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Periotic Morphology in the Trichosurin Possums *Strigocuscus celebensis* and *Wyulda squamicaudata* (Diprotodontia, Phalangeridae) and a Revised Diagnosis of the Tribe Trichosurini

KIRSTEN CROSBY[1] AND CHRISTOPHER A. NORRIS[2]

ABSTRACT

The morphology of the periotic in the extant trichosurin possums *Strigocuscus celebensis* and *Wyulda squamicaudata* is described and compared with that of various species of extant and extinct phalangerid marsupials. The periotic morphologies of *S. celebensis* and *W. squamicaudata* show a number of similarities with those of brushtailed possums of the genus *Trichosurus*, strengthening the case for a monophyletic tribe Trichosurini consisting of these three genera. Comparisons with periotics of possums from the Tertiary Riversleigh deposits of Queensland that were previously assigned on the basis of craniodental anatomy to *Trichosurus* and *Strigocuscus* suggest that, despite some similarities, the three extant trichosurins may be more closely related to each other than to the Riversleigh taxa. A revised morphological diagnosis of the Trichosurini is provided, incorporating these data.

INTRODUCTION

The lesser Sulawesi cuscus *Strigocuscus celebensis* and the scaly-tailed possum *Wyulda squamicaudata* are small to medium-size members of the marsupial family Phalangeridae. Both species bear a superficial resemblance to members of the most diverse and abundant group of phalangerids, the true cuscuses of the genus *Phalanger*. In the case of

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S. celebensis this similarity led to inclusion of the species in *Phalanger* (e.g., Tate, 1945), a situation which prevailed as the accepted taxonomy until comparatively recently. By contrast, *Wyulda* has always been recognized as a distinct taxon, with craniodental characters that indicate a close affinity to the brushtailed possums of the genus *Trichosurus*.

The division of the Phalangeridae into two groups, the monogeneric cuscuses and the two genera of possums, remained unchallenged until the phylogenetic revision of Flannery et al. (1987), who proposed that cuscuses were paraphyletic with respect to the possums. The Phalangeridae were divided into two subfamilies, the Ailuropinae, containing a single species *Ailurops ursinus*, and the Phalangerinae, containing all the remaining species of phalangerid. The Phalangerinae were divided into a further two groups: the tribes Phalangerini and Trichosurini. Flannery et al. (1987) resurrected the generic name *Strigocuscus* from synonymy within *Phalanger* and placed the genus within the Trichosurini, along with *Wyulda* and *Trichosurus*. As originally defined by Flannery et al., *Strigocuscus* contained four species formerly included within *Phalanger*: *S. celebensis*, *S. gymnotis*, *S. ornatus*, and *S. rothschildi*. A fifth taxon, *S. mimicus*, was raised from subspecific status within *Phalanger orientalis*. Subsequent studies have removed all species but *S. celebensis* from within the group and added a new species, *S. pelengensis* (George, 1987; Springer et al., 1990; Norris, 1992; Flannery, 1994; Hamilton and Springer, 1999), previously a subspecies of *S. celebensis* (Tate, 1945). The generic placement of this taxon is still under debate.

A study by Norris (1994) described the periotic bones of various phalangerid species and categorized three periotic morphologies which more or less corresponded to the divisions originally proposed by Flannery et al. (1987), together with the narrower definition of *Strigocuscus* made by later authors. Norris only studied one trichosurin periotic in detail, that of *Trichosurus vulpecula*. No loose periotic of either *S. celebensis* or *W. squamicaudata* was available for examination.

The fact that periotic morphology in phalangerids corresponded so closely to the phylogenetic divisions created by analysis of a broad character set of morphological and molecular characters suggested that a study of this region in specimens of fossil phalangerids from Tertiary deposits at Riversleigh, Australia, might provide insights into the early evolution and diversification of the group. In superficial morphology, the Riversleigh species appear to be trichosurin. However, they also possess a number of cranial characters that are plesiomorphic for phalangerids as a whole. Flannery et al. (1987) hinted at this in their list of synapomorphies for the trichosurins, where they noted that the Riversleigh species *Trichosurus dicksoni* exhibited the plesiomorphic state for some characters. A comparison of the periotic of this species and of *Strigocuscus reidi*, also from Riversleigh, showed a very different morphology than that of *T. vulpecula*, as discussed by Norris (1994). In fact, examination of these, and other, extinct taxa from Riversleigh suggest that a much broader range of periotic morphologies may be present within the group than is apparent from its extant members. Since other craniodental characters of these fossil species suggest that the majority of them have trichosurin affinities (K.C., in prep.), a broader knowledge of the periotic anatomy of the living trichosurins is required. To this end, periotics of *Strigocuscus celebensis* and *Wyulda squamicaudata* were dissected from skulls housed in the Department of Mammalogy at the American Museum of Natural History (AMNH) and studied in detail.

