The bony labyrinth of late Permian Biarmosuchia: palaeobiology and diversity in non-mammalian Therapsida

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Biarmosuchia, as the basalmost group of Therapsida (the stem group of mammals), are important for understanding mammalian origins and evolution. Unlike other therapsid groups, the bony labyrinth of biarmosuchians has not yet been studied, despite insightful clues that bony labyrinth morphology can provide to address palaeobiology and phylogeny of extinct animals. Here, using CT scanning, surface reconstruction and a 3D geometric-morphometric protocol of 60 semi-landmarks on the bony labyrinth of 30 therapsids (including three Mammaliaformes), it is demonstrated that bony labyrinth morphology of biarmosuchians is very distinctive compared to that of other therapsids. Despite the primitive nature of their cranial morphology, biarmosuchians display highly derived traits in the structure of the bony labyrinth. The most noticeable are the presence of a long and slender canal linking the vestibule to the *fenestra vestibuli*, an enlarged and dorsally expanded anterior canal, and the absence of a secondary common crus (except for one specimen), which sets them apart from other non-mammalian therapsids. These characters provide additional support for the monophyly of Biarmosuchia, the most recently recognized major therapsid subclade. Although implications of the derived morphology of the biarmosuchian bony labyrinth are discussed, definitive interpretations are dependent on the discovery of well-preserved postcranial material. It nevertheless sheds light on a previously overlooked diversity of bony labyrinth morphology in non-mammalian therapsids.

Keywords: Biarmosuchia, Therapsida, bony labyrinth, inner ear, geometric-morphometric.

INTRODUCTION

Understanding the evolution of the different parts of the ear region is central to understanding synapsid and mammalian palaeobiology (Stokstad 2003; Walsh *et al*. 2009; Ekdale 2013; Benoit *et al*. 2013a,b,c; Kemp 2016; Luo *et al*. 2016). The classic well-established evolutionary series of transformation of the middle ear from the postdentary-bones continues to attract much scientific interest (Allin 1975; Rubidge & Sidor 2001; Kemp 2005, 2016; Luo 2011; Luo *et al*. 2016; Ramírez-Chaves *et al*. 2016). Evolution of the inner ear, on the other hand, can be partly reconstructed from casts of the bony labyrinth, i.e. the osseous capsule that housed the inner ear inside the skull (Stokstad 2003; Ekdale 2013; Benoit *et al*. 2013a–d; Georgi *et al*. 2013; Walsh *et al*. 2013). New X-ray computed tomographic scanning techniques (CT scanning) have enabled reconstruction of the internal cast of the bony labyrinth allowing palaeoneurologists to more easily trace the evolution of bony labyrinth morphology in the fossil record. As the bony labyrinth houses the organs of both balance and hearing, its morphology facilitates the accurate reconstruction of various palaeobiological traits in extinct tetrapods. These include head posture (Girard 1929; Vidal *et al*. 1986; Stokstad 2003; Sereno *et al*. 2007; Benoit *et al*., in press), locomotion (Spoor *et al*. 2002, 2007; Stokstad 2003; Silcox *et al*. 2009), auditory capabilities (West 1985; Meng & Fox 1995; Manoussaki *et al*. 2008; Walsh *et al*. 2009; Laaß 2015a,b, 2016), adaptations for life under water (Spoor *et al*. 2002; Neenan & Scheyer 2012; Georgi *et al*. 2013; Benoit *et al*. 2013a), and social group size and communication (Walsh *et al*. 2009; Benoit *et al*. 2013c). In addition, the structure of the bony labyrinth has been used to reconstruct the phylogeny of extinct species (Lebrun *et al*. 2010; Benoit *et al*. 2013c, 2015).

Because of its relevance to mammalian evolution, bony labyrinth morphology has been documented for most groups of non-mammalian Therapsida (NMT) (Fig. 1), particularly that of cynodonts and dicynodonts (e.g. Olson 1944; Cox 1962; Keyser 1965; Sigogneau 1974; Luo 2001; Kielan-Jaworowska *et al*. 2004; Ivakhnenko 2008; Castanhinha *et al*. 2013; Rodrigues *et al*. 2013; Laaß & Schillinger 2015; Laaß 2015a,b, 2016; Benoit *et al*., in press). Despite this, the structure of the bony labyrinth of the

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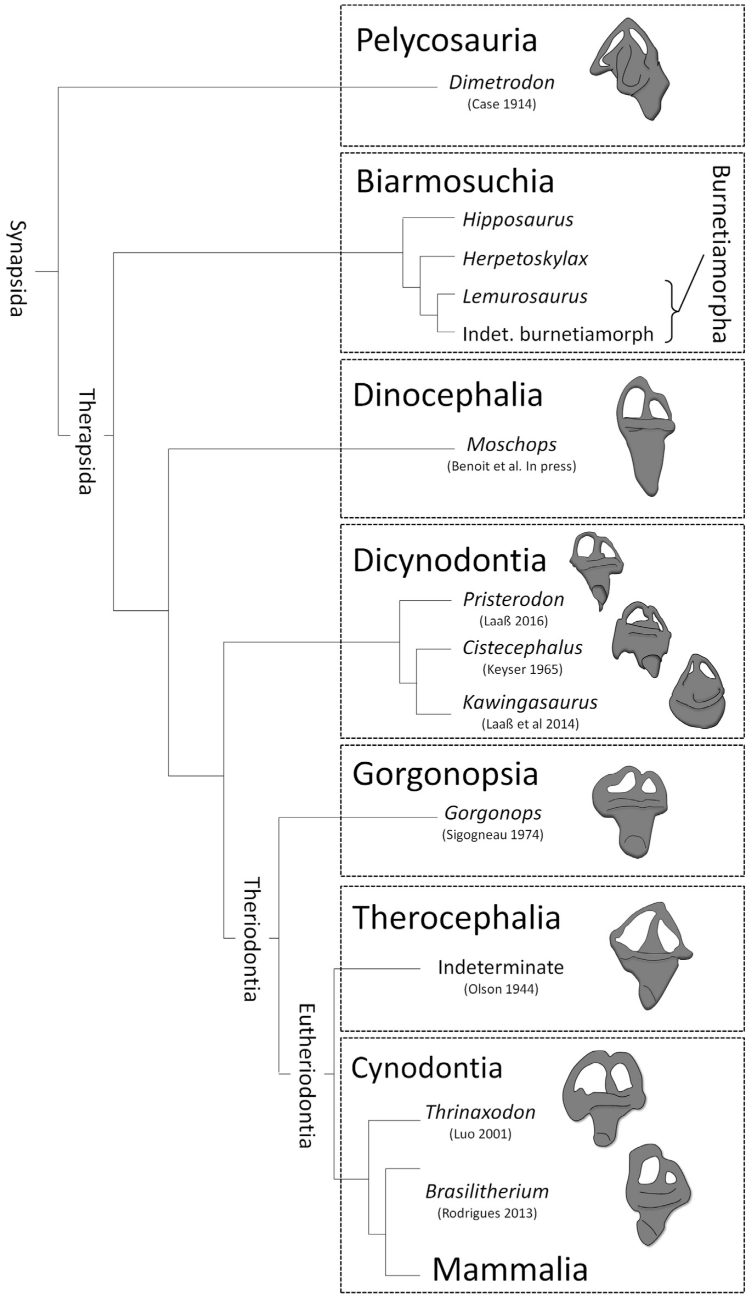

Figure 1. Phylogeny of Therapsida showing the phylogenetic relationships of the Biarmosuchia studied here. Bony labyrinth redrawn after the references cited directly in the figure. Phylogeny after Rubidge & Sidor (2001).

Biarmosuchia, the most basal major therapsid clade (Rubidge & Sidor 2001; Liu *et al*. 2009), has not yet been described and,yet it is of great importance for understanding the most distant evolutionary origin of mammalian traits at the deep root of the therapsid clade.

Before Biarmosuchia was recognized as a distinct clade of Therapsida (Hopson & Barghusen 1986; Sigogneau-Russell 1989; Rubidge & Sidor 2001) they were considered to be gorgonopsians (Sigogneau 1970). Few biarmosuchian genera are represented by more than the holotype material, and many of these specimens are poorly preserved or distorted (e.g. Rubidge & Sidor 2001, 2002; Sidor 2003; Sidor & Welman 2003; Sidor *et al*. 2004; Smith *et al*. 2006; Sidor & Rubidge 2006; Rubidge *et al*. 2006; Sidor & Smith 2007; Ivakhnenko 2008; Kruger *et al*. 2015; Kammerer *et al*. 2016; Day *et al*. 2016). The application of various recently developed imaging techniques could elucidate palaeobiological characteristics of biarmosuchians, such as locomotion, which have not been addressed. Here, synchrotron and CT scanning, and an advanced protocol of semi-landmark-based geometric morphometrics (Perrier *et al*. 2016) were applied to quantify and compare the bony labyrinth morphology of five biarmosuchian genera to that of 24 other therapsids, shedding new light on the deep evolutionary roots of the therapsid bony labyrinth.

MATERIALS AND METHODS

Scanning

For this study, the skulls of five biarmosuchians were scanned: two genera (*Hipposaurus* and *Herpetoskylax*) belonging to the basal paraphyletic non-burnetiamorph biamosuchians (‘Hipposauridae’ and ‘Ictidorhinidae’, respectively) (Sidor & Rubidge 2001; Sidor & Smith 2007; Kruger *et al*. 2015; Day *et al*. 2016); the burnetiamorph *Lemurosaurus* (two skulls), and an additional specimen of a presumably new burnetiamorph species (SAM-PK-11112, hereby refer to as indet. burnetiamorph) (see Fig. 1).

The scans of the biarmosuchian skulls were compared to scans of 25 other synapsids, including five Anomodontia, two Gorgonopsia, four Therocephalia, one Dinocephalia, ten non-mammaliaform Cynodontia and three Mammaliaforms. A list of the specimens scanned with taxonomic assignment, details of the scanning device, voxel size, and stratigraphic position is provided in Supplementary Data 1. Three-dimensional renderings of bony labyrinths were obtained using manual segmentation under Avizo 8 (FEI VSG, Hillsboro OR, USA).

Geometric morphometrics of 3D surfaces

We used a protocol of 60 three dimensional semi-landmarks, modified from Perier *et al*. (2016), to characterize the shape of the three semicircular canals (20 semi-landmarks per canal) of 30 therapsid skulls (Fig. 2A). The semi-landmarks were placed using the software ISE-MeshTools (Lebrun 2008; Lebrun, *et al*. 2010; http://morphomuseum.com/meshtools). Using this software, curves were defined in the centre of the lumen of each semicircular canal, from the centre of its ampulla to its opposite limb. The curves were converted into 20 equidistant semi-landmarks, which were then analysed using MorphoTools (Specht *et al*. 2007; Lebrun 2008). Due to the conservative symmetry of the bony labyrinth in mammals (see Welker *et al*. 2009; Billet *et al*. 2012), the semi-landmark protocol was applied only to the left bony labyrinth. When damaged, deformed or not preserved, the left bony labyrinth was substituted by a mirror image of the right. Each specimen's semi-landmark configuration was represented by its centroid size and by its multidimensional shape vector in a linearized Procrustes shape space, using generalized least-squares fitting (Rohlf 1990). These data were subsequently analysed using a principal components analysis (PCA) of shape (Dryden & Mardia 1998).

