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The labyrinthine morphology of *Pronycticebus gaudryi* (Primates, Adapiformes)

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Abstract The publication of a well preserved Eocene primate, *Darwinius masillae* (Cercamoniinae, Notharctidae), has revived the debate on the phylogenetic relationships of Adapiformes and extant primates (Franzen et al., PLos ONE 4(5):e5723, 2009). Recently, Lebrun et al. (J Anat 216:368–380, 2010) showed that the morphology of the bony labyrinth of strepsirrhine primates conveys a strong phylogenetic signal. The study of labyrinthine morphology may thus bring a new piece of evidence to resolve phylogenetic relationships within a group. The investigation of the labyrinthine morphology of another Cercamoniinae, *Pronycticebus gaudryi,* reveals no synapomorphy with the labyrinths of modern anthropoids. On the contrary, *Pronycticebus* is closer in labyrinthine shape to extant strepsirrhines, which supports the hypothesis that the Cercamoniinae and other Adapiformes are the sister group of toothcombed primates.

Keywords Adapiformes · Geometric morphometrics · Inner ear · Primates · Strepsirrhini

Introduction

The recent description of *Darwinius masillae* (Cercamoniinae, Notharctidae), a well-preserved Eocene primate, has revived the debate on the phylogenetic relationships of Adapiformes and anthropoid primates (Franzen et al. 2009). Several decades ago, a few researchers had argued that extant anthropoids share an adapiform ancestor (Franzen 1994; Gingerich 1973, 1975, 1981; Gingerich and Schoeninger 1977; Rasmussen 1986, 1990). Since then, phylogenetic analyses of primate relationships have favoured the hypothesis that Adapiformes are stem strepsirrhines (see, for instance, Kay et al. 1997; Marivaux et al. 2005; Ni et al. 2004; Ross et al. 1998; Seiffert et al. 2005). However, Franzen et al. (2009) have revived the hypothesis of a special link between Adapiformes and anthropoids, claiming that *Darwinius masillae* was part of a group "representative of the early haplorhine diversification". This view was criticised by Williams et al. (2010), in a review of the anatomical features differentiating haplorhine and strepsirrhine primates. Williams et al. (2010) argued that *Darwinius* is certainly not a haplorhine, and gave further support to the hypothesis that Adapiformes are basal strepsirrhines (but see Gingerich et al. 2010).

In this paper, we analyse the phylogenetic relationships of Adapiformes with other primates from the perspective of the morphology of the inner ear. Morphological variation of the bony labyrinth across taxa reflects differences in locomotor behaviour (Silcox et al. 2009; Spoor and Zonneveld 1998; Spoor et al. 2007; Walker et al. 2008) and hearing performance (Coleman and Boyer 2012; Coleman and

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Colbert 2010; Coleman et al. 2010; Echteler et al. 1994; Gleich et al. 2005; Kirk and Gosselin-Ildari 2009; West 1985). This structure is thus highly functionally constrained. Nevertheless, a part of labyrinthine morphological variation may still convey phylogenetic information. Basilar membrane length, the number of spiral turns and cochlear volume relate to low frequency and high frequency sensitivity (Coleman and Boyer 2012; Echteler et al. 1994; Kirk and Gosselin-Ildari 2009; West 1985). However, other aspects of the morphology of the cochlea, such as its general geometry and orientation relative to the semi-circular canal system, are less likely to reflect hearing performance. Concerning the semi-circular canal system, even though canal radius tends to increase with agility, semi-circular canal morphology conveys a strong phylogenetic signal (Spoor et al. 2007). As large species tend to be less agile than small ones, a possible way to maximise the phylogenetic information conveyed by this structure is to remove the allometric component of labyrinthine morphological variation.

Building on these hypotheses, Lebrun et al. (2010) proposed a protocol analysis designed to capture the allometry-free component of the geometry of the semi-circular canal system, and the general orientation and geometry of the cochlea within the labyrinth. These authors showed that in strepsirrhine primates the geometry of the bony labyrinth conveys a strong phylogenetic signal. Also, they showed that change in labyrinthine morphology is adequately described with an evolutionary random walk model, i.e. random phenotypic dispersal in morphospace. Under this hypothesis, average shapes calculated for each node of a phylogenetic tree give an estimate of the inner ear morphology of the respective last common ancestors (LCAs). Lebrun et al. (2010) showed that the morphology of Eocene Adapinae is close to the inferred state of the ancestral toothcombed primate labyrinthine morphology. In addition, adapine labyrinthine morphology is close to that of Malagasy primates, which supports the hypothesis that Adapiformes are the sister group of toothcombed primates.

The morphology of the inner ear of *Darwinius masillae* is not preserved (Hurum 2011). However, a more complete and undistorted cranium of another member of Cercamoniinae, *Pronycticebus gaudryi*, is available for study. The ear region of *Pronycticebus* is well preserved. The bullae were intact when the specimen was discovered (Grandidier 1904), and were subsequently partially prepared. A small segment of a free ectotympanic ring was exposed and described by Simons (1962) as *Loris*-like. Other students instead described the ear region of *Pronycticebus* as *Lemur*-like, a free-floating ectotympanic ring actually found in Malagasy primates (Couette et al. 2011; Le Gros Clark 1934; Saban 1963; Szalay 1971), giving support to the strepsirrhine status of *Pronycticebus*. Because the bullae of the type specimen are filled with a hard calcitic matrix, the specimen was never completely dissected. However, CT scan techniques allow for virtual and non-invasive dissection of that region. Investigation of the morphology of the labyrinth of *Pronycticebus* was carried out, and study of its morphological affinities with that of extant primates and other Eocene primate taxa will provide an independent piece of evidence to test hypotheses about the phylogenetic relationships of Adapiformes with other primates (Lebrun et al. 2011). Our earlier analyses showed that primate labyrinthine morphology is consistent at the family level, and exhibits an even higher degree of consistency at the subfamily level (Lebrun et al. 2010). Building upon these findings, we make the assumption that the labyrinths of *Darwinius masillae* and of *Pronycticebus gaudryi* share strong morphological affinities. Also, the teeth of *Darwinius* show derived similarities with those of *Agerinia* (Herbomel and Godinot 2011), and *Agerinia* and *Pronycticebus* have been considered as closely related (Godinot 1998; Szalay 1971). Hence, *Darwinius* is probably quite closely related to *Pronycticebus gaudryi*, and the labyrinth of the latter is likely a good proxy for that of *Darwinius masillae*.

Materials and methods

Comparative sample

We compare the labyrinth of *Pronycticebus* with a broad sample of extant and extinct primates, in order to have a good representation of present and past primate labyrinthine morphological diversity. The comparative dataset consists of 93 inner ears of primates (see Table 1). Thirty-nine inner ears belong to modern strepsirrhine taxa, representing 14 lemuroid and 9 lorisoid genera. Forty-two modern haplorhine specimens were digitised, representing 16 genera of platyrrhines, 20 genera of catarrhines and the genus *Tarsius*. Concerning the fossil sample, 11 inner ears of Adapiformes were included, representing 3 adapine genera and the cercamoniine *Pronycticebus*. Finally, 2 inner ears of fossil Omomyiformes belonging to the Microchoerinae subfamily were analysed (see Table 1). Only left inner ears were integrated in the sample when preserved. For the four adapine specimens which had only their right inner ear preserved, virtual mirror images of their right labyrinth were produced and used for analysis.

Data acquisition

X-ray micro-computed tomography (μCT) and synchrotron X-ray microtomography (SR-μCT) were used to acquire 3D data. Most fossil specimens were scanned at the European Synchrotron Radiation Facility (ESRF) on beam lines ID17

Table 1 List and protocol of data acquisition of the specimens used in the analyses

Genus	Species	Family	Collection[a]	No.	Ear (L/R)	Voxel size (μm)[b]	Scanner	Age
Lemurs								
Allocebus	*trichotis*	Cheirogaleidae	MNHN MO	2002-1	L	36	Scanco μCT80	Adult
Cheirogaleus	*major*	Cheirogaleidae	MNHN MO	2002_87	L	50	Scanco μCT80	Adult
Cheirogaleus	*medius*	Cheirogaleidae	AIM-ZU	8128	L	74	Scanco μCT80	Adult
Microcebus	*murinus*	Cheirogaleidae	AIM-ZU	AS-1815	L	36	Scanco μCT80	Adult
Microcebus	*murinus*	Cheirogaleidae	AIM-ZU	5065-12	L	36	Scanco μCT80	Adult
Microcebus	*rufus*	Cheirogaleidae	MNHN MO	1882-1550	L	36	Scanco μCT80	Adult
Mirza	*coquereli*	Cheirogaleidae	AIM-ZU	1869-198	L	36	Scanco μCT80	Adult
Phaner	*furcifer*	Cheirogaleidae	MNHN MO	1962-2712	L	36	Scanco μCT80	Adult
Eulemur	*fulvus*	Lemuridae	MONTP	No n°	L	60	ESRF ID19	Subadult
Eulemur	*mongoz*	Lemuridae	AIM-ZU	1214	L	74	Scanco μCT80	Adult
Eulemur	*rubriventer*	Lemuridae	AIM-ZU	10599	L	74	Scanco μCT80	Adult
Hapalemur	*griseus*	Lemuridae	AIM-ZU	5055	L	74	Scanco μCT80	Adult
Lemur	*catta*	Lemuridae	AIM-ZU	9601	L	74	Scanco μCT80	Adult
Varecia	*variegata*	Lemuridae	AIM-ZU	As 805	L	74	Scanco μCT80	Adult
Avahi	*laniger*	Indriidae	AIM-ZU	1827	L	74	Scanco μCT80	Adult
Avahi	*occidentalis*	Indriidae	AIM-ZU	13884	L	74	Scanco μCT80	Adult
Indri	*indri*	Indriidae	AIM-ZU	AS-919	L	74	Scanco μCT80	Adult
Daubentonia	*madagascariensis*	Daubentoniidae	MONTP	No n°	L	60	ESRF ID19	Adult
Daubentonia	*madagascariensis*	Daubentoniidae	AIM-ZU	AS-1843	L	74	Scanco μCT80	Adult
Lepilemur	*dorsalis*	Lepilemuridae	MNHN MO	2002-6	L	50	Scanco μCT80	Adult
Lepilemur	*leucopus*	Lepilemuridae	AIM-ZU	5058	L	74	Scanco μCT80	Adult
Lepilemur	*mustelinus*	Lepilemuridae	MNHN	2002-3	L	50	Scanco μCT80	Adult
Lepilemur	*ruficaudatus*	Lepilemuridae	AIM-ZU	11054	L	74	Scanco μCT80	Adult
Lepilemur	*ruficaudatus*	Lepilemuridae	AIM-ZU	10614	L	74	Scanco μCT80	Adult
Propithecus	*diadema*	Indriidae	AIM-ZU	7255	L	74	Scanco μCT80	Adult
Propithecus	*verreauxi*	Indriidae	AIM-ZU	AS-131	L	74	Scanco μCT80	Adult
Galagos								
Euoticus	*elegantulus*	Galagidae	AIM-ZU	7712	L	45.71	ESRF ID17	Adult
Galago	*alleni*	Galagidae	AIM-ZU	7925	L	45.71	ESRF ID17	Adult
Galago	*moholi*	Galagidae	MNHN MO	1885-196	L	36	Scanco μCT80	Adult
Galago	*senegalensis*	Galagidae	AIM-ZU	6591	L	45.71	ESRF ID17	Adult
Galagoides	*demidoff*	Galagidae	AIM-ZU	6535	L	45.71	ESRF ID17	Adult
Otolemur	*crassicaudatus*	Galagidae	AIM-ZU	1841	L	45.71	ESRF ID17	Adult
Otolemur	*garnetti*	Galagidae	AIM-ZU	AS926	L	45.71	ESRF ID17	Adult
Lorises								
Arctocebus	*calabarensis*	Lorisidae	AIM-ZU	7730	L	98	EMPA	Adult
Loris	*tardigradus*	Lorisidae	AIM-ZU	9950	L	45.71	ESRF ID17	Adult
Nycticebus	*coucang*	Lorisidae	AIM-ZU	10586	L	74	Scanco μCT80	Adult
Perodicticus	*potto*	Lorisidae	AIM-ZU	7425	L	60	ESRF ID17	Adult
Pseudopotto	*martini*	Lorisidae	AIM-ZU	6698	L	50	Scanco μCT80	Adult
Platyrrhines								
Aotus	*trivirgatus*	Cebidae	AIM-ZU	1775	L	45.71	ESRF ID17	Adult
Callithrix	*jacchus*	Cebidae	AIM-ZU	10168	L	74	Scanco μCT80	Adult
Callimico	*goeldi*	Cebidae	AIM-ZU	10317	L	74	Scanco μCT80	Adult
Cebuella	*pygmaea*	Cebidae	AIM-ZU	7162	L	74	Scanco μCT80	Adult
Leontopithecus	*rosallia*	Cebidae	AIM-ZU	11070	L	74	Scanco μCT80	Adult
Saguinus	*leucopus*	Cebidae	AIM-ZU	11043	L	74	Scanco μCT80	Adult
Alouatta	*belzebul*	Atelidae	AIM-ZU	10943	L	74	Scanco μCT80	Adult