MATERIALS AND METHODS

The right periotic was dissected from the skull of AMNH 196502, an adult female specimen of *Strigocuscus celebensis*. The skull of AMNH 196919, an adult female specimen of *Wyulda squamicaudata*, was prepared from the alcohol-preserved carcass of this animal by dermestid beetle action, and the left periotic was dissected. Detailed descriptions of the two bones were made, and the morphology was compared with specimens of a variety of extant and extinct phalangerid taxa (table 1).

For the most part, the terminology em-

TABLE 1
Material Examined

Number	Species	Specimen
OUM 7994	*Ailurops ursinus*	periotic
BMNH 96.6.24.7	*Ailurops ursinus*	periotic
OUM 4844	*Trichosurus vulpecula*	periotic
OUM 4351	*Trichosurus vulpecula*	periotic
BMNH 0.1.25.1	*Phalanger rothschildi*	sagittally sectioned skull
BMNH 62.10.21.3	*Phalanger ornatus*	sagittally sectioned skull
BMNH 50.997	*Phalanger carmelitae*	sagittally sectioned skull
AMNH 196502	*Strigocuscus celebensis*	periotic
AMNH 196919	*Wyulda squamicaudata*	periotic
QMF 13078	*Strigocuscus reidi*	periotic
QMF 13077	*Trichosurus dicksoni*	periotic
QMF 50395	unnamed phalangerid from Riversleigh	periotic
OUM 679	*Bettongia leseueri*	periotic
OUM 7971	*Pseudocheirus occidentalis*	periotic

ployed in this paper follows MacIntyre (1972), with modifications from Wible (1990) and Norris (1994). There are certain structures on the periotic, however, whose homology needed to be further evaluated before they could give solid phylogenetic information. These were the rostral tympanic process, the ectotympanic process, and the crista promontorii medioventralis. Problems with these structures include whether they are homologous with those seen in other groups, as well as their relative positions.

MacPhee (1981) defined the rostral tympanic process (RTPP) as being a ‘‘tympanic process that arises (apparently always periosteally) from all or part of the ventral surface of the pars cochlearis.’’ Wible (1990), in a study of periotics of Cretaceous marsupials, described a crest that ‘‘arises from the promontorial surface in front of the fenestra cochleae and runs towards the midline along the posterior edge of the medial expansion.’’ He noted that this crest is in the same position as the RTPP in modern marsupials and that the morphology of this crest in his Petrosal Type A (probably a species of *Pediomys*) resembles the RTPP of phalangerids. Norris (1994) described the RTPP in *Trichosurus vulpecula* as the medial border of the pars cochlearis, a ‘‘sharp ridge running antero-ventrally to fuse with the margin of the trigeminal fossa.’’ In direct contrast to this, however, Marshall et al. (1995: p. 75) contended that phalangerids have a smooth promontorium with no RTPP.

The confusion arises because the RTTP identified by Wible in *Didelphis* is only the apex of a much larger structure; this extends both rostrally and medially from the summit of the mound formed by the underlying cochlea, which we term the cupula cochleae. In phalangerids, the cupula intrudes into this structure, and the ventrally extended process seen in *Didelphis* is absent. As a result, there appear to be two structures on the ventral surface of the pars cochlearis: a crest running anteriorly from the cupula cochleae onto the promontorium (the RTTP of Norris, 1994), and a variably developed, ventrally oriented process. The latter structure was labeled by Norris (1994) as the ectotympanic process (ECTP). In fact, this process is merely the caudo-lateral extension of the RTTP (fig. 1). Thus, in this paper, we have subsumed the ECTP sensu Norris (1994) into the RTPP.

