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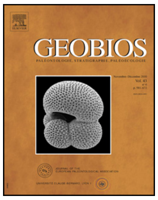

Original article

Homoplasy in the ear region of Tethytheria and the systematic position of Embrithopoda (Mammalia, Afrotheria)☆

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ABSTRACT

The ear region of mammals has long been considered as morphologically very conservative and accordingly, phylogenetically useful. In this study, the anatomy of the petrosal and bony labyrinth (osseous inner ear) of *Numidotherium* (Proboscidea) and *Arsinoitherium* (Embrithopoda) are investigated and compared in order to assess the evolution of ear region characters in proboscideans and embrithopods. Using a cladistic analysis across Paenungulata based on ear region characters only, we found that *Arsinoitherium* is surprisingly best placed as a crown proboscideans to the exclusion of *Numidotherium* and *Phosphatherium*, which results in the paraphyly of proboscidean. The clade Proboscidea is actually well supported by dental and post-cranial characters, and we propose that this result underlines the great amount of morphological convergences in the ear region of Embrithopoda and Proboscidea, possibly due to convergent evolution of capabilities toward infrasonic hearing.

1. Introduction

Scarce but rich North African Paleogene deposits have provided a great amount of fossil mammals since the last century (Andrews, 1906; Mahboubi et al., 1986; Hartenberger et al., 1998, 2001; Rasmussen and Simons, 2000; Gheerbrant et al., 2003; Tabuce et al., 2008; Gheerbrant, 2009; Ravel et al., 2011; see Seiffert, 2010 for an overview). Africa was partly isolated from other continents during the Paleogene (Gheerbrant and Rage, 2006; Tabuce et al., 2008), and given the great scarcity of Paleogene localities in Africa, these fossils are dramatically important to understand the early evolution of the endemic mammalian fauna of this continent. The radiation of ungulate-like orders belonging to the clade Paenungulata – namely the Hyracoidea (hyraxes), Proboscidea (elephants), Sirenia (sea-cows) and Embrithopoda (e.g., arsinoitheres) – represents one of the major events of this endemic evolutionary history (Gheerbrant et al., 2005a). The radiation of paenungulates during the Paleogene produced a great diversity of species with various forms and sizes, ranging from the rabbit-sized *Microhyrax* (Tabuce et al., 2001) to the giant rhinoceros-like *Arsinoitherium* (Andrews, 1906), and various ecologies, from the fully aquatic sea-cows and semi-aquatic hippopotamus-like *Moeritherium* (Clementz et al., 2008; Liu et al., 2008) to the deer-like *Antilohyrax* (Rasmussen and Simons, 2000).

Phylogenetic relationships within paenungulates are still disputed. Consensually, Proboscidea and Sirenia are gathered together in the clade Tethytheria, while Hyracoidea are set apart as a basal offshoot of Paenungulata (Tassy and Shoshani, 1988; Gheerbrant et al., 2005b; Poulakakis and Stamatakis, 2010; Kuntner et al., 2011), but in some phylogenetic analyses based on molecular data, Hyracoidea are the sister group of Sirenia (Stanhope et al., 1998; Springer et al., 2004). Among Paenungulata, the phylogenetic position of the embrithopod *Arsinoitherium* is also a long-standing question. Andrews (1906), who described first the Fayum vertebrate fauna, related it to Hyracoidea. Then, *Arsinoitherium* was subsequently considered as a basal taxon of Tethytheria (Tassy and Shoshani, 1988; Gheerbrant et al., 2005b), the sister-group of Proboscidea (Court, 1990, 1992b; Fischer and Tassy, 1993; Asher et al., 2003), or even the sister-group of Sirenia (Seiffert, 2007).

The study of the ear region morphology to elucidate the systematic and phylogeny of Paenungulata is a long-standing practice, and as such it has often been a subject of intensive debate. For example, Fischer (1990) proposed that the fusion of the cochlear canaliculus (cochlear aqueduct) with the *fenestra cochleae* was a synapomorphy of a (Proboscidea, Sirenia) clade. Court (1990), observing the same pattern in *Arsinoitherium*, concluded that it could be a synapomorphy of the whole Tethytheria (Proboscidea, Sirenia, Embrithopoda and other extinct relatives).