Bony labyrinth measurements

Measurements of the bony labyrinth (Table 1) were taken using Avizo 8 (VSG) software and following the protocol illustrated in Fig. 2. The length of the vestibule was measured, including the cochlear recess when present, but excluding the exceedingly long canal joining the *fenestra vestibuli* to the vestibule in some biarmosuchians. The radius of curvature of a semicircular canal is half the mean of its width plus its length. The width of a semicircular canal was measured from the centre of the lumen of each opposing limb (Fig. 2C). The height 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. 2C). The length corresponds to the length of the canal taken at the centre of the lumen of the canal (Fig. 2C). The ventral expansion of the posterior semicircular canal (Vep) (equivalent to the sagittal labyrinthic index of Spoor & Zonneveld [1995]) was measured when the plane of the lateral semicircular canal was parallel to the horizon. According to Spoor & Zonneveld (1995) this measure is the ratio of the distances between the level of the ventralmost point of the lumen of the posterior semicircular canal and the plane of the lateral semicircular canal, and that between the level of the dorsalmost point of the posterior canal and the plane of the lateral semicircular canal (Fig. 2B). The dorsal expansion of the anterior semicircular canal (Dea) (equivalent to the extension of the anterior semicircular canal projecting to the dorsalmost point of the posterior semicircular canal of Schmelzle *et al*. [2007]) was measured when the plane of the lateral semicircular canal was parallel to the horizon and the plane of the posterior semicircular canal was perpendicular to the field of view. This measure is the ratio of the distances between the level of the dorsalmost point of the lumen of the posterior semicircular canal and the level of the dorsalmost point of the lumen of the anterior one, and the length between the dorsalmost point of the lumen of the posterior semicircular canal and the ventralmost point of the anterior semicircular canal and the surface of the vestibule (Fig. 2B). The angle between the plane of the lateral semicircular canal and the main axis of the skull was measured as shown in figure 2D.

For comparison of relative semicircular canal size (Supplementary Data 2) we used sources from the literature to build a dataset of average semicircular canal radius of curvature and body masses for 280 extant and extinct species, including mammals, reptiles, amphibians, and NMT (see Supplementary Data 2 for details). Body mass was sourced from literature (Tables 1; Supplementary Data 2) but when not available it was estimated based on skull length using the equations of Benoit *et al*. (in press). The coefficient of agility was calculated using the equation of Spoor *et al*. (2007) and Silcox *et al*. (2009) using body mass and the average semicircular canal radius (Table 1). Estimations of the auditory range of detectable airborne sounds (predicted range of audible frequencies and mean best frequency) were calculated using the equations of Walsh *et al*. (2009).

Bony labyrinth description

It has long been established that the bony labyrinth morphology does not fully reflect that of the membranous labyrinth in extant species (Gray 1907, 1908). Structures such as the secondary common crus, sacculus and utriculus on the bony labyrinth look very different from the corresponding structures on the membranous labyrinth, and others such as the osseous semicircular canals only approximate the morphology of their homologues on the membranous organ. For simplicity and readability, most of the literature (e.g. Olson 1944; Ekdale 2013; Ruf *et al*. 2009; Luo *et al*. 2011) use the membranous labyrinth terminology to describe the bony labyrinth of extinct species. Accordingly, only the bony labyrinth is described and discussed here, and no assumption is made on the morphology of the membranous labyrinth, unless specified.

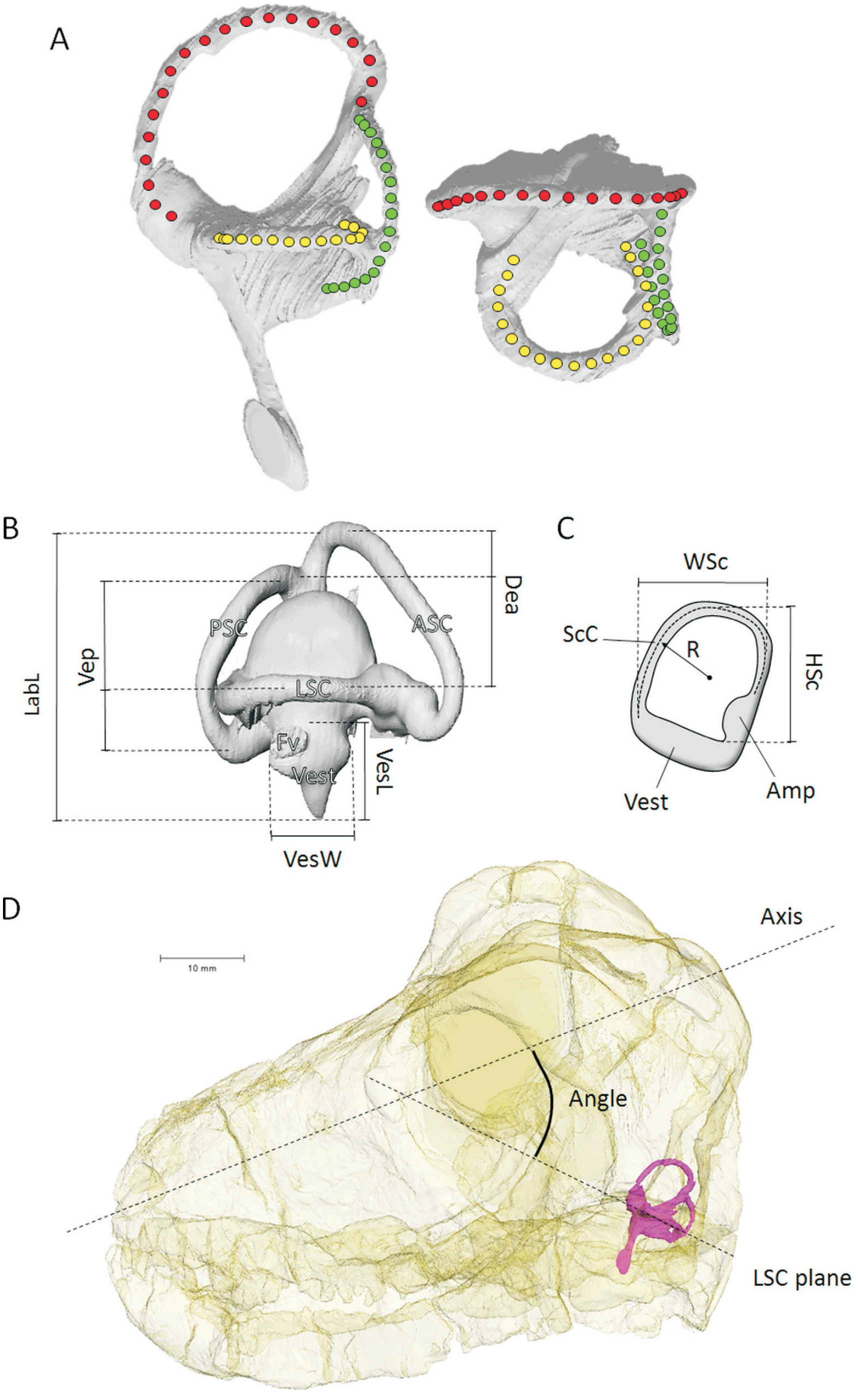

Figure 2. Methods. **A,** The protocol of 60 semi-landmarks used to perform the PCA on shape. **B** and **C,** measurement protocol of the bony labyrinth (**B**) and semicircular canals (**C**). **D**, Measurement of the angle between the skull and lateral semicircular canal. A, bony labyrinth of *Lemurosaurus pricei* (BP/1/816); B, bony labyrinth of *Iguana* sp.; **C**, drawing of an isolated semicircular canal; **D**, reconstruction of the bony labyrinth in the transparent skull of *Lemurosaurus pricei* (BP/1/816). Abbreviations: Amp, ampulla; Angle, angle between the skull and lateral semicircular canal; ASC, anterior semicircular canal; Axis, main axis of the skull; Dea, dorsal expansion of the anterior semicircular canal; Fv, *fenestra vestibuli*; HSc, semicircular canal height; LabL, length of the bony labyrinth; LSC, lateral semicircular canal; LSC plane, plane of the lateral semicircular canal; PSC, posterior semicircular canal; R, radius of curvature of the semicircular canal; ScC, semicircular canal; Vep, ventral expansion of the posterior canal; Vest, vestibule; VesL, length of the vestibule; VesW, width of the vestibule; WSc, semicircular canal width.

DESCRIPTIONS AND RESULTS

Unlike most non-mammaliaform therapsids (NMT) in which the medial wall of the vestibule, common crus, ampullae, and anterior and lateral semicircular canals are not ossified (Olson 1944; Sigogneau 1974; Luo 2001; Kielan-Jaworowska *et al*. 2004; Ivakhnenko 2008; Castanhinha *et al*. 2013; Rodrigues *et al*. 2013; Laaß & Schillinger 2015; Laaß 2015a,b, 2016; Benoit *et al*., in press), the bony labyrinth of biarmosuchians is well-encapsulated. Only a small part of the vestibule and the semicircular canal ampullae are medially opened. The vestibule is short in biarmosuchians. In all taxa except *Hipposaurus*, the *fenestra vestibuli* is located at the distal end of a long and thin osseous canal that goes through the thickened bone of the basicranium (Fig. 3). In contrast, the vestibule is short and conical in *Hipposaurus*, and the *fenestra vestibuli* communicates directly with the exterior surface, which is the most generalized condition among

Table 1. Measurements of the skulls and bony labyrinths, and estimation of hearing range, best hearing frequency and agility of the therapsids studied. Abbreviations: Dea, dorsal expansion of the anterior canal; SC, semicircular canal; SCR, semicircular canal radius; Vep, ventra expansion of the posterior canal. In the 'length of bony labyrinth column', numbers in brackets represent measurments including the length of the slender canal leading to the *fenestra vestibuli*. In the 'Vestibule length column', numbers in brackets represent measurements of the cochlear canal in mammals.

		Skull length (mm)	Basicranial axis length (mm)	Body mass (g)	Length of bony labyrinth (mm)	Vestibule length (mm)	Ratio vestibule/ basicranial axis	Hearing range after Walsh *et al*. 2009 (Hz)	Mean best hearing frequency after Walsh *et al*. 2009 (Hz)
Moschops	Dinocephalia	340.19	106.27	327367	36.49	21.81	0.21	8228.00	4680.38
Hipposaurus	Biarmosuchia	193.92	67.94	23213	25.45	9.45	0.14	7824.27	4461.38
Herpetoskylax	Biarmosuchia	112.77	31.05	4490	16.47 (17.86)	6.48 (9.94)	0.21	8248.16	4691.32
Lemurosaurus BP/1/816	Biarmosuchia	75.20	17.85	1327	9.87 (15.12)	2.19 (7.02)	0.12	7724.13	4407.06
Lemurosaurus NMQR 1702	Biarmosuchia	118.53	34.21	5219	16.36 (17.25)	6.52 (7.46)	0.19	8138.60	4631.89
Indet. SAM-PK-11112	Biarmosuchia	119.49	32.21	5348	17.59 (23.62)	7.21 (13.86)	0.22	8341.61	4742.01
Pristerodon	Dicynodontia	67.65	23.59	967	14.22	6.62	0.28	8688.23	4930.04
Indet. BP/1/155	Gorgonopsia	134.69	45.58	7682	15.12	8.22	0.18	8075.39	4597.60
Scylacocephalus	Gorgonopsia	99.26	34.13	3056	13.61	7.63	0.22	8339.86	4741.06
Choerosaurus	Therocephalia	93.07	31.45	2571	8.17	3.90	0.12	7732.17	4411.42
Microgomphodon	Therocephalia	86.96	36.31	2052	13.77	7.98	0.22	8316.77	4728.54
Euchambersia NHMUK 5696	Therocephalia	121.04	?	5560	?	?	?	?	?
Euchambersia BP/1/4009	Therocephalia	83.74	25.71	1832	11.64	4.50	0.18	8043.63	4580.37
Olivierosuchus	Therocephalia	96.08	34.72	2770	?	?		6975.20	4000.80
Cynosaurus BP/1/1563	Cynodontia	49.70	17.18	387	6.22	2.22	0.13	7764.00	4428.69
Cynosaurus BP/1/3926	Cynodontia	115.83	46.18	4868	12.58	6.43	0.14	7825.15	4461.86
Thrinaxodon BP/1/4263	Cynodontia	70.88	20.20	1112	8.82	3.41	0.17	8005.68	4559.79
Thrinaxodon 4757.79 BP/1/7199	Cynodontia	72.54	22.79	1192	5.11	5.21	0.23	8370.7	
Galesaurus	Cynodontia	93.42	34.34	2629	10.70	5.34	0.16	7924.44	4515.72
Trirachodon AM 461	Cynodontia	95.62	28.24	2730	10.29	1.57	0.06	7314.57	4184.89
Trirachodon BP/1/4658	Cynodontia	101.45	33.85	3263	9.82	6.22	0.18	8095.97	4608.77
Trirachodontid indet.	Cynodontia	45.54	12.96	299	6.74	2.40	0.19	8105.63	4614.00
Lumkuia	Cynodontia	59.05	17.37	645	6.91	2.25	0.13	7765.91	4429.72

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Table 1 (continued)

		Skull length (mm)	Basicranial axis length (mm)	Body mass (g)	Length of bony labyrinth (mm)	Vestibule length (mm)	Ratio vestibule/ basicranial axis	Hearing range after Walsh *et al*. 2009 (Hz)	Mean best hearing frequency after Walsh *et al*. 2009 (Hz)
Tachyglossus	Mammaliaform	108.50	25.71	3996	9.89	(9.98)	–	–	–
Ornithorhynchus	Mammaliaform	85.25	10.70	1933	8.36	(7.34)	–	–	-
Megazostrodon	Mammaliaform	29.84	10.44	87	4.66	3.10	0.30	8787.78	4984.04
Lystrosaurus NMQR 3593	Dicynodontia	101.63	33.67	3281	30.32	12.21	0.36	9188.85	5201.60
Lystrosaurus NMQR815	Dicynodontia	101.79	32.26	3296	28.48	16.80	0.52	10154.13	5725.22
Patranomodon	Anomodontia	63.64	16.35	806	10.56	4.91	0.30	8808.36	4995.20
Massetognathus	Cynodontia	89.18	21.55	2214	9.33	5.20	0.24	8448.16	4799.81
Eodicynodon	Dicynodontia	99.77	35.59	3103	17.41	7.56	0.21	8271.87	4704.18
		Vestibule width (mm)	Ant SC radius (mm)	Ant SC length (mm)	Lat SC radius (mm)	Lat SC length (mm)	Post SC radius (mm)	Post SC length (mm)	Average SCR (mm)
Moschops	Dinocephalia	14.73	5.73	20.28	4.27	12.08	4.06	12.30	4.69
Hipposaurus	Biarmosuchia	9.42	6.07	22.13	3.52	9.26	4.42	18.58	4.67
Herpetoskylax	Biarmosuchia	5.18	3.76	14.83	3.03	9.41	2.25	10.62	3.01
Lemurosaurus BP/1/816	Biarmosuchia	4.41	3.43	12.00	2.19	6.10	2.22	9.17	2.61
Lemurosaurus NMQR 1702	Biarmosuchia	4.93	3.87	13.85	2.34	6.70	3.06	12.60	3.09
Indet. SAM-PK-11112	Biarmosuchia	5.08	4.58	16.16	3.71	12.77	3.02	8.66	3.77
Pristerodon	Dicynodontia	3.67	2.87	9.29	2.43	6.58	2.38	7.54	2.56
Indet. BP/1/155	Gorgonopsia	4.36	3.15	10.30	2.22	8.13	2.34	7.28	2.57
Scylacocephalus	Gorgonopsia	3.86	2.91	9.88	?	?	2.08	6.70	2.50
Choerosaurus	Therocephalia	2.73	2.22	6.89	1.58	4.76	1.73	4.77	1.84
Microgomphodon	Therocephalia	3.71	2.46	7.85	?	?	?	?	2.46
Euchambersia NHMUK 5696	Therocephalia	?	3.91	13.31	2.84	9.36	2.61	8.57	3.12
Euchambersia BP/1/4009	Therocephalia	4.50	3.13	9.07	2.75	8.23	3.07	9.09	2.98
Olivierosuchus	Therocephalia	?	?	?	2.94	?	?	?	2.94
Cynosaurus BP/1/1563	Cynodontia	2.56	1.74	5.98	1.18	3.09	1.24	4.10	1.39
Cynosaurus BP/1/3926	Cynodontia	4.51	2.65	9.02	1.63	4.56	2.16	7.68	2.14

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Table 1 (continued)

		Vestibule width (mm)	Ant SC radius (mm)	Ant SC length (mm)	Lat SC radius (mm)	Lat SC length (mm)	Post SC radius (mm)	Post SC length (mm)	Average SCR (mm)
Thrinaxodon BP/1/4263	Cynodontia	3.23	1.94	7.78	1.93	4.81	1.56	3.88	1.81
Thrinaxodon BP/1/7199	Cynodontia	3.56	1.96	6.43	1.50	4.42	1.79	5.60	1.75
Galesaurus	Cynodontia	3.81	2.15	6.98	1.54	4.06	1.71	6.03	1.80
Trirachodon AM 461	Cynodontia	1.28	2.82	9.40	2.17	6.27	2.46	7.05	2.48
Trirachodon BP/1/4658	Cynodontia	5.65	2.73	9.40	2.20	6.41	2.13	6.80	2.35
Trirachodontid indet.	Cynodontia	1.43	1.75	5.59	1.40	3.85	1.18	4.04	1.45
Lumkuia	Cynodontia	2.35	1.61	5.98	1.39	4.31	1.50	4.96	1.50
Tachyglossus	Mammaliaform	2.08	2.31	7.51	1.45	5.08	1.81	6.96	1.86
Ornithorhynchus	Mammaliaform	1.52	1.77	5.07	1.31	4.03	1.75	4.74	1.61
Megazostrodon	Mammaliaform	1.18	1.93	2.91	–	–	–	–	1.93
Lystrosaurus NMQR 3593	Dicynodontia	5.69	3.78	14.36	2.96	10.41	3.82	13.25	3.52
Lystrosaurus NMQR815	Dicynodontia	5.95	4.17	13.91	3.08	9.54	3.49	12.57	3.58
Patranomodon	Anomodontia	3.13	2.99	10.69	2.26	7.94	1.68	7.83	2.31
Massetognathus	Cynodontia	4.28	2.42	8.58	1.80	6.39	2.08	6.29	2.10
Eodicynodon	Dicynodontia	9.08	4.39	14.78	2.97	9.06	3.50	11.39	3.62

		Coefficient of agility	Vep	Dea	Angle between anterior and lateral canals (°)	Angle between posterior and lateral canals (°)	Angle between anterior and posterior canals (°)	Angle between the cranial axis and the plan of the the horizontal canal (°)	
Moschops	Dinocephalia	4	–	0.51	90.10	73.93	75.69	76	
Hipposaurus	Biarmosuchia	6	1.43	0.78	86.21	81.03	93.31	11	
Herpetoskylax	Biarmosuchia	5	2.15	0.77	78.67	72.77	128.47	26	
Lemurosaurus BP/1/816	Biarmosuchia	6	1.51	0.95	82.62	88.41	91.97	37	
Lemurosaurus NMQR 1702	Biarmosuchia	5	1.30	1.42	73.19	75.24	133.54	25	
Indet. SAM-PK-11112	Biarmosuchia	6	–	0.54	77.07	101.12	82.08	20	
Pristerodon	Dicynodontia	6	–	0.24	80.61	76.72	77.80	18	

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Table 1 (continued)

		Coefficient of agility	Vep	Dea	Angle between anterior and lateral canals (°)	Angle between posterior and lateral canals (°)	Angle between anterior and posterior canals (°)	Angle between the cranial axis and the plan of the the horizontal canal (°)
Indet. BP/1/155	Gorgonopsia	4	–	0.19	76.27	83.24	86.02	18
Scylacocephalus	Gorgonopsia	5	–	0.25	77.54	74.01	75.84	33
Choerosaurus	Therocephalia	4	–	0.28	84.02	80.09	97.84	52
Microgomphodon	Therocephalia	5	?	?	86.37	87.45	?	32
Euchambersia NHMUK 5696	Therocephalia	5	–	0.16	78.91	87.74	76.02	19
Euchambersia BP/1/4009	Therocephalia	6	–	0.09	44.94	102.96	80.36	30
Olivierosuchus	Therocephalia	6	?	?	78.25	76.80	?	31
Cynosaurus BP/1/1563	Cynodontia	4	–	0.25	76.43	73.48	81.67	12
Cynosaurus BP/1/3926	Cynodontia	4	–	0.46	77.54	80.57	95.76	21
Thrinaxodon BP/1/4263	Cynodontia	4	–	0.28	76.54	93.66	113.94	29
Thrinaxodon BP/1/7199	Cynodontia	4	–	0.07	80.64	95.51	94.00	33
Galesaurus	Cynodontia	4	–	0.24	78.40	81.06	82.12	60
Trirachodon AM 461	Cynodontia	5	–	0.00	88.56	74.80	73.84	18
Trirachodon BP/1/4658	Cynodontia	4	–	0.07	78.63	82.13	82.91	24
Trirachodontid indet.	Cynodontia	4	–	0.32	78.11	86.08	89.61	22
Lumkuia	Cynodontia	4	–	0.00	70.23	75.92	88.69	23
Tachyglossus	Mammaliaform	3	–	0.16	65.03	97.40	100.09	24
Ornithorhynchus	Mammaliaform	3	–	0.24	70.94	92.02	91.41	9
Megazostrodon	Mammaliaform	7	–	–	–	–	–	44
Lystrosaurus NMQR 3593	Dicynodontia	7	–	0.30	82.89	75.06	80.08	–23
Lystrosaurus NMQR815	Dicynodontia	7	–	0.27	75.99	76.51	78.87	–19
Patranomodon	Anomodontia	6	–	0.56	80.91	90.25	73.49	21
Massetognathus	Cynodontia	4	–	0.34	80.77	67.55	79.05	24
Eodicynodon	Dicynodontia	7	–	0.20	80.35	85.76	79.60	35

therapsids (Olson 1944; Cox 1962; Keyser 1965; Sigogneau 1974; Luo 2001; Kielan-Jaworowska *et al*. 2004; Ivakhnenko 2008; Castanhinha *et al*. 2013; Rodrigues *et al*. 2013; Laaß & Schillinger 2015; Laaß 2015a,b, 2016; Benoit *et al*., in press). There is no cochlear recess, except in one specimen of *Lemurosaurus* (NMQR 1702) which shows a distinct papilla medial to the vestibule (Fig. 3E) comparable to those observed in some cynodonts, dicynodonts and therocephalians (Luo 2001; Kielan-Jaworowska *et al*. 2004; Castanhinha *et al*. 2013; Rodrigues *et al*. 2013; Laaß 2015a,b; Fig. 4D, G, I–K).

There is no evidence for the separation of the sacculus and utriculus of the vestibule in any of our specimens. As in other NMT, the three ampullae are opened medially to the brain cavity in biarmosuchians, except in one *Lemurosaurus* (BP/1/816) in which the posterior ampulla only is not ossified medially. All three ampullae are prominent except in *Herpetoskylax,* in which the lateral ampulla is distinctly smaller (Fig. 3C). All NMT have a secondary common crus, which corresponds to the fusion of the ventral arm of the posterior canal with the posterior arm of the lateral canal (Olson 1944; Cox 1962; Keyser 1965; Sigogneau 1974; Luo 2001; Kielan-Jaworowska *et al*. 2004; Ivakhnenko 2008; Castanhinha *et al*. 2013; Rodrigues *et al*. 2013; Laaß & Schillinger 2015; Laaß 2015a,b, 2016; Benoit *et al*., in press; Fig. 4A–K). As a result, the entrance into the posterior ampulla is shared by both osseous canals. A short secondary common crus is present in the indet. burnetiamorph, with the two canals being separated until they fuse at the entry of the posterior ampulla (Fig. 3F), but not in the other biarmosuchians studied (Fig. 3). Instead, *Lemurosaurus*, *Herpetoskylax*, and *Hipposaurus* display an apomorphic condition in which there is no secondary common crus (Fig. 3). In these taxa, the lateral and posterior canals are fused for a short section, distal to the vestibule. However, instead of entering the posterior ampulla together as in other therapsids, the posterior canal projects ventrally and separates from the lateral canal (Fig. 3). Therefore, the lateral canal enters the vestibule dorsal to the posterior ampulla, independent of the posterior canal. In *Lemurosaurus*, the posterior canal enters the vestibule through the posterior ampulla (Fig. 3D, E), but in the basal biarmosuchians *Hipposaurus* and *Herpetoskylax* the posterior canal enters the vestibule directly, medial to the posterior ampulla (Fig. 3A, B). As a result, neither the posterior nor the lateral canals enter the vestibule through the posterior ampulla in these two taxa (Fig. 3A, B), which is a unique condition among therapsids and mammals (Olson 1944; Cox 1962; Keyser 1965; Sigogneau 1974; Luo 2001; Stokstad 2003; Kielan-Jaworowska *et al*. 2004; Ivakhnenko 2008; Castanhinha *et al*. 2013; Rodrigues *et al*. 2013; Ekdale 2013; Benoit *et al*. 2013a–d, 2015, in press; Georgi *et al*. 2013; Walsh *et al*. 2013; Laaß & Schillinger 2015; Laaß 2015a,b, 2016; Fig. 4). This ventral expansion of the posterior canal (Vep) is more pronounced in *Herpetoskylax* than in other biarmosuchians (Table 1).

As in mammals, the anterior canal is the largest of the semicircular canals in NMT in terms of length and radius (Table 1) and encircles the floccular fossa of the endocast. In *Lemurosaurus, Herpetoskylax*, and the indet. burnetiamorph, the anterior canal is more than 50% larger than the posterior one, which is very large for a therapsid (Table 1). *Moschops* is the only other NMT in our sample to approach this condition, with the anterior canal about 40% larger than the posterior one (Table 1). The dorsal expansion of the anterior canal (Dea) also reaches more than 50% of the height of the posterior canal in biarmosuchians and *Moschops*, which indicates the great enlargement of this canal (Table 1). The radius of the posterior canal is also proportionately larger in *Lemurosaurus*, *Herpetoskylax*, and *Hipposaurus* because of the ventral expansion of the ventral posterior canal (Table 1).

In the PCA of shape, most of the variation is explained by axis PC1 (34.03%). Axes PC2 and PC3 explain 27.79% and 10.89% of the variation, respectively. Shape differences on PC1 mostly affects the lateral canal and its relative position with respect to the ampullary arm of the posterior canal (presence or absence of a secondary common crus) (Fig. 5). Shape differences on PC2 mostly affect the relative size of the anterior canal and its dorsal projection (Fig. 5). All NMT are mixed in the scatter plots, but the Biarmosuchia is the only therapsid group that is isolated by the geometry of the semicircular canals (Fig. 5). Both axes distinguish biarmosuchians from other NMT, with the greatest degree of differenciation being on axis PC2. PC3 captures more minor differences in the angle between the common crus and the lateral canal, and the width of the lateral semicircular canal (Fig. 5). Four of the biarmosuchians fall outside the range of morphological variation of semicircular canal of other NMT (Fig. 5), which reflects the unique configuration of their semicircular canals (e.g. the absence of secondary common crus, the Dea). One noticeable exception is the indet. burnetiamorph (SAM-PK-K11112) which appears close to a gorgonopsian (*Scylacocephalus*) but still stands apart from all other NMT on both scatter plots (Fig. 5). This position of SAM-PK-K11112 in the geometric morphometric analysis may reflect the presence of a secondary common crus in this specimen, which strongly affects the 3D conformation of semicircular canals, as described above.

The average radius of curvature of the semicircular canals is relatively larger in biarmosuchians, the dinocephalian *Moschops*, anomodonts, the gorgonopsian *Scylacocephalus*, the cynodont *Trirachodon* (AM 461) and the therocephalians *Euchamberia*, *Olivierosuchus* and *Microgomphodon*, than in the indet. gorgonopsian, the therocephalian *Choerosaurus* and most cynodonts (Fig. 6). Like most non-cynodont therapsids (apart from one specimen of *Trirachodon*), the biarmosuchians have a quotient of agility above 5 (Table 1). Non-mammalian cynodonts and *Moschops* have a quotient value of 4 while the monotremes have a value of 3 (Table 1). The anomodonts have the largest semicircular canal radius compared to body size, with values reaching up to 7 (Table 1).

DISCUSSION

The morphology of the bony labyrinth in NMT is often assumed to be conservative with respect to that of mammals (Sigogneau 1974; Luo 2001; Laaß 2015; Angielczyk

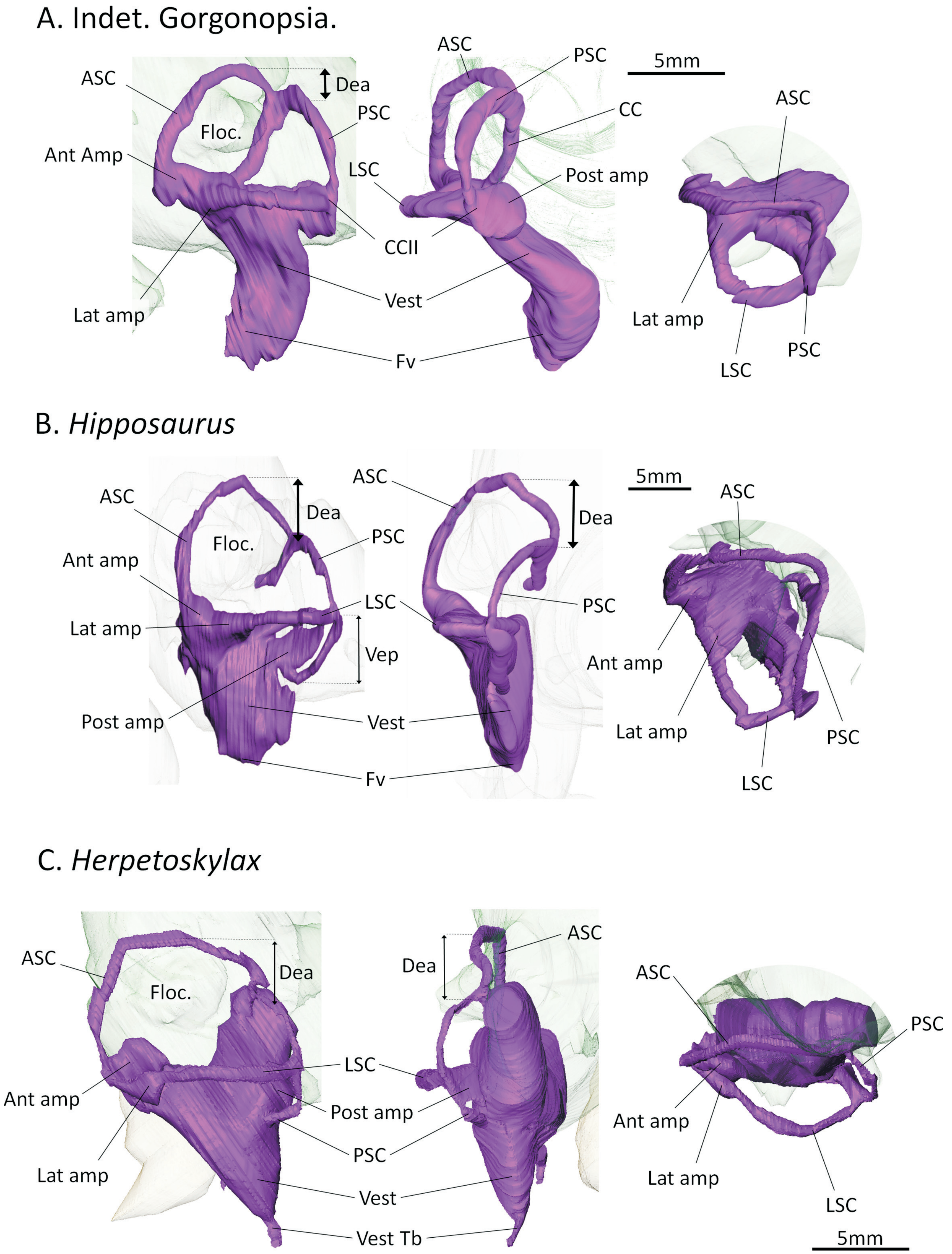

Figure 3. The bony labyrinth of Biarmosuchia. **A**, an indeterminate gorgonopsia (BP/1/155) for outgroup comparison; **B**, *Hipposaurus* (CG-WB123); **C**, *Herpetoskylax hopsoni* (BP/1/3924). Abbreviations: Ant amp, anterior ampulla; ASC, anterior semicircular canal; CC, common crus; CCII, secondary common crus; Dea, dorsal expansion of the anterior semicircular canal; Floc., floccular (subarcuate) fossa; Fv, *fenestra vestibuli*; Lat amp, lateral ampulla; LSC, lateral semicircular canal; Post amp, posterior ampulla; PSC, posterior semicircular canal; Vep, ventral expansion of the posterior canal; Vest, vestibule; Vest tb, vestibular tube. The brain endocast is in transparent. Scale bar, 5 mm.

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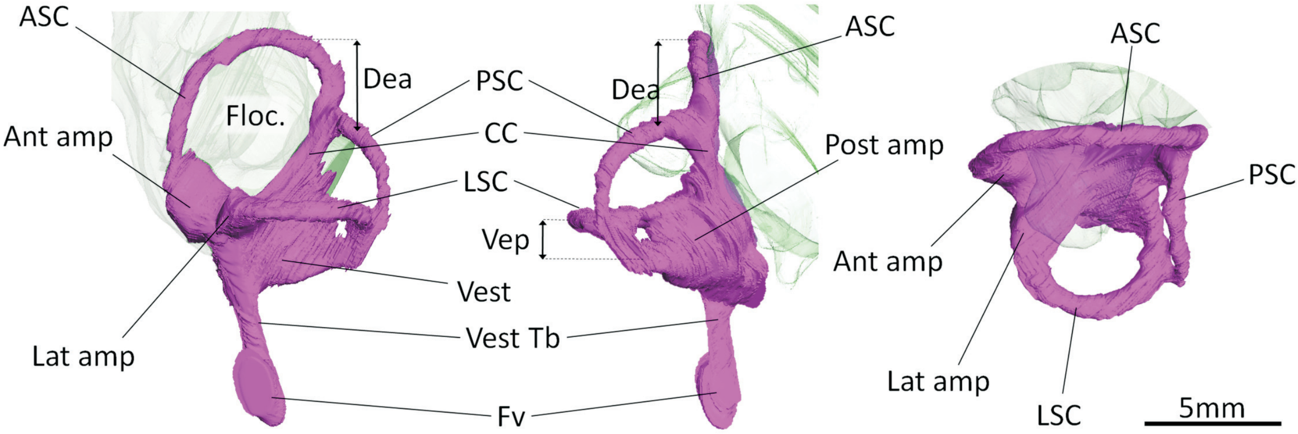
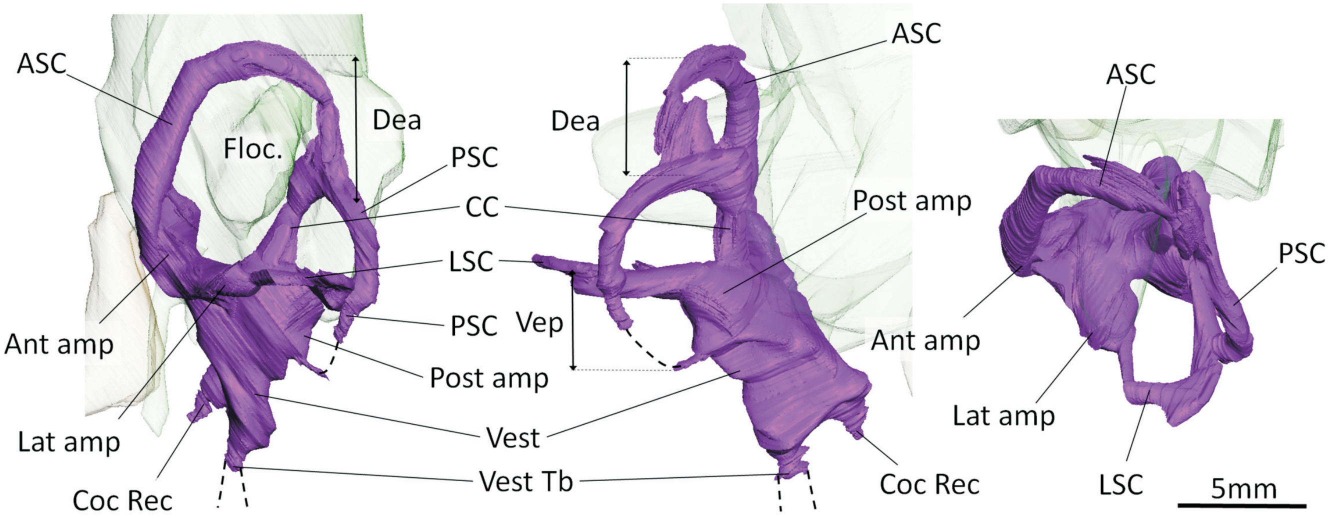
D. *Lemurosaurus* (BP/1/816)



E. *Lemurosaurus* (NMQR 1702)



F. SAM-PK-K11112

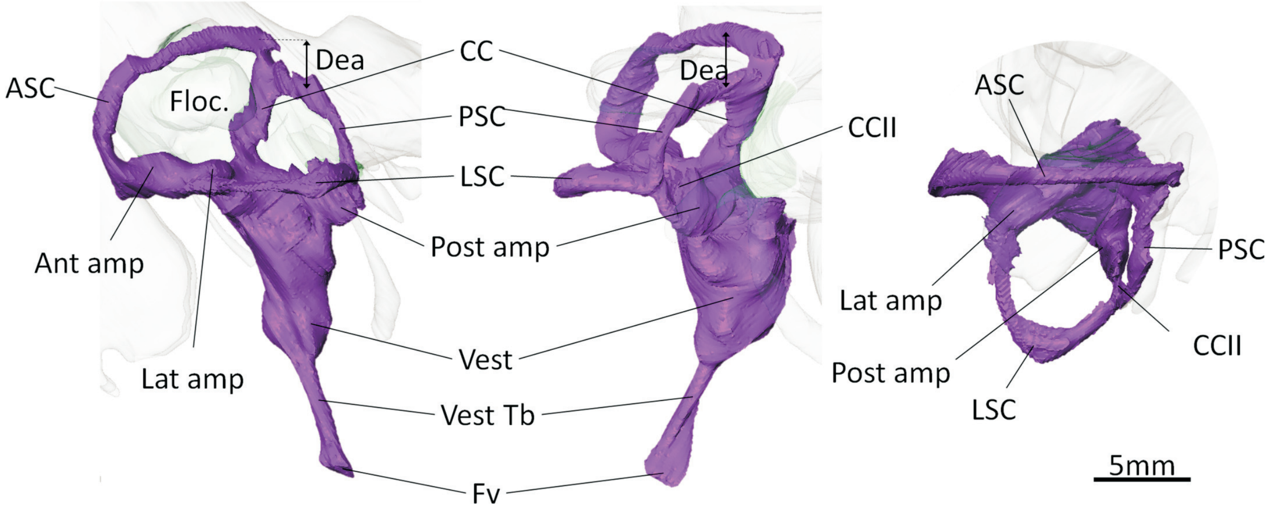


Figure 3 (continued) **D,** *Lemurosaurus pricei* (BP/1/816); **E,** *Lemurosaurus pricei* (NMQR 1702); **F,** indet. burnetiamorph (SAM-PK-K11112).

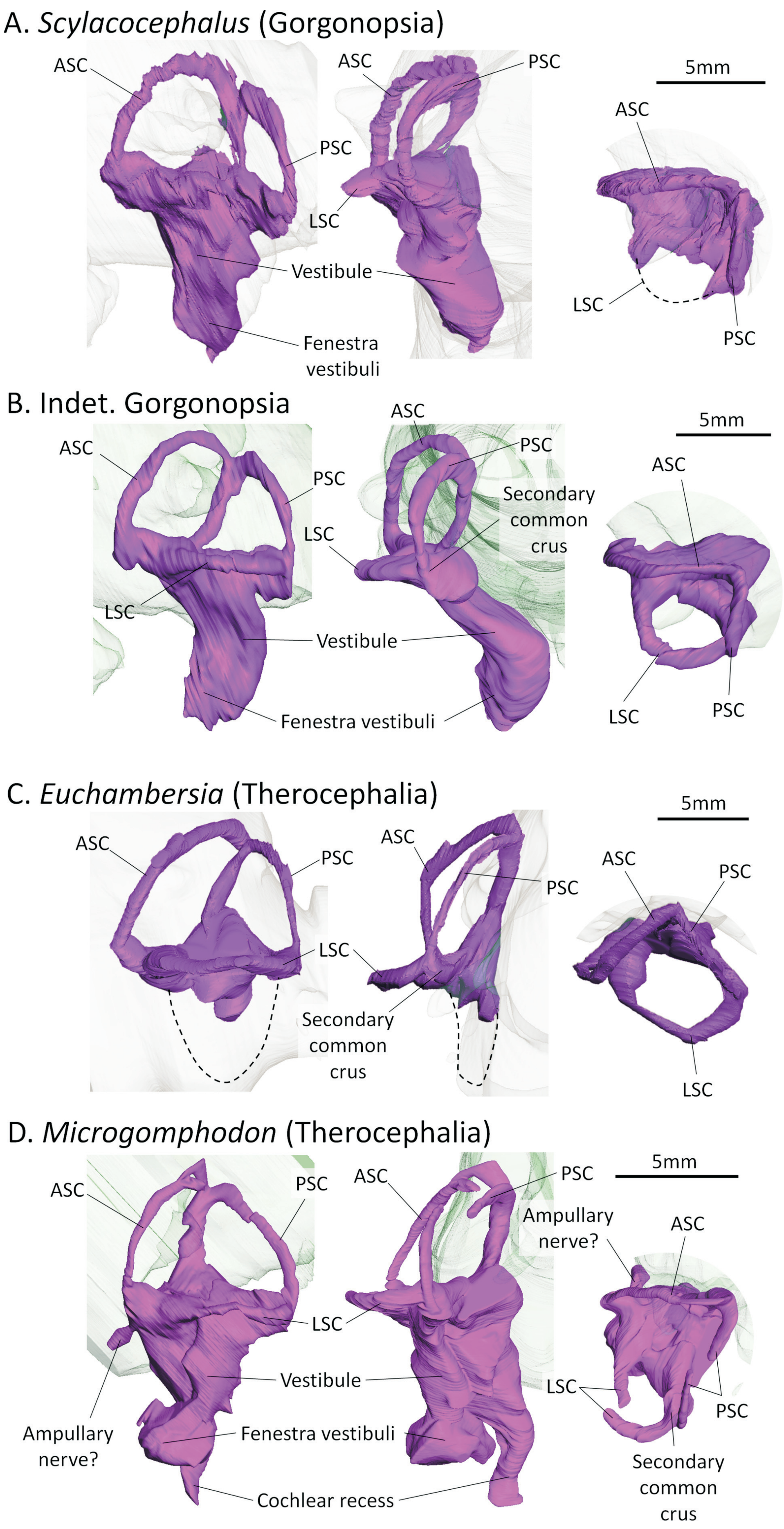


Figure 4. The bony labyrinth in a variety of therapsids examined for this study. **A,** *Scylacocephalus watermeyeri* (BP/1/216); **B,** an indeterminate gorgonopsia (BP/1/155); **C,** *Euchambersia mirabilis* (BP/1/4009); **D,** *Microgomphodon oligocynus* (SAM-PK-10160). Abbreviations: ASC, anterior semicircular canal; LSC, lateral semicircular canal; PSC, posterior semicircular canal.

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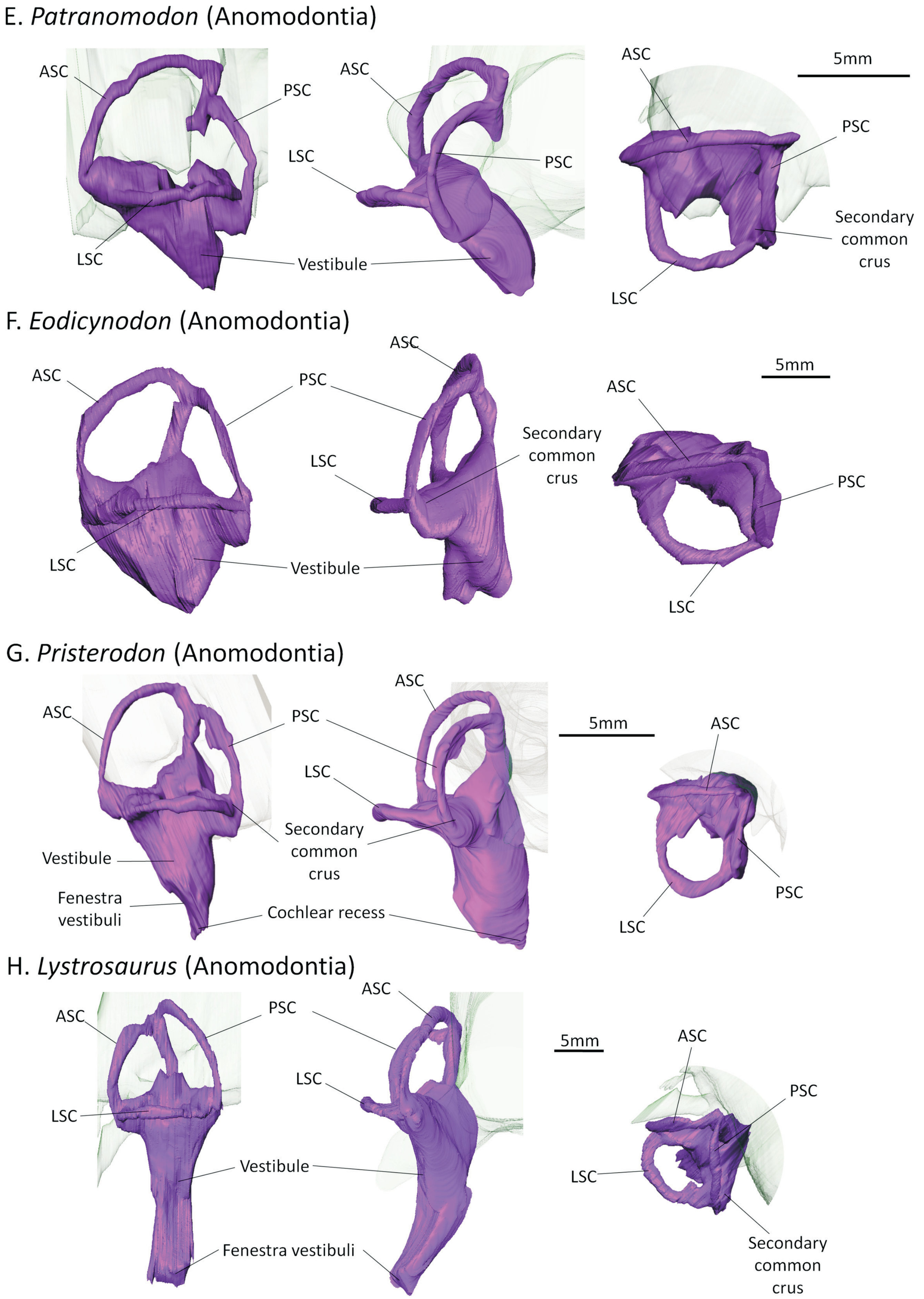

Figure 4 (continued). **E,** *Patranomodon nyaphulii* (NMQR 3000); **F,** *Eodicynodon oosthuizeni* (NMQR 2978); **G,** *Pristerodon* sp. (BP/1/2642); **H,** *Lystrosaurus declivis* (NMQR 815).

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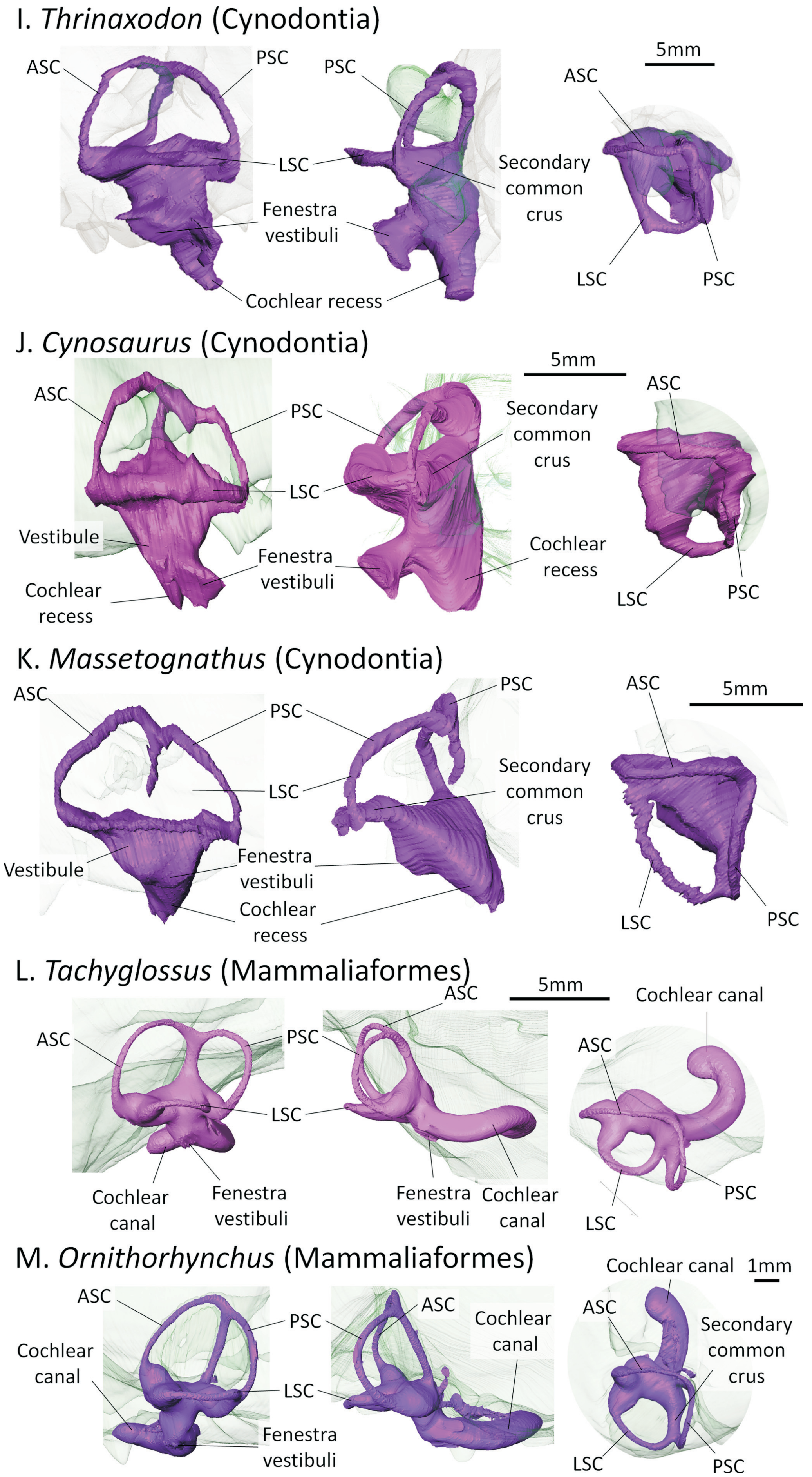

Figure 4 (continued) **I,** *Thrinaxodon liorhinus* (BP/1/7199); **J,** *Cynosaurus suppostus* (BP/1/3926); **K,** *Massetognathus pascuali* (BP/1/4245); **L,** *Tachyglossus aculeatus* (MS86); **M,** *Ornithorhynchus anatinus* (BP/4/908). From left to right: lateral, posterior and dorsal view of the bony labyrinth.

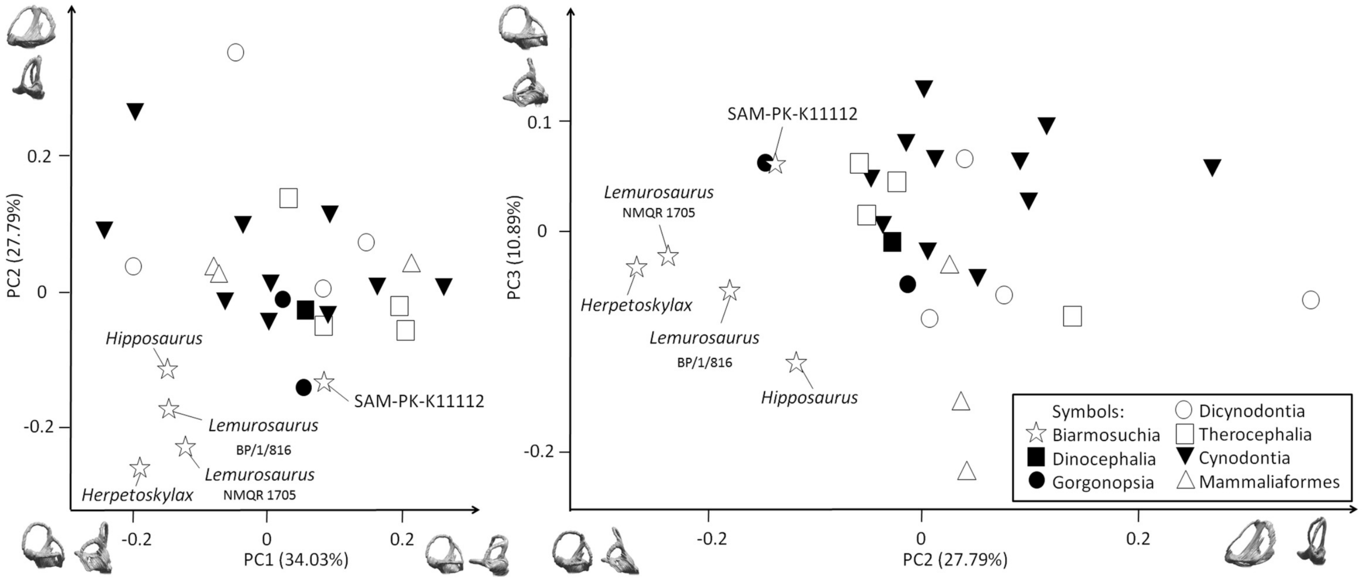

Figure 5. Results of the PCA on shape.

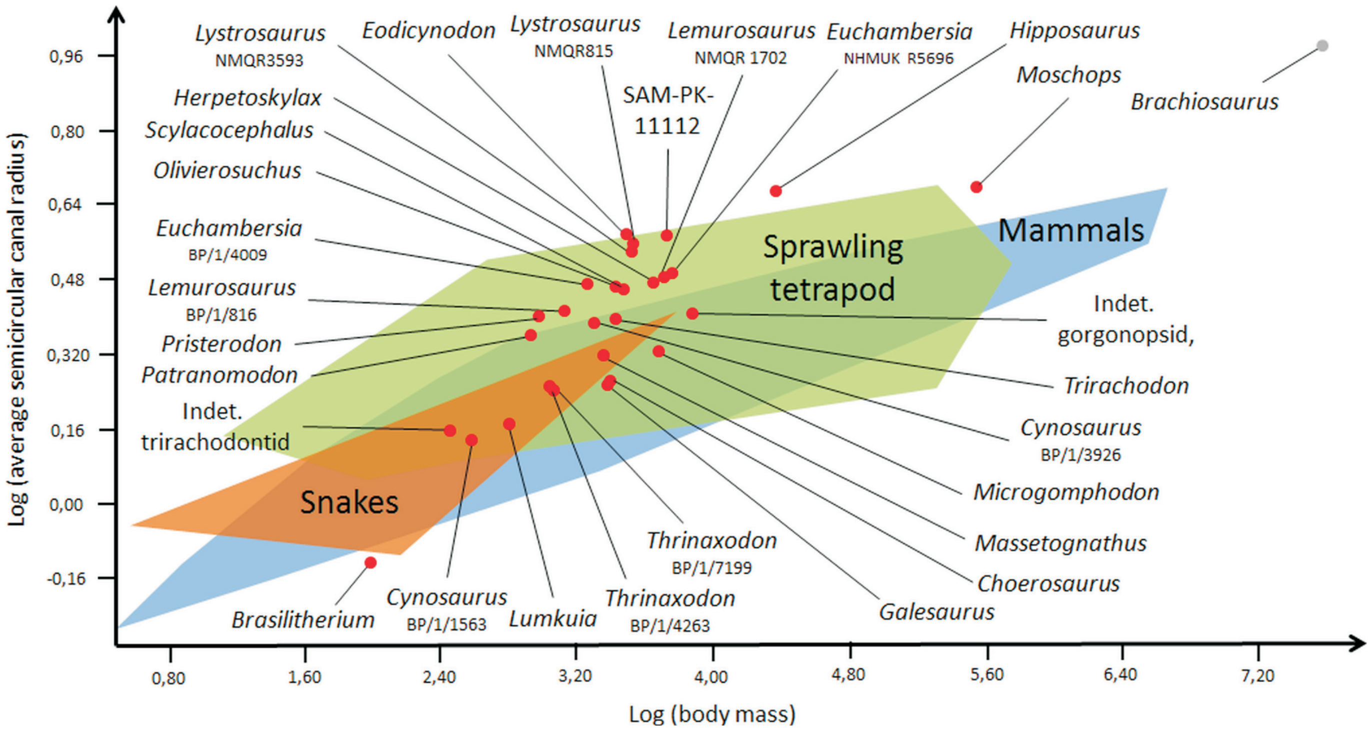

Figure 6. Comparison of average semicircular canal radius of curvature and body mass in tetrapods (Supplementary Data 2).

et al. 2016), similar to that of early 'pelycosaur' grade synapsids (Case 1914). Because there is no cochlear canal, the bony labyrinth in NMT shows little variation of vestibule morphology compared to that of mammals. In addition, the radius of curvature of the semicircular canals are usually subequal, and the posterior and lateral canals usually share a secondary common crus (Olson 1944; Cox 1962; Keyser 1965; Sigogneau 1974; Luo 2001; Kielan-Jaworowska *et al*. 2004; Ivakhnenko 2008; Castanhinha *et al*. 2013; Rodrigues *et al*. 2013; Laaß & Schillinger 2015; Laaß 2015a,b, 2016; Benoit *et al*., in press; Fig. 4). The unique and autapomorphic bony labyrinth morphology of biarmosuchians demonstrate that bony labyrinth morphology in therapsids is in fact more diverse than previously recognized. The large dorsal expansion of the anterior semicircular canal (Dea), absence of a secondary common crus in all but one of our specimens (SAM-PK-11112), and the presence of a long and slender canal joining the vestibule to the distant *fenestra vestibuli* (except in *Hipposaurus*) clearly set biarmosuchians apart as a distinct group of NMT. The status of the Biarmosuchia as a higher taxon was recognized only recently (Sigogneau-Russell

1989; Hopson & Barghusen 1986; Rubidge & Sidor 2001) and, given the highly autapomorphic morphology of their bony labyrinth, this study of their bony labyrinth provides further support to their clade status. These highly distinctive characters provide an opportunity to consider the palaeobiological implications of these new data.

Cochlear recess and auditory capabilities

We here describe the presence of a recess medial to the vestibule in the biarmosuchian *Lemurosaurus* (NMQR 1702) which could correspond to a cochlear recess. In biarmosuchians more derived than *Hipposaurus* (Fig. 1), the vestibule elongates ventrally into a slender canal leading to the *fenestra vestibuli* (Fig. 3), but this is probably not homologous to the cochlear recess since the cochlear recess does not open distally into the *fenestra vestibuli* (Luo 2001). The cochlear recess is the antecedent of the coiled cochlear canal of mammals and was previously recognized only in cynodonts (i.e. *Cynosaurus*, *Thrinaxodon*, *Massetognathus*, *Probelesodon*, *Probainognathus*, *Yunnanodon* and *Brasilitherium*) for which it constitutes a synapomorphy (Luo 2001; Kielan-Jaworowska *et al*. 2004; Rodrigues *et al*. 2013; Fig. 4I–K). In contrast, despite substantial ossification in this area, a cochlear recess is absent in most Biarmosuchia and Anomodontia, and all Dinocephalia and Gorgonopsia studied so far (Olson 1944; Sigogneau 1974; Araujo *et al*. 2017; Benoit *et al*., in press). The probable presence of the cochlear recess in the biarmosuchian *Lemurosaurus* broadens the phylogenetic occurrence of this character among therapsids. Among our comparative sample, a cochlear recess is also present in the therocephalian *Microgomphodon* but not in other therocephalians in which the vestibule is weakly ossified medially (Olson 1944; Fig. 4D). Recently, the presence of a cochlear recess was also hypothesized in two dicynodonts, *Niassodon mfumukasi* and *Pristerodon* sp. (Castanhinha *et al*. 2013; Laaß 2015a, 2016). In the cistecephalid *Kawingasaurus fossilis*, Laaß (2015b) identified a dramatically enlarged vestibule, a feature strongly correlated with fossoriality, but found no cochlear recess. A cochlear recess is absent in the basal anomodonts *Patranomodon* and *Eodicynodon* (Fig. 4E, F). Therefore, apart from Cynodontia, a cochlear recess is present in isolated taxa only among Anomodontia (two occurences), Therocephalia (one occurence) and Biarmosuchia (one occurence). In addition to its absence in more basal representatives of these clades, this strongly suggests that the presence of a distinct and ossified cochlear recess evolved multiple times among therapsids. Just as coiling of the membranous cochlea is not reflected by the bony cochlear canal in monotremes (Gray 1908), the absence of an ossified cochlear recess does not imply that the corresponding membranous structure, the basilar papilla, was absent. For example, a small membranous basilar papilla is present in sarcopterygian fishes but does not reflect on their bony labyrinth (Fritzsch 1987; Manley 2012). More data are required to address the evolution of this structure in NMT, but given the presence of a possible cochlear recess in a basal species such as *Lemurosaurus*, it may be hypothesized that an enlarged basilar papilla, which is ancestral to the membranous cochlea, was already present in the last common ancestor of therapsids.

Estimations of auditory capability based on vestibular length (Table 1) show that the presence or absence of a cochlear recess does not greatly influence the predicted range of detectable airborne frequencies or the mean best hearing frequency in therapsids (Table 1). According to Walsh *et al*.'s equation (Walsh *et al*. 2009), the predicted hearing capabilities of air-borne sound of therapsids averages 4–5 kHz ± 4–5 kHz (Table 1), which overlaps the highest values of those measured in extant reptiles (Walsh *et al*. 2009). These values are less than 20 kHz, which corresponds to the lower limit of frequencies that only mammals can detect (Manley 2012). Althought there are some uncertainties that may affect the accuracy of this prediction (e.g. the nature and position of the tympanum in NMT and the effect of the morphology of the stapes [Gaetano & Abdala 2015; Kemp 2016]), it remains consistent with current consensus that mammals evolved high frequency hearing capabilities only later in the Mesozoic (Meng & Fox 1995; Laaß 2015a, 2016; Kemp 2016; Luo *et al*. 2016).

Semicircular canals and locomotion

Compared to other therapsids, the Biarmosuchia have a disproportionately large anterior semicircular canal (Fig. 3; Table 1). An enlarged anterior canal is not uncommon among tetrapods, including mammals (Gray 1907, 1908; Walsh *et al*. 2009; Ekdale 2013), but it is rare among NMT and elsewhere has only been documented in the dinocephalian *Moschops* and *Brasilitherium* (Fig. 3; Table 1; Rodrigues *et al*. 2013; Benoit *et al*., in press). In biarmosuchians and *Moschops* a prominent dorsal expansion of the anterior canal (Dea) is also present (Table 1). The morphology of the anterior canal could be linked to that of the floccular fossa and the corresponding paraflocular lobe of the cerebellum (Sanchez-Villagra 2002). A larger flocular fossa may result in a larger anterior canal (Sanchez-Villagra 2002), but in dinocephalians the floccular fossa is shallow, unlike the condition in biarmosuchians and most other NMT (Fig. 3; Laaß & Kaestner 2017; Benoit *et al*., in press). Actually, there seems to be no direct link between the presence of a large and deep flocular fossa and the size of the anterior canal in NMT (Olson 1944; Cox 1962; Keyser 1965; Sigogneau 1974; Luo 2001; Kielan-Jaworowska *et al*. 2004; Ivakhnenko 2008; Castanhinha *et al*. 2013; Rodrigues *et al*. 2013; Laaß & Schillinger 2015; Laaß 2015a,b, 2016; Araujo *et al*. 2017; Fig. 4) though, this would need to be quantitatively addressed.

Semicircular canals record the rotation of the head in three dimensions in tetrapods (Graf & Klam 2006; Malinzak *et al*. 2012). It is thus hypothesized that their size is correlated to head mobility and agility in tetrapods (Spoor *et al*. 2002; Stokstad 2003; Clarke 2005; Georgi *et al*. 2013) and enlargement of the anterior canal would reflect greater vertical mobility of the head (Clarke 2005). However, the body masses of dinocephalians and biarmosuchians differ greatly (Table 1), and the orientation of the anterior semicircular canal with respect to the skull in *Moschops* and biarmosuchians is also very different. Indeed, the angle between the cranial axis and the plane of the horizontal canal approximates 80° in *Moschops* whereas in Biarmosuchians it smaller (Table 1). This may reflect a difference in neutral head posture (Benoit *et al*., in press). *Lystrosaurus* is remarkable in this respect as it is the only NMT to display an angle value below zero, which means the head was likely held high (Table 1). The differences in both body mass and bony labyrinth orientation makes it difficult to imagine that a common pattern of head motion are the reason for the similarity in anterior semicircular canal enlargement in *Moschops* and biarmosuchians.

Herpetoskylax, *Hipposaurus* and *Lemurosaurus* are the only NMT currently known that do not have a complete secondary common crus (Fig. 3B, C; Olson 1944; Cox 1962; Keyser 1965; Sigogneau 1974; Luo 2001; Kielan-Jaworowska *et al*. 2004; Ivakhnenko 2008; Castanhinha *et al*. 2013; Rodrigues *et al*. 2013; Laaß & Schillinger 2015; Laaß 2015a,b, 2016; Benoit *et al*., in press; Fig. 4A–K). Fusion of the osseous lateral and posterior semicircular canals into a secondary common crus, and fact that both canals share the same ampulla (the posterior ampulla) to enter the vestibule, is a primitive feature for therapsids and mammals (Ekdale 2013; Luo *et al*. 2011) and is present in all other therapsids and Mesozoic mammals studied to date (e.g. *Henkelotherium*, *Haldanodon* and *Dryolestes*) (Ruf *et al*. 2009, 2013; Luo *et al*. 2011). It is also present in the extant monotreme *Ornithorhyncus* (but not *Tachyglossus*, Fig. 4L, M), a variety of marsupials (e.g. *Didelphys*), as well as some placental mammals (e.g. *Orycteropus*, *Equus*) (Gray 1907 1908; Ekdale 2013; Benoit *et al*. 2015).

Lemurosaurus, *Herpetoskylax*, and *Hipposaurus* depart from this ancestral anatomy since the posterior and lateral semicircular canals are not completely fused. In these taxa, the posterior canal projects ventrally and only merges with the lateral canal at the level where they cross each other (Fig. 3). This condition, though unique among NMT, is sporadically represented in some extant placental mammals (e.g. the Hyracoidea, *Dasypus*, some Macroscelididae; Ekdale 2013; Benoit *et al*. 2013d) and reptiles (Fig. 2; Jones & Spells 1963 ; Ramprashad *et al*. 1986; Olori 2010).

Herpetoskylax and *Hipposaurus* share a unique condition with no equivalent in any known extant or extinct species. Their posterior canal enters directly into the vestibule without passing through the corresponding posterior ampulla (Fig. 3). As a result, the ampulla appears isolated from both the lateral and posterior semicircular canals (Fig. 3). Another interpretation for this morphology would be to consider that the posterior ampulla is extremely small or absent and that the structure here identified as the posterior ampulla is neomorphic. *Herpetoskylax* and *Hipposaurus* are two of the most basal biarmosuchians (e.g. Sidor & Rubidge 2006; Kruger *et al*. 2015; Day *et al*. 2016). Given that this very particular condition is not present in the basalmost burnetiamorph *Lemurosaurus* (Fig. 3D, E) and that a secondary common crus is present in the unidentified burnetiamorph SAM-PK-11112 (Fig. 3F), it appears possible that the secondary common crus displayed by the latter was re-acquired secondarily after it was lost in more basal species. In this case, the absence of a secondary common crus was only transitory in the evolution of biarmosuchians. Another possibility would be that *Herpetoskylax* and *Hipposaurus* comprise a distinct clade, which is not supported by any phylogenetic analysis to date (Sidor & Welman 2003; Smith *et al*. 2006; Sidor & Smith 2007; Kruger *et al*. 2015; Kammerer *et al*. 2016; Day *et al*. 2016).

Because of the lack of fossil material, the postcranial anatomy of biarmosuchians is poorly documented, limited to few limb bones and vertebrae in *Biarmosuchus* and *Hipposaurus*, and little is known about their locomotion (Olson 1962; Sigogneau 1970; Sues 1986; Signogneau-Russell 1989). It appears that their postcranial skeleton was similar to that of gorgonopsians and other basal therapsids, which were able to adopt both a sprawling posture or a more parasagittal gait, as opposed to epicynodonts, which were more permanently parasagittal (Olson 1962; Jenkins 1971; Signogneau-Russell 1989; Kemp 2005). The average radius of semicircular canals indicates that biarmosuchians, along with *Moschops*, anomodonts, *Scylacocephalus* and some therocephalians did have a larger semicircular canal radius than other therapsids, including most cynodonts (Fig. 6). Indeed, all cynodonts have semicircular canal radii that fall within the range of variation observed in extant mammals, whereas biarmosuchians, anomodonts and many other therapsids are different (Fig. 6).

Based on the correlation demonstrated between semicircular canal radius, agility and locomotion in mammals (Spoor *et al*. 2002, 2007; Silcox *et al*. 2009), it is tempting to interpret this difference as reflecting a more mammal-like posture in the derived cynodonts (Jenkins 1971). In contrast, the more basal forms, such as biarmosuchians, anomodonts and dinocephalians, would have had a more sprawling posture. The fact that radius of curvature of the semicircular canals of basal theriodonts (gorgonopsian and therocephalians) are spread between these two groups possibly reflects an intermediate postural behaviour (Fig. 6).

However, the calculation of agility scores based on semicircular radius (Spoor *et al*. 2007; Silcox *et al*. 2009) gives a different signal. It predicts that biarmosuchians, gorgonopsians and anomodonts were more agile than most cynodonts and *Moschops* (Table 1). On the one hand, these higher scores may reflect a more diverse range of locomotory possibilities permitted by the use of both a 'reptile-like gait' and 'mammal-like gait' in biarmosuchians, gorgonopsians and anomodonts, whereas cynodonts and *Moschops* were more constrained to a single type of posture, perhaps more parasagittal. But on the other hand, this is inconsistent with the fossil record of footprints attributed to dinocephalians, which supports a partial sprawling posture (Gand *et al*. 2000; Surkov *et al*. 2007) and the hypothesis that some dicynodonts evolved a more upright posture independently because of the biomechanical constraints imposed by their large body size (Blob 2001; Fröbisch 2006). Finally, the range of semicircular canal radii of sprawling tetrapods overlaps that of mammals and NMT (Fig. 6). This means that, based on the average radius of the semicircular canals alone (and the so calculated coefficient of agility), it is impossible to discriminate between sprawling and parasagittal forms. Thus the question of whether the very derived semicircular canal anatomy of the biarmosuchians reflects a different type of locomotion will have to be addressed when well-preserved postcranial material becomes available.

CONCLUSION

With their large pachyostosed, ornamented cranial structures and intermeshing incisors, biarmosuchians constitute a fascinating, yet poorly understood radiation of early NMT (Rubidge & Sidor 2001; Kemp 2005; Day *et al*. 2016). Along with these traits, the study performed here has identified additional potential synapomorphies that support the clade. It also highlights an unexpected diversity of morphology of the bony labyrinth in NMT which, and along with other recent studies (Castanhinha *et al*. 2013; Rodrigues *et al*. 2013; Laaß & Schillinger 2015; Laaß 2015a,b, 2016; Benoit *et al*., in press), strongly suggests that the auditory system of different NMT taxonomic groups was not as homogenous as previously postulated (Luo 2001; Kielen Jaworowska *et al*. 2004; Kemp 2016; Luo *et al*. 2016). Finally, the unique morphology of the semicircular canals in biarmosuchians, with no extant equivalents, suggests a highly derived type of locomotion. Future studies and reappraisal of the scarce postcranial material of biarmosuchians will certainly shed some light on this very autapom

INSTITUTIONAL ABBREVIATIONS

AM	Albany Museum, Grahamstown, South Africa
BP/1	Evolutionary Studies Institute, Johannesburg, South Africa
CG	Council for Geosciences, Pretoria, South Africa
MS	School of Anatomical Sciences, Johannesburg, South Africa
NHMUK	Natural History Museum, London, United Kingdom
NMQR	National Museum, Bloemfontein, South Africa
SAM-PK	Iziko Museum, Cape Town, South Africa

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