The final structure that is in question is the crista promontorii medioventralis (CPM). MacIntyre (1972) defined this as a ridge running anteriorly from the margin of the posterior lacerate foramen that forms the boundary between the cerebellar and tympanic faces. In MacIntyre’s figure this structure is shown as lying lateral to the sulcus of the inferior petrosal sinus (SIPS). In the periotics of *Wyulda* and phalangerins, however, the ventral edge of the cerebellar face can extend

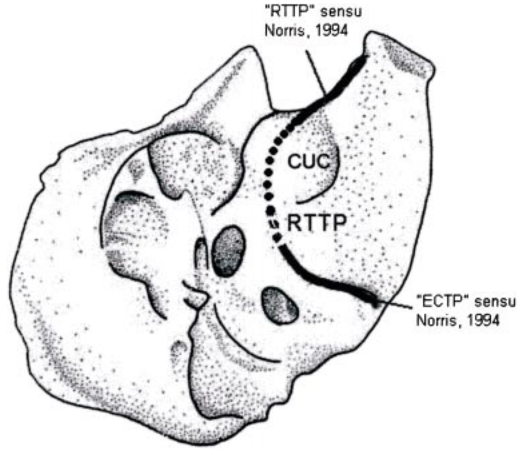

Fig. 1. Tympanic view of a generalized phalangerid petrosal, with a line showing the crest of the rostral tympanic process (RTTP). The cupula cochleae (CUC) intrudes into the RTTP, splitting it into two portions, which Norris (1994) identified as the rostral and ectotympanic processes (''RTTP'' and ''ECTP''). In fact, both structures are part of the RTTP.

down medial to the SIPS, forming a ventrally directed flange. In these cases, the lowest point on the pars cochlearis, and the apparent margin between the cerebellar and tympanic faces, tends to be the ventral edge of this flange. Despite this, however, we continue to apply the term CPM to the crest that runs lateral to the SIPS, as this is the structure that most closely resembles the original definition of MacIntyre.

Terminology of the nerves and blood vessels surrounding the periotic follows Archer (1976). In this paper, the term ''trichosurin'' refers only to the modern species. Riversleigh specimens are discussed separately, as their exact phylogenetic position has not yet been determined (this includes the two described Riversleigh species, *Trichosurus dicksoni* and *Strigocuscus reidi*).

DESCRIPTIONS OF PERIOTIC MORPHOLOGY

Strigocuscus celebensis

The overall morphology of the periotic in *S. celebensis* is remarkably similar to that of *Trichosurus vulpecula* (Norris, 1994), particularly in its elongate promontorium, which accounts for almost half the total length of the pars cochlearis, and small internal auditory meatus (fig. 2). However there are a number of distinctive features not shared with *Trichosurus* (table 2). The caudal margin of the subarcuate fossa is greatly thickened, reducing the overall size of the opening. At the anterior margin of the fossa, an overhang in the crista petrosa produces a small, pocketed area. As in *Trichosurus*, the crista petrosa is expanded to form part of the septum separating the middle and posterior cranial fossae and is notched anterodorsally for the passage of the prootic sinus. However, unlike in *Trichosurus*, this expansion does not result in the development of a large, platelike lamella or lead to the crista petrosa becoming contiguous with the tegmen tympani. In *Strigocuscus*, the crista petrosa is a comparatively small, robust structure, which is clearly separated from the tegmen tympani. It is comparatively low at the point where it meets the margin of the subarcuate fossa, and it is grooved along its lateral margin by the sulcus of the prootic sinus. In *Trichosurus* this sulcus is deflected laterally by the expansion of the crista petrosa, but in *Strigocuscus* it follows a more or less straight dorsal-ventral path.