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However, later works dealing with the petrosal of the early proboscideans *Numidotherium* (Court and Jaeger, 1991), *Moeritherium* (Court, 1994a) and *Phosphatherium* (Gheerbrant et al., 2005b), and re-description of the skull and ear region of the stem sirenian *Prorastomus* (Savage et al., 1994; Court, 1994a) provided new evidence that the merging of both apertures was acquired convergently among Tethytheria. The presence of an Eustachian sac (guttural pouch) was also proposed by Fischer (1989) to support a Perissodactyla-Hyracoidea relationship, whereas the new phylogenetic framework based on molecular studies (Stanhope et al., 1998; Asher et al., 2003) precludes the homology of the guttural pouch in these taxa (see also Fischer and Tassy, 1993; Endo et al., 1998, 2009).

The ear region anatomy, including the petrosal and bony labyrinth (cast of the inner ear), has been widely used for phylogenetic reconstructions and taxonomic discussions, especially among afrotherians (Court, 1990; Ekdale, 2009, 2011; Wible, 2012; Benoit et al., 2013a, b). Hence, to understand their evolution across phylogeny has become a central question of mammalian palaeontology. Here we propose a reappraisal of the evolutionary history of the ear region of Tethytheria based on a study using X-ray microtomography (CT scan) of the petrosal of *Arsinoitherium* and *Numidotherium*.

2. Material and methods

2.1. Taxon sampling

Numidotherium koholense is the type species of the genus *Numidotherium*, one of the oldest and basalmost proboscideans (Mahboubi et al., 1986; Gheerbrant and Tassy, 2009). It comes from the late early Eocene (Ypresian) of El Kohol in Algeria (Mahboubi et al., 1984, 1986; Coster et al., 2012). Regarding the great amount of fossil data yet accumulated for this taxon, *Numidotherium koholense* is of unquestionable phylogenetical importance (Sanders et al., 2010a). Indeed, this species is to date the best-known early proboscidean in terms of cranial and postcranial morphology (Mahboubi et al., 1984, 1986; Court, 1994b) as well as ontogenetic and sexual variability (Noubhani et al., 2008). Its basicranial morphology has never been described in detail though some specimens (e.g., UOK5) are well preserved. A short description of the petrosal has yet been provided (Court and Jaeger, 1991) but it was limited to the openings of the *pars cochlearis*. In the same manner the description of the bony labyrinth (Court, 1992a) is based solely on a well-preserved natural cast of the cochlear canal, but the semicircular canals remain unknown. The specimen described here (petrosal and bony labyrinth) is the isolated and unreferenced petrosal of *Numidotherium koholense* already described by Court and Jaeger (1991). Description of the basicranial morphology is based on specimens UOK1 (holotype) and UOK5 (KB3).

Arsinoitherium zitteli is the best-known Embrithopoda (Andrews, 1906; Court, 1990, 1992b, 1993). The morphology of the basicranium and petrosal of *Arsinoitherium* has been already fully described by Court (1990, 1992b) and will not be reassessed here. The description of the bony labyrinth of *Arsinoitherium* is based on the specimen BMNH 8800 which belongs to a juvenile specimen from the Oligocene of the Jebel Qatrani Formation (Andrews, 1906; Court, 1990).

Comparisons were made with the published data on the stem proboscideans *Phosphatherium* (Gheerbrant et al., 2005b) and *Moeritherium* (Andrews, 1906; Tassy, 1981; Court, 1994a), the Pleistocene Elephantimorpha from the Friesenhahn Cave, Texas (Ekdale, 2011), the stem sirenians *Prorastomus* and the recently described Tunisian taxon from Chambi (Savage et al., 1994; Court, 1994a; Benoit et al., 2013a), extant *Trichechus* (Robineau, 1969; Court, 1994a; Ekdale, 2009; Benoit et al., 2013a), the desmostylian *Desmostylus* (Hay, 1915; Uno and Kimura, 2004), and the hyracoid genus *Procavia* (Cifelli, 1982; Kondrashov, 1998; Ekdale, 2009). We also used scans of specimens of extant elephants *Elephas* (N177) and *Loxodonta* (MHN-Aix-VE-2011-69), and the hyracoid *Procavia* (UM2-N-76; MNHN 1901-685a; MNHN 1901-685f) made by ourselves.

2.2. CT scanning acquisition

The petrosal of *Arsinoitherium* was scanned at the British Museum of Natural History (London, United-Kingdom) using a *Metris X-Tek HMX ST 225 CT scanner* with a resolution of 79 μm (200 kV; 140 μA). The petrosal of *Numidotherium koholense* was scanned at the MRI Micro-CT imaging station Skyscan 1076 (*Montpellier, France*) with a voxel size of 36.7 μm (100 kV; 100 μA); the skulls of this species (UOK1, UOK5) were scanned at the University Hospital of Lapeyronie (Montpellier, France) using a *MultiDetector CT scanner Lightspeed VCT* with a voxel size of 420 μm (140 kV; 80 mA). Comparison specimens were scanned at the MRI Micro-CT imaging station Skyscan 1076 *(Montpellier, France)* with a resolution of 36.7 μm (100 kV; 100 μA) (*Procavia*), at the University Hospital of Lapeyronie *MultiDetector CT scanner Lightspeed VCT* (Montpellier, France) with a resolution of 420 μm (140 kV; 80 mA) (*Elephas*), and at the Clinique du Parc (Castelnau-le-Lez, France) using a *MultiDetector CT scanner Somatom* Definition AS, Siemens *Health care* with a resolution of 283 μm (120 kV; 100 mA) (*Loxodonta*). Images *segmentation* and 3D digital reconstructions of petrosals and bony labyrinth were done using Avizo 6.3 (VSG) software.

2.3. Measurements

Measurements of the bony labyrinth (Table 1; Benoit et al., 2013b) were taken using Avizo 6.3 software. Fig. 1 sums up the measurement protocol. Semicircular canal plane angles are measured when the plane of each semicircular canal is perpendicular to the field of view (Fig. 1 (A–C)). The length of the semicircular canal corresponds to the length of the canal taken at the centre of the lumen of the canal (Fig. 1 (D)). The radius (of curvature) of a semicircular canal is half the mean of its width plus its height (Ekdale, 2009). The width of a semicircular canal was measured from the centre of the lumen of each opposing limbs (Fig. 1 (D)). The height of a semicircular canal was taken perpendicular to the respective width, and was measured as the greatest distance from the wall of the vestibule to the centre of the lumen of the canal (Fig. 1 (D)). The cochlear ratio, or aspect ratio of the cochlea (Ekdale, 2009), corresponds to the quotient between the width and the height of the cochlear canal when viewed in profile (Fig. 1 (E)). The relative height of the basal turn (Benoit et al., 2013b) is the ratio between the height of the basal turn of the cochlear canal and the height of the cochlear canal at the level of the maximum height of the spiral in profile view (Fig. 1 (E)). The vestibulo-cochlear angle is the angle between the plane of the basal turn of the cochlear canal and the axis of the common crus (Fig. 1 (E)). The stapedial ratio (Segall, 1970) is the quotient between the length and the width of the *fenestra vestibuli* (oval window; Fig. 1 (F)); the greater this value, the more oval the *fenestra vestibuli*. Because the outlines of this aperture mould the shape of the stapedial footplate, this ratio is also used as a proxy to describe the shape of the stapedial footplates (Segall, 1970). The number of turns of the cochlear spiral (cochlear coiling) corresponds to the number of degrees accomplished by the cochlear canal from its apex to the end of the primary bony lamina (Fig. 1 (F); Geisler and Luo, 1996). The diameter of the cochlear canal corresponds to the width between the posteriormost point of the centre of the lumen of the cochlear canal and the anteriormost