Table 1 (continued)

Genus	Species	Family	Collection[a]	No.	Ear (L/R)	Voxel size (µm)[b]	Scanner	Age
Ateles	*paniscus*	Atelidae	AIM-ZU	10754	L	74	Scanco µCT80	Adult
Lagothrix	*infumata*	Atelidae	AIM-ZU	10663	L	74	Scanco µCT80	Adult
Brachyteles	*arachnaoides*	Atelidae	AIM-ZU	11065	L	74	Scanco µCT80	Adult
Callicebus	*personatus*	Pithecidae	AIM-ZU	10677	L	74	Scanco µCT80	Adult
Cebus	*apella*	Cebidae	AIM-ZU	10802	L	74	Scanco µCT80	Subadult
Saimiri	*sciureus*	Cebidae	AIM-ZU	9159	L	74	Scanco µCT80	Adult
Cacajao	*rubicundus*	Pithecidae	AIM-ZU	10709	L	74	Scanco µCT80	Subadult
Chiropotes	*satanas*	Pithecidae	AIM-ZU	10911	L	74	Scanco µCT80	Adult
Pithecia	*Pithecia*	Pithecidae	AIM-ZU	8608	L	74	Scanco µCT80	Adult
Catarrhines								
Cercocebus	*torquatus*	Cercopithecidae	AIM-ZU	9887	L	74	Scanco µCT80	Subadult
Cercopithecus	*mona*	Cercopithecidae	AIM-ZU	12213	L	74	Scanco µCT80	Adult
Chlorocebus	*aethiops*	Cercopithecidae	AIM-ZU	6812	L	74	Scanco µCT80	Adult
Colobus	*polykomos*	Cercopithecidae	AIM-ZU	12522	L	74	Scanco µCT80	Adult
Erythrocebus	*pattas*	Cercopithecidae	AIM-ZU	AS-1748	L	74	Scanco µCT80	Juvenile
Macaca	*fascicularis*	Cercopithecidae	AIM-ZU	13483	L	74	Scanco µCT80	Adult
Macaca	*mulatta*	Cercopithecidae	AIM-ZU	9401	L	74	Scanco µCT80	Infant
Mandrillus	*sphinx*	Cercopithecidae	AIM-ZU	7603	L	74	Scanco µCT80	Juvenile
Miopithecus	*talapoin*	Cercopithecidae	AIM-ZU	7602	L	74	Scanco µCT80	Adult
Nasalis	*larvatus*	Cercopithecidae	AIM-ZU	AS-484	L	74	Scanco µCT80	Adult
Papio	*papio*	Cercopithecidae	AIM-ZU	10890	L	74	Scanco µCT80	Infant
Piliocolobus	*badius*	Cercopithecidae	AIM-ZU	6390	L	74	Scanco µCT80	Adult
Presbytis	*comata*	Cercopithecidae	AIM-ZU	10751	L	74	Scanco µCT80	Adult
Presbytis	*melalophos*	Cercopithecidae	AIM-ZU	10659	L	74	Scanco µCT80	Adult
Procolobus	*verus*	Cercopithecidae	AIM-ZU	6362	L	74	Scanco µCT80	Adult
Pygathrix	*nemaeus*	Cercopithecidae	AIM-ZU	10772	L	74	Scanco µCT80	Adult
Semnopithecus	*entellus*	Cercopithecidae	AIM-ZU	12520	L	74	Scanco µCT80	Subadult
Theropithecus	*gelada*	Cercopithecidae	AIM-ZU	8793	L	74	Scanco µCT80	Juvenile
Trachypithecus	*vetulus*	Cercopithecidae	AIM-ZU	10736	L	74	Scanco µCT80	Adult
Hylobates	*larvatus*	Hominoidae	AIM-ZU	AS-1465	L	74	Scanco µCT81	Juvenile
Gorilla	*gorilla*	Hominoidae	AIM-ZU	5563	L	500×90×90	Med. Scanner	Adult
Pan	*troglodytes*	Hominoidae	AIM-ZU	5717	L	500×90×90	Med. Scanner	Adult
Tarsiers								
Tarsius	*bancanus*	Tarsiidae	AIM-ZU	PAL-44	L	36	Scanco µCT80	Adult
Tarsius	*bancanus*	Tarsiidae	AIM-ZU	AS-1838	L	36	Scanco µCT80	Adult
Tarsius	*syrichta*	Tarsiidae	AIM-ZU	AS-1732	L	78	EMPA	Adult
Tarsius	*spectrum*	Tarsiidae	AIM-ZU	AS-1821	L	36	Scanco µCT80	Adult
Fossils								
Adapiformes								
Palaeolemur	*betillei*	Adapidae	MHN BX	Bor-613	L	30	ESRF ID19	Adult
Adapis	*sp.*	Adapidae	MONTP	ACQ208	L	45.7	ESRF ID17	Adult
Adapis	*sp.*	Adapidae	MONTAU	MAPHQ 223	R	30	ESRF ID19	Adult
Adapis	*sp.*	Adapidae	MONTAU	MAPHQ 51	L	30	ESRF ID19	Adult
Adapis	*parisiensis*	Adapidae	CAMBRIDGE	M538	L	87.6	X-Tek HMX160	Adult
Adapis	*sp.*	Adapidae	MÜNCH	XV-1869-1530	L	30	ESRF ID19	Adult
Adapis	*sp.*	Adapidae	MÜNCH	XV-1869-2	L	30	ESRF ID19	Adult
Adapis	*sp.*	Adapidae	BASEL	QW1530	R	30	ESRF ID19	Adult
Adapis	*sp.*	Adapidae	BASEL	QW1	R	50	Scanco µCT80	Adult

