

Digital reconstruction of the inner ear of *Leptictidium auderiense* (Leptictida, Mammalia) and North American leptictids reveals new insight into leptictidan locomotor agility

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Abstract Leptictida are basal Paleocene to Oligocene eutherians from Europe and North America comprising species with highly specialized postcranial features including elongated hind limbs. Among them, the European *Leptictidium* was probably a bipedal runner or jumper. Because the semicircular canals of the inner ear are involved in detecting angular acceleration of the head, their morphometry can be used as a proxy to elucidate the agility in fossil mammals. Here we provide the first insight into inner ear anatomy and morphometry of Leptictida based on high-resolution computed tomography of a new specimen of *Leptictidium auderiense* from the middle Eocene Messel Pit (Germany) and specimens of the North American *Leptictis* and *Palaeictops*. The general morphology of the bony labyrinth reveals several plesiomorphic mammalian features, such as a secondary crus commune. *Leptictidium* is derived from the leptictidan groundplan in lacking the secondary bony lamina and having proportionally larger

semicircular canals than the leptictids under study. Our estimations reveal that *Leptictidium* was a very agile animal with agility score values (4.6 and 5.5, respectively) comparable to Macroscelidea and extant bipedal saltatory placentals. *Leptictis* and *Palaeictops* have lower agility scores (3.4 to 4.1), which correspond to the more generalized types of locomotion (e.g., terrestrial, cursorial) of most extant mammals. In contrast, the angular velocity magnitude predicted from semicircular canal angles supports a conflicting pattern of agility among leptictidans, but the significance of these differences might be challenged when more is known about intraspecific variation and the pattern of semicircular canal angles in non-primate mammals.

Keywords Leptictida · *Leptictidium* · Inner ear · Bony labyrinth · Semicircular canals · Locomotion

Kurzfassung Leptictida sind basale Eutheria aus dem Paläozän bis Oligozän von Europa und Nordamerika, die Arten mit hochspezialisiertem Postcranialskelett umfassen; so haben manche Arten deutlich verlängerte Hinterbeine. Hierzu gehört die europäische Form *Leptictidium*, die möglicherweise ein bipeder Läufer oder Hüpfen war. Da die Bogengänge des Innenohres die Winkelbeschleunigung des Kopfes detektieren, kann deren Morphometrie genutzt werden, um die Agilität fossiler Säuger zu rekonstruieren. Erstmals werden hier die Innenohranatomie und – morphometrie der Leptictida vorgestellt, die auf hochauflösenden Computertomografiescans eines neuen Exemplares von *Leptictidium auderiense* aus dem mittleren Eozän der Grube Messel (Deutschland) sowie weiteren Exemplaren der nordamerikanischen Formen *Leptictis* und *Palaeictops* basieren. Generell zeigt die Morphologie des Innenohres, dass die untersuchten Arten zahlreiche

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plesiomorphe Säugermerkmale zeigen, wie z. B. ein sekundäres Crus commune. *Leptictidium* ist vom Grundplan der Leptictida abgeleitet, da es keine Lamina spiralis ossea secundaria besitzt und proportional größere Bogengänge als die anderen untersuchten Leptictida aufweist. Es zeigt sich, dass *Leptictidium* ein recht agiles Tier mit Agilitätswerten von 4.6 bzw. 5.5 war, die mit denen der Macroscelidea und rezenten biped hüpfenden Placentalia vergleichbar sind. *Leptictis* und *Palaeictops* haben geringere Agilitätswerte (3.4 bis 4.1), wie bei den meisten rezenten Säugern, die einen eher generalisierten Lokomotionstyp (z. B. terrestrisch, cursorial) aufweisen. Im Gegensatz dazu zeigt die Berechnung der Winkelbeschleunigungs-Magnitude, die von den Winkeln zwischen den Bogengängen abgeleitet wird, ein gegenteiliges Agilitätsmuster innerhalb der Leptictida, wobei diese Unterschiede weiterer Überprüfungen bedürfen, sobald mehr über die intraspezifische Variabilität der Bogengangwinkel in Nicht-Primaten bekannt ist.

Schlüsselwörter Leptictida · *Leptictidium* · Innenohr · knöchernes Labyrinth · Bogengänge · Lokomotion

Abbreviations

AMNH	Division of Paleontology, American Museum of Natural History, New York, USA
F-AM	Frick Collection, Division of Paleontology, American Museum of Natural History, New York, USA
SMF	Senckenberg Forschungsinstitut und Naturmuseum Frankfurt, Germany
SMF-ME	Senckenberg Forschungsinstitut und Naturmuseum Frankfurt, Germany, Messel Collection
SZ	Zoologische Schausammlung, Tübingen, Germany
USNM	Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington DC, USA

Introduction

Terrestrial Paleogene faunas contain various insectivore-like eutherian mammals. Among them, the order Leptictida, a group of small to medium-sized animals with elongate snouts, archaic dentition, and elongated hind limbs, is an intriguing taxon, whose relationships are still debated. Representatives of the order Leptictida have been found in North America, Europe, and perhaps Asia (see Kellner and McKenna 1996). The core of the order, however, consists of the Leptictidae, a family known from the Paleocene to the Oligocene of North America, which is

best represented by the genera *Palaeictops* and especially *Leptictis* (Novacek 1977). *Palaeictops*, a rat-sized animal, is known from the early to the middle Eocene (Rose 1999; Gunnell et al. 2008). With a great number of skulls identified from Eocene–Oligocene sites, some well-preserved skeletons and even some brain endocasts, *Leptictis* is certainly the best known leptictidan (Moodie 1922; Butler 1956; Novacek 1977, 1982, 1986; Rose 2006b).

The fossil record of the order Leptictida also extends into Europe, albeit no attested members of the family Leptictidae seem to have been present there (Hooker 2013). The European side of the order is actually represented from the Paleocene to the Eocene by the family Pseudorhyncocyonidae (Russell 1964; Sigé 1974, 1975; Storch and Lister 1985; Mathis 1989; McKenna and Bell 1997; Hooker 2013). Besides the poorly known name-bearing genus *Pseudorhyncocyon* (Phosphorites du Quercy, Late Eocene, France), the Paleocene *Diaphyodectes* and *Phakodon*, as well as the Eocene *Fordonia*, this family is best characterised by the well-documented genus *Leptictidium* (see Hooker 2013). First described by Tobien (1962) from the Messel Pit (Middle Eocene, Germany), *Leptictidium* is known by several complete skeletons belonging to three species discovered at this site (Koenigswald and Storch 1987). Additional but more fragmentary remains of other *Leptictidium* species have been found at Abbey Wood, Croydon and Ferry Cliff (Early Eocene, UK) (Hooker 2013), Geiseltal (Middle Eocene, Germany) (Storch and Lister 1985; Hooker 2013), and Phosphorites du Quercy (Late Eocene, France) (Mathis 1989; Hooker 2013).

As is well known, the Messel Pit fossils are often very well preserved and almost complete skeletons, which can sometimes show the imprint of fur and have preserved stomach contents (Koenigswald and Wuttke 1987; Schaal and Ziegler 1992; Koenigswald et al. 1998; Habersetzer and Schaal 2004). In the case of *Leptictidium*, the stomach contents revealed that these animals were omnivores, feeding on insects, lizards, small mammals, and perhaps even some leaves (Maier et al. 1986). Their elongated snout bears features interpreted as linked to the presence of a proboscis (Storch and Lister 1985). Although *Leptictidium* is one of the most common medium-sized mammals found in the middle Eocene deposits of Messel, details of its anatomy and ecology are still poorly known and are the subject of debates.

For over a century, the relationships of Leptictida have been debated. They have been described as stem Placentalia or alternatively are allied to certain crown Placentalia such as Afrotheria, Lipotyphla, Primates, Tupaiidae, and even Lagomorpha (e.g., Leidy 1868; Matthew 1909; Gregory 1910; Simpson 1945; McKenna 1966, 1975; Szalay 1966, 1977; Butler 1972, 1988; Novacek 1986; MacPhee and Novacek 1993; Asher 1999; Asher et al. 2002, 2003;

Rose 2006a; Wible et al. 2007, 2009). Recently, a comprehensive study based on morphological data from fossil and extant mammals combined with molecular sequences suggests a sister-group relationship of Leptictida and Macroscelidea, with both nested within Afrotheria (O’Leary et al. 2013). Conversely, on the basis of new fossil specimens and a revision of all European Pseudorhyncocyonidae, Hooker (2013) proposed the Pseudorhyncocyonidae to be the sister-group of a clade comprising Leptictidae, Pantolestia, and Palaeonodonta. This phylogeny results in the paraphyly of Leptictida. However, Hooker’s phylogenetic analysis is dominated by dental characters. Notably, the inner ear of leptictidans, which is otherwise a highly relevant intracranial structure phylogenetically, is poorly represented in these studies due to the lack of available data [for data matrices see MorphoBank Project 773; <http://morphobank.org/permalink/?P773> and additional supporting information S3 in Hooker (2013)]. In this regard, a natural inner ear endocast of *Leptictis dakotensis* is the only available data source to date (Novacek 1986: fig. 30). However, the inner ear is partly hidden by the endocast of the brain cavity, and thus anatomical information is scarce. Given the potential importance of leptictidans to disentangle the origin and relationships of many higher taxa, a better knowledge of their internal cranial anatomy appears to constitute an important and necessary step towards a better resolution of basal eutherian phylogeny.

