The petrosal and inner ear of the Late Jurassic cladotherian mammal *Dryolestes leiriensis* and implications for ear evolution in therian mammals

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*Dryolestes leiriensis* is a Late Jurassic fossil mammal of the dryolestoid superfamily in the cladotherian clade that includes the extant marsupials and placentals. We used high resolution micro-computed tomography (µCT) scanning and digital reconstruction of the virtual endocast of the inner ear to show that its cochlear canal is coiled through 270°, and has a cribriform plate with the spiral cochlear nerve foramina between the internal acoustic meatus and the cochlear bony labyrinth. The cochlear canal has the primary bony lamina for the basilar membrane with a partially formed (or partially preserved) canal for the cochlear spiral ganglion. These structures, in their fully developed condition, form the modiolus (the bony spiral structure) of the fully coiled cochlea in extant marsupial and placental mammals. The CT data show that the secondary bony lamina is present, although less developed than in another dryolestoid *Henkelotherium* and in the prototribosphenidan *Vincelestes*. The presence of the primary bony lamina with spiral ganglion canal suggests a dense and finely distributed cochlear nerve innervation of the hair cells for improved resolution of sound frequencies. The primary, and very probably also the secondary, bony laminae are correlated with a more rigid support for the basilar membrane and a narrower width of this membrane, both of which are key soft-tissue characteristics for more sensitive hearing for higher frequency sound. All these cochlear features originated prior to the full coiling of the therian mammal cochlea beyond one full turn, suggesting that the adaptation to hearing a wider range of sound frequencies, especially higher frequencies with refined resolution, has an ancient evolutionary origin no later than the Late Jurassic in therian evolution. The petrosal of *Dryolestes* has added several features that are not preserved in the petrosal of *Henkelotherium*. The petrosal characters of dryolestoid mammals are essentially the same as those of *Vincelestes*, helping to corroborate the synapomorphies of the cladotherian clade in neural, vascular, and other petrosal characteristics. The petrosal characteristics of *Dryolestes* and *Henkelotherium* together represent the ancestral morphotype of the cladotherian clade (*Dryolestoidae + Vincelestes + extant Theria*) from which the extant therian mammals evolved their ear region characteristics.

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INTRODUCTION

The mammalian petrosal bone is ossified from the cartilaginous otic capsule in mammalian development. It contains the inner ear that is crucial for hearing (Gray, 1908; De Beer, 1937; Williams *et al.*, 1989). The petrosal is a dense and durable bone often preserved in fossils. It has complex external morphological features that can be a useful source for phylogenetic information, and has been well studied in a wide range of Mesozoic mammals (see the recent reviews by Kielan-Jaworowska, Cifelli & Luo, 2004;
Rougier & Wible, 2006). The intricate morphological features of the inner ear bony labyrinth are also likely to be informative for phylogenetic inference (Allin & Hopson, 1992; Meng & Fox, 1995a; Luo, 2001; Ruf et al., 2009; Ekdale & Rowe, 2011). However, because the interior structures of the petrosal were not accessible without traditional, often destructive, approaches until recently, the inner ear has been documented for far fewer taxa of the Mesozoic mammals. Following a previous study on the petrosal and inner ear structure of the Late Jurassic dryolestoid mammal Henkelotherium guimarotae (Ruf et al., 2009), here we present a new study of the petrosal and inner ear structure of another dryolestoid, Dryolestes leiriensis (Martin, 1999) by microcomputed tomography (µCT) and digital reconstruction of the ear structures. The inner ear bony labyrinth of Dryolestes was briefly described (Luo et al., 2011a), and here we present a more detailed description and illustration of its inner ear structure.

Dryolestoids are an extinct Mesozoic mammal group that is distantly related to modern marsupials and placentals (Fig. 1). On the basis of dental and postcranial characters (Ji, Luo & Ji, 1999; Luo, Ji & Yuan, 2007b; Luo & Wible, 2005; Luo et al., 2007a, b; Rougier et al., 2007), dryolestoids are more closely related to extant marsupials and placentals than the more ancestral ‘symmetrodonts’ (Hu et al., 1997; Li & Luo, 2006). In the current framework of Mesozoic mammal phylogeny, dryolestoids are placed more basal than prototribosphenidans, such as Vincelestes (Rougier, 1993), and than the northern tribosphenic mammals, known as boreosphenidans (Luo, Cifelli & Kielan-Jaworowska, 2001a; Kielan-Jaworowska et al., 2004; Martin & Rauhut, 2005; Luo, 2007). They represent a basal, extinct group of the Cladotheria clade (sensu McKenna & Bell, 1997) that is defined by the common ancestor of the Dryolestoidia, Vincelestes, boreosphenidans mammals, and the extant marsupials and placentals.

The divergence and earliest evolution of modern marsupials and placentals was a major event in mammalian history (de Muizon, Cifelli & Céspedes, 1997; Rougier, Wible & Novacek, 1998; Ji et al., 2002; Luo et al., 2003, 2011b; Kielan-Jaworowska et al., 2004; Bininda-Emonds et al., 2007; Wible et al., 2007, 2009). As dryolestoids are stem relatives to the extant marsupials and placentals, their features are important for inferring the plesiomorphic morphotype, or groundplan, from which the diverse marsupials and placentals have evolved (Krebs, 1991; Martin, 1997, 1999; Ruf et al., 2009) (Fig. 1). The petrosal characteristics and inner ear structure of D. leiriensis can add to a growing body of comparative analyses of the petrosal and inner ear structure of early mammals, including basal metatherians and eutherians (Wible, 1990; Marshall & de Muizon, 1995; Meng & Fox, 1995a; de Muizon, 1998; Rougier et al., 1998; Wible et al., 2001; Wible, Novacek & Rougier, 2004; Ekdale, Archibald & Averianov, 2004; Ladevèze, 2004, 2007; Ladevèze & de Muizon, 2007, 2010; Sánchez-Villagra et al., 2007; Sánchez-Villagra & Schmelze, 2007; Ladevèze, Asher & Sánchez-Villagra, 2008; Ekdale & Rowe, 2011), the prototribosphenidan Vincelestes (Rougier, Wible & Hopson, 1992; Rougier, 1993), the dryolestoid Henkelotherium (Ruf et al., 2009), the

Figure 1. Phylogeny of the main comparative taxa and names of major clades used in this study.
spalacotheroid *Zhangheotherium* (Hu *et al*., 1997), multituberculates (Kielan-Jaworowska, Presley & Poplin, 1986; Miao, 1988; Luo & Ketten, 1991; Lillegraven & Hahn, 1993; Wible & Hopson, 1995; Hurum, 1998; Wible & Rougier, 2000; Ladévéze *et al*., 2010), eutriconodonts (Wible & Hopson, 1993; Rougier, Wible & Hopson, 1996; Wang *et al*., 2001), and many mammaliaforms (Kermack, Mussett & Rigney, 1981; Lillegraven & Krusat, 1991; Crompton & Luo, 1993; Lucas & Luo, 1993; Wible & Hopson, 1993; Luo, Crompton & Lucas, 1995; Luo, 2001). Traditional studies on early mammal inner ears had to rely on fortuitously broken petrosals that exposed the internal structures (Lillegraven & Krusat, 1991; Lillegraven & Hahn, 1993; Rougier, 1993; Meng & Wyss, 1995; Meng & Fox, 1995b; Fox & Meng, 1997) or by destructive sectioning of fossils (Kielan-Jaworowska *et al*., 1986; Graybeal *et al*., 1989; Luo *et al*., 1995; Hurum, 1998; Luo, 2001). The application of µCT in recent studies of mammalian inner ears (Schmelzle, Sánchez-Villagra & Maier, 2007; Ladévéze *et al*., 2008, 2010; Horovitz *et al*., 2009; Ruf *et al*., 2009) has been advantageous in being nondestructive and more amenable for quantitative analyses (e.g. Spoor *et al*., 2002; Schmelzle *et al*., 2007; Ekdale, 2010, 2011; Macrini *et al*., 2010). In our study, CT scans revealed the hidden morphology that could not be exposed through conventional mechanical preparation, and made it possible to obtain quantitative measurements (Figs 2–5; Table 1).

**MATERIAL AND METHODS**

The left petrosal of *D. leiriensis* [Guimarota Mammal Collection (Gui Mam) 2/81] will be housed in the Museo Geológico (Lisboa, Portugal) under specimen number 6807 (Figs 6–11). The petrosal is preserved together with broken pieces of the parietal, the squamosal, and the supraoccipital that are dislocated, incomplete, and compressed, but nonetheless still recognisable. The entire specimen was originally discovered from coal matrix, and has been conserved in translucent resin plastic (Drescher, 2000). The endocranial and occipital aspects of the petrosal were exposed through mechanical preparation. However, its lateral and ventral aspects are buried in the matrix and embedding plastic, and can only be visualized by virtual reconstruction through µCT scanning.

The petrosal was an isolated specimen but there is no doubt that it belongs to *D. leiriensis* (Martin, 1999) because of its unique morphology, such as the therian-like cochlear ganglion canal, apomorphic features of the petrosal of dryolestoids and crown therians, and comparatively large size. The Late Jurassic Guimarota Coal Mine has yielded abundant fossil mammals. To date, more than 7000 dental specimens, more than 700 dentaries and about 20 crushed skulls or partial skulls have been recovered (Krebs, 2000; Martin & Krebs, 2000; Martin, 2001). The Guimarota mammalian species with abundant specimens are: the docodont *Haldanodon exspectatus* (Kühne & Krusat, 1972; Henkel & Krusat, 1980; Krusat, 1980; Lillegraven & Krusat, 1991; Martin, 2005), the dryolestoids *D. leiriensis*, *Krebsotherium lusitanicum* (Martin, 1999), *Henkelotherium guimarotae*, *Drescheratherium acutum*, and several multituberculate species (Hahn & Hahn, 1998a, b, c, d; Kielan-Jaworowska *et al*., 2004). Other mammalian species are rare, and represented by very limited numbers of specimens (Martin & Krebs, 2000). Clearly this petrosal (Museo Geológico 6807) does not belong to any multituberculate as it has many morphological differences from, and is much larger than, the known petrosals of the Guimarota multituberculates (Hahn, 1988). In the Guimarota assemblage, *Ha. exspectatus* and *D. leiriensis* are of similar size and they both are much larger than the other mammalian taxa, including the dryolestoids *K. lusitanicum* (Martin, 1999) and *Drescheratherium acutum* (Krebs, 1998). However, the many petrosal and inner ear apomorphies of *Dryolestes* are distinctive from the plesiomorphic petrosal features of the mammaliaform *Haldanodon*, in which the petrosals are unequivocally associated with taxonomically diagnostic jaws and teeth (Lillegraven & Krusat, 1991; Wible & Hopson, 1993; Luo, 1994; Rougier *et al*., 1996; Luo *et al*., 2002).

Although very similar in the petrosal and inner ear characters to *He. guimarotae* (Gui Mam 138/76b; Ruf *et al*., 2009), *D. leiriensis* is much larger than, and therefore clearly distinguishable from the former. The type specimen of *He. guimarotae* (Gui Mam 138/76a, b) has a mandibular length of 17.5 mm (Krebs, 1991); its promontorium is 2.2 mm long from the posterior rim of the fenestra vestibuli to the anterior pole of the promontorium, and 1.8 mm wide from the petrosal–basioccipital suture to the primary facial foramen (Ruf *et al*., 2009). *Dryolestes leiriensis* is larger, with the mandibular length ranging from an estimated 30 mm (Gui Mam 22/76) to 34 mm in length (Gui Mam 40/76). The petrosal assigned here to *Dryolestes* (Museo Geológico 6807, Gui Mam 2/81) has a preserved length of promontorium of 4.5 mm, and the width of the promontorium is 2.7 mm. The petrosal of *He. guimarotae* is about 45–50% of that of *D. leiriensis* by measurable dimensions of the promontorium (Ruf *et al*., 2009). These petrosals are completely ossified and unlikely to be juvenile specimens. The size differences between the petrosals of *Dryolestes* and *Henkelotherium* are in good concordance with the size differences between their mandibles.
The petrosal of *D. leiriensis* was scanned by two \( \mu \)CT scanners. The first scan was on the OMNI-X Universal HD600 Scanner at the Center of Quantitative Imaging (CQI), the Energy Institute, Pennsylvania State University, State College, Pennsylvania, USA. The images have 1024 \( \times \) 1024 pixel dimensions and a voxel size of 0.025 \( \times \) 0.025 \( \times \) 0.028891 mm. The second scanning was on the scanner v|tome|x s (GE Sensing & Inspection Technologies GmbH phoenix X-ray) at the Steinmann-Institut für Geologie, Mineralogie und Paläontologie, Universität Bonn, Germany. The images have 1024 \( \times \) 1024 pixel dimensions and a voxel size of 0.010158 \( \times \) 0.010158 \( \times \) 0.010158 mm.

To increase the resolution of the region of interest.

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Figure 3. Dryolestes leiriensis left petrosal and inner ear bony labyrinth (Gui Mam 2/81). Micro-computed tomography scan transverse slices of the para cochlearis and the vestibular region. A–I, anterior–posterior series from the anterior end to the approximately middle portion of the inner ear bony labyrinth. Abbreviations: ac, aqueductus cochleae; asc, anterior semicircular canal; asca, anterior semicircular canal ampulla; av, aqueductus vestibuli; bpl, base for the primary bony lamina of basilar membrane (wall of spiral ganglion canal); bsl, base of the secondary bony lamina of basilar membrane (bony reinforcement of spiral ligament); cc, crus commune; cgc, incomplete and remnant canal for spiral ganglion (=base of the primary bony lamina); co, cochlear canal basal portion [the first half-turn (180° arc) from the sacculo-utricular junction]; co-a, cochlear canal apical portion [the apical quarter-turn (270–180° arc) from the sacculo-utricular junction]; csf, cavum supracochleare floor (remnant); fc, fenestra cochleae; fc, foramina of cochlear nerve VIII (partial tractus spiralis foraminosus, or the cribriform plate); fn + fut, shared space of the facial nerve VII and utricular nerve VIII; fut, foramen for utricular nerve VIII; fv, fenestra vestibuli; iam, internal acoustic meatus; ips, inferior petrosal sinus; ivc, inflection point between the vestibule and cochlea; pfc, prefacial commissure; pff, primary facial foramen; sa, saccule; stf, stapedial muscle fossa; ut, utricle.
(the cochlear canal), we used the software DATOS|X-RECONSTRUCTION (GE Sensing & Inspection Technologies GmbH phoenix X-ray) to virtually halve the voxel size (0.005079 mm) from the raw data set, which further increased the resolution of fine structures. The reconstructions of the petrosal and the bony labyrinth of the inner ear were completed by the manual segmentation function of

**Figure 4.** *Dryolestes leiriensis* left petrosal and the inner ear bony labyrinth (Gui Mam 2/81). Micro-computed tomography scan transverse slices of the vestibular and canaliclar regions. Continued from Figure 1: J–R, anterior–posterior series from approximately the middle to the posterior end of the inner ear bony labyrinth. Abbreviations: ac, aqueductus cochleae; asc, anterior semicircular canal; asca, anterior semicircular canal ampulla; av, aqueductus vestibuli; cc, crus commune; fc, feneatra cochleae; fv, fenestra vestibuli; lsc, lateral semicircular canal; lsca, lateral semicircular canal ampulla; nc, nuchal crest component of pars canalicularis; psc, posterior semicircular canal; psca, posterior semicircular canal ampulla; ptc, post-temporal canal (incomplete, preserved as an open groove); sa, saccule; saf, subarcuate fossa; scc, secondary crus commune; sss, sigmoid sinus groove; ut, utricule.
Figure 5. Dryolestes leiriensis left petrosal and inner ear bony labyrinth (Gui Mam 2/81). Microcomputed tomography scan horizontal (frontal) slices of the pars cochlearis and the vestibular region. A–D, ventral–dorsal series from the lower part of the basal cochlear turn to the apex of the cochlea. Abbreviations: asc, anterior semicircular canal; av, aqueductus vestibuli; bpl, base for primary bony lamina of basilar membrane (= wall of spiral ganglion canal); bsl, secondary bony lamina of basilar membrane (bony reinforcement of spiral ligament); cgc, cochlear ganglion canal; co, cochlear canal basal portion [the first half-turn (180° arc) from the sacculo-utricular junction]; co-a, cochlear canal apical portion (the apical quarter-turn 180–270° arc) from the sacculo-utricular junction; dus, division (crest) between utricle and saccule; fc, fenestra cochleae; fcn, foramina for cochlear nerve fibres VIII (= cribriform plate); fn, primary facial nerve foramen VII; fsa, foramen for saccular nerve VIII; fut, foramen for utricular nerve VIII; fut + fn, shared space for facial nerve and vestibular nerve (inside the internal acoustic meatus); fv, fenestra vestibuli; iam, internal acoustic meatus; ips, inferior petrosal sinus; ivc, inflection point between the vestibule and cochlea; lsc, lateral semicircular canal; lss, sigmoid sinus sulcus; ptc, post-temporal canal (partial, without squamosal wall); sa, saccule; saf, subarcuate fossa; sss, sigmoid sinus sulcus; stf, stapedial muscle fossa; ut, utricle.
Table 1. Measurement of petrosal and inner ear structures of *Dryolestes leiriensis*

| Petrosal                        | Width (mm) | Length (mm) |
|--------------------------------|------------|-------------|
| Promontorium                   | 3.15       | >4.5        |
| Fenestra vestibuli             | 0.47       | 0.53        |
| Fenestra cochleae (ventral view)| 0.13       | 0.27        |

| Cochlear bony labyrinth structures | Coiling along length | Estimated length (mm) |
|-----------------------------------|----------------------|------------------------|
| Cochlear canal                    | ~270°                | 3.3                    |
| Primary bony lamina length        |                      | 1.6                    |
| Secondary bony lamina length      |                      | 1.17                   |
| Angle of cochlear basal-turn to lateral semicircular canal | 145° | |

| Semicircular canal structures     | Estimated diameter (width–height average) (mm) | Width (mm) | Height (mm) |
|----------------------------------|-----------------------------------------------|------------|-------------|
| Basal cochlear turn diameter     | 0.99                                          | 0.96       | 1.02        |
| Apical cochlear turn diameter    | 0.77                                          | 0.85       | 0.68        |

|                               | Width (mm) | Height (mm) | Arc radius (inner curvature) (mm) | Lumen diameter (mm) |
|--------------------------------|------------|-------------|----------------------------------|---------------------|
| Anterior semicircular canal    | 2.31       | 2.22        | 1.13                             | 0.21                |
| Posterior semicircular canal   | 1.56       | 1.50        | 0.77                             | 0.22                |
| Lateral semicircular canal     | 1.55       | 1.46        | 0.75                             | 0.22                |
| Average radius of all semicircular canals | 0.88 | |

*For measurement landmarks see the text.
Measurements based on the second microcomputed tomography scanning by the scanner at Steinmann-Institut für Geologie, Mineralogie und Paläontologie, Universität Bonn.
Scan resolution 0.010158 mm; virtually half voxel size 0.005079 mm; all measurements of inner ear features were from AVIZO 5.1.

The software AMIRA 4.1 and AVIZO 5.1. Linear measurements (Table 1) were taken from the virtual endocast of the bony labyrinth with the AVIZO 5.1 software.

For morphological terminology of the inner ear of extant and Mesozoic mammals, we mostly followed Fleischer (1973), Williams et al. (1989), and Ruf et al. (2009). For the petrosal morphological characters, we followed Wible (1990), Wible & Hopson (1995), Rougier et al. (1996), Luo, Crompton & Sun (2001b), Kielan-Jaworowska et al. (2004), Rougier & Wible (2006), and Ruf et al. (2009). Names of the Mesozoic mammaliaform taxa and main clades are summarized in Figure 1.

Estimation of the agility scores from the size of semicircular canals requires body mass (Spoor et al., 2007; Silcox et al., 2009; Macrini et al., 2010). Here we used the mandibular length as a proxy to estimate the body mass, following Foster (2009) and using the data on mandible length from Martin (1999). It was estimated that *D. leiriensis* weighs an average of 130 g with a range from 100 to 160 g.

Samples of available petrosal specimens are small for any Mesozoic mammal taxa. With a single specimen of *D. leiriensis*, we could not assess the variation of its morphological features. Recent studies on variability of the inner ear bony labyrinth in mammals (Ekdale, 2009, 2010) demonstrated that, upon ossification of the petrosal, the inner ear bony structures show no significant variations in the marsupial *Monodelphis*. We follow the assumption established by these studies (e.g. Ekdale, 2010).
PETROSAL MORPHOLOGY

The petrosal in pretribosphenic mammals consists of the pars cochlearis, the pars canaliculiris or the mastoid region, the lateral trough, and the anterior lamina (see the reviews by Kielen-Jaworowska et al., 2004; Rougier & Wible, 2006). Both the pars cochlearis and the pars canaliculiris are well preserved (Fig. 2). However, the lateral trough is damaged and incomplete, although the remnant of its floor is still attached to the pars cochlearis and is visible (Fig 2, Figure 6. Dryolestes leiriensis left petrosal (Gui Mam 2/81). A, ventromedial view of the pars cochlearis. B, ventral view of the pars cochlearis. Abbreviations: ac, aqueductus cochleae canal opening (intramural in jugular notch); boc, basioccipital contact (and suture); cif, crista interfenestralis; cp, crista parotica; csf, cavum supracochleare floor (incompletely preserved as a ridge); ctp, caudal tympanic process; eoc, exoccipital contact (and suture); er, epitympanic recess; fc, fenestra cochleae; fi, fossa incudis; fv, fenestra vestibuli; hf, hiatus Fallopii (for greater superficial petrosal nerve VII, incomplete open notch); ips, inferior petrosal sinus – posterior opening of the canal (on tympanic surface); ipsa?, inferior petrosal sinus – anterior opening of the canal (intramural and in the basioccipital-petrosal suture; putative); jf, jugular foramen (exposed as open notch); me, mastoid exposure of pars canaliculiris of petrosal (on the occipital aspect of the skull); mps, medial promontorial sulcus (with uncertain soft-tissue homology); pa, parietal (fragments); pa, pila antotica (incomplete); pica, promontorial sulcus for internal carotid artery; pp, paroccipital process (ventral projection); pf, primary facial nerve foramen; pr, promontorium; pss, prootic sinus sulcus (canal incompletely preserved as open groove); pst, proximal stapedial artery sulcus; ptc, post-temporal canal (for arteria and vena diploëtica magna); ptr, postpromontorial tympanic recess; rcm, resin plastic and coal matrix as preserved in Gui Mam 2/81; rsa?, ramus superior of stapedial artery sulcus (incompletely preserved as open groove, putative); sff, secondary facial foramen (for hyomandibular branch of facial nerve VII, preserved as open notch); smn, stylomastoid notch (putative); stf, stapedial muscle fossa; th?, tympanohyal attachment base; ttf, tensor tympani muscle fossa; ‘?’, unidentifiable bone fragments.

**Figure 6.** Dryolestes leiriensis left petrosal (Gui Mam 2/81). A, ventromedial view of the pars cochlearis. B, ventral view of the pars cochlearis. Abbreviations: ac, aqueductus cochleae canal opening (intramural in jugular notch); boc, basioccipital contact (and suture); cif, crista interfenestralis; cp, crista parotica; csf, cavum supracochleare floor (incompletely preserved as a ridge); ctp, caudal tympanic process; eoc, exoccipital contact (and suture); er, epitympanic recess; fc, fenestra cochleae; fi, fossa incudis; fv, fenestra vestibuli; hf, hiatus Fallopii (for greater superficial petrosal nerve VII, incomplete open notch); ips, inferior petrosal sinus – posterior opening of the canal (on tympanic surface); ipsa?, inferior petrosal sinus – anterior opening of the canal (intramural and in the basioccipital-petrosal suture; putative); jf, jugular foramen (exposed as open notch); me, mastoid exposure of pars canaliculiris of petrosal (on the occipital aspect of the skull); mps, medial promontorial sulcus (with uncertain soft-tissue homology); pa, parietal (fragments); pa, pila antotica (incomplete); pica, promontorial sulcus for internal carotid artery; pp, paroccipital process (ventral projection); pf, primary facial nerve foramen; pr, promontorium; pss, prootic sinus sulcus (canal incompletely preserved as open groove); pst, proximal stapedial artery sulcus; ptc, post-temporal canal (for arteria and vena diploëtica magna); ptr, postpromontorial tympanic recess; rcm, resin plastic and coal matrix as preserved in Gui Mam 2/81; rsa?, ramus superior of stapedial artery sulcus (incompletely preserved as open groove, putative); sff, secondary facial foramen (for hyomandibular branch of facial nerve VII, preserved as open notch); smn, stylomastoid notch (putative); stf, stapedial muscle fossa; th?, tympanohyal attachment base; ttf, tensor tympani muscle fossa; ‘?’, unidentifiable bone fragments.
6, 7). The anterior lamina of the petrosal is unknown as the area where it would be expected is missing. To facilitate an overview of the incomplete, although still identifiable, structures of the *Dryolestes* petrosal, and to orientate the incomplete structures to the better preserved landmarks, we provide a conjectural restoration in Figure 2.

**Ventral Side of Petrosal**

The promontorium, the ventral eminence of the pars cochlearis, is externally convex and has an oval to oblong outline (Figs 6, 7: pr). The width of the promontorium is about 3.5 mm from the basioccipital suture to the broken edge of the primary facial foramen (Fig. 6: boc; Fig. 7: pff).
length from the anterior border of the fenestra vestibuli to the preserved anterior edge of the promontorium is about 4.5 mm, but this is an underestimate because the anterior pole of the promontorium is incomplete. The anterolateral part of the promontorium shows a small, groove-like depression that we interpreted to be the attachment site of the tensor tympani muscle. This tensor tympani fossa is located between the remnant part of the lateral trough floor and the transpromontorial groove for the internal carotid artery (Figs 6, 7: ttf).

The fenestra vestibuli (oval window) has a slightly oval outline of 0.53 mm in length and 0.47 mm in width, with a stapedial footplate ratio of 1.3. This value is far lower than the stapedial ratios of 1.6 or higher for basal eutherian and placental mammals (Wible et al., 2001; Macrini et al., 2010). The fenestra vestibuli has an elevated lateral rim and the fenestra...
opening faces posteroventrally (Figs 6, 7: fv). As a result of this posteroventral orientation, the window appears to be more or less circular when seen in the straight ventral view (Fig. 6B). The fenestra cochleae (round window) has an elevated ventral rim, and is orientated posteromedially (Figs 5, 6: fc). In posteroventral view, the round window is almost perfectly circular (not illustrated), but it appears to have an oval outline in straight ventral view (Fig. 5).

The fenestra vestibuli and the fenestra cochleae are widely separated by the crista interfenestralis, a broad and low ridge on the posterior promontorial surface (Fig. 6: cif) (sensu Wible et al., 1995). The stapedial muscle fossa is represented by a shallow depression directly posterior to the oval window (Figs 6, 7: stf). The medial margin of the stapedial fossa is aligned with the crista interfenestralis, although not connected to it.

The petrosal has a broad, shallow depression medial to the crista parotica and lateral to the fenestra vestibuli, the crista interfenestralis, and the stapedial fossa. The depression is more similar to its counterpart in the spalacotheroid Zhangheotherium (Hu et al., 1997) and a putative petrosal of the symmetrodont Gobitheriodon (Wible et al., 1995), than to the same area in the more derived Vinceletes (Rougier et al., 1992). In our putative restoration of the petrosal of Dryolestes (Fig. 2), the lateral trough is wider posteriorly, but anteriorly is narrow as interpreted for Henkelotherium and as seen in Vinceletes (Rougier et al., 1992; Ruf et al., 2009). This speculative restoration can be revised if shown to be otherwise by more complete fossils discovered in the future.

The caudal tympanic process is represented by an elevated, crest-like area posterior to the fenestra cochleae and is separated from the fenestra by a

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**Figure 9.** Dryolestes leiriensis left petrosal mastoidea (Gui Mam 2/81). A, B, posterior view of the pars mastoidea of petrosal (stereophotographs). C, posterior view of petrosal (camera lucida drawing). D, structure identification. Abbreviations: ac, aqueductus cochleae canal opening (intramural in jugular notch); boc, basioccipital contact (and suture); eoc, exoccipital contact surface; ips, inferior petrosal sinus – posterior opening of the canal (on tympanic surface); me, mastoid exposure of pars canaliculis of petrosal (on the occipital aspect of the skull); nc, nuchal (lambdoidal) component of pars canaliculis of petrosal; oev, occipital emissary vascular foramen; pp, (posterior) paroccipital process of petrosal; ptc, post-temporal canal (for the arteria and vena diploëtica magna); soc, supraoccipital contact (and suture).
transverse, shallow postpromontorial tympanic recess (Figs 2, 6, 7: ctp, ptr). This recess is present in some multituberculates, the spalacotheroid Zhangheotherium, the prototribosphenidan Vincelestes, metatherians, and eutherians (Wible, 1990; Rougier et al., 1992, 1998; Wible et al., 1995; 2001; Hu et al., 1997; de Muizon, 1998; Wible & Rougier, 2000; Ladevèze, 2004, 2007; Ladevèze & de Muizon, 2010).

The paroccipital process is a pyramidal protuberance, posterior to the stapedial muscle fossa and in the posterior end of the preserved petrosal (Figs 6, 7: pp). The process is continuous with a prominent vertical crest on the occipital aspect of the petrosal. Anteriorly the paroccipital process is in continuation with the crista parotica, which we interpret to be represented by a low and heavily worn crest. A deep pit lateral to the crest of the crista parotica is tentatively identified to be the fossa incudis, the attachment site of the short process of the incus (Figs 6, 7: cp, fi), as in many Mesozoic and extant mammals (Wible & Hopson, 1993; Luo & Crompton, 1994). The area of the petrosal lateral to the crista parotica is incomplete and damaged, so we can only very tentatively interpret the epitympanic recess lateral and anterolateral to the crista parotica (Figs 2, 6, 7: er?). Between the stapedial muscle fossa and the paroccipital process, there is a small, shallow notch that we interpret to be the stylomastoid notch (Figs 6, 7: smn). Located next to the tympanohyal attachment site on the crista parotica, this notch would be the exit point of the facial nerve from the tympanic cavity, as seen in extant mammals.

The interpretation of the features around the paroccipital area of Dryolestes is based on the fact...
that the paroccipital process, the stylomastoid notch, the crista parotica, and its fossa incudis, are arranged in a similar topographical relationship in eutriconodonts, monotremes, *Vincelestes*, and a large number of basal eutherians and metatherians (Wible, 1990; Rougier et al., 1992; Wible & Hopson, 1993; Luo, 1994; Meng & Fox, 1995a; Wible et al., 2001; Ekdale et al., 2004; Ladevèze, 2004, 2007; Ladevèze & de Muizon, 2007, 2010).

The ventral surface of the promontorium shows several grooves that are interpreted to be the homologous vascular features of crown therian mammals (Wible, 1986, 1987; Rougier et al., 1992). The proximal stapedial artery groove is represented by a dis-
distinct sulcus that extends from the posterior part of the promontorium posterolaterally into the rim of the fenestra vestibuli (Figs 6, 7: pst). The promontorium has a shallow but distinct sulcus that is interpreted here as the course for the internal carotid artery. It starts on the posterior part of the promontorium anterior to the fenestra cochleae, then curves anterolaterally toward the preserved anterior apex of the promontorium. The main segment of the transpromontorial groove for the internal carotid artery is longitudinal along the length of the promontorium (Figs 6–8: pica). We interpret that the internal carotid artery splits into an anterior and longitudinal vessel (the main internal carotid artery) and the proximal stapedial artery (see the restoration in Fig. 1A), which is also the case in Vincelestes (Rougier et al., 1992), the Cretaceous eutherian Prokennalestes (Wible et al., 2001), some zhelestids (Ekdale et al., 2004), and in placental mammals in general (Wible, 1986). The longitudinal segment of the internal carotid artery groove is observed in Henkelotherium (Ruf et al., 2009). However, the proximal stapedial artery groove and the promontorial sulcus are not recognizable for Henkelotherium because of damage to the fossil. The medial part of the promontorium in Dryolestes shows another longitudinal groove that is present parallel both to the basiocipital suture, and to the transpromontorial groove of the internal carotid. This groove is here called the medial promontorial sulcus and is interpreted also as a vascular groove (Figs 6–8: mps), but its homology is uncertain. A similar groove is present in this position in some placental ungulate mammals (Cifelli, 1982), and this is interpreted to be for a vein – likely to be the inferior petrosal sinus (Wible, 1986).

**MEDIAL MARGIN OF PETROSAL**

The petrosal and the basiocipital are disarticulated along their suture, exposing the rugose contact surface of the pars cochlearis (Figs 6, 8, 9: boc). The jugular foramen is represented by a rounded notch in the medial and posterior corner of the promontorium (Figs 2, 5, 8, 10: jf), bound anteriorly by the petrosal–basiocipital contact and posteriorly by the petrosal–exoccipital contact (Figs 8–11: eoc). In extant mammals, the topographically homologous notch forms the lateral border of the jugular foramen for cranial nerves IX, X, and XI and blood vessels (Kuhn, 1971; Zeller, 1989, 1993; Evans, 1993; Wible & Hopson, 1995; Wible, 2003). The external opening of the aqueductus cochleae (for the perilymphatic duct) is located on the lateral wall of the jugular foramen. The aqueductus canal is the connection of the scala tympanica within the cochlear canal to the subarachnoid meninx outside the petrosal but inside the cranial cavity (Williams et al., 1989). The canal enters the saccular space in the inner ear bony labyrinth very close to the fenestra cochleae (Fig. 3G, I: ac, fc).

There is a network of longitudinal canals in the pars cochlearis and parallel to the suture of the petrosal and the basiocipital. This canal network is interpreted to be the inferior petrosal sinus plexus, a venous structure (Figs 3, 5: ips). This canal network has a single posterior opening by the anterior border of the jugular foramen ventral (external) to the petrosal–basiocipital suture (Figs 8–10: ips). The single canal of the inferior petrosal sinus is split anteriorly into two (or more) parallel canals that form a plexus within the porous bone in the pars cochlearis. At the anterior end of the promontorium, the canal has a relatively large opening (Figs 8–11: ipsa). However, the connection from this opening to the more anterior vascular structures is not known because of damage. The inferior petrosal sinus canal (or a network of canals) is also present in Henkelotherium, with some anastomastic channels to the inner ear labyrinth (Ruf et al., 2009). A similar inferior petrosal sinus feature is also known in Vincelestes (Rougier et al., 1992) and a wide range of other Mesozoic mammaliaforms including Morganucodon (Kermack et al., 1981) and Haldanodon (Lillegraven & Krusat, 1991).

**LATERAL ASPECT OF PETROSAL**

The lateral aspect of the petrosal forms the floor and the sidewall of the braincase in the intact skulls of other Mesozoic mammals and monotremes (Kuhn, 1971; Zeller, 1989; Rougier et al., 1992, 1996). However, the petrosal of Dryolestes is damaged where the anterior lamina would be expected, so the anterior lamina is unknown (Figs 6–8: rcm). The remnant floor of the cavum supracochleare, which is the roof of the lateral trough in intact skulls of other mammals, is still recognizable in the CT scans. The floor of the cavum supracochleare demarcates the bony space that would contain the geniculate ganglion of the facial nerve (Figs 3, 6, 7: csf). The cavum supracochleare is positioned lateral to the cochlear housing, and is separated from the endocranial aspect of the cochlear housing by a well-developed prefacial (also known as the ‘suprafacial commissure,’ Figs 10, 11: pfc). As the ventral floor of the cavum supracochleare is damaged, and the cavum is broken open, the primary facial foramen is clearly visible in the lateral view (Fig. 7B: pff). The facial nerve passes through the prefacial commissure from the internal acoustic meatus. The cavum epiperticulare, the space for the trigeminal ganglion (V), is damaged; therefore, it is not possible to speculate whether the cavum supracochleare (for the facial nerve ganglion, VII) would
be confluent with the cavum epitericum (for the trigeminal nerve ganglion, V) in Dryolestes, as in eutriconodont mammals (Rougier et al., 1996), or if the two cava for the trigeminal and the geniculate ganglia would be more separate as in Vincelestes (Rougier et al., 1992).

The hiatus Fallopii, the foramen for the greater petrosal nerve of the facial nerve, is broken yet discernible (interpretive reconstruction in Fig. 2). The hiatus is broken and represented by a small incisure near the broken anterior floor of the cavum supracochleare with a sulcus leading anteriorly, presumably also for the greater petrosal nerve (Figs 6, 7: hf), as in Henkelotherium (Ruf et al., 2009). In both Henkelotherium and Dryolestes, the incomplete hiatus is located in exactly the same position as in the intact petrosals of other mammals, such as Vincelestes (Rougier et al., 1992). The secondary facial foramen is also preserved as an open notch on the remnant cavum supracochleare floor (Figs 6, 7: sff). A sulcus for the facial nerve leads posteriorly from the secondary facial foramen. The facial sulcus extends along the medial side of the crista parotica, and further posteriorly bypasses the stapedial muscle fossa, toward the stylomastoid notch (Fig. 7A: smn).

The prootic sulcus and canal, a channel for the prootic sinus vein (Wible & Hopson, 1995), is represented by a shallow, although recognizable, sulcus on the endocranial surface of the petrosal anterolateral to the subarcuate fossa (Figs 10, 11: pss, prc). The tympanic aperture of the prootic sinus canal is located lateral to the secondary facial foramen and anterior to the shallow concave area of the post-tympanic sinus. We interpret that the lateral trough floor is broken at a fracture through the tympanic opening of the prootic canal and the secondary facial foramen, both of which are partially preserved but are restored in our interpretive illustration (Fig. 2A). The entire course of the prootic sinus can be reliably interpreted for Dryolestes because its course, as preserved, is identical to the counterparts in other Mesozoic mammals (Kermack et al., 1981; Kielan-Jaworowska et al., 1986; Rougier et al., 1992, 1996; Wible et al., 1995, 2001; Hu et al., 1997; Luo et al., 2001b). The tympanic aperture of the prootic canal is next to the facial nerve pathway, so we interpret that the lateral head vein, the tributary vessel from the prootic sinus, would share the same pathway as the facial nerve in the tympanic cavity (Wible & Hopson, 1995; Rougier & Wible, 2006).

The virtual reconstruction of the petrosal shows a faint vertical groove that extends from the tympanic cavity just posterior to the prootic canal opening, and dorsally to the anterior end of the post-temporal canal. This canal is interpreted, tentatively, to represent the course for the superior ramus of the stapedial artery, as in Vincelestes (Rougier et al., 1992). The canal for the superior ramus of the stapedial artery would be intramural, but is exposed in the broken petrosal as an open groove (Figs 6, 7: rsa?).

The post-temporal canal is a prominent feature on both the lateral and the occipital aspects of the mastoid part of the petrosal (Figs 3–11: ptc). This canal is the conduit for the arteria and vena diploëtica magna in extant mammals in which this feature is known (Wible, 1987; Wible & Hopson, 1995). It is bounded in the intact skull laterally by the squamosal and medially by the mastoid of the petrosal (pars cochlearis). As the squamosal bone is damaged and dislocated in the Dryolestes specimen, the canal is exposed as an open groove on the petrosal. The openly exposed channel of the post-temporal canal is bordered by the dorsal squamosal contact from above, and the ventral squamosal contact from below (Fig. 6: sqv, sqd). Its anterior opening is connected to the incomplete groove for the superior ramus of the stapedial artery (Figs 6, 7: rsa) and its posterior opening is on the posterior (occipital) aspect of the petrosal.

**POSTERIOR ASPECT OF PETROSAL**

The mastoid exposure of the pars canalicularis (pars mastoidae) makes up the entire posterior (occipital) aspect of the petrosal (Fig. 9: me). Its occipital surface is broadly concave. The lateral and dorsal borders of the mastoid rise to contribute to the nuchal (lambdoidal) crest (Fig. 9: nc). The posterior opening of the post-temporal canal is on the nuchal crest and divides the crest in a dorsal segment and a ventral segment. The post-temporal canal opening has a funnel shape, with a shallow, vertical groove running ventrally from the opening on the posterior surface of the petrosal. The medial border of the mastoid has a long, rugose edge that represents the contact with the supraoccipital in the intact skull. The petrosal–supraoccipital contact shows a notch, one third of the way from the top. We interpret that this notch is for the occipital emissary vein (Figs 9, 11: oev), as in Canis (Evans, 1993). On the ventral segment of the petrosal–supraoccipital contact, there are two vascular foramina of unknown homology (Fig. 11: f1, f2). The petrosal–exoccipital contact is represented by a concave and rugose area on the ventromedial part of the mastoid (Figs 9–11: ecco). The ventral end of the petrosal–exoccipital contact forms the posterior margin of the jugular foramen (Fig. 11: jf). The ventral area of the mastoid has a prominent vertical ridge parallel to the petrosal–exoccipital contact; this ridge ends in the posterior paroccipital process on the ventral aspect of the petrosal (Fig. 9: pp).
ENDOCRANIAL SURFACE OF PETROSAI

The endocranial surface of the petrosal has three prominent features: the subarcuate fossa, the internal acoustic meatus, and the prefacial commissure. The subarcuate fossa is the largest feature (Figs 4, 5, 9, 11: saf), and is represented by a large concavity with its endocranial margin formed by the underlying anterior semicircular canal. The subarcuate fossa accommodates the paraflocculus of the cerebellum in the extant mammals in which this feature is present (Evans, 1993; Wible, 2003; Macrini, Rougier & Rowe, 2007a; Macrini, Rowe & VandeBerg, 2007b; Sanchez-Villagra et al., 2007). The concavity of the fossa is not uniform in Dryolestes; two parts of the fossa are deeper than the rest of the concave surface. The deepest part is in its posteroventral portion enclosed by the posterior semicircular canal (Fig. 4 M, N). The area surrounded by the lateral semicircular canal is also relatively deep (Fig. 5C, 5D).

The opening for the aqueductus vestibuli (for the endolymphatic duct) is near the medial border of the subarcuate fossa (Figs 10, 11: av). It is a short canal from the endocranial surface of the petrosal to the utricle, connecting with the utricle just below the expanded base of the crus commune of the anterior and posterior semicircular canals (Figs 4J, 12, 13: av, cc). The transverse sinus groove is represented by a shallow depression dorsal to the subarcuate fossa (Fig. 11: tsg). The transverse sinus groove bifurcates ventrally, and leads into two vascular grooves. The sigmoid sinus sulcus extends ventrally in a curved groove along the medial margin of the subarcuate fossa, and then joins the jugular foramen (Fig. 11: sss). At the jugular foramen, the sigmoid sinus and the inferior petrosal sinus would both join the internal jugular vein (Evans, 1993). Within the shallow sigmoid sinus groove there is a large nutritive foramen. Another major vascular sulcus on the endocranial surface of the petrosal around the anterolateral margin of the subarcuate fossa is the prootic sinus sulcus, which is ventrally connected to the endocranial opening of the prootic canal (Fig. 11: pss, prc), as seen in many extant mammals with this feature (Wible & Hopson, 1995).

The internal acoustic meatus is in the middle of the slightly concave endocranial surface of the pars cochlears. The posterior periphery of the internal acoustic meatus has a more elevated margin; but its anterior periphery is shallow, and graded into and transitional with the surrounding concave surface of the pars cochlears (Figs 10, 11: iam). Subdivided by a low transverse septum, the internal acoustic meatus has two depressions. The depression dorsal to the transverse septum contains a smaller, more posteriorly positioned vestibular nerve foramen (Fig. 10: ts, vn) for the vestibular branch of the cranial nerve VIII, which can be traced from the meatus into the utricular part of the vestibule on CT scans (Figs 4, 5: fut).

The anterior foramen in the upper depression of the internal acoustic meatus is the primary facial foramen, the passage of the facial nerve (VII) into the cavum supracochlea. The anterolateral border of the internal acoustic meatus is formed by the prefacial commissure that has a saddle-like shape in the lateral and endocranial views (Figs 7, 10, 11: pfc). The CT scans show a small channel connecting the saccular cavity in the bony labyrinth that is interpreted to be the conduit of the saccular nerve (Fig. 5: fsa). The endocranial segment of the primary facial nerve foramen is broadly confluent with the space for the cochlear and utricular nerves (Figs 3: fcn, fn, fut, pff).

The lower depression in the internal acoustic meatus shows the foramina of the cochlear nerve fibres. Seen in both light microscopy and CT scans, a small posterior part in the depression for the cochlear nerve foramina is broken and open, possibly by an earlier mechanical preparation. The anterior area of the foramina of the cochlear nerve fibres are somewhat obscured by glue or protective coating under light microscopy, but is clearly imaged by the high-resolution CT scans (Figs 3, 5: fcn).

The CT scans clearly show numerous, minute foramina of the cochlear nerve fibres in a curved pattern on the ossified cribriform floor of the internal acoustic meatus (Figs 3, 5: iam, fcn), corresponding to the curvature of the basal cochlear turn (Figs 12, 13: fcn-eg). In extant mammals, each of these foramina transmits an individual cochlear nerve fibre strand into the bony cochlear canal. These foramina are arranged in a spiral tract that corresponds to the coiled cochlear canal, known as the tractus spiralis foraminosus (Fleischer, 1973; Williams et al., 1989). This spiral tract is known in the Late Cretaceous metatherians and eutherians (Meng & Fox, 1995a, b), but can now be further traced to the Late Jurassic Dryolestes (Figs 12–15).

The distribution of the cochlear foramina here differs from the monotreme condition in which the distribution of the cochlear foramina is not spiral (Fox & Meng, 1997: Fig. 7; Luo et al., 2011a), despite the overall sieve-like appearance in the ossified floor of the internal acoustic meatus in extant monotremes (Fox & Meng, 1997). The curved tract of the foramina for the cochlear nerve fibres in Dryolestes (Figs 11–14: fcn) adds a new observation for dryolestoids on a key feature that is not preserved in the only petrosal specimen of Henkelotherium (Ruf et al., 2009). The relationship of these foramina to the ganglion canal and the primary bony lamina in the cochlear canal is described below.
**Bony Labyrinth of Cochlear Canal**

The virtual endocast of the bony cochlear canal is curved in its basal part but coiled toward the apex of the cochlea (Figs 11, 12: co, co-a). The proximal end (basal-most point) of the cochlear canal is an important landmark for estimating the degree of the coil, and for measuring the length of the cochlear canal. As the soft tissue of the membranous cochlear duct is nested inside the bony canal, the length of the cochlear canal in fossil mammals represents the upper limit for the length of the cochlear duct, and approximates the length of the basilar membrane and the organ of Corti, relevant for hearing functions (Geisler & Luo, 1996; Ekdale, 2009).
The cochlear duct is a soft-tissue structure and is almost never preserved in fossils. However, the proximal (basal) end of the cochlear duct can be established by its topographical relationship to several bony features: (1) by the proximal end of the basilar membrane gap marked by the primary and the secondary bony laminae (Figs 3, 5, 12: bpl, bsl); (2) by the most proximal foramen of the foramina for cochlear nerve fibres (Figs 12, 13: p-fcn); (3) by the junction of the aqueductus cochleae bony canal and the fenestra cochleae; or (4) by the point of inflection between the vestibule and the base of cochlea (Figs 5A, 12B: ivc). In extant therian mammals, all four criteria can be potentially useful, but how each can be applicable depends on the detailed construction of the cochlear canal, as explained below.

The cochlear duct is defined by the presence of the organ of Corti, which consists of the hair cells (neurones) and their support cells, positioned on the basilar membrane (Williams et al., 1989; Durrant &...
The basilar membrane gap is represented by the primary and secondary bony laminae that can be fossilized. When the proximal ends of the bony laminae can be directly observed either by serial sectioning, or by μCT scans, they are the beginning point of the basilar membrane. This landmark has been used in previous studies of cetaceans, whose petrosals usually have well-ossified primary and secondary bony laminae.

**Figure 14.** Interpretation of neural and related bony structures in the cochlear canal of *Dryolestes*. A, virtual reconstruction of the inner ear bony labyrinth from microcomputed tomography. B, structures in cross-section. Yellow, interpretive reconstruction of the cochlear nerve fibres perforating the cochlear nerve VIII foramina (= tractus foraminosus spiralis). Blue, the extent of the spiral ganglion along the cochlear canal, inferred from the basal wall of the ganglion canal. Grey, reconstruction of the incomplete primary bony lamina. The cribiform plate (tractus spiralis foraminosus) and the base of the primary bony lamina are preserved. However, the edge of the primary bony lamina can only be inferred.

**Figure 15.** Evolutionary pattern of cochlear canal in therian mammals (cross-sections of the cochlear canal near the foramen (foramina) of the cochlear nerves. A, *Sinoconodon* (modified from Luo et al., 1995). B, *Morganucodon* (after Luo, 2001). C, the monotreme *Ornithorhynchus* (modified from Fleischer, 1973: Abb. 78). D, generalized eutriconodont (Z.-X. Luo, unpubl. data). E, *Nemegtbaatar* (modified from Hurum, 1998). F, *Dryolestes*. G, *Homo sapiens* (modified from Fleischer, 1973). Nodes same as in Figure 1: 1, mammaliaforms; 2, crown Mammalia; 3, theriiforms; 6, cladotherians; 8, crown therians.
secondary bony laminae (e.g. Wever et al., 1971; Fleischer, 1976a; Ketten & Wartzok, 1990; Ketten, 1992; Luo & Eastman, 1995; Geisler & Luo, 1996; Luo & Marsh, 1996). However, not all mammals have the secondary bony lamina for the basilar membrane (reviewed by Fleischer, 1973; Ketten, 1992; Ruf et al., 2009). In fossil mammals without a clearly developed secondary bony lamina, the proximal end of the basilar membrane gap can be difficult to identify. On fossil endocasts of the inner ear with poorly preserved bony laminae, there is no indication of the soft-tissue junction where the basilar member is attached in extant mammals (Williams et al., 1989; Durrant & Lovrinic, 1995).

The second direct landmark for the proximal or posterior end of the cochlear duct is the proximal-most entry point of the cochlear nerve fibres, a reliable landmark for the organ of Corti (Figs 5, 12; p-fcn). As they mark, very closely, the proximal end of the cochlear duct, traces of the most proximal position of the cochlear nerve fibre on the endocast can be useful for determining the starting point of the cochlear canal.

In extant mammals, the proximal end of the organ of Corti begins near the junction of the aqueductus cochleae (= perilymphatic duct) and the proximal scala tympani. The latter is interconnected to the fenestra cochleae (Bast & Anson, 1949; Williams et al., 1989; Evans, 1993). On the virtual endocast of Dryolestes, the aqueductus cochleae and the fenestra cochleae are distinctive (Figs 12, 13: ac, fc); their position provides an additional reference point for the proximal end of the cochlear canal. The topographical relationship of the aqueductus cochleae and the fenestra cochleae on the Dryolestes endocast is similar to that in extant mammals. It represents a useful, although secondary, osteological landmark for the beginning point of the cochlear duct. However, this landmark is only visible from the endocranial or the posteromedial perspectives of the endocast.

It is not always possible to observe directly the internal structures of the cochlear canal in fossils, such as the starting point of the basilar membrane gap, and the proximal entry point of the cochlear nerve fibres. CT scan image resolution is variable for measuring cochlear length. Ekdale (2009) assessed the accuracy of both the proximal end of the basilar membrane gap, and the inflection of the vestibule and cochlea, for measuring cochlear length. He concluded that differences in measurement of the cochlear coiling and length, as based on these two different landmarks, are small.

For Dryolestes, the point of inflection between the vestibule and the cochlea is clearly marked on the well-preserved endocast surface (Figs 5A, 12B: ivc). It can be used here as a secondary landmark for the cochlear canal, as used by West (1985), Meng & Fox (1995b), and Ekdale (2009). The close approximation of the point of inflection to the proximal end of the basilar membrane can be corroborated by several additional observations in extant mammals. In the endolymphatic labyrinth of the human inner ear (Bast & Anson, 1949; Williams et al., 1989), the ductus reuniens connects the saccule to the proximal end of the cochlear duct (scala media). The saccule is also connected to the aqueductus vestibuli (endolymphatic duct), which is enclosed within a bony canal (canal of the endolymphatic duct). The 'bending' of the cochlear duct from the saccule occurs near the junction of the endolymphatic duct (Williams et al., 1989). In the serial CT scans and on the endocast of Dryolestes, the entry point of the aqueductus vestibuli can be clearly observed (Figs 3G–I, 5B: av). The entry of the aqueductus vestibuli into the inner ear bony labyrinth and its association with the inflection point of the vestibule and cochlea are reliable constraints for locating the
proximal end of the cochlear duct. As the inflection of the vestibule and the cochlea is more pronounced in their anterior aspect, but barely noticeable in the posterior aspect, application of this landmark also has a limitation.

The proximal end of the cochlear duct can be recognized in Dryolestes by both the proximal-most entry point of the cochlear nerve fibre (= the posterior-most foramen of the tractus spiralis foraminosus) and by the point of inflection between the vestibule and cochlea (Figs 12, 13: p-fcn, ivc). The secondary bony lamina for the basilar membrane is present, although weakly developed in Dryolestes. Limited by the image resolution, we could only approximate the starting point of the basilar membrane gap by the inflection of the vestibular cavity and the proximal entry of the cochlear nerve fibres (West, 1985; Meng & Fox, 1995b; Ekdale, 2009). Measured from this point distally along the groove of the primary bony lamina and towards the distal apex of the cochlea, the total length of the cochlear canal is 3.3 mm in Dryolestes (Table 1). Based on the same landmarks, the entire cochlear canal is coiled through an arc of about 270°, forming about three quarters of a complete turn in Dryolestes (Figs 12–14). The canal is relatively straight near the base, but its curvature becomes more pronounced distally (Figs 5, 12, 13). The apical half-turn forms an almost perfect circular arc around the distal point of the foramina for the cochlear nerve fibres.

The basal cochlear turn and middle segment have a nearly circular outline in cross-section (Figs 2, 13), with a canal diameter of 0.99 mm, averaged from the height (1.02 mm) and the width (0.96 mm) at the level immediately anterior of the fenestrae vestibule and cochleae. Near its apex, the cochlea has an oval outline in cross-section (Fig. 2: co-a), measured at 0.68 mm for the height and 0.85 mm for the width (average diameter 0.77 mm) at the level posterior to the narrowing cross-section in the apical turn of the cochlear canal. The apical part of the cochlear canal endocast is compressed dorsoventrally (Figs 12A, 13B: co-a). Although the petrosal is incomplete in other areas, the pars cochlearis appears to be undistorted in Dryolestes. It is unlikely that the slight compression of the apical cochlea would be caused by the post mortem compression of the pars cochlearis in fossilization, a possibility that could not be ruled out for Henkelotherium because its promontorium is not as well preserved (Ruf et al., 2009). Therefore, the relatively flattened apical part of the cochlear canal is a bona fide anatomical feature for both Henkelotherium and Dryolestes. In all characters relating to the shape and proportions of the cochlear endocast, Dryolestes is identical to Henkelotherium (Ruf et al., 2009).

**Primary bony lamina and cochlear ganglion canal**

The Dryolestes inner ear bony labyrinth is better preserved than that of Henkelotherium. As a result, we can add new observations on several cochlear characters, and corroboration for other features already known from Henkelotherium (Ruf et al., 2009). The medial (cranial) surface of the cochlear canal endocast shows the casts of the spiral cochlear nerve fibres (Figs 12–14: fcn in yellow). The nerve fibres perforate through the tractus spiralis foraminosus of the ossified cribriform floor in the deepest part of the internal acoustic meatus. Each foramen represents an individual cochlear nerve fibre’s separate entrance into the cochlear labyrinth (Fig. 5).

The primary bony lamina of the basilar membrane and the spiral cochlear ganglion canal are two inter-related structures in the cochlear bony labyrinth in extant therian mammals (Fleischer, 1973, 1976b; Williams et al., 1989; Luo et al., 2011a). The primary lamina is a bony structure that serves as the conduit for the axons of hair cells and the spiral ganglion, and physically supports the medial margin of the basilar membrane. Thus, the primary lamina is the most reliable osteological correlate to infer the presence of modern therian-like cochlear innervation, and the extent of such innervation along the length of the cochlear canal. The spiral cochlear ganglion canal is embedded in the base of the primary bony lamina. In the echolocating mammals with a hypertrophied spiral ganglion, the large canal of the spiral ganglion bulges into the scala tympani compartment of the cochlear canal (Fleischer, 1976a; Luo & Eastman, 1995; Luo & Marsh, 1996). However, in most therian mammals (e.g. humans, Bast & Anson, 1949), the spiral cochlear ganglion is small enough that it is just an integral part of the base of the primary bony lamina.

In Dryolestes, both the primary bony lamina and the ganglion canal are clearly visible in the CT scans (Fig. 5: pbl, cgc), and their presence is reflected on the endocast surface (Figs 12, 13: pbl, fcn-cg). The endocranial surface of the cochlear canal endocast has a clear and strongly curved tract that represents the numerous tiny foramina that perforated into the spiral ganglion canal (Figs 12–14). Along the outside (radial side) of the curved tract of the spiral foramina, there is a deep and well-defined groove (Figs 12, 13: bpl) that represents the base of the primary bony lamina for the basilar membrane (= lamina spiralis ossea primaria) in the intact cochlear canal. By the preserved base of the primary bony lamina (Fig. 14B), we estimate that it is 1.6 mm in length.

The basal part of the bony lamina forms the wall of the cochlear ganglion canal (Fig. 5A, B: cgc). By
tracing the CT scans of the well-formed wall of the ganglion canal, we were able to reconstruct that the cochlear ganglion extends through the cochlear ganglion canal along the basal two thirds of the cochlear canal length (Fig. 14: cochlear ganglion). The wall of the ganglion canal thins distally and opens into the apical part of the cochlear canal (Fig. 5A, B). We interpret that the edge of the primary bony lamina is either not fully ossified or is too thin to be detectable in the CT scans (Fig. 14B: grey pattern represents the incomplete primary lamina). Either way, it is conservative to conclude that Dryolestes has preserved the basal portion of the primary bony lamina, and nearly completely preserved the ganglion canal embedded in the lamina (Fig. 14).

Dryolestes has the modern therian-like innervation of the cochlea, as seen in Homo sapiens (Williams et al., 1989) and other extant mammals (Fleischer, 1973), although there is also some difference. In extant therians, the primary bony lamina and spiral ganglion canal extend to the apex of the entire fully coiled cochlea. By comparison, the primary bony lamina in Dryolestes is present for the proximal two thirds of the cochlea (the first 180°), absent in the apical one quarter turn of this cochlea with 270° of coiling.

The primary bony lamina base of Dryolestes bears strong resemblance to that in Henkelotherium. In Henkelotherium, the base for the primary bony lamina is well preserved along about half of the basal cochlear canal length. However, the impression of this bony lamina is absent in the coiled apical quarter of the canal (Ruf et al., 2009: fig. 6). The length of the cochlear duct is 2.7 mm, shorter than the 3.3 mm cochlear length of Dryolestes, and is proportionate to the overall smaller size of the cochlea in Henkelotherium.

We suggest that, for the Dryolestoida as a whole, the entire cochlear duct (scala media) was innervated in the same way as in extant therian mammals, with the primary bony lamina transmitting the axons of the hair cells and supporting the medial (axial) margin of the basilar membrane. However, the bony laminar base is fully ossified only along the proximal half-turn of the cochlear canal (Fig 5B: bpl) and the canal for the cochlear ganglion was fully developed (Fig 5: cgc). The wall of the ganglion canal extends to more than the first half-turn of the cochlea in the horizontal sections (Fig. 5) but the canal opens distally into the apical quarter-turn of the cochlea. The shorter and apically open cochlear ganglion canal of Dryolestes and Henkelotherium represents a plesiomorphic condition to the longer ganglion canal extending into the apex in modern therians.

**APEX OF COCHLEAR CANAL**

We interpret that the apical third of the cochlea of Dryolestes differs from the innervation pattern of extant monotremes. In extant monotremes (Pritchard, 1881; Denker, 1901; Alexander, 1904; Fox & Meng, 1997), the apical portion of the cochlear duct contains the lagena, an auditory sensory structure of all amniote vertebrates. The lagena contains a patch of sensory epithelium in the cochlear duct, has hair cells similar to those of the vestibular macula but has no inner or outer hair cells that are characteristic of the hearing organ (organ of Corti) of the cochlear duct. Moreover, the lagena is topographically separated from the organ of Corti in the monotremes Ornithorhynchus (platypus) (Ladhams & Pickles, 1996) and Tachyglossus (echidna) (Alexander, 1904; Ladhams & Pickles, 1996). In the pars cochlearis of monotremes, a separate nerve canal leads from the internal acoustic meatus to the lagena in the apical portion of the cochlear canal, and is physically separated from the cribriform plate of the cochlear nerve fibres to the organ of Corti (Alexander, 1904; Luo et al., 2011a: Fig. 2).

By contrast, the organ of Corti in therian mammals is embedded between the cochlear duct and the scala tympani. The apical portion of the cochlea that contains the organ of Corti has the full complement of cochlear compartments of the scala vestibuli, cochlear duct (= scala media), and the scala tympani, as does the rest of the cochlea (Pye, 1970, 1977, 1979; Williams et al., 1989). The cochlear nerve fibre innervation extends, distally, to the apical turn of the cochlear canal. The apex of the cochlea has neither a lagena nor a separate lagenar nerve, the same as in extant marsupials and placentals (Luo et al., 2011a).

In the pars cochlearis of Dryolestes, there is no separate, monotreme-like lagena nerve. This excludes the possibility that Dryolestes had a lagena at the apical end of the cochlear duct like that in monotremes. Although the primary bony lamina is not seen in the apical quarter turn of the cochlea by uCT scans, the innervation in the apical turn was the same as in the rest of the cochlea, and was therian-like. The axons of the hair cells would have been enclosed by a weakly ossified (or even cartilaginous) primary bony lamina, or some similar supporting structure.

**SECONDARY BONY LAMINA**

Dryolestes has a secondary bony lamina for the basilar membrane, although it is weakly developed (Figs 3H, 5B: bsl). The secondary bony lamina (= lamina spiralis ossea secundaris) is present in the basal-most part of the cochlear canal between the fenestra cochleae and
the fenestra vestibuli (Figs 3F–I, 5B: sbl). On the virtual cochlear endocast, the secondary bony lamina starts at the fenestra cochleae and extends distally for a short distance (about 1.2 mm) on the radial (outer) wall of the cochlear canal endocast (Figs 12, 13: sbl), before grading and fading into the uniformly smooth surface of the cochlear endocast. In Henkelotherium, the secondary bony lamina of the basilar membrane is much better developed and extends further distally than in Dryolestes (Ruf et al., 2009). This feature can be variable amongst dryolestoids, although this may be an artefact of preservation. For dryolestoids as a whole, the secondary lamina is less developed than in the Cretaceous prototribosphenidan Vincelestes (Rougier, 1993) and Cretaceous metatherians and eutherians (Meng & Fox, 1995a, b; Ekdale, 2009). The laminar gap between the primary and secondary bony laminae cannot be measured accurately in Dryolestes because of the poor preservation of these laminae (Figs 14, 15).

Bony Labyrinth of Vestibule and Semicircular Canals

As in extant mammals the saccule of Dryolestes is located in the anteroventral part of the vestibule in the cross-sections of the CT scans (Figs 3–5: sa). The saccular nerve channel can be clearly identified (Fig. 5A: fsa). The saccular cavity is partially represented by a round and elevated area that is posterior to the fenestra vestibuli and opposite to the position of the fenestra cochleae and the aqueductus cochleae entry point on the inner ear endocast (Fig. 12: sa, f, fc, ac). On the medial aspect of the vestibule, the point of inflection of the vestibule and cochlea can serve as a landmark to separate the utricle and the saccule (Fig. 3: ivc, ut, sa). On the posteroventral side, a division marks the separation between the saccule and the utricle (Fig. 5: dus). The utricle–saccule division is represented as a groove on the endocast (Figs 12, 13: dus). This structure is anteriorly continuous and merges with the inflection point of the vestibule and cochlea. On the cranial and anterior aspects of the endocast, there is no bony landmark to separate the saccule and the utricle because the two structures share a common space in the vestibule, as in all extant mammals.

The anterior semicircular canal rises from its ampulla and ends in the crus commune, the shared passage with the posterior semicircular canal. The anterior semicircular canal ampulla is almost spherical (Fig. 12: asc). By height and radius, the anterior semicircular canal is larger than the posterior and the lateral semicircular canals (Table 1). The posterior semicircular canal is confluent with the anterior semicircular canal in the crus commune (Fig. 12: cc). Posteriorly it forms a short secondary crus commune with the lateral semicircular canal, before entering into the posterior semicircular canal ampulla, which appears to be large because of the combined space of the secondary crus commune and the ampulla (Figs 12, 13: scc, psca). As the passages of the crus commune and the secondary crus commune are shared, the independent portion of the posterior semicircular canal is relatively short, and has the shortest arc, height, and length amongst the three semicircular canals (Table 1). The lateral semicircular canal begins from the lateral semicircular canal ampulla and ends in the secondary crus commune. The plane of the lateral semicircular canal forms a 145° angle to the imaginary axis through the basal (and relatively straight) part of the cochlear canal, similar to that in Henkelotherium (Ruf et al., 2009). Dryolestes and Henkelotherium are also similar in having the secondary crus commune (Ruf et al., 2009). The secondary crus commune is a systematically variable feature, absent in most crown therians, but present in some (although not all) notoungulate placental mammals (Macrini et al., 2010) and several Mesozoic eutherians (Ekdale & Rowe, 2011).

We followed Schmelzle et al. (2007) in measurement of the semicircular canals. The radius of the inner curvature of the semicircular canals was calculated by measuring the height and width of each arc using the formula 0.5 × [height + width]/2. The height was defined as the maximum distance between the external surface of the vestibule and the inner arc of the canal; the width was measured perpendicular to the height. The height of the posterior semicircular canal was measured between the dorsal border of the posterior ampulla and the farthest point on the inner arc. The lumen diameter of each semicircular canal was measured at the farthest point from the vestibule and posterior ampulla, respectively, according to the height of the canals (see Table 1).

The radii of the semicircular canals are indicators of agility of mammalian locomotion and habits (Spoor et al., 2007). Agility scores can be estimated by regression of the semicircular canal against body mass in order to infer the habits and locomotor function of extinct mammals (Silcox et al., 2009; Macrini et al., 2010). We estimate that adults of D. leiriensis had an average body mass of 130 g from an average mandible length of 34.7 mm by the regression analysis first developed by Foster (2009). The average radius of the three semicircular canals is 0.88 mm (Table 1), and it has an average agility score of 3.2. By comparison to extinct mammals with similar agility scores (Spoor et al., 2007), Dryolestes could have been either an arboreal or a terrestrial mammal, but was not gliding, flying, saltatorial, or aquatic.
DISCUSSION

SYSTEMATIC DISTRIBUTION OF PETROSAL CHARACTERS

The *Dryolestes* petrosal specimen adds new information to the known petrosal characters of dryolestoids, in addition to those preserved in *Henkelotherium* (Ruf et al., 2009). Several of these are the shared derived characters of dryolestoids, *Vincelestes*, and crown therians. Both *Dryolestes* and *Henkelotherium* are more similar to *Vincelestes* and crown therians, in having a more bulbous and oval-shaped promontorium related to the stronger coiling of the cochlear canal, than to the spalacotheroid ‘symmetrodonts,’ triconodontids, and multituberculates (Luo & Ketten, 1991; Cromp-...
perilymphatic duct from the inner ear labyrinth to the jugular foramen, as best exemplified by *Ornithorhynchus*. The fenestra cochleae is fully formed because the exit of the perilymphatic duct from the membranous labyrinth is confluent with the ‘foramen’ cochleae. There are several cladotherian apomorphies on the tympanic side of the mastoid. The caudal tympanic process has resulted in raising the posterior margin of the tympanic cavity. Related to this, the postromontorial tympanic recess, the concave space between this caudal tympanic process and the fenestra cochleae, becomes larger in trechnotherians than in ‘pre-trechnotherian’ mammaliaforms.

**IMPLICATIONS FOR HEARING EVOLUTION**

We speculate that the development of such neomorphic features as the postromontorial tympanic recess and the separate fenestra cochleae and aqueductus cochleae may have functional ramifications. Foremost, the derived processus recessus in the post-terior pars cochlearis helps to separate the fenestra cochleae, which functions to release the residual sound pressure from the perilymphatic space, from the perilymphatic duct that drains the perilymphatic space (Zeller, 1985). This may lead to improved acoustic isolation of the inner ear labyrinth from the middle ear tympanic cavity (Ruf et al., 2009) by reducing the size of the fenestra cochleae and the canal size of the perilymphatic foramen. We further speculate here that the space expansion of a larger postromontorial tympanic recess of the tympanic cavity is related to the pressure-release function of the fenestra cochleae, which co-evolved with the postromontorial tympanic recess in the trechnothe-rian clade, and are retained as plesiomorphies in dryolestoids.

The most significant implications of the newly revealed inner ear morphology of *Dryolestes* are for the evolutionary origins of the cochlear innervation for modern marsupials and placentals. The modern therian mammalian auditory neural pathway consists of the following structures: the hair cells of the organ of Corti convert the vibration of sound waves to a neural signal, which is relayed through the spiral ganglion canal. The cochlear ganglion cells are bipolar and their cell nuclei are contained in the ganglion canal. The cochlear ganglion cells are connected distally to the hair cells in the organ of Corti, and proximally to the brain (Lewis, Leverenz & Bialek, 1985; Williams et al., 1989; Durrant & Lovrinic, 1995). The neural structures of this pathway have osteologi-cal correlates in extant therians:

1. The canals of the primary bony lamina: the individual fascicles of the cochlear nerve fibres from the ganglion cells to the hair cells are enclosed in the pores of the habenula perforata – the tiny nerve canals inside the edge of the primary bony lamina;
2. The cochlear ganglion canal: the neurone bodies of cochlear ganglion cells are enclosed in the bony canal, embedded inside the base of the primary bony lamina or the modiolus of the pars cochlearis; and the bony wall of the ganglion canal forms the base of the primary bony lamina;
3. The tractus spiralis foraminosus (‘cribriform plate’): the individual fascicles of the cochlear nerve fibres connecting the ganglion cells to the central nervous system are enclosed by the minute foramina and tubules between the internal acoustic meatus and the spiral ganglion canal.

These extant therian bony structures with functional significance are now known for *Dryolestes* (Figs 3–5, 15F). By the phylogenetic position of dryolestoids (Fig. 15) and their first appearance in the Middle Jurassic in the fossil record, we extrapolate that the origin of modern therian cochlear innervation is an evolutionary innovation of the cladotherian group. With this sophisticated cochlear innervation, the early cladotherians appear to have developed more sensitive hearing of sound of higher frequencies and to have had refined resolution of frequencies, as in extant marsupials and placentals.

In addition to the new cochlear innervation, other features of the inner ear also imply better development of hearing function. The primary, and very probably also the secondary, bony laminae are correlated with a more rigid support for both edges of the basilar membrane. The presence of the bony laminae also narrows the width of this membrane in the basal part of the cochlea. These are soft-tissue characteristics for more sensitive hearing of higher frequency sound (Fleischer, 1976a; Ketten, 1992). Although the systematic distribution of the secondary bony lamina is not universal amongst extant marsupials and placentals (reviewed by Fleischer, 1973; Ruf et al., 2009), there is strong evidence that this feature evolved before the rise of extant marsupials and placentals, in basal members of cladotherians (Ruf et al., 2009). It is likely that the extant therian-like hearing sensitivity evolved before the common ancestor of crown therians.

Chronologically, the evolutionary origins of the living therian-like innervation of the cochlea, and the structural organization of both the bony and membranous labyrinths, occurred no later than the Late Jurassic, the geological age of *Dryolestes* and *Henkelotherium*, and possibly as early as the Middle Jurassic, to which the earliest-known dryolestoid fossil is dated (Freeman, 1979; Kielan-Jaworowska et al., 2004).
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