Table 1 (continued)

Genus	Species	Family	Collection[a]	No.	Ear (L/R)	Voxel size (μm)[b]	Scanner	Age
Lepdatapis	*sp.*	Adapidae	MONTP	ACQ209	R	45.71	ESRF ID19	Adult
Pronycticebus	*gaudryi*	Adapidae	MNHN	QU11056	L	36	SkyScan 1076	Adult
Omomyiformes								
Microchoerus	*erinaceus*	Omomyidae	MONTP	PR-1771	L	36	Scanco μCT80	Adult
Necrolemur	*antiquus*	Omomyidae	MONTAU	MAPHQ 289	L	30	ESRF ID19	Adult

[a] *AIM-ZU* Antropologisches Institut und Museum Zürich; *MHN BX* Musée d'Histoire Naturelle de Bordeaux; *MÜNCH* Museum und Institut für Palaeontologie München; *MNHN MO* Muséum National d'Histoire Naturelle, Laboratoire Mammifères et Oiseaux, Paris; *MONTAU* Musée d'Histoire Naturelle de Montauban; *BASEL*, Naturhistorisches Museum Basel; *MONTP*, Institut des Sciences de l'Evolution de Montpellier. *CAMBRIDGE* Museum of Zoology of Cambridge

[b] Except for *Pan* and *Gorilla*, all scans have cubic voxels

and ID19 (see Table 1). Synchrotron tomography results in high contrast and spatial resolutions data (Tafforeau et al. 2006), which greatly facilitate segmentation of the bony labyrinth cavities filled by dense sediment when fossils are highly mineralised (Lebrun et al. 2010). Digital volume data of *Pronycticebus gaudryi* were obtained via high resolution micro-CT on a SkyScan 1076 scanner. Three-dimensional surfaces representing the bony labyrinths were produced with Amira 3.1.1 (Visage Imaging) and Avizo 6.3.1 (Visualization Sciences Group) via thresholding using the half maximum height technique (Spoor et al. 1993) and manual segmentation. The choice of the threshold value could affect to some extent the reconstruction of the semicircular canals and of the cochlea (Coleman and Colbert 2007). Fortunately, thresholding effects do not affect the location of the lumen centre of the semicircular canals and the cochlea (Gunz et al. 2012; Lebrun et al. 2010). As such, labyrinthine shape was quantified with 22 landmarks, located at the centres of the lumina of the semicircular canals, of the ampullae, and of the cochlear helix (see Supporting Information Figure S1), following the protocol of Lebrun et al. (2010).

Data analysis

Using generalised least-squares fitting (Rohlf 1990) and principal components analysis (PCA) of shape (Dryden and Mardia 1998), the form of each specimen's landmark configuration was represented by its centroid size S, and by its multidimensional shape vector v in linearised Procrustes shape space. In order to take into account potential confounding effects of size allometry on primate labyrinthine shape (Lebrun et al. 2010), size-corrected shapes were obtained as follows. Regression of Procrustes coordinates by the logarithm of centroid size were computed for Lorisoidea, Lemuroidea, Catarrhines, Platyrrhines, Adapiformes, Omomyiformes, and Tarsiiformes, yielding group-specific allometric shape vectors (*ASVg*). The *ASVg* represent directions in shape space which characterise group-specific allometric patterns of labyrinthine shape variation. A common allometric shape vector (*ASVc*), obtained as the mean of all the *ASVg*, provided a direction in shape space that minimises potential divergence in labyrinthine allometric patterns across taxonomic groups. All labyrinths were then projected on *ASVc*, the residuals representing the size-independent component of labyrinthine shape. Size-independent shape variation was analysed by PCA of shape using the interactive software package MORPHOTOOLS (Lebrun 2008; Specht 2007; Specht et al. 2007).

In order to assess the morphological affinities of *Pronycticebus* with extant primates, Adapinae and Microchoerinae, phenetic trees were produced as follows. For each group (Adapinae, Microchoerinae, Lemuroidea, Lorisoidea, *Tarsius*, Catarrhines, Platyrrhines), an average size-corrected labyrinthine shape was produced. Taxa were then clustered using the NJ (neighbour joining) procedure. A landmark-based random sampling procedure, as described in Lockwood et al. (2004), was executed 1,000 times. The associated consensus NJ tree was computed using PHYLIP (Felsenstein 1989).

Results

Visualising patterns of size-corrected labyrinthine shape variation in morphospace and in physical space permits characterisation of high-level taxon-specific morphologies (Fig. 1): lorisoids, lemuroids, anthropoids, *Tarsius,* adapiforms and omomyiforms are well discriminated in PC1–PC2 space (32.05 % of total shape variation), without almost any overlap. The labyrinth of *Pronycticebus* is closest in morphology to that of Adapinae and of Lemuroidea families such as Lepilemuridae, Lemuridae and Cheirogaleidae, and differs substantially from that of anthropoids (see Table 2). Anthropoid labyrinths show extension in the anteromedial to posterolateral direction, whereas the labyrinths of extant strepsirrhines and *Tarsius* tend to be compressed in this direction.

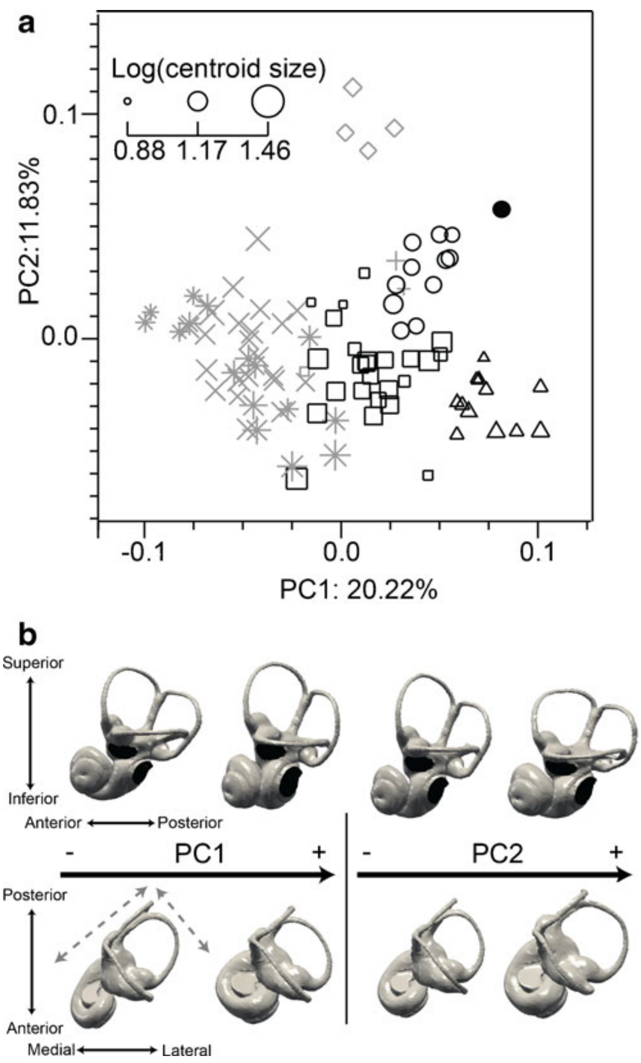

Fig. 1 Principal components analysis (PCA) of labyrinthine size-corrected shape variation. **a** Graphing the first two components of shape space, *PC1* and *PC2*, shows differences in labyrinthine morphology across anthropoids, extant strepsirrhines, Eocene primates and *Tarsius. Black symbols* strepsirrhines, *grey symbols* haplorhines, *triangles* Lorisoidea, *squares* Lemuroidea, *Ooen circles* Adapinae *filled circle Pronycticebus*, *stars* Platyrrhines, *X* Catarrhines, *diamonds Tarsius*; + Microchoerinae. *Symbol size* variation represents labyrinthine centroid size variation. **b** Patterns of labyrinthine shape variation associated with PC1 and PC2, respectively. *Grey arrows* anteromedial-to-posterolateral and anterolateral-to-posteromedial directions

Table 2 Procrustes and allometric corrected distance between the labyrinthine shape of *Pronycticebus* and that of extant and extinct primate family-specific mean labyrinthine shapes

Family	Procrustes distance	Allometry-corrected distance
Adapiformes		
Adapidae	0.091	0.085
Lorisoidea		
Galagidae	0.149	0.143
Lorisidae	0.171	0.166
Lemuroidea		
Cheirogaleidae	0.132	0.121
Daubentoniidae	0.177	0.144
Indridae	0.138	0.137
Lemuridae	0.127	0.125
Lepilemuridae	0.111	0.111
Tarsiiformes		
Omomyidae	0.145	0.140
Tarsiidae	0.139	0.125
Platyrrhines		
Atelidae	0.168	0.165
Cebidae	0.192	0.174
Pitheciidae	0.167	0.167
Catarrhines		
Cercopithecidae	0.156	0.148
Hylobatidae	0.179	0.178
Hominidae	0.194	0.192

The lateral canal of anthropoids is extended in the anteromedial to posterolateral direction while that of prosimians shows extension in the anterolateral to posteromedial direction (see Fig. 1b, deformations along PC1). In *Pronycticebus,* Adapinae and Microchoerinae, the posterior semi-circular canal assumes a high position relative to the lateral canal (see Figs. 2 and 3), which results in partial fusion of the lateral and posterior semi-circular canals. Fossil specimens are well discriminated from extant strepsirrhines, anthropoids and *Tarsius* in PC1–PC2 space. Furthermore, the semi-circular canals of these Eocene primates are round, and their three semi-circular canals are of approximately similar size. This condition differs from that found in *Tarsius* and small-bodied anthropoids: their anterior canal is relatively smaller (see also Fig. 1b). The common crus of *Pronycticebus* is orthogonal to

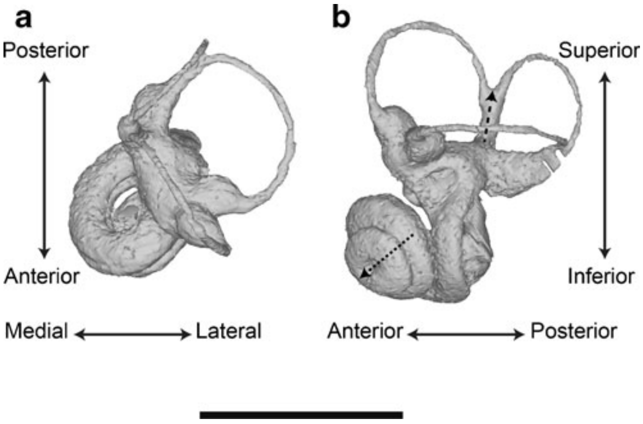

Fig. 2 Left bony labyrinth of *Pronycticebus gaudryi.* The labyrinth is positioned in superior (**a**) and lateral (**b**) views (by convention, the lateral semicircular canal is positioned horizontally). Specimen: QU 11056. *Scale bar* 5 mm. *Dashed arrows* give the orientation of the common crus and of the cochlea. Note that the common crus is orthogonal to the plane of the lateral semi-circular canal

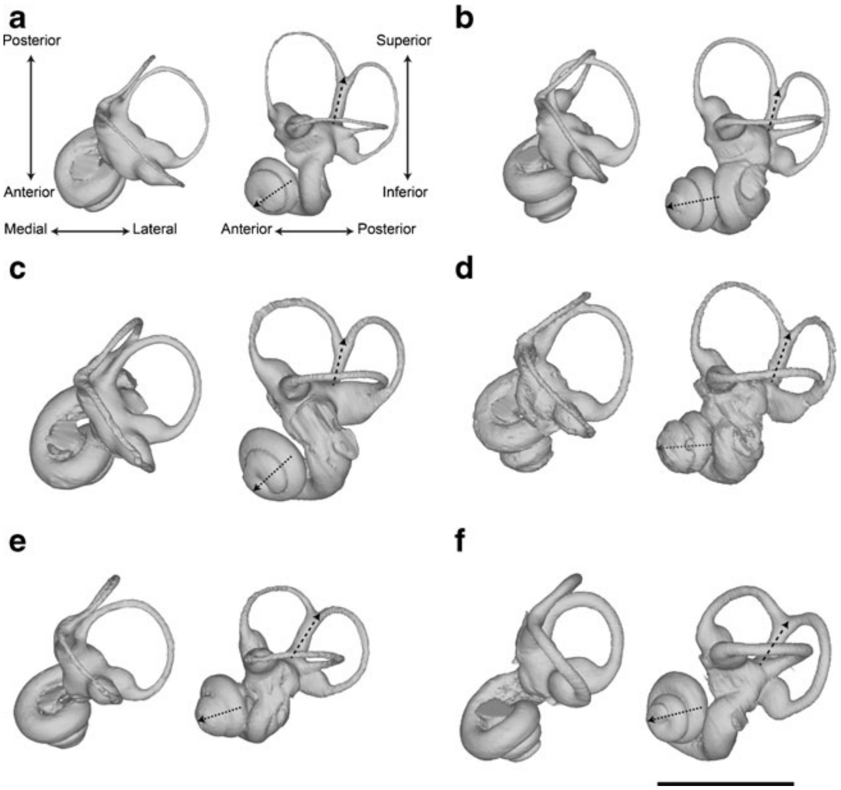

Fig. 3 Left bony labyrinths of primates of **a** *Cheirogaleus major*, **b** *Galago moholi*, **c** *Adapis sp.*, **d** *Microchoerus erinaceus*, **e** *Tarsius spectrum*, **f** *Callithrix jacchus*. For each specimen, the labyrinth is positioned in superior (*left*) and lateral (*right*) views. Specimens: **a** MNHN MO 2002-87, **b** MNHN MO 1885-196, **c** MUNCH XV-1869-1530, **d** MONTP PR-1771, **e** AIM-ZU AS1821, **f** AIM-ZU 10168. *Scale bar* 5 mm. Taxa of similar labyrinthine size to that of *Pronycticebus* were chosen. *Dashed arrows* give the orientation of the common crus and of the cochlea

the plane of the lateral semi-circular canal, a condition that can also be observed in small-bodied Adapinae, like *Adapis*, and in some lemurs, such as *Cheirogaleus*, and in Lorisidae. The common crura of microchoerine primates, of *Tarsius* and Anthropoidea tend to point posteriorly (see Fig. 3).

Pronycticebus, *Adapis* and Lemuroidea exhibit similarities in cochlear shape, orientation and number of turns, measured following West (1985); their cochleae exhibit between 2 and 2.5 turns. In Lemuroidea, Lorisoidea and Adapiformes, the turns of the cochlear spiral are in broad and close contact, which gives this structure a relatively more globose and flattened aspect. In contrast, the cochlear orientation and aspect of *Tarsius* and Microchoerinae resembles that of small anthropoids such as *Callithrix* (see Fig. 3): Microchoerinae, *Tarsius* and anthropoids exhibit cochleae oriented more anteriorly than those of Adapiformes and Lemuroidea (see Figs. 2 and 3). Also, the second turn of their cochleae tends to stay further away from the plane of the first turn.

The phenetic similarity tree based on inner ear morphology is illustrated in Fig. 4. This tree gives indications about the affinities of taxon-specific labyrinthine shapes, and does not reflect the current view of primate phylogeny. This phenetic tree groups together extant platyrrhines and catarrhines, while Adapinea and *Pronycticebus* branch close to each other, and are distant from extant anthropoids. Microchoerinae and *Tarsius* branch together, but appear also distant from anthropoids.

Discussion

Our results show that inner ear morphology is a useful taxonomic marker, supporting the results of Lebrun et al. (2010). Our data show that the inner ear of *Pronycticebus* is morphologically closest to that of adapine Adapiformes, which indicates that inner ear morphological variation of Adapiformes is small. This result confirms that the inner ear of *Pronycticebus* can reasonably be used as a proxy for that of other putative Cercamoniinae primates like *Darwinius*.

Primate inner ear symplesiomorphies

The Eocene primates analysed in this study share similarities in the semi-circular canal system: their semi-circular canals are round and are of largely similar size, their posterior canal assumes a relatively high position, a consequence of which is its partial fusion with the lateral canal. We propose that these shared Adapiformes/Omomyiformes features represent symplesiomorphies of primate labyrinthine morphology.

Labyrinthine shape variation and cranial evolution

Our results suggest that, despite being a functionally constrained structure, a substantial residual part of primate labyrinthine morphology conveys non-functional information. This residual morphological variation may be related to

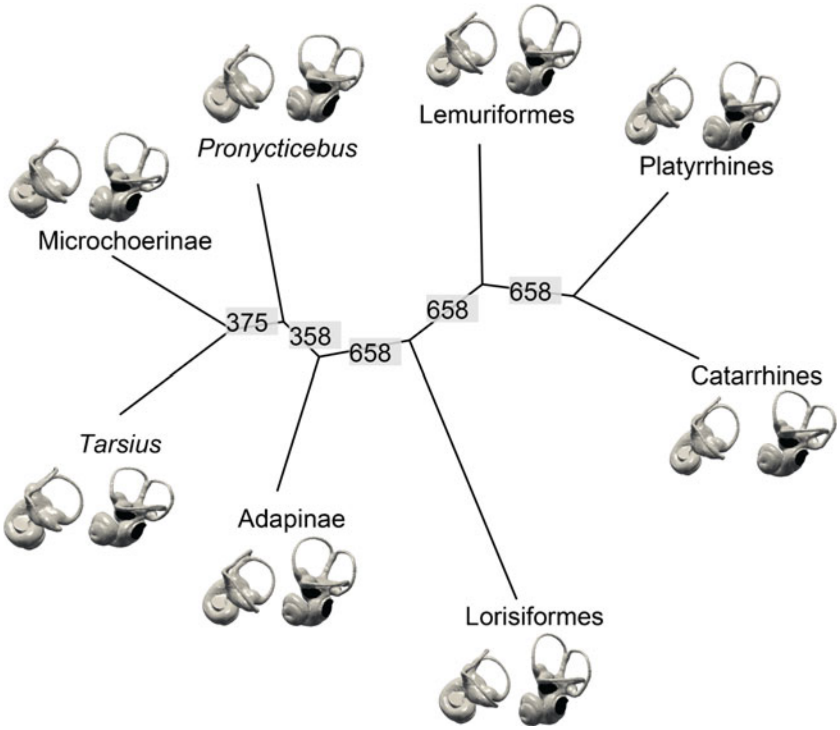

Fig. 4 Phenetic neighbour joining tree based on inner ear morphology (average labyrinthine shape of taxa) reflecting bony labyrinth morphological affinities (size-corrected shape distances) between Adapinae, *Pronycticebus*, Lemuroidea, Lorisoidea, Microchoerinae, *Tarsius*, Platyrrhines, Catarrhines. Bootstrap values for 1,000 resamplings are given at each node

specific cranial morphological characters. We observed in fossil Adapinae and Microchoerinae that the bony channels of the posterior limb of the lateral canal are merged with the inferior part of the posterior canal, forming a second common crus. The presence of a second common crus is found in a variety of extant and extinct placental and non-placental mammals (see, for instance, Benoit et al. 2012; Ekdale 2009; Hyrtl 1845; Schmelzle et al. 2007). In all extant specimens observed in this study, the posterior canal assumes a lower position relatively to the lateral canal, the consequence of which is the absence of fusion of the inferior part of the posterior canal with the posterior limb of the lateral canal. It may be asked how the presence of a second common crus in Eocene Adapinae and Microchoerinae and its absence in all extant primate specimens observed here relate to primate cranial evolution. Primates, and in particular anthropoids, exhibit a well-documented general evolutionary trend towards increased encephalisation during the Cenozoic (Jerison 1973, 1979; Radinski 1977), that is toward increasing their relative brain size. Evolving larger brain size implies modifications of the morphology of the braincase, and has a potential impact on the otic capsules and the surrounding petrous bone (Jeffery and Spoor 2004). The coronal orientation of the petrous bone has been shown to correlate with relative brain size in primates (Spoor 1997), which may influence the geometry of the labyrinth, and in particular the relative position of the semi-circular canals and the orientation of the cochlea. Also, in modern humans, the petrous bone is wedged between the cerebral temporal lobe and the cerebellum (see, for instance, Jeffery and Spoor 2004). This configuration is found in other extant primate species, such as *Otolemur garnetti*, *Tarsius syrichta* and *Callithrix jacchus* (see Fig. S2). In these species, the regions of the petrous bone holding the anterior and posterior canals are in close contact with the cerebral temporal lobes and the cerebellum. In *Adapis parisiensis*, the petrous bone being more laterally positioned relative to the brain, the position and shape of the posterior and anterior canals are less likely to be influenced by brain structures (see Fig. S2). The lower position of the posterior canal relative to the lateral canal in modern forms may be the result of a “packing” issue subsequent to the increasing volume of the brain during evolution. The orientation of the cochlea and the shape of the semi-circular canals may also covary with other aspects of cranial morphology, such as basicranial flexion. In order to better understand the non-functional component of primate labyrinthine morphological variation, a comprehensive covariation analysis between cranial and inner ear morphology is required.

Morphological differences between the two primate suborders

Researchers working on the dentitions of the earliest Omomyiforms and Adapiformes note only little difference (Gingerich 1986; Godinot 1978; Simons 1962; Szalay 1976). Hopefully, other cranial structures are useful to discriminate among primate groups. The middle ear region has long been studied (e.g. Gregory 1915, 1920; MacPhee and Cartmill 1986; Saban 1963), and differences in vascularisation and pneumatisation are found between both suborders. Our results suggest that the inner ear is another structure that differs in morphology between both suborders. Despite the morphological similarities cited above, the inner ear of Eocene microchoerines on the one hand, and that of adapine Adapiformes and *Pronycticebus*, on the other, can be well distinguished, in particular in their cochlear and common crus orientation and in their cochlear aspect.

Tarsius and Omomyiformes on the one hand and extant anthropoids on the other differ in overall labyrinthine shape (see Figs. 1, 4). However, several inner ear characters link these extant and extinct haplorhines. Omomyiformes and *Tarsius* share similarities in the orientation of the common crus and shape of the canals (see Fig. 3). And even though Tarsiers have more spiral turns and have longer cochleae than Omomyids (Coleman and Boyer 2012), they share with small anthropoids some other aspects of morphology of the cochlea. We found that *Tarsius*, microchoerines and small anthropoids have anteriorly oriented cochleae exhibiting a second turn staying away from the plane of the first turn, and posteriorly oriented common crura. These three characters are candidate synapomorphies for the inner ears of haplorhines. On the other hand, extant and extinct strepsirrhine inner ears share morphological similarities. The inner ears of Adapinae and *Pronycticebus* are close in morphology to those of Malagasy lemurs. Lebrun et al. (2010) suggested that, within extant strepsirrhines, the inner ear condition of Lemuroidea is primitive, while that of Lorisoidea is derived. Furthermore, Lebrun et al. (2010) found morphological affinities between the inner ears of Lemuroidea and Adapiformes and that of the demopteran *Cynocephalus*, the three semicircular canals of which are straight, round and approximately of similar size. However, as the inner ears of the dermopteran *Galeopterus* and of the scandantian *Tupaia* differ widely from those of primates, it cannot be ruled out that the similarities observed between *Cynocephalus* on the one hand, and Adapiformes and Lemuroidea on the other, represent morphological convergences. As such, it cannot yet be assessed whether the labyrinthine similarities observed in Adapidae and Lemuroidea represent shared derived features within strepsirrhine primates rather than primate inner ear symplesiomorphies.

Is there evidence for a link between Adapiformes and Haplorhini?

There is virtually no similarity between the inner ears of Adapiformes and those of extant anthropoids, which gives no tangible arguments that would support the hypothesis of Franzen et al. (2009) that *Darwinius*, and other notharctid Adapiformes represent a group of primates which gave rise to anthropoids. Our results, on the other hand, do not contradict the classical hypothesis linking Adapiformes and toothcombed strepsirrhines, based on wrist and ankle synapomorphies (Beard et al. 1988).

The sample of fossil primates analysed here does not allow one to securely define synapomorphies of strepsirrhine inner ears. Such inferences would require the inclusion of other Adapiformes and earlier Omomyiformes. Also, extant anthropoids labyrinthine morphology may be well derived, as illustrated by the clear division of Adapiform–Omomyiform inner ear in PC1–PC2 space on the one hand and of those of modern anthropoids on the other. Though shared characters exist between the inner ears of *Tarsius,* Omomyidae and small bodied anthropoids, further research is needed to assess whether they represent haplorhine synapomorphies.

Comparisons with inner ears of Eocene eosimiid (Beard et al. 1996; Jaeger et al. 1999) and of late Eocene African anthropoids (Seiffert et al. 2005) are thus required to understand the morphological evolution of this structure within haplorhines.

Conclusion

No synapomorphy was found between the labyrinths of *Pronycticebus* and those of modern anthropoids. On the contrary, *Pronycticebus* is closer in labyrinthine shape to extant strepsirrhines, which better supports the hypothesis that Cercamoniinae and other Adapiformes are the sister group of toothcombed primates. Also, candidate synapomorphies of haplorrhine inner ear have been proposed, which are absent in Adapiformes primates. Our results call for further comparative analyses including the inner ear of early Eocene Adapiformes for which the cranium is preserved, such as *Cantius,* and of early Eocene Omomyiformes such as *Teilhardina* and of fossil anthropoids.

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