Dorsally, the lamella that is often seen around the posterodorsal margin of the peri-

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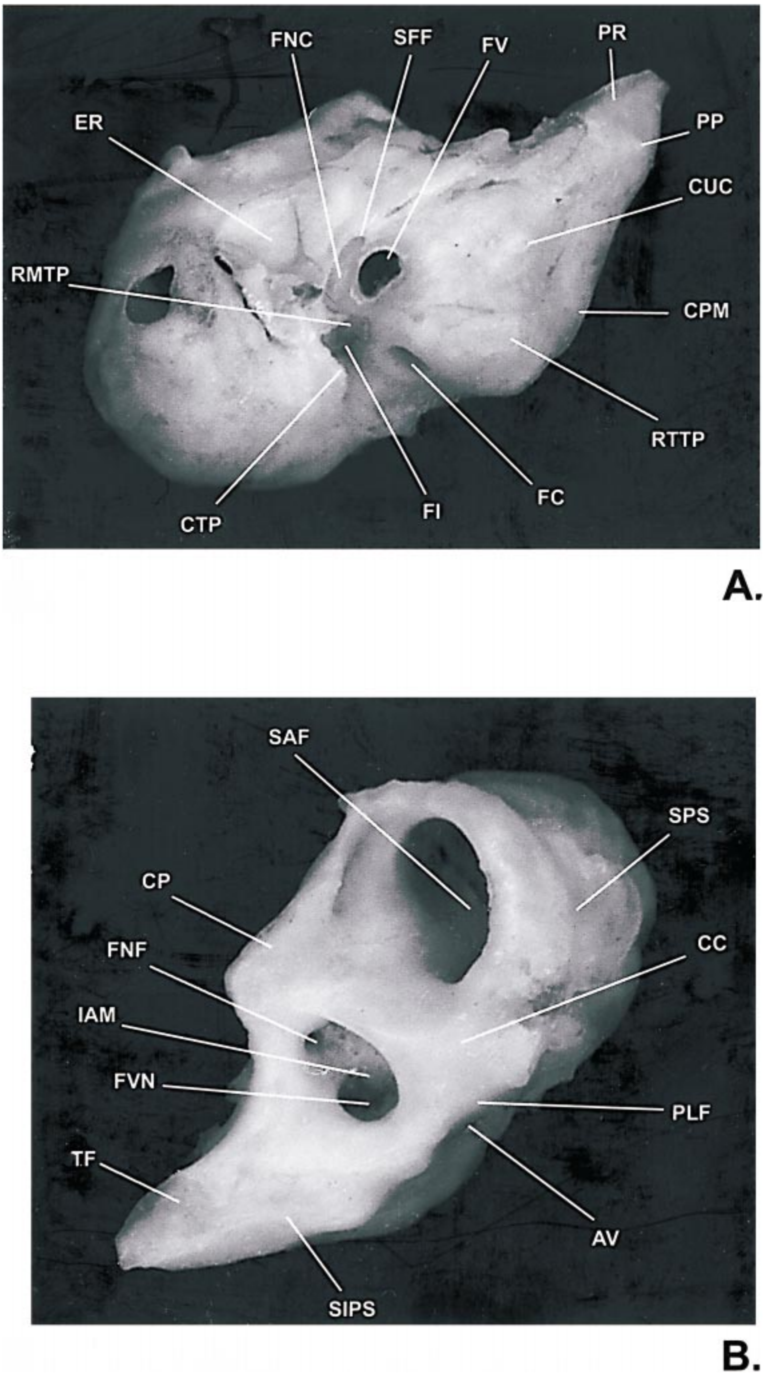
Fig. 2. Periotic of AMNH 196502, *Strigocuscus celebensis*. **A.** Tympanic face. **B.** Cerebellar face. Abbreviations: AV, aqueductus vestibuli; CC, crus commune; CP, crista petrosa; CPM, crista promontorii medioventralis; CTP, caudal tympanic process; ER, epitympanic recess; FC, fenestra cochleae; FI, fossa incudis; FNC, facial nerve canal; FNF, facial nerve foramen; FV, fenestra vestibuli; FVN, foramen of the vestibulocochlear nerve; IAM, internal auditory meatus; PLF, posterior lacerate foramen; PP, pustular process; PR, promontorium; RMTP, recessus mesotympanicus; SAF, subarcuate fossa; SFF, secondary facial foramen; SIPS, sulcus of the inferior petrosal sinus; SPS, sulcus of the prootic sinus. TF, trigeminal nerve fossa. Approximately 10× life size.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CTP
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A.
SAF
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CC
FNF
IAM
FVN
PLF
TF
AV
SIