils (Maier, 1980), but recent work has shown that a concomitant part of this rearrangement is a truncated and relatively vertical orientation of the nasolacrimal canal (NLC), a change which keeps the opening of the ‘tear duct’ or nasolacrimal duct (NLD) in close proximity to the entrance to the VNO (Fig. 1; Rossie and Smith, 2007). This osteological feature would seem to have great potential for testing the phylogenetic affinities of Paleogene fossils, but our current knowledge of the trait’s distribution rests on

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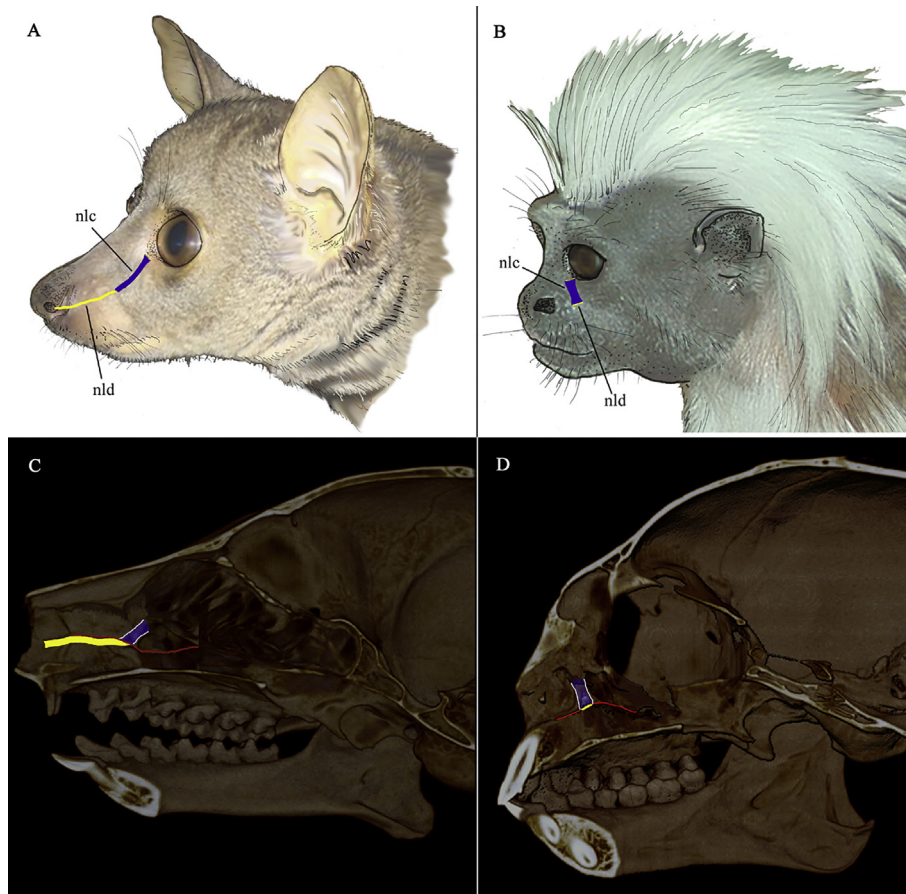


Figure 1. Nasolacrimal canal and duct in strepsirrhines (A, C) and haplorhines (B, D). The canal is oriented obliquely in strepsirrhines and more vertically in haplorhines. Bony canal in the lacrimal and maxillary bones is depicted in blue. The epithelial nasolacrimal duct (yellow) travels through the canal to reach the nasal cavity, but in strepsirrhines it continues anteriorly within the nasal mucosa in a furrow along the underside of the maxilloturbinal to reach the vestibule before opening. Three-dimensional reconstructions from computer tomography scans of *Galagoides* (C) and *Saguinus* (D) reveal the position of the canal and duct in relation to the internal nasal cavity. The maxilloturbinal has been digitally resected, leaving only the cut edge of its basal lamella, depicted in red. Abbreviations: nlc = nasolacrimal canal, nld = nasolacrimal duct. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

a very small comparative sample (Rossie et al., 2006; Tabuce et al., 2009). Here we employ high-resolution computed tomography to reveal the nasolacrimal morphology of a broad sample of 28 extant haplorhine and strepsirrhine species along with nine Paleogene genera for which well-preserved crania are known. *Microchoerus*, *Pseudoloris*, *Tetonius*, *Omomys*, *Rooneyia*, and *Shoshonius* are examined as potential Eocene haplorhines, and *Notharctus* is included as a representative of Eocene strepsirrhines. The Oligocene *Parapithecus* and *Aegyptopithecus* are also included in order to document the condition in a stem anthropoid and a stem catarrhine, respectively.

2. Materials and methods

Fossil crania of *Microchoerus*, *Notharctus*, and *Aegyptopithecus* were scanned using the X-TEK X-ray subsystem on the OMNI-X HD-600 CT scanner at the Center for Quantitative Imaging at Penn State University. *Microchoerus* was scanned at a slice thickness of 0.04154 mm, *Notharctus* at 0.0553 mm, and *Aegyptopithecus* at 0.0769 mm. *Shoshonius*, *Rooneyia*, *Parapithecus*, and extant primates were scanned at the High Resolution X-ray CT Facility at the University of Texas, Austin. *Shoshonius* was scanned at a slice thickness of 0.032 mm, *Parapithecus* at 0.048 mm, and *Rooneyia* at 0.0867 mm. Skulls of extant primates were scanned with a variety of protocols appropriate to their size, ranging from slice thickness

of 0.2237 mm–0.05353 mm. *Omomys* and *Tetonius* were scanned on the AMNH Microscopy and Imaging Facility's (MIF) GE Phoenix v|tome|x s 240 scanner at slice thicknesses of 0.033395 and 0.028961, respectively. *Pseudoloris* was scanned with a Viscom scanner at a slice thickness of 0.137 mm. All image data were reconstructed as 16 bit TIFF images, which were rendered as 3D images using VoxBlast 3.1 (VayTek, Inc.) software.

The orientation of the nasolacrimal canal was quantified as the angle between the postcanine tooththrow and NLC (Fig. 2). This was calculated for one specimen each of 28 extant primate species (2 catarrhines, 10 platyrrhines, *Tarsius*, 8 lorisooids, 7 lemuroids) using the angle measurement tool of the ImageJ image analysis program (Rasband, 2016). The line defining the tooththrow is a secant passing through the lateral alveolar border of P³ and the lateral alveolar border of the penultimate tooth (because the position of the last molar is highly variable). The NLC line is a secant passing through the center of the orbital and nasal openings of the canal. Because the two samples (haplorhines and strepsirrhines) are composed of a different number of specimens, and exhibit different variances, they were compared using a Mann-Whitney U-test and Kolmogorov-Smirnov test in Microsoft Excel (2013). *Parapithecus* and *Aegyptopithecus* were included in the statistical comparison because their haplorhine taxonomic status is unquestioned. The raw image data from which these measurements were made are available from the corresponding author upon request.

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