A subject of particular debate is the mode of locomotion of Leptictida and *Leptictidium* in particular. Analysis of an almost complete skeleton of *Leptictis dakotensis* by Rose (2006b) revealed that it exhibits a significant elongation of its hind limbs, which is usually associated with cursorial and saltatorial locomotion; the forelimbs were probably also used for digging. Rose (1999: 369) inferred that the North American leptictids “were quadrupedal mammals that progressed slowly most of the time, with occasional bouts of rapid quadrupedal running and hopping”. The comparison of the species *Leptictidium nasutum* with *Leptictis dakotensis* revealed that the size difference between front and hind legs was even more pronounced in *Leptictidium* (Rose 2006b). Furthermore, a significant difference from all known Eocene–Oligocene leptictids (even *Palaeictops* and the Palaeocene *Prodiacodon*) is the total absence of fusion between tibia and fibula in *Leptictidium* (Storch and Lister 1985). This combination of derived (longer hind limbs) and plesiomorphic (tibia–fibula unfused) traits indicates a different type of locomotion for *Leptictidium*, which has been suggested to be a bipedal runner or hopper (Maier et al. 1986; Frey et al. 1993; Christian 1999). Unfortunately, completely bipedal mammals are rare, and it is thus difficult to find an appropriate living model to compare with *Leptictidium*. Interestingly,

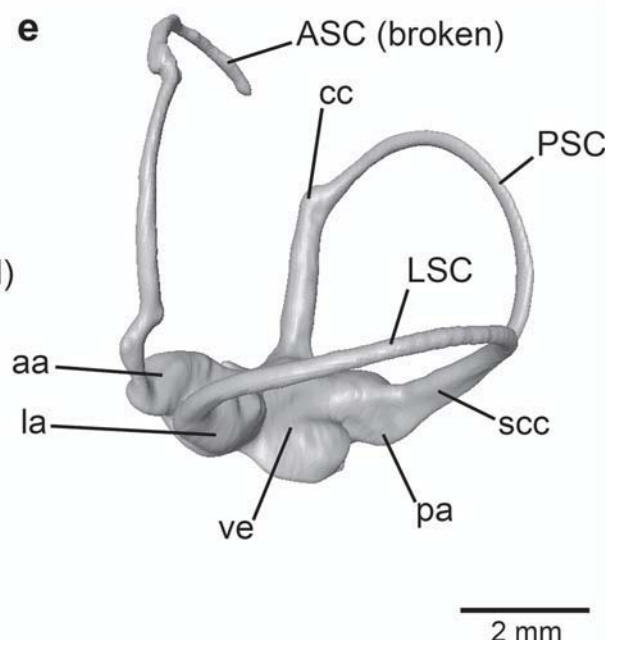
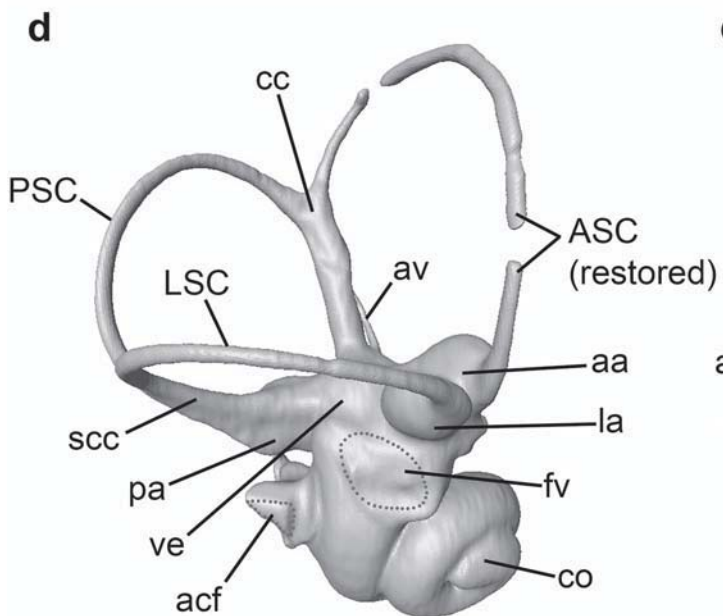
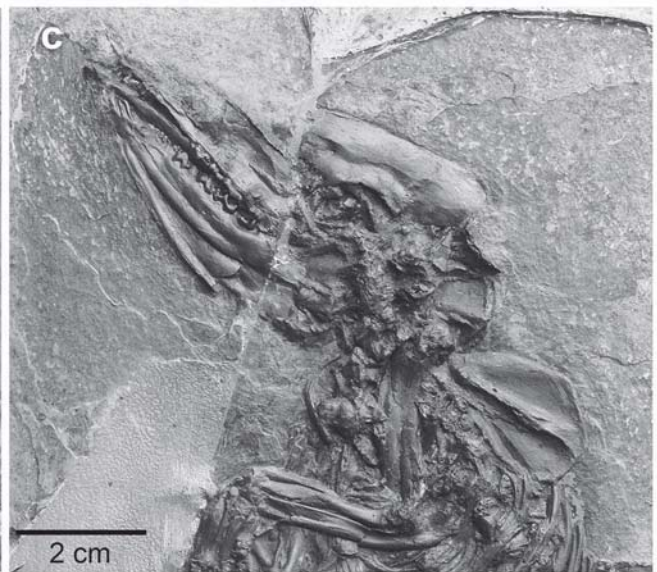
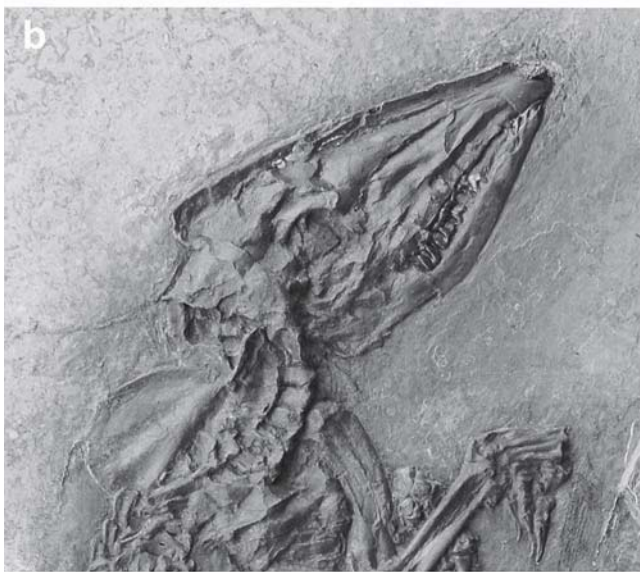
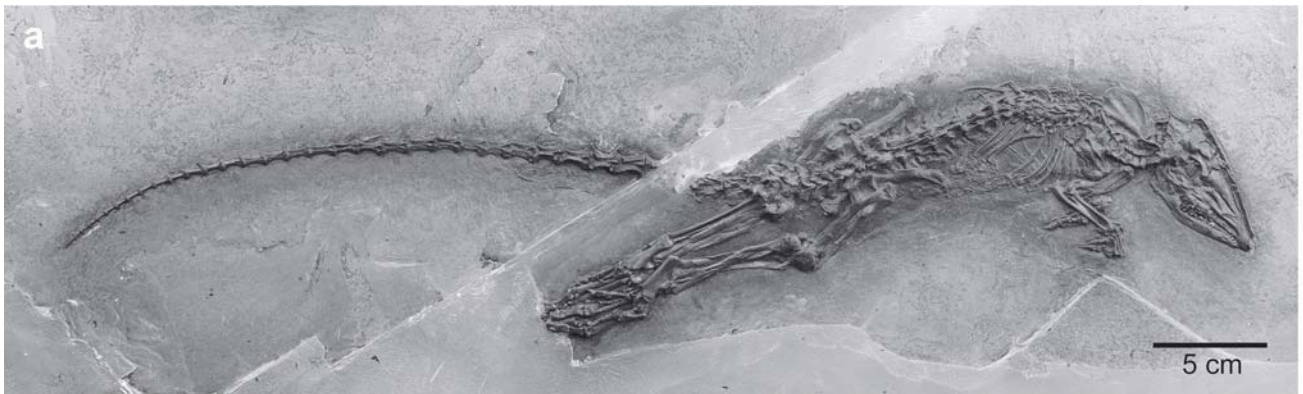
the best extant analogues for leptictidan locomotion are, besides bipedal saltators like *Aepyprymnus*, *Dipodomys* and *Pedetes*, the possibly closely related Macroscelidea (in particular *Rhynchocyon*), which run quadrupedally using a typical swift, cursorial half-bound gait, primarily powered by the hind limbs (Rathbun 1973, 2009).

Besides postcranial anatomy, the shape and proportions of vestibular labyrinth structures also record configurations related to locomotion and posture, which in turn can be used as a reliable proxy to characterise locomotor behaviour and agility in extant, and, by extrapolation, extinct mammals (e.g., Spoor et al. 2007; Walker et al. 2008; Silcox et al. 2009; David et al. 2010; Macrini et al. 2010; Malinzak et al. 2012; Ryan et al. 2012; Berlin et al. 2013). To date, nothing is known about this pattern in Leptictida.

Here we provide the first detailed description of the inner ear bony labyrinth of a new specimen of *Leptictidium auderiense*, which has been recently recovered. *Leptictidium auderiense* is the smallest of three species known from Messel (Koenigswald and Storch 1987). This specimen (SMF-ME-11377) is unique in preserving the inner ear, which was virtually reconstructed using high-resolution computed tomography (μ CT). Accordingly, the aim of the present study is to describe and interpret the inner ear anatomy in *Leptictidium* and to compare it with leptictids represented by *Leptictis* and *Palaeictops*. Our study also elucidates the locomotor agility of *Leptictidium* and other Leptictida in comparison with extant mammals. Finally, in view of the pivotal position of Leptictida in mammalian phylogeny, knowledge of additional aspects of their anatomy, especially the phylogenetically informative ear, will prove useful for interpreting relationships among basal placentals and other eutherians.

Materials and methods

We investigated an unpublished specimen of *Leptictidium auderiense* (SMF-ME-11377) that was recently (September 2011) discovered in the black oil shale of the Messel Pit Fossil Site (Germany; middle Eocene, Early Lutetian, MP 11, approximately 47 Ma; Schaal and Ziegler 1992; Koenigswald et al. 1998; Lenz et al. 2011, 2014) in the framework of the ongoing, long-term excavation programme (begun in 1975) of the Senckenberg Forschungsinstitut und Naturmuseum Frankfurt (Abteilung Paläoanthropologie und Messelforschung). Split through the sagittal plane, the complete skull and articulated skeleton are preserved on two slabs (plate A and B) that were prepared using the epoxy resin transfer method (Fig. 1a–c). For comparison, we included two additional leptictid species in our study. The investigated specimen of *Leptictis* sp., AMNH 80213 is the posterior part of the skull



◀ **Fig. 1** *Leptictidium auderiense* SMF-ME-11377, lateral view of the complete specimen on plate A (a) and close-ups of the skull and shoulder girdle of plate A (b) and plate B (c). Virtual 3D reconstruction of the right (d) and left (e) bony labyrinth in nearly lateral view. Dotted lines indicate the location of the fenestra vestibuli and aperture of cochlear fossula. aa anterior ampulla, acf aperture of cochlear fossula, av aqueductus vestibuli, ASC anterior semicircular canal, cc crus commune, co cochlea, fv fenestra vestibuli, la lateral ampulla, LSC lateral semicircular canal, pa posterior ampulla, PSC posterior semicircular canal, scc secondary crus commune, ve vestibule

and basicranium and was collected at Fitters Ranch (Stark County, North Dakota, USA; late Eocene, Chadronian). The size of this specimen is comparable to that of *Leptictis dakotensis* (Novacek 1986). *Palaeictops* sp. (USNM 495155) is represented by a partial skull associated with several postcranial remains, which were assigned by Rose (1999) to a group of intermediate-sized individuals of that genus. In order to include *Macroscelidea* in the morphometric analysis, we investigated the macerated skull of *Macroscelides proboscideus*, SZ 7379. For further morphological comparison of the inner ear, we mainly refer to the works of Novacek (1986: *Leptictis dakotensis* and other leptictids), and Ekdale and Rowe (2011: zhelestids). Due to the generally moderate or minor intra-individual and intraspecific variation of the inner ear in mammals (Welker et al. 2009; Ekdale and Rowe 2011; Billet et al. 2012), we confined our study to the right bony labyrinth in one specimen per species.

Leptictidium auderiense (SMF-ME-11377) was scanned with the μ CT device TomoScope HV500 (Werth Messtechnik GmbH) at the Fraunhofer Anwendungszentrum CTMT in Deggendorf, Germany, with a resolution (isotropic voxel size) of 34.67 μ m. *Leptictis* (AMNH 80213), *Palaeictops* (USNM 495155), and *Macroscelides* (SZ 7379) were scanned with the μ CT device vltomelx s (GE phoenix|x-ray) at the Steinmann-Institut für Geologie, Mineralogie und Paläontologie, Bonn, Germany. *Leptictis* was processed with an isotropic voxel size of 26.49 μ m, *Palaeictops* with 17.13 μ m (8.57 μ m virtual resolution), and *Macroscelides* with 28.72 μ m. The μ CT data were used to render virtual endocasts of the bony labyrinth by segmentation with the software Avizo® (FEI Visualization Sciences Group).

Anatomical observations are discussed against the background of cladistic analyses from O'Leary et al. (2013) and Hooker (2013), with Leptictidae being a more derived group than Pseudorhyncocyonidae within a probably paraphyletic Leptictida in the latter. Pending future studies further testing the monophyly of the taxon Leptictida, we continue to use this term in the present contribution as an entity gathering Pseudorhyncocyonidae and Leptictidae.

Measurements were taken on the virtual surface of the bony labyrinths with Avizo 6 and 7®. The radius of curvature of each semicircular canal was calculated by the height and the perpendicular width using the formula $0.5(\text{height} + \text{width})/2$, according to Schmelzle et al. (2007). In order to obtain suitable data for comparison with the data set of Spoor et al. (2007), i.e., the height and width as maximum distance from the vestibule to the center of the canal, we calculated the mean of the inner and outer curvature of the canals. The number of cochlear turns was calculated according to West (1985) by using a projection line from the inflection point of the fenestra cochleae to the apex of the cochlear canal. The cochlear length was measured along the outer curvature from the anterior border of the fenestra vestibuli to the apex of the cochlea (Ruf et al. 2009). Measurements for the cochlea aspect ratio (cochlear height divided by cochlear width) and bony labyrinth volume were conducted according to Ekdale (2010, 2013). The inner ear height (IEH) was calculated according to Billet et al. (2013), and measured as the linear distance between the dorsal apex of the crus commune and the ventral apex of the cochlea. The stapedial ratio is a proxy for stapedial footplate size, and is calculated as length divided by width of the fenestra vestibuli (Segall 1970).

Angular measurements were conducted following the protocol of Ekdale (2010). However, the points for the ObliqueSlice tool in Avizo® were modified in that they were set on the outer curvature of the semicircular canals and the basal turn of the cochlea, respectively. The angle between the lateral semicircular canal and the cochlear basal turn was only measured in the lateral perpendicular view of both planes. In *Leptictidium*, the plane of the broken anterior semicircular canal was estimated by setting one point at the base of the crus commune.

The radius of curvature of the semicircular canals of the investigated specimens was compared to body mass following Spoor et al. (2007) and Silcox et al. (2009), a correlation that allows estimation of the degree of locomotor agility. For this purpose, we used the following estimates of body mass of the investigated species. Based on cranial and postcranial measurements, the mean body mass of *Leptictidium auderiense* SMF-ME-11377 is estimated to be around 466 or 627 g (95 % prediction limit) following the methods of Gingerich (1990) and Koenigswald et al. (2009) respectively; for our analyses, we use both values. Our investigated *Leptictis* specimen is similar in size to *Leptictis dakotensis* and is referred to as *Leptictis*, aff. *L. dakotensis* (Novacek 1986). Thus, we used the body mass range of *Leptictis dakotensis* (700 to 1000 g) estimated by Rose (2006b), which is in concordance with the estimation by Novacek (1982). *Palaeictops* was smaller than the other investigated leptictid and probably had a maximum body mass of about 500 g (Rose 1999).

However, comparison of the skeletal dimensions of *Leptictis* (Rose 2006b) with *Leptictidium auderiense* (cast of SMF 83/7) and *Rhynchocyon* shows that all three are very close in size. The *Palaeictops* specimen is still noticeably smaller in elements that can be compared, larger than *Petrodromus* (200 g, Silva and Downing 1995) and smaller than *Rhynchocyon* (490 g, Silva and Downing 1995). Based on these comparisons, it seems more likely that *Leptictis* weighed 400 to 600 g, and *Palaeictops* slightly more than half that, maybe 300 to 400 g (Table 1). These estimations were additionally used for analysis of the agility in the investigated Leptictida.

As Macroscelidea were not included in the original analysis by Spoor et al. (2007), we virtually reconstructed the bony labyrinth of an extant specimen of *Macroscelides proboscideus* (SZ 7397), which has a mean body mass ranging from 38 to 70 g (Silva and Downing 1995); we used the approximate average of 54 g for comparison (Table 1). We also included inner ear measurements by Cox and Jeffery (2010) of the largest living macroscelidean, *Rhynchocyon cirnei*, in our study.

Then we plotted the \log_{10} of the mean radius of curvature of all three semicircular canals (SCR) of the investigated Leptictida and Macroscelidea against the \log_{10} of the body mass (BM) in an existing regression analysis comprising 210 terrestrial therian species (Spoor et al. 2007: fig. 1b). The agility scores (AGIL) of the investigated species were calculated according to the method of Silcox et al. (2009) based on the following equations, which include the body mass (BM) and the radius of curvature (R) of the anterior (ASC), lateral (LSC), and posterior semicircular canals (PSC), and the mean radius of curvature of the three canals (SC), respectively:

$$\text{ASCR: } \log_{10}\text{AGIL} = 0.850 - 0.153 (\log_{10}\text{BM}) + 0.706 (\log_{10}\text{ASCR})$$

$$\text{LSCR: } \log_{10}\text{AGIL} = 0.959 - 0.1670 (\log_{10}\text{BM}) + 0.854 (\log_{10}\text{LSCR})$$

$$\text{PSCR: } \log_{10}\text{AGIL} = 0.881 - 0.151 (\log_{10}\text{BM}) + 0.677 (\log_{10}\text{PSCR})$$

$$\text{SCR: } \log_{10}\text{AGIL} = 0.948 - 0.188 (\log_{10}\text{BM}) + 0.962 (\log_{10}\text{SCR})$$

These equations tend to underestimate agility scores for heavy taxa, but provide more accurate results for lighter taxa (Billet et al. 2013).

Because our investigated species are small taxa with body mass values that are very close to each other, our results provide at least a relative scale of locomotor agility that enables comparison among these taxa.

Recent investigations of 3D kinematic experiments and angular arrangement of the semicircular canals in primates show that the angles of the canal planes are highly

correlated with sensitivity and fast head rotations, and therefore locomotor agility (Malinzak et al. 2012).

Thus, we calculated the variance from 90° among angles between the three semicircular canals [$90\text{var} = (\text{sum of } (n) \text{ squared deviations from } 90^\circ)/(n-1)$], in order to estimate possible corresponding patterns of head rotation and locomotor agility within Leptictida, independently from body mass (Malinzak et al. 2012).

Systematic paleontology of the studied material

Order Leptictida McKenna, 1975

Family Leptictidae Gill, 1872

Genus *Leptictis* Leidy, 1868

Genus *Palaeictops* Matthew, 1899

Family Pseudorhyncocyonidae Sigé, 1974

Genus *Leptictidium* Tobien, 1962

Leptictidium auderiense Tobien, 1962

Results

Anatomical description

Leptictidium auderiense

The right bony labyrinth of *Leptictidium* is preserved on SMF-ME-11377 plate B; however, the anterior semicircular canal is broken and one part is preserved on plate A (Fig. 1). The left bony labyrinth is only represented by the pars canalicularis with a broken and distorted anterior semicircular canal also located on plate B (Fig. 1e). Thus, we only refer to the right bony labyrinth in the following description and analysis. The measurements on the virtual endocasts are summarized in Table 1.

The bony labyrinth of *Leptictidium* is characterized by relatively large, thin, and distinctly arcuate semicircular canals (Figs. 1d, 2a, b, 3a). The anterior semicircular canal could be restored virtually, but its shape remains ambiguous; most probably it had a pronounced circular shape, like the posterior semicircular canal. The lateral semicircular canal is elliptical, oriented posterolaterally. The lateral and posterior semicircular canals are quite planar, but the anterior semicircular canal is concave medially, as is evident from the anterior profile (Figs. 2a, b, 3a). Based on the height and width of the semicircular canals (see Table 1) the radii of curvature (R) of the canals were calculated. The anterior semicircular canal ($R = 2.18 \text{ mm}$) is larger than the posterior one ($R = 1.91 \text{ mm}$). The lateral semicircular canal of *Leptictidium* is the smallest, with a radius of curvature of 1.83 mm . The lateral semicircular canal extends laterally

Table 1 Measurements of the right bony labyrinth of the investigated species

	<i>Leptictidium auderiense</i> SMF-ME-11377	<i>Leptictis</i> sp. AMNH 80213	<i>Palaeictops</i> sp. USNM 495155	<i>Macroscelides proboscideus</i> SZ 7397	<i>Rhynchocyon cirnei</i> (Cox and Jeffery 2010)
ASC height	4.38 mm ^a	3.16 mm	3.05 mm	2.31 mm	
ASC width	4.34 mm ^a	3.27 mm	3.01 mm	2.45 mm	
LSC height	3.48 mm	2.31 mm	2.03 mm	1.74 mm	
LSC width	3.82 mm	2.68 mm	2.27 mm	2.49 mm	
PSC height	3.82 mm	2.73 mm	2.62 mm	1.79 mm	
PSC width	3.81 mm	2.81 mm	2.40 mm	1.96 mm	
ASCR	2.18 mm ^a	1.61 mm	1.52 mm	1.19 mm	2.13 mm
LSCR	1.83 mm	1.25 mm	1.08 mm	1.06 mm	1.79 mm
PSCR	1.91 mm	1.39 mm	1.26 mm	0.94 mm	1.89 mm
SCR	1.97 mm	1.42 mm	1.29 mm	1.06 mm	1.94 mm
Angle ASC/LSC	70.2° ^a	75.6°	90.2°	105.4°	
Angle LSC/PSC	88.9°	86.3°	92.7°	92.4°	
Angle ASC/PSC	87.6° ^a	90.7°	93.6°	91°	
Angle LSC/co	26.4°	11.8°	32.7°		
Co height	3.44 mm	3.0 mm	2.38 mm		
Co width	5.31 mm	4.38 mm	3.44 mm		
Co aspect ratio	0.65	0.69	0.69		
Co length	16.05 mm	18.02 mm	14.4 mm		
Co volume	9.79 mm ³	10.22 mm ³	6.34 mm ³		
Bl volume	19.08 mm ^{3a}	16.37 mm ³	9.18 mm ³		
Contribution of co volume to total bl volume	51.31 %	62.43 %	69.06 %		
IEH	6.44 mm	5.3 mm	4.75 mm		
Stapedial ratio	1.32 (1.2 mm h/ 0.91 mm w)	1.8 (1.28 mm h/ 0.7 mm w)	1.72 (0.95 mm h/ 0.55 mm w)		
Ratio ASCR/LSCR	1.19	1.29	1.41		
Ratio ASCR/PSCR	1.14	1.16	1.21		
Ratio PSCR/LSCR	1.04	1.11	1.17		
Ratio SCR/IEH	0.31	0.27	0.27		
BM	466g ^b 627g ^c	700–1000g ^d 400–600g ^f	500g ^e 300–400g ^f	54g ^g	490g ^g
log ₁₀ ASCR	0.339	0.207	0.182	0.076	0.328
log ₁₀ LSCR	0.263	0.097	0.033	0.025	0.253
log ₁₀ PSCR	0.295	0.143	0.100	−0.029	0.275
log ₁₀ SCR	0.295	0.152	0.111	0.025	0.289
log ₁₀ BM	2.668 2.797	2.845–3.000 2.602–2.778	2.699 2.477–2.602	1.732	2.690
AGIL ASCR	4.8 4.6	3.5–3.6 3.7–4.0	3.7 3.8–4.0	4.4	4.7
AGIL LSCR	5.5 5.2	3.5–3.7 3.8–4.1	3.4 3.6–3.8	4.9	5.3
AGIL PSCR	4.8 4.6	3.4–3.5 3.6–3.9	3.5 3.6–3.8	4.0	4.6
AGIL SCR	5.4 5.1	3.4–3.6 3.7–4.0	3.5 3.7–3.9	4.4	5.3

Table 1 continued

	<i>Leptictidium auderiense</i> SMF-ME-11377	<i>Leptictis</i> sp. AMNH 80213	<i>Palaeictops</i> sp. USNM 495155	<i>Macroscelides proboscideus</i> SZ 7397	<i>Rhynchocyon cirnei</i> (Cox and Jeffery 2010)
90var	199.51	110.77	10.15	121.96	
log ₁₀ 90var	2.30	2.04	1.01	2.09	

AGIL agility score, *ASC* anterior semicircular canal, *ASCR* radius of curvature of ASC, *bl* bony labyrinth, *BM* body mass, *co* cochlea, *h* height, *IEH* inner ear height, *LSC* lateral semicircular canal, *LSCR* radius of curvature of LSC, *PSC* posterior semicircular canal, *PSCR* radius of curvature of PSC, *SCR* average radius of curvature of all three semicircular canals, *90var* variance from 90° among angles between semicircular canals of one side, *w* width

^a Measurements are based on restoration of broken ASC

^b BM calculated following the method of Gingerich (1990)

^c BM calculated following the method of Koenigswald et al. (2009)

^d BM according to Rose (2006b)

^e BM according to Rose (1999)

^f Body mass estimation based on comparison of skeletal size of Leptictida and extant Macroscelididae

^g BM according to Silva and Downing (1995)

almost as far as the anterior semicircular canal (Fig. 3a). The inner ear height (IEH) is 6.47 mm and the ratio SCR/IEH is 0.31.

The posterior leg of the lateral semicircular canal is fused with the ventral leg and ampulla of the posterior semicircular to form a secondary crus commune (Figs. 1d, 2b, 3b); this fusion is restricted to the bony structures and does not affect the soft tissue of the semicircular canals (Sánchez-Villagra and Schmelzle 2007). Consequently, in anterior view, the plane of the lateral semicircular canal is on the same level as the lower leg of the posterior semicircular canal, and the sagittal labyrinthine index is 0.0 and thus coded as low (Fig. 2a). The ampullae of the semicircular canals are distinct, but not prominently inflated (Fig. 3a). The aqueductus vestibuli leaves the vestibule anterior to the crus commune and runs medially (Figs. 2a, 3a). However, the crus commune of the *Leptictidium* specimen SMF-ME-11377 shows a break that extends into the aqueductus vestibuli; thus, the latter is incomplete distally. The elliptical and spherical recesses (utricle and saccule, respectively) are continuous and no distinct separation is visible on the endocast of *Leptictidium*.

The angle between the plane of the lateral semicircular canal and the basal turn of the cochlear canal is 26.4°. The fenestra vestibuli is elliptical (Fig. 1d), and is 1.2 mm high and 0.91 mm wide, resulting in a very low stapedial ratio of 1.32. The fenestra cochleae is hidden inside a small cochlear fossula; the external aperture of the cochlear fossula (see Wible et al. 2009) is elliptical, but very small and facing laterally (Figs. 1d, 2b). The canaliculus cochleae is a short and wide bony channel (Figs. 2b, 3a). The cochlea of *Leptictidium* has almost two full turns and appears to be planispiral, but has an aspect ratio of 0.65 that is rated as high (Figs. 1d, 2a, 3b; Table 1). The cochlear

canal is 16.05 mm long and contributes 51.31 % to the total bony labyrinth volume (Table 1). As is evident in the ventral view, the cochlear turns are well in contact but do not cover each other. The cochlear spiral shows an apical lacuna that corresponds to the bony modiolus, which transmits the branches of the vestibulocochlear nerve (cranial nerve VIII) (Fig. 3b). While the primary bony lamina is a prominent internal feature of the cochlear duct, there is no evidence for a secondary bony lamina, either on the virtual endocast or in the μ CT images (Fig. 4a).

Leptictis and *Palaeictops*

It is evident from the virtual endocasts that both *Leptictis* and *Palaeictops* show the same general morphology of the bony labyrinth as *Leptictidium*. Their semicircular canals are also thin and distinctly arcuate, but are proportionally smaller than in the latter (Figs. 2c–f, 3c, e), as also revealed by the ratio SCR/IEH, which is 0.27 in both North American species. As in *Leptictidium*, the anterior semicircular canal is the largest and shows more planar deviation, whereas the lateral semicircular canal is the smallest (Fig. 2c, e; see Table 1 for radii of curvature). However, the shapes of the anterior and posterior semicircular canals of *Palaeictops* are similar to those of *Leptictidium* but different from the oval anterior and slightly triangular posterior semicircular canals in *Leptictis* (Fig. 2c–f). The lateral semicircular canals of *Leptictis* and *Palaeictops* are different from that of *Leptictidium* in being more rounded and smaller relative to the anterior and posterior semicircular canals (for ratios of semicircular canals see Table 1). Both *Leptictis* and *Palaeictops* have a prominent secondary crus commune, and therefore a sagittal labyrinthine index of 0.0 (Figs. 2c, e, 3b, d–f). The ampullae of the

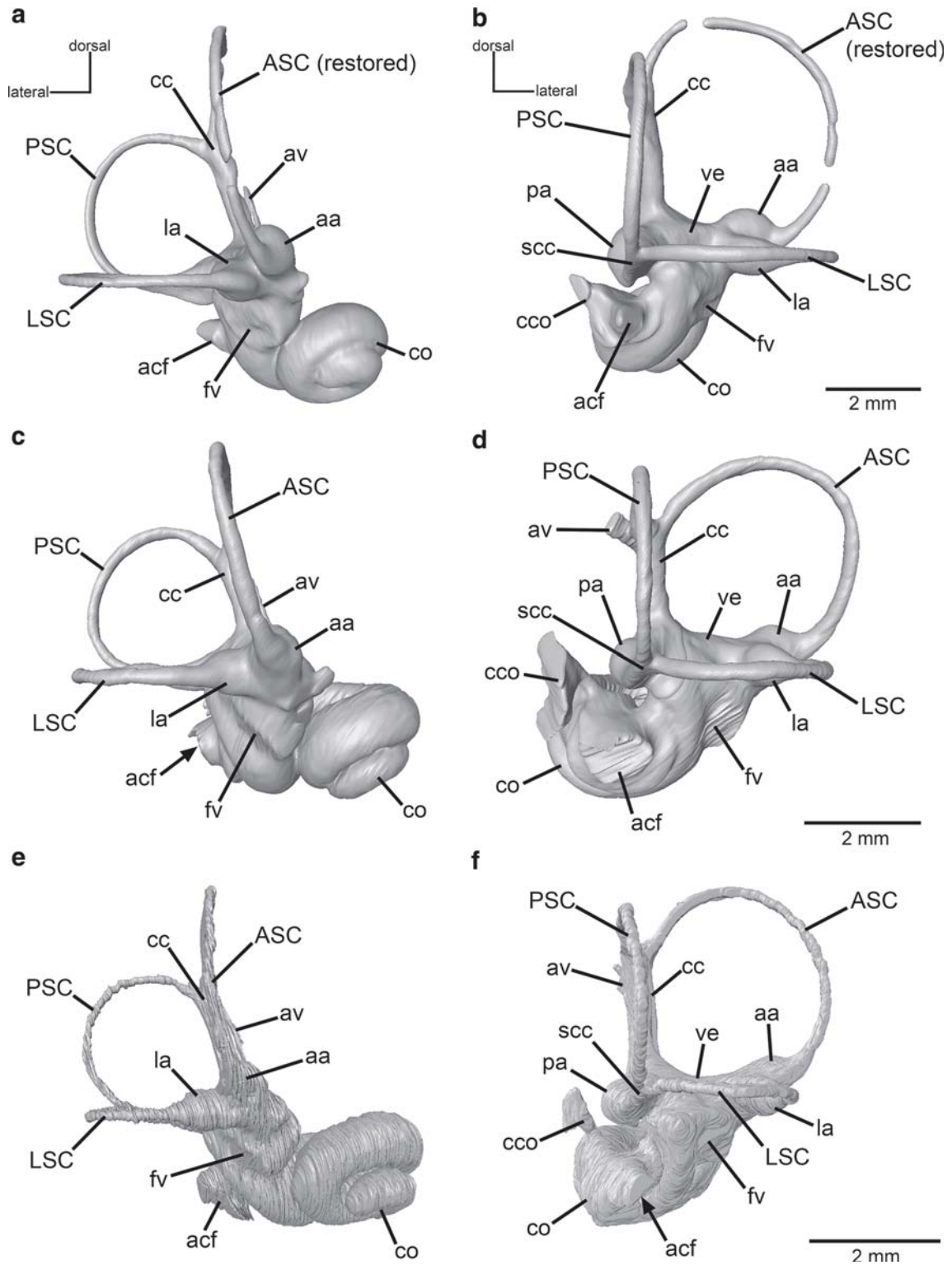


Fig. 2 Comparison of the right bony labyrinth of *Leptictidium auderiense* SMF-ME-11377 (**a, b**), *Leptictis* sp. AMNH 80213 (**c, d**), and *Palaeictops* sp. USNM 495155 (**e, f**) in anterolateral view (**a, c, e**) and posterolateral view (**b, d, f**). *aa* anterior ampulla, *acf* aperture of cochlear fossula, *av* aqueductus vestibuli, *ASC* anterior

semicircular canal, *cc* crus commune, *cco* canaliculus cochleae, *co* cochlea, *fv* fenestra vestibuli, *la* lateral ampulla, *LSC* lateral semicircular canal, *pa* posterior ampulla, *PSC* posterior semicircular canal, *sbl* secondary bony lamina, *scc* secondary crus commune, *ve* vestibule

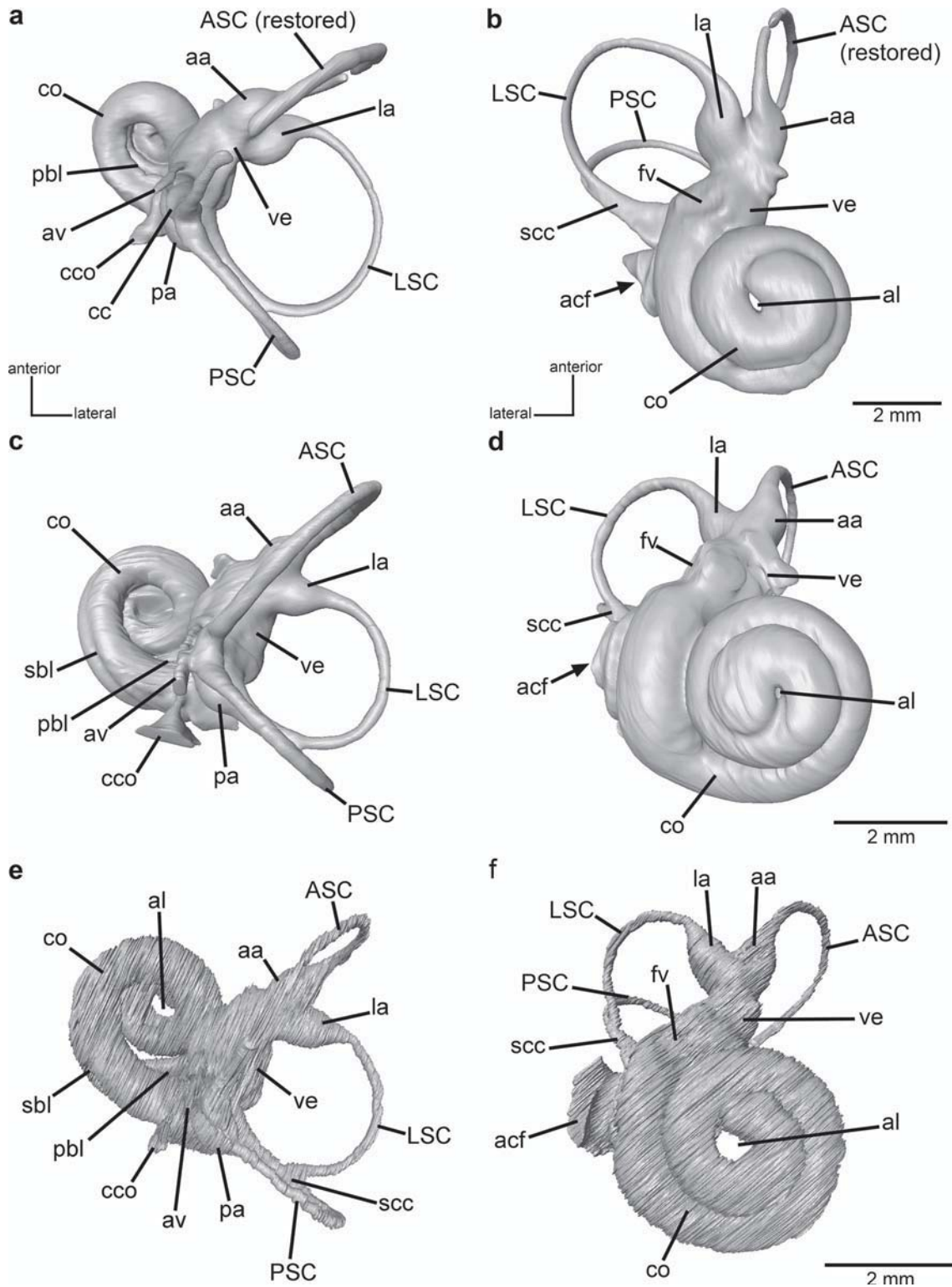
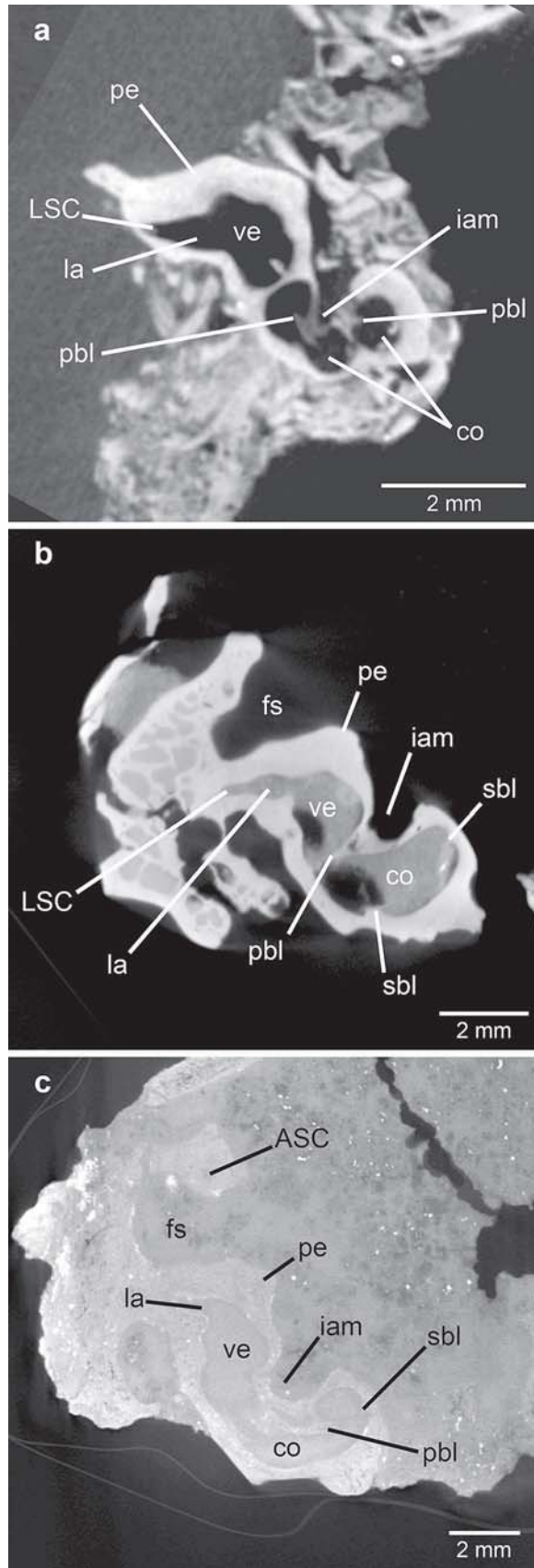


Fig. 3 Comparison of the right bony labyrinth of *Leptictidium auderiense* SMF-ME-11377 (**a, b**), *Leptictis* sp. AMNH 80213 (**c, d**), and *Palaeictops* sp. USNM 495155 (**e, f**) in dorsal view (**a, c, e**) and apex view of cochlea (**b, d, f**). aa anterior ampulla, acf aperture of cochlear fossula, al apical lacuna, av aqueductus vestibuli, ASC

anterior semicircular canal, cco canaliculus cochleae, co cochlea, fv fenestra vestibuli, la lateral ampulla, LSC lateral semicircular canal, pa posterior ampulla, pbl primary bony lamina, PSC posterior semicircular canal, sbl secondary bony lamina, scc secondary crus commune, ve vestibule



◀ **Fig. 4** Transverse μ CT images of the right bony labyrinth of (a) *Leptictidium auderiense* SMF-ME-11377, (b) *Leptictis* sp. AMNH 80213, and (c) *Palaeictops* sp. USNM495155. ASC anterior semicircular canal, co cochlea, fs fossa subarcuata, iam internal acoustic meatus, pbl primary bony lamina, pe petrosal, sbl secondary bony lamina, ve vestibule

semicircular canals are also not inflated much. The aqueductus vestibuli of *Leptictis* and *Palaeictops* leaves the vestibule anterior very close to the crus commune and then curves dorsoposteriorly along the medial side of the latter, and thus shows a different pattern than in *Leptictidium* (Figs. 2d, f, 3c, e). However, due to a break through the distal opening, the aqueductus vestibuli is incomplete in *Palaeictops*. As in *Leptictidium*, there is no clear evidence on the virtual endocasts of the investigated leptictids of a separation of the elliptical from the spherical recesses (Fig. 2c–f). Compared to *Leptictidium*, *Leptictis* has a smaller (more acute) angle between the lateral semicircular plane and basal turn of the cochlea (11.8°), whereas *Palaeictops* has a larger angle (32.7°). The stapedial ratios of *Leptictis* (1.8) and *Palaeictops* (1.72) clearly show that their fenestrae vestibuli are more elliptical than that of *Leptictidium*. Furthermore, the two leptictids have a more inflated cochlear fossula showing a large external aperture (Figs. 2c–f, 3d, f). The canaliculus cochleae of *Leptictis* is a short but distinct canal that opens into a broad, fan-shaped opening on the surface of the petrosal (Figs. 2d, 3c); in *Palaeictops*, the canaliculus cochleae shows a similar pattern, but the opening is much smaller (Figs. 2f, 3e).

Concerning the general shape of the cochlea, both Leptictidae under study have a roughly planispiral cochlea like *Leptictidium*, but their cochlear aspect ratio is even higher (0.69, see Table 1). In certain features of the cochlea, *Palaeictops* again resembles *Leptictidium* more than *Leptictis*. *Palaeictops* (USNM 495155) has almost two cochlear turns and a prominent apical lacuna, but *Leptictis* (AMNH 80213) has 2.25 turns and the apical lacuna is tiny (Fig. 3d, f). The number of turns in the investigated *Leptictis* specimen differs from the observations by Novacek (1986: 60 and fig. 30b), who mentions almost three full turns on the natural endocast of the bony labyrinth of *Leptictis dakotensis* (F-AM 96730). The contribution of the cochlea to the total volume of the bony labyrinth is higher than in *Leptictidium*: 62.43 % in *Leptictis* and 69.06 % in *Palaeictops*, which means that the two leptictids under study have proportionally larger cochleae and smaller semicircular canals than *Leptictidium*. Whereas the primary bony lamina is prominent in all investigated specimens, a secondary bony lamina is only

present on the proximal half of the basal cochlear turn in *Leptictis* and *Palaeictops* (Figs. 3c, e, 4b, c).

Estimation of locomotor agility

The size of the semicircular canals was compared to body mass, a correlation that allows detection of degree of agility (Spoor et al. 2007). Plotted in the regression analysis of Spoor et al. (2007), *Leptictidium* clusters with other highly agile mammals (represented by dark triangles in Fig. 5) and shows values similar to *Chinchilla laniger*, *Xerus erythropus*, *Saimiri sciureus* (all AGIL 6, see supplementary data in Spoor et al. 2007), and *Rhynchocyon cirnei* (see below). Thus, *Leptictidium* has significantly larger semicircular canals in terms of radius of curvature than most similar-sized species (Fig. 5). Even if a higher body mass (627 g) is estimated, *Leptictidium* still falls among the fast-moving species.

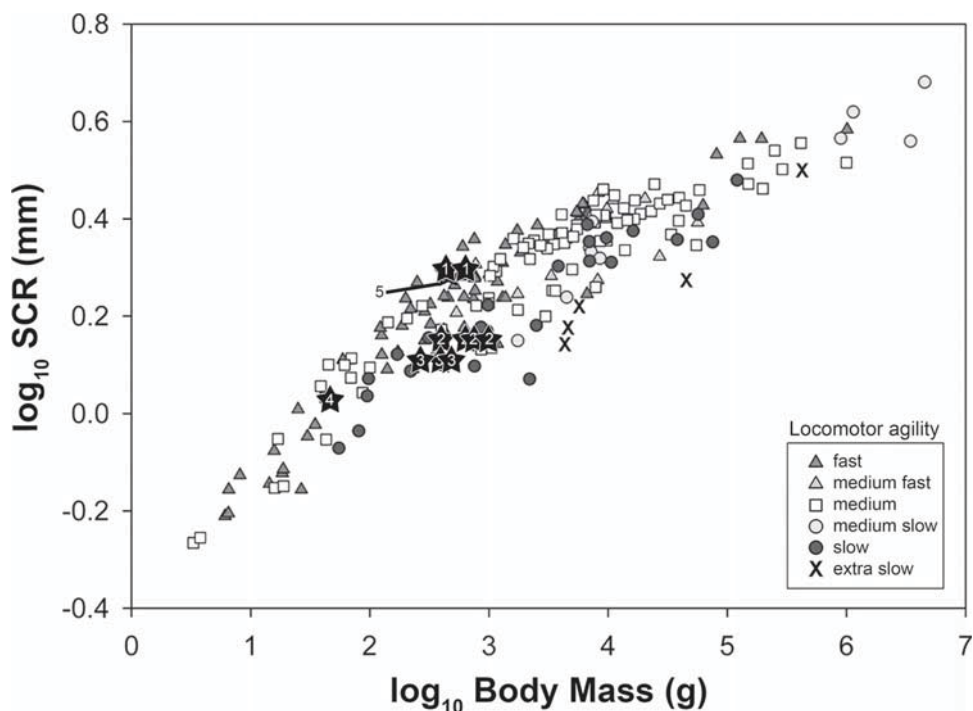
In contrast, *Leptictis* clearly plots below most similar-sized species in an area rather corresponding to slow-moving animals (Fig. 5), although certain medium-moving and fast-moving species, e.g., *Isoodon obesulus* (AGIL 4), *Erinaceus europaeus* (AGIL 4), and *Pteropus giganteus* (AGIL 6), also fall in this range. Moreover, given the fact that the body mass of the *Leptictis* specimen might be overestimated, even a lower body mass comparable to the lower range of *Leptictidium* still falls among the slow to medium agile species and would clearly lie below *Leptictidium* in the regression analysis.

Palaeictops also clusters at the bottom of the sampling among slow to medium-moving animals, and is therefore well in line with a lighter *Leptictis* (Fig. 5). The Macroscelidea *Macroscelides* and *Rhynchocyon*, with their relatively large semicircular canals, show the same pattern as *Leptictidium* in plotting at the upper border of the curve, which is suggestive of high agility (Fig. 5).

In addition, we estimated the agility scores of the investigated species using the equations by Silcox et al. (2009), which include the radius of curvature of the semicircular canal, as well as the body mass (Table 1). These equations are derivatives of the regression analysis by Spoor et al. (2007) and allow estimating of the agility score for each semicircular canal separately, as well as for the mean radius of curvature of the three canals.

In *Leptictidium*, the locomotor agility score of the mean radius of curvature of the three semicircular canals is 5.1 and 5.4, respectively, depending on body mass estimation. Individually, the lateral semicircular canal shows higher agility scores (5.2 and 5.5) than the other two canals (both 4.6 and 4.8). These agility scores indicate a medium to medium-fast type of agility according to the scale presented by Spoor et al. (2007). The investigated leptictids clearly show lower agility scores based on the estimated body masses. The mean radius agility score of *Leptictis* ranges from 3.4 to 4.0, in which the lateral semicircular canal indicates a slightly higher agility (3.5–4.1), followed by the anterior semicircular canal (3.5–4.0) and the posterior one (3.4–3.9). These values suggest a medium-slow

Fig. 5 Relationship between mean radius of curvature of semicircular canals (SCR) and body mass in terrestrial living and fossil mammals (after Spoor et al. 2007). The agility score of the species is indicated by symbols. The black stars indicate the mapped Leptictida and Macroscelidea. Coding: 1, range of *Leptictidium auderiense* SMF-ME-11377; 2, range of *Leptictis* sp. AMNH 80213; 3, *Palaeictops* sp. USNM 495155; 4, *Macroscelides proboscideus* SZ 7397; 5, *Rhynchocyon cirnei* (from Jeffery and Cox 2010)



to medium agility. *Palaeictops* falls in the same agility classes in having a mean radius agility score from 3.5 to 3.9, but in contrast to the other two genera, it shows a different pattern. The highest score is not derived from the lateral but from the anterior semicircular canal (3.7–4.0), followed by the posterior (3.5–3.8) and the lateral semicircular canal (3.4–3.8).

In comparison, *Macroscelides* and *Rhynchocyon* both have higher agility scores than *Leptictis* and *Palaeictops*, but scores that are rather similar to those of *Leptictidium*, indicating a medium to medium-fast agility. In *Macroscelides* the mean radius agility score is 4.4 and the lateral semicircular canal reveals the highest value (4.9), followed by the anterior semicircular canal (4.4) and the posterior semicircular canal (4.0). *Rhynchocyon* has a mean radius agility score of 4 based on field observations, but a score of 5.3 based on the given measurements in Cox and Jeffery (2010) and the equations by Silcox et al. (2009). The lateral semicircular canal also yields an agility score of 5.3, whereas the anterior and posterior semicircular canals have smaller values (4.7 and 4.6, respectively).

Following Malinzak et al. (2012), we also estimated the rotational head speed as a proxy for locomotor agility. The planes between the semicircular canals in *Leptictidium* all form angles that are lower than 90° (Table 1). The angle between the anterior and posterior semicircular canals is 87.6°, that between the anterior and lateral canals is 70.2°, and the angle between the lateral and the posterior canals is 88.9°. Thus, *Leptictidium* has a rather large variance from 90° (90var) among the angles of the three semicircular canals; its $\log_{10}90\text{var}$ is 2.30. In contrast, the angles between the semicircular canal planes of *Palaeictops* are all greater than 90° (93.6°, 90.2°, and 92.7°, respectively) and the $\log_{10}90\text{var}$ is only 1.01. The angular pattern of *Leptictis* is in between, as the angle between the anterior and lateral semicircular canal is also higher than 90° (90.7°), but the other two angles are smaller than 90° (75.6° and 86.3°), as in *Leptictidium*, resulting in a $\log_{10}90\text{var}$ of 2.04. Both *Leptictis* and *Palaeictops* show the greatest angle between the anterior and posterior semicircular canals, but in *Leptictidium* the greatest angle is between the lateral and posterior canals. Like *Leptictidium* and *Leptictis*, *Macroscelides* also shows the greatest angular deviation between the anterior and lateral semicircular canals. However, in being 105.4°, this angle is clearly larger than 90°, but the resulting $\log_{10}90\text{var}$ of 2.09 is pretty close to that of *Leptictis* (Table 1). A plot of the investigated Leptictida in the “primate regression analysis” ($\log_{10}90\text{var}$ versus \log_{10} AVM) of Malinzak et al. (2012) indicates that *Palaeictops* would have a much higher head angular velocity magnitude (AVM) than the other two leptictidans, even higher than almost all primates of that study (Fig. 6a). *Leptictidium* and *Leptictis* plot at lower AVM values than

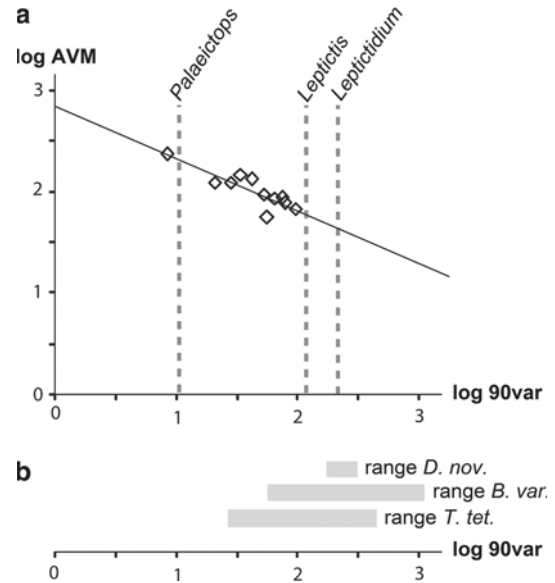


Fig. 6 Relationship between angular velocity magnitude and variation of the spatial orientation of the semicircular canals in Primates, Xenarthra, and the investigated Leptictida. **a** Primate equation (species represented by diamonds) with plotted Leptictida (after Malinzak et al. 2012), **b** range of variance from 90° of the semicircular canals in selected Xenarthra (based on Billet et al. 2013). 90var variance from 90° among angles between semicircular canals of one side of the head, AVM angular velocity magnitude, *B. var.*, *Bradypus variegatus*; *D. nov.*, *Dasyurus novemcinctus*; *T. tet.*, *Tamandua tetradactyla*

Palaeictops and below the primates, with *Leptictis* showing a slightly higher AVM than *Leptictidium*.

Discussion

As Leptictida may be early-diverging members of the placental clade, we first compared their bony labyrinth morphology with that of Upper Cretaceous eutherians, including the unnamed zhelestids from the Bissekty Formation, *Ukhaatherium gobiensis*, *Kulbeckia kulbecke*, and *Zalambdalestes lechei*, which represent the eutherian morphotype in many respects (Ekdale and Rowe 2011). Furthermore, we compared our observations to the study by Ekdale (2013) and added the Leptictida under study to his data matrix on six bony labyrinth characters (see Table 2).

The general bony labyrinth morphology of the investigated Leptictida resembles the pattern observed in these Upper Cretaceous eutherians. Based on the study by Ekdale and Rowe (2011) and further recent works (Ruf et al. 2009; Luo et al. 2012; Ekdale 2013, 2015), we propose that thin and distinctly arcuate semicircular canals and the presence of a secondary crus commune, as present in all of our Leptictida, are plesiomorphic features of the leptictidan groundplan (in the sense of Hennig 1950). Mesozoic

Table 2 Characters of the bony labyrinth in the investigated species (taken from Ekdale 2013)

Character	1	2	3	4	5	6
<i>Leptictidium auderiense</i> SMF-ME-11377	0	0	0	1	0	1
<i>Leptictis</i> sp. AMNH 80213	0	0	0	1	1	1
<i>Palaeictops</i> sp. USNM 495155	0	0	0	1	0	1

Character coding: 1, entry of posterior limb of lateral semicircular canal: (0) secondary common crus, (1) posterior ampulla, (2) vestibule; 2, position of plane of lateral semicircular canal relative to posterior semicircular canal when labyrinth is in anterior view: (0) low (sagittal labyrinthine index =0.0), (1) high (sagittal labyrinthine index >0.0); 3, largest semicircular canal arc radius of curvature: (0) anterior canal, (1) lateral canal, (2) posterior canal; 4, shape of cochlear spiral: (0) low (aspect ratio ≤ 0.55), (1) high (aspect ratio >0.55); 5, number of cochlear turns: (0) 1–2 turns ($\sim 360^\circ$ – 720°), (1) 2–3 turns (720° – 1080°), (2) over 3 turns ($>1080^\circ$); 6, percent volume of total bony labyrinth contributed by cochlea: (0) $\leq 50\%$, (1) 51–75 %, (2) $> 75\%$

eutherians all have a lower number of cochlear turns (about 1–1.5) than the leptictidans under study, which corresponds to the general pattern observed in many living mammals, with approximately two cochlear turns (e.g., Fleischer 1973; Ekdale and Rowe 2011; Ekdale 2013). Thus, Leptictida are derived compared to the eutherian groundplan in having more than one cochlear turn (Meng and Fox 1995; Ekdale and Rowe 2011; Ekdale 2015). The precise pattern in *Leptictis* remains ambiguous, because our observation of 2.25 cochlear turns in *Leptictis* sp. (AMNH 80213) differs from the three turns described by Novacek (1986) for *Leptictis dakotensis* (F-AM 96730). However, this inconsistency might be a consequence of different species, high intraspecific variation, or misinterpretation of the natural endocast. The ampullae of the leptictidans studied here are less pronounced than those of zhelestids, *Ukhaatherium gobiensis*, *Kulbeckia kulbecke*, and *Zalambdalestes lechei* (Ekdale and Rowe 2011). Thus, the slender ampullae of Leptictida might represent an apomorphic feature.

There is clearly no evidence from the bony labyrinth morphology for a close relationship of the investigated Leptictida and Macroscelidea (Benoit et al. 2013; Ekdale 2013; pers. observ.), as was suggested recently by O’Leary et al. (2013). There is also no evidence for this relationship in the data matrix based on Ekdale (2013) that supports our interpretation that the Leptictida are plesiomorphic in many respects and differ from *Macroscelides* (Table 2). For instance, *Macroscelides* shows a different pattern of general bony labyrinth features than the leptictidans under study with proportionally smaller and elliptical semicircular canals and prominent bulbous ampullae. Absence of the secondary crus commune is a derived feature in *Macroscelides*, though the lateral and posterior semicircular canals can have a punctiform connection, if they touch each other. The cochlea of *Macroscelides* also has 2.25

turns, but its shape is very different in being much more conical, though it also has a high cochlear aspect ratio (Benoit et al. 2013; Ekdale 2013; pers. obs). However, the latter is one of the highest among the investigated Afrotheria in the study of Ekdale (2013).

Palaeictops and *Leptictis* have a secondary bony lamina that is almost as long as in zhelestids (Ekdale and Rowe 2011). Such a structure is present not only in zhelestids, but also already in the Upper Jurassic stem-therians *Dryolestes leiriensis* and *Henkelotherium guimarotae*, as well as in many placentals (Meng and Fox 1995; Ruf et al. 2009; Ekdale and Rowe 2011; Luo et al. 2011, 2012; Ekdale 2013). Thus, we propose that the secondary bony lamina is a plesiomorphic character of Leptictida and Theria as well. The secondary bony lamina is reduced several times independently in modern mammals (Fleischer 1973; Ekdale 2015). *Leptictidium auderiense* also shows a derived pattern concerning the absence of the secondary bony lamina. This feature might be an adaptation to lower frequencies, because absence of the secondary bony lamina decreases the stiffness of the basilar membrane and therefore its sensitivity for higher frequencies. In extant mammals, the reduction or loss of the secondary bony lamina, often correlated with a freely mobile malleus, as well as a proportionally longer basilar membrane are adaptations to lower frequencies (Fleischer 1973; West 1985). However, we do not yet have data on middle ear ossicles of Leptictida, and the definite length of the basilar membrane remains ambiguous.

The stapedial ratio is a proxy for stapedial footplate size, commonly used in phylogenetic analyses of extant species, for which monotremes have a ratio of 1.0, marsupials below 1.8, and placentals above 1.8 (Segall 1970; Wible 1990; Ekdale et al. 2004; Ekdale 2013). However, our leptictidans all show a stapedial ratio of 1.8 and below, which means that their stapedial footplate is not very elongate. The comprehensive work of Ekdale (2013) on placental bony labyrinths, covering all living orders, clearly indicates that there are several exceptions to the simplified classification of Segall (1970), and that the stapedial ratio might represent a continuous character. Further confirmed exceptions in placentals are found in extinct notoungulates, litopterns, and in the living artiodactyl *Moschiola* (Macrini et al. 2010; Orliac et al. 2012; Billet and de Muizon 2013; Billet et al. 2015), suggesting that exceptions are common in reality, and that this classification may need revision. In our case, the leptictidans also fall in the range of marsupials described by Segall (1970). *Leptictidium* is the most extreme (stapedial ratio 1.32), whereas *Leptictis* and *Palaeictops* are very close to the traditional threshold considered for the distinction between marsupials and placentals (1.8 and 1.72, respectively). A low stapedial ratio could represent a convergent

evolution of a more rounded fenestra vestibuli within several groups of placentals, or a retained plesiomorphic feature of therians, as monotremes actually have a round fenestra vestibuli (see above). More data on stapedial ratios in basal therians are needed to elucidate the phylogenetic value of this feature.

As *Leptictidium* on one hand, and *Leptictis* and *Palaeictops* on the other hand, may represent two parallel evolutionary lineages within Leptictida, the polarisation of certain inner ear characters remains ambiguous in the absence of available data for phylogenetically more basal Leptictida. Nonetheless, it is evident from the morphological comparison that the cochlear part of the bony labyrinth of *Leptictidium* is more similar to that of *Palaeictops* than to that of *Leptictis*. Thus, we can hypothesize that the latter represents a derived pattern within the North American clade, and that the European Pseudorhyncocyonidae retained certain plesiomorphic cochlear features.

In contrast, the semicircular canals, which are associated with the sense of balance, clearly show a different pattern in the two families. *Leptictidium* is derived from the leptictidan groundplan in having proportionally larger semicircular canals, as evidenced from the morphometric analysis, and its lateral semicircular canal is proportionally larger (relative to other canals) than in the two leptictid species under study (Table 1). This suggests adaptation to faster horizontal head movements and higher agility (e.g., Schmelzle et al. 2007; Cox and Jeffery 2010; see discussion below), and may reflect the different hypothesized locomotor adaptations in the postcranial skeleton of European and North American leptictidans.

Maier et al. (1986) first suggested that *Leptictidium* was a bipedal runner, not a saltator, because its unfused tibia and fibula and the weak sacroiliac joint (involving only one sacral vertebra) could cause weakness or instability of these joints, which would in turn be inconsistent with saltation. This mode of locomotion would have no representatives in the modern world. Conversely, Frey et al. (1993) advocated that the unfused tibio-fibula did not inhibit bipedal hopping, as can be seen in macropodids. Likewise, *Pedetes* and lagomorphs can jump, although their sacroiliac joint involves only one sacral vertebra. These authors thus concluded that *Leptictidium* was a rapid bipedal saltator like *Pedetes*. Later, Christian (1999) argued that the dorsoventrally flexible lumbar region, long and slender ilium, short sacrum, and narrow foot of *Leptictidium* are also more consistent with bipedal hopping than bipedal running. Finally, Rose (2006b) suggested that the skeleton of *Leptictidium* showed substantial evidence for a hind-limb propelled locomotion that was bipedal when speed was necessary, but also that its forelimbs were adapted for digging. This author added that the failure to

find a comparable extant mammal indicates that “the Messel form was not exactly like any living mammal in these behaviours, and probably was unusual, if not unique, in its precise mode of bipedal progression” (Rose 2006b: 54). *Leptictis* and *Palaeictops* are different in having longer (although still shortened) forelegs, and bipedal saltation is likely not to have been the primary mode of locomotion of these species (Rose 1999, 2006b). Morphofunctional studies by Rose (1999) suggest that *Palaeictops* was a terrestrial mammal that showed some adaptation for digging. Moreover, it probably usually moved slowly on four legs (as do many specialized runners and hoppers), but may have performed short quadrupedal runs (even hops) for short periods of time (Rose 1999).

These conclusions are supported by the relationship of the semicircular radius of curvature and body mass of the investigated leptictidans plotted into the regression analysis of Spoor et al. (2007), and by their agility scores (Fig. 5). *Leptictidium* plots on the same regression level as many other highly agile animals analyzed by Spoor et al. (2007), including the bipedal saltators *Dipus sagitta* and *Pedetes capensis*, as well as the Macroscelidea we added. The highest agility scores of *Leptictidium* (5.1–5.5) fall in the range of extant saltatory mammals (5–6), in agreement with the hypothesized very agile, saltatory locomotion.

Conversely, *Leptictis* and *Palaeictops* show a medium-slow to medium agility, based on their predicted agility scores (3.4–3.7), which correspond to the scores of most extant mammals comprising terrestrial, cursorial, scansorial, arboreal, and semiaquatic locomotion (Spoor et al. 2007). Considering the body mass estimation of the Leptictida, even a somewhat lower or higher body mass of the three species would not significantly affect the semicircular canal size versus body mass ratio, and the different locomotor agilities would still be reflected by morphometry. However, though the locomotion of the North American leptictids, based on their limb skeleton, has been regarded as resembling in some respects that of the living Macroscelidea (Rose 2006b), this study indicates that their agility scores are not consistent with this idea and suggest less agile locomotion. Other investigated saltatory species, such as the lagomorphs *Lepus europaeus* and *Oryctolagus cuniculus* (agility scores of 5), plot in the area between the investigated species (for details see supplementary data in Spoor et al. 2007).

Configuration of the semicircular canal planes relative to orthogonality is correlated with rotational head speed within primates. The closer the angles are to 90°, the faster the head rotations are (Malinzak et al. 2012). Our agility predictions in the investigated Leptictida based on this method clearly conflict with the results from the analysis of the radius of curvature based on the work of Spoor et al. (2007). For instance, *Palaeictops* would show the highest

angular velocity magnitude (AVM), very close to the fast-leaping *Galago moholi*, which is the most agile primate in the study of Malinzak et al. (2012). *Leptictidium* and *Leptictis* would have almost similar but lower AVM values, below the primates, with *Leptictidium* showing the lowest AVM (Fig. 6a). These results suggest that *Palaeictops* was a very agile species, whereas *Leptictis* and *Leptictidium* were even less agile than the slow loris *Nycticebus pygmaeus*, with *Leptictidium* being the least agile. We also calculated the $\log_{10}90\text{var}$ of Macroscelidea (Benoit et al. 2013; pers. obs.), which range from 1.29 to 2.40. Thus, the Macroscelidea would cover almost the whole range of primates in the regression analysis of Malinzak et al. (2012), and most macroscelidean species (e.g., *Rhynchocyon cirnei* and *Macroscelides proboscideus*) would also plot with *Leptictis* and *Leptictidium*.

However, the analysis by Malinzak et al. (2012) is almost exclusively based on primates, and might not be easily transposable to other mammalian orders. Moreover, not enough is known about the intraspecific and interspecific variation of angles between the semicircular canals. Malinzak et al. (2012) included only two non-primate species, *Cynocephalus volans* and *Bradypus variegatus*, in their study. The semicircular canal angles predict very high AVM values for the gliding mammal *Cynocephalus*, whereas the suspensory sloth plots at lower AVM. Billet et al. (2012) demonstrated high variability in the bony labyrinth of tree sloths, which includes the deviation of semicircular canal angles from orthogonality. The range of $\log_{10}90\text{var}$ in *Bradypus variegatus* (1.73–3.08; calculated from Billet et al. 2012: ESM-2) is very large and actually covers a large part of the range of primates (Fig. 6b). Accordingly, including only one specimen of *Bradypus* in such a study should be taken with reserve. The intraspecific variation of semicircular canal angles within species with a generally more constant morphology, such as the xenarthrans *Dasybus novemcinctus* and *Tamandua tetradactyla*, may actually also result in a largely varying $\log_{10}90\text{var}$ (calculated from angle values in Billet et al. 2012: ESM-2) that depends on which individual is considered. Among five specimens of *Tamandua tetradactyla*, the $\log_{10}90\text{var}$ varies a good deal from 1.42 to 2.63; it varies less, from 2.25 to 2.49, among six specimens of *Dasybus novemcinctus* (Fig. 6b). This pattern suggests that the differences in $\log_{10}90\text{var}$ observed between our leptictidan taxa may not exceed the range of intraspecific variation observed in some extant species, and thus may not strictly correspond to differences in agility. Recently, Berlin et al. (2013) also observed a negative relationship between mean vestibular sensitivity and 90var in a sample of diverse extant mammals, in agreement with the negative relationship between angular head velocities and 90var demonstrated by Malinzak et al. (2012). However, Berlin

et al. (2013) point out that not only the orientation of the semicircular canals, but the radius as well, may be constrained by locomotor agility. Furthermore, the correlation coefficients of the regressions in Berlin et al. (2013) are relatively modest, which in addition to the existence of non-negligible intraspecific variation, makes the relationship between semicircular canal orientation and vestibular sensitivity difficult to use at present.

In conclusion, the bony labyrinth morphology of the investigated Leptictida shows several plesiomorphic features, but no potentially derived shared characters that could support the recently proposed sister-group relationship to Macroscelidea (O’Leary et al. 2013). The bony labyrinth of *Leptictis* is more derived than that of *Palaeictops* in many respects, and *Leptictidium* resembles the pattern of the more basal leptictid *Palaeictops*. However, the proportionally enlarged semicircular canals in *Leptictidium* suggest a greater agility than in the two leptictids under study. The agility score of *Leptictidium* (based on Spoor et al. 2007 and Silcox et al. 2009) falls in the range of Macroscelidea and bipedal saltatory rodents, and supports a specialized and highly agile locomotion, as demonstrated by its postcranial adaptations (Maier et al. 1986; Frey et al. 1993; Christian 1999), although the exact type of locomotion—bipedal saltation and/or bipedal running—still remains ambiguous based on the available data. The conflicting results of the 90var analysis (based on Malinzak et al. 2012) need to be put on hold until more data on intraspecific variability and on the validity of this correlation for non-primate mammals are available. In order to confirm the leptictidan groundplan and to understand the discrepancy between agility score patterns and overall postcranial anatomy in the investigated Leptictida, a more thorough study should involve all available species of *Leptictidium* and *Leptictis*, as well as specimens of *Prodiacodon*. Nevertheless, it is hoped that this account will make anatomical information of the inner ear in Leptictida available to a wider audience, which should be pertinent for phylogenetic and comparative functional analyses of a variety of mammals.

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