



News and Views

The bony labyrinth of *Oreopithecus bambolii*

Lorenzo Rook^{a*}, Luca Bondioli^b, Franco Casali^c, Massimo Rossi^c,
Meike Köhler^d, Salvador Moyá Solá^d, Roberto Macchiarelli^e

^a *Dipartimento di Scienze della Terra and Museo di Storia Naturale (Sezione di Geologia e Paleontologia), Università di Firenze, via La Pira 4, 50121 Firenze, Italy*

^b *Museo Nazionale Preistorico Etnografico “L. Pigorini”, Sezione di Antropologia, p.le G. Marconi 14, 00144 Roma, Italy*

^c *Dipartimento di Fisica, Settore di Fisica Biomedica, Università di Bologna, viale Berti Pichat 6/2, 40127 Bologna, Italy*

^d *Institut de Paleontologia M. Crusafont, c/Escola Industrial 23, 08201 Sabadell, Spain*

^e *Laboratoire de Géobiologie, Biochronologie et Paléontologie humaine, CNRS UMR 6046, Université de Poitiers, 40 av. du Recteur Pineau, 86022 Poitiers, France*

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Introduction

Since the time of its first description (Gervais, 1872), the taxonomic and phylogenetic status, as well as the positional behavior, of *Oreopithecus bambolii* have represented some of the most controversial issues in paleoprimatology (see Alba et al., 2001b; Begun, 2002). Although its has a varied and controversial taxonomic interpretive history, today *Oreopithecus* is broadly accepted as a hominoid belonging to the great ape and human clade (Harrison and Rook, 1997; Moyá Solá and Köhler, 1997).

The late Miocene northern Tyrrhenian palaeogeographic setting in which *Oreopithecus* lived was a stable, insular system forming the Tusco-Sardinian archipelago, and granting temporary isolation from the mainland within a peculiar

endemic ecosystem (Hürzeler and Engesser, 1976; Moyá Solá et al., 1999b). Surviving in isolation until 7.0–6.5 Ma, *Oreopithecus* was the last European apelike primate to become extinct (Rook et al., 2000; Bernor et al., 2001).

In this biogeographic context, *Oreopithecus* developed a number of homininlike adaptations (homoplasies), together with peculiar cranial and dental morphological characteristics that have been considered similar to the ancestral catarrhine, cercopithecoid, or hominid conditions (Hürzeler, 1958, 1968; Simons, 1960; Delson, 1979; Szalay and Delson, 1979; Köhler and Moyá Solá, 1997; Moyá Solá et al., 1999a; Rook et al., 1999; Alba et al., 2001b). Most of the *Oreopithecus* cranio-dental anatomy has recently been interpreted as a derived structural adaptation to selective pressures favoring neoteny by heterochrony (Alba et al., 2001b). Nonetheless, integrated into a large-bodied ape-like *châssis*, the fossil displays a wide thorax, short trunk and legs, high intermembral index, extensive elbow mobility, and widely abductable hallux (Moyá Solá and Köhler, 1997). These constitute the unique mosaic of

* Corresponding author. Tel.: +39-55-2757-520;
fax: +39-55-218-628

E-mail addresses: lrook@geo.unifi.it (L. Rook),
luca.bondioli@fastwebnet.it (L. Bondioli), casali@bo.infn.it
(F. Casali), moyass@diba.es (S. Moyá Solá),
roberto.macchiarelli@univ-poitiers.fr (R. Macchiarelli).

hominid-, hominin-, and cercopithecoidlike features which legitimizes its characterization as an “enigmatic anthropoid” (Delson, 1987).

In the abundant collection of *Oreopithecus* odontoskeletal remains recovered at Baccinello, Tuscany, BAC-208 consists of a fragmentary cranium including the left petrosal bone (Moyá Solá and Köhler, 1997). Preliminary radiographic inspection indicated that its internal structures are well-preserved, presenting the opportunity to study the morphology of the bony labyrinth.

We present here a virtually complete *Oreopithecus* bony labyrinth electronically reconstructed from high-resolution μ CT-scanning. Extensive comparative investigation has shown a remarkable diversity in the bony labyrinth of extant and extinct mammal taxa (Spoor et al., 2002), and has demonstrated its potential for yielding information about phylogenetic relationships and locomotor agility (Spoor, 1993, 2003; Spoor et al., 1994, 1996, 2002, 2003; Spoor and Zonneveld, 1998; Spoor and Leakey, 2001). The latter relationship is based on the semicircular canal system's contribution to the sensory control of locomotion, including stabilization of the head and eyes, by recording the angular motion of the head (Schwartz and Tomlinson, 1994). The body-size related arc-sizes of the semicircular canals (SCs) are known to be a determinant of their sensitivity (Oman et al., 1987; Muller, 1994).

The primary aim of this contribution is to provide anatomical information on the still poorly documented ancestral condition of the hominid (i.e., great ape and human) bony labyrinth (Spoor, 1996, 2003). The *Oreopithecus* canal sizes, anterior canal shape, and torsion of the posterior canal are here considered in a comparative primate context, in which extant great apes are characterized by (i) smaller canal arc sizes for their body mass (most strikingly when compared to hylobatids); (ii) a lower anterior canal arc; and (iii) a reversed torsion of the posterior canal (Spoor and Zonneveld, 1998). A further aim of this study is to detect morphological and morphometric clues in the bony labyrinth that could help in discriminating between locomotor and positional behaviors that have been suggested for *Oreopithecus* [slow-moving arboreality (Wunderlich et al., 1999;

Begun, 2002) vs. a rather extant great-ape-like locomotor mode (Köhler and Moyá Solá, 1997; Rook et al., 1999)].

Materials and methods

The specimen

BAC-208 is a crushed fragmentary cranium of a young individual preserving both M^1 (isolated) and M^2 (still in their crypts). A virtually complete, undeformed left petrosal bone is present in an excellent state of preservation. Its endocranial aspect shows a well-developed and deep internal acoustic meatus.

Body mass estimate

In order to appropriately compare the size of the bony labyrinth, body mass constitutes a fundamental reference variable (Spoor and Zonneveld, 1998). Body mass assessment in *Oreopithecus* has been extensively discussed (Jungers, 1987, 1990; Moyá Solá and Köhler, 1997; Alba et al., 2001a,b). *Oreopithecus* is commonly reported as a relatively large-sized fossil hominoid, whose body weight is estimated to have been between 30–35 kg (Begun, 2002).

Comparisons of dental size/body size proportions of *Oreopithecus* with its putative ancestor *Dryopithecus* (see Harrison and Rook, 1997; Moyá Solá and Köhler, 1997) and with the extant great apes indicate that *Oreopithecus* has proportionally small teeth (Alba et al., 2001a; see also Hürzeler, 1958, 1968; Moyá Solá and Köhler, 1997). Accordingly, dental size-derived estimates systematically underestimate its body mass (Jungers, 1987, 1990; Moyá Solá and Köhler, 1997; Alba et al., 2001a,b).

The only *Oreopithecus* fossil preserving a relatively complete postcranium suitable for body mass assessment is IGF 11778 (Straus, 1958), for which a body mass of 32 kg has been estimated (Jungers, 1987, 1990). Accordingly, for the purposes of the present analysis, this value has been assumed as representative of the fossil taxon, including the individual BAC-208. Body mass

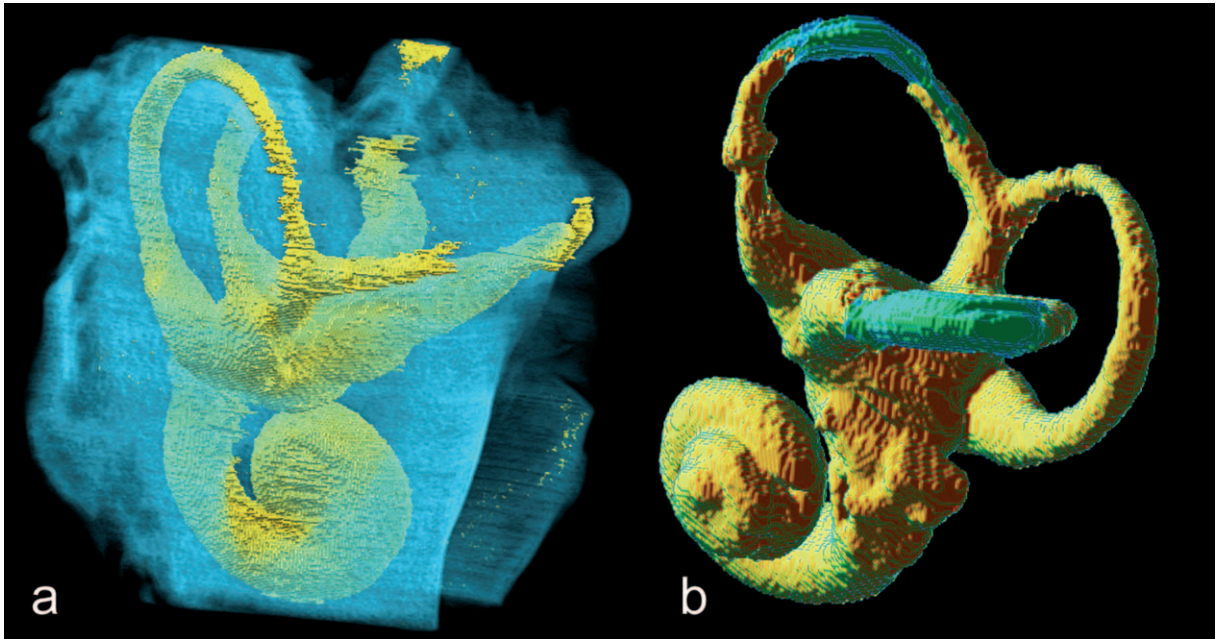


Fig. 1. BAC-208 (left petrosa): three-dimensional reconstruction of the bony labyrinth. a: unrestored, with translucent petrosal bone (not standard medial perspective); b: lateral view with partially reconstructed anterior and lateral semicircular canals.

estimates for the extant primate taxa used in the present comparative analyses (Figs. 2 and 3) are from Smith and Jungers (1997).

Canal size correction for body mass

For the purposes of the present analysis, canal sizes were corrected for body mass as standardized residuals from the log–log regressions of these variables. These were calculated from the whole extant primate sample, including *Homo*, as given in Spoor and Zonneveld (1998). The *Oreopithecus* measures and body mass estimate were not used in the regression calculation.

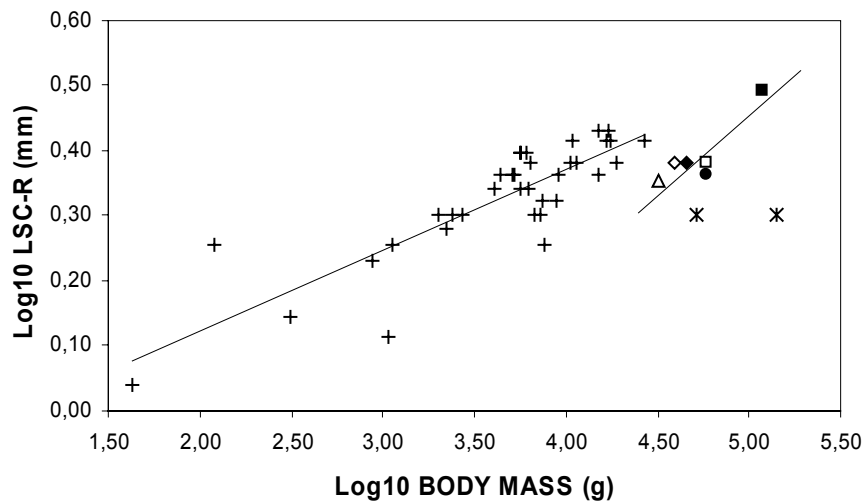
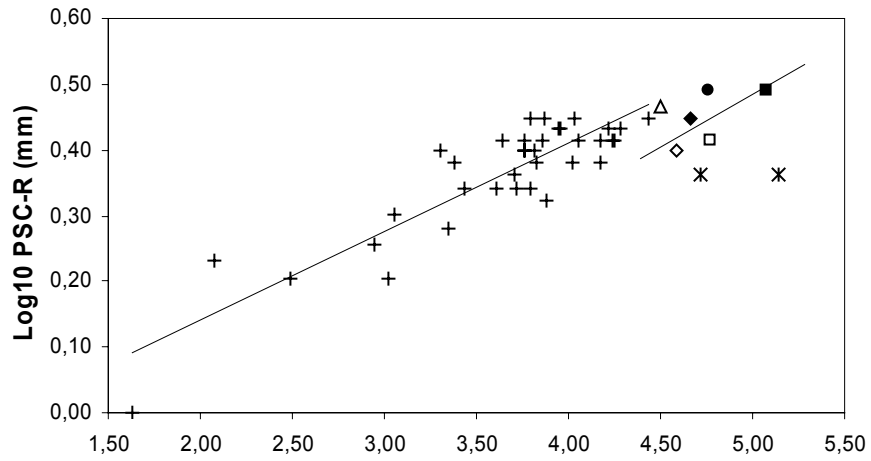
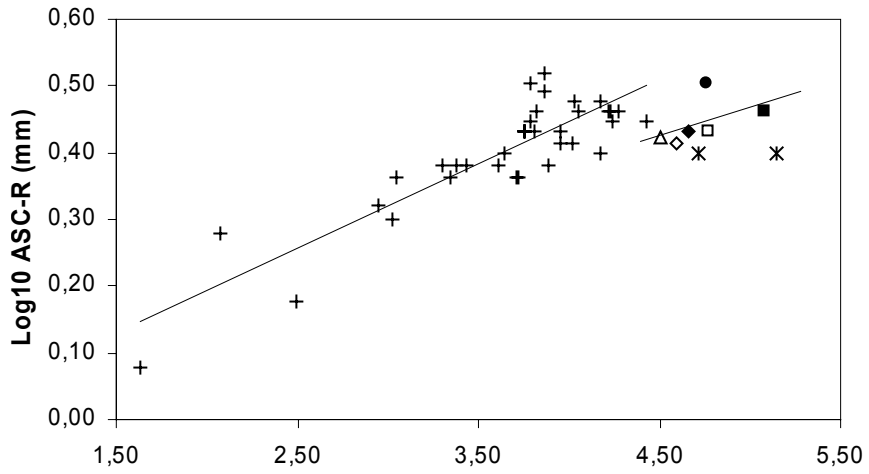
Microtomographic analysis

The microtomographic analysis was performed using the μ CT-scan system at the University of Bologna by M.R. It consists of a 200 kVp, 3 mA, microfocus X-ray tube, a high precision programmable stand, and an X-ray detector. The detector is a thin $\text{Gd}_2\text{O}_2\text{S:Tb}$ phosphor layer (30 mg/cm^2) deposited on a 2:1 fiberoptic taper (FOT), optically

coupled to a cooled CCD camera. The functional detection area is $30 \times 15 \text{ mm}^2$. The cone beam geometry with the small focal spot of the X-ray tube (up to $8 \mu\text{m}$) allows the magnification of small samples, increasing the effective spatial resolution (Rossi et al., 2004).

The data set obtained for the BAC-208 petrosal consists of a 16 bit volume of $760 \times 760 \times 490$ isotropic voxels with a voxel size of $29.05 \mu\text{m}$. To facilitate independent elaboration and analysis of this high-resolution record, we have made the original data available in raw format at <http://www.geo.unifi.it/ricerca/bambolii.htm>.

To maintain consistency with the currently available extensive reference database (Spoor and Zonneveld, 1998; Spoor et al., 2002), all linear and angular measurements of the BAC-208 labyrinth (Table 1) were taken by F. Spoor from planar reformatted images in the transverse and sagittal planes, derived from the original image stack. Statistical analyses, using the comparative database provided by Spoor and Zonneveld (1998), were performed using SPSS, (SPSS Inc.).



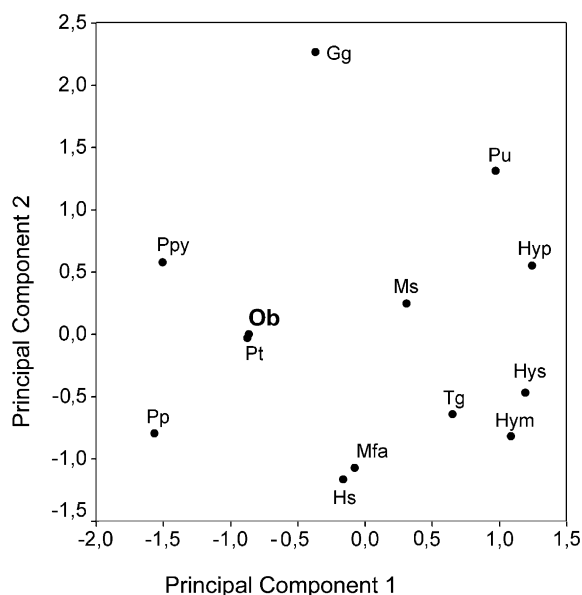


Fig. 3. Principal components analysis of semicircular canals size corrected for body mass. Variables used: radii of curvature of the semicircular canals measured to the center of the lumen and corrected by body mass (ASC-R, PSC-R, LSC-R); semicircular canals height/width ratio (ASC h/w, PSC h/w, LSC h/w). Unrotated and normalized factor scores. Factors 1 and 2 sum up 77% of total variation (56% and 21%, respectively). Gg: *Gorilla gorilla*; Hs: *Homo sapiens*; Hym: *Hylobates moloch*; Hyp: *Hylobates pileatus*; Hys: *Hylobates syndactylus*; Mfa: *Macaca fascicularis*; Ms: *Mandrillus sphinx*; Ob: *Oreopithecus bambolii* (BAC-208); Pp: *Pan paniscus*; Ppy: *Pongo pygmaeus*; Pt: *Pan troglodytes*; Pu: *Papio ursinus*; Tg: *Theropithecus gelada*. BAC-208 measurements are from μ CT; measurements of extant taxa are from Spoor and Zonneveld (1998).

Volume rendering and imaging were made by means of AVS/Express 6.1 (Advanced Visual Systems, Inc.).

Results and discussion

The three-dimensional reconstruction of the *Oreopithecus* bony labyrinth is shown in Fig. 1a

(unrestored) and Fig. 1b with minor parts of the anterior and lateral semicircular canals reconstructed. In the morphology and relative proportions of the semicircular canals, the BAC-208 bony labyrinth resembles the extant great ape condition (see Figures 4 and 5 in Spoor and Zonneveld, 1998). The *Oreopithecus* specimen does not show the small canals typical of *Megaladapis*, the only known large primate with canals smaller than those of the great apes (Spoor, 1993). Fig. 2 shows the allometric relationships of the radii of curvature of primate semicircular canals. While *Oreopithecus* lies on the extant great ape regression line for the anterior and the lateral semicircular canals, its posterior canal is relatively large. Nonetheless, the latter falls within the range of intra-specific variation shown by the extant great apes (Spoor and Zonneveld, 1998). Moreover, the *Oreopithecus* specimen falls well above *Megaladapis* for all three canals.

In BAC-208, the shape index of the anterior semicircular canal (ASC h/w; Table 1) is close to the great ape values (*Oreopithecus*=73; *Pan paniscus*=81; *Pan troglodytes*=80; *Gorilla gorilla*=71; *Pongo pygmaeus*=73), while it differs from both the extant human (87) and the average cercopithecoid condition (94).

A peculiar feature shown by BAC-208 is the orientation of the cochlea (COt<VSC; Table 1), whose apex projects more laterally than in other primate taxa (*Oreopithecus*=144; *H. sapiens*=116; *P. paniscus*=118; *P. troglodytes*=120; *G. gorilla*=116; *P. pygmaeus*=117; average cercopithecoid condition=120). A very modest torsion of the anterior semicircular canal (ASCtor) seems to be an additional, unique *Oreopithecus* characteristic (*Oreopithecus*=2; *H. sapiens*=16; *P. paniscus*=8; *P. troglodytes*=13; *G. gorilla*=15; *P. pygmaeus*=20; average cercopithecoid condition=10). The torsion of the posterior semicircular canal (PSCtor) is also

Fig. 2. Bivariate double logarithmic plot of body mass and radius of curvature of the anterior (ASC-R; top), posterior (PSC-R; middle), and lateral (LSC-R; bottom) semicircular canals. Cross: non-hominid primates; asterisk: *Megaladapis edwardsi*; open triangle: *Oreopithecus*; open diamond: *Pan paniscus*; solid diamond: *Pan troglodytes*; black square: *Gorilla gorilla*; open square: *Pongo pygmaeus*; solid circle: *Homo sapiens*. Values for extant species are from Spoor and Zonneveld (1998), and those for *M. edwardsi* are from Spoor (1993). Note that the latter species has two different body size estimates according different authors: 52 kg after Jungers (1978) and 140 kg after Fleagle (1988).

Table 1

Canonical bony labyrinth dimensions, indexes, and angles (see Spoor and Zonneveld, 1998) assessed for BAC-208, *Oreopithecus bambolii*

Abbreviation	Description	
ASC-R	Radius of curvature of the anterior semicircular canal measured to the center of the lumen	2.7
PSC-R	Radius of curvature of the posterior semicircular canal measured to the center of the lumen	2.9
LSC-R	Radius of curvature of the lateral semicircular canal measured to the center of the lumen	2.3
ASC h/w	Shape index (height/width \times 100) of the anterior semicircular canal	73
PSC h/w	Shape index (height/width \times 100) of the posterior semicircular canal	104
LSC h/w	Shape index (height/width \times 100) of the lateral semicircular canal	88
ASCtor	Torsion of the anterior semicircular canal	2
PSCtor	Torsion of the posterior semicircular canal	-1
LSCtor	Torsion of the lateral semicircular canal	na
ASCm<PSCm	Angle between the orientation of the arc of the anterior semicircular canal at its greatest width in the transverse plane and the orientation of the arc of the posterior semicircular canal at its greatest width in the transverse plane	101
LSCt<VSC	Angle between the axis of symmetry of the lateral semicircular canal in transverse plane and the reference line in the transverse plane bisecting the anteroposteriorly opening angle between the arc orientations of the two vertical semicircular canals	129
CCR<LSCm	Angle between the orientation of the common crus in the sagittal plane and the orientation of the arc of the lateral semicircular canal at its greatest width in the transverse plane	105
APA<LSCm	Angle between the ampullar line connecting the centers of the anterior and posterior ampullae, projected onto the sagittal plane, and the orientation of the arc of the lateral semicircular canal at its greatest width in the transverse plane	36
SLI	The sagittal labyrinthine index (see Table 2 and Fig. 1b in Spoor and Zonneveld, 1998)	42
CO-R	Radius of curvature of the basal turn of the cochlea measured to the center of the lumen	1.9
CO h/w	Shape index (height/width \times 100) of the basal turn of the cochlea	148
COt<VSC	Angle between the orientation of the basal turn of the cochlea in the transverse plane and the reference line in the transverse plane bisecting the anteroposteriorly opening angle between the arc orientations in the two vertical semicircular canals	144
VC<LSCm	Angle between the vestibulocochlear line connecting the center of the arc of the lateral semicircular canal and the lateralmost point of the second cochlear turn projected onto the sagittal plane and the orientation of the arc of the lateral semicircular canal at its greatest width in the transverse plane	140
COs<LSCm	Angle between the orientation of the basal turn of the cochlea in the sagittal plane and the orientation of the arc of the lateral semicircular canal at its greatest width in the transverse plane	40

Linear dimensions in mm; angles in degrees; na: not available. All measurements performed by F. Spoor. For a detailed description and graphical display of the variables, as well as for an extensive comparative database in extant primates (including *Homo*), see Spoor and Zonneveld (1998).

moderate in *Oreopithecus* (-1) and closer to the average cercopithecoid condition (-3.5) rather than to the human (-9) and the great ape values (*P. paniscus*=6; *P. troglodytes*=7; *G. gorilla*=2; *P. pygmaeus*=8). Thus, like in other anatomical areas, *Oreopithecus* cochlear morphology presents a mix of shared and unique features.

Results of a principal component analysis of semicircular canal size and shape, as estimated by the body mass-corrected radii (ASC-R, PSC-R, LSC-R) and their shape indices (ASC h/w, PSC h/w, LSC h/w), are shown in Fig. 3. The analysis includes extant great and lesser apes, together with

a selected number of medium- to large-bodied cercopithecoids. Factor 1 accounts for 56% of the observed variation and positively correlates with all variables. On this axis, *Oreopithecus* clusters with *Pan troglodytes*, away from the lesser apes and large cercopithecoids (Fig. 3). Factor 2, which accounts for 21% of the variation, contrasts the dimensions of the anterior and posterior semicircular canals with those of the lateral one, while for the shape indices it contrasts the anterior against the lateral and the posterior canals. On this axis, *Oreopithecus* again clusters with *Pan* (Fig. 3).

An additional external morphological feature of the investigated petrosal bone that points to the great ape status of *Oreopithecus* is the absence of the *fossa subarcuata*. On BAC-208, rather than a true fossa extended through the arc of the anterior semicircular canal, only a very shallow residual depression is detectable on its cranial aspect. Even though the fossa can be obliterated in some large non-hominoid primates (e.g., in *Theropithecus oswaldi*; Spoor and Leakey, 1996, 2001), a condition similar to that shown by *Oreopithecus* has been observed also in *Dryopithecus* (Moyá Solá and Köhler, 1995, 1997).

On the whole, the outer and inner morphology of the *Oreopithecus* BAC-208 petrosal bone strongly resembles the extant great ape condition. In particular, the comparative analysis of the bony labyrinth of this late Miocene hominid shows (1) extant great-ape-like canal sizes (though less so for the posterior canal), (2) an anterior canal shape similar to that of the great apes, and (3) a posterior canal torsion not typically great ape (positive value), but not far from the *Gorilla* mean. As previously indicated by the analysis of the 10 myr-old *Dryopithecus brancoi* from Rudabanya (Spoor, 1996; Spoor et al., 1996; Spoor and Zonneveld, 1998), the results reported here reinforce the idea that the extant great ape labyrinth is close to the late Miocene condition.

With reference to the question of positional/locomotor behavior in *Oreopithecus* (see Begun, 2002), our results are compatible with a locomotor regime encompassing an agility of movements within the range of the extant great ape locomotor repertoire; conversely, they do not support for *Oreopithecus* a (sloth- or koalalike) highly suspensory, arboreal, slow-moving positional behavior similar, for instance, to the condition suggested for *Megaladapis* (Walker, 1974; Jungers, 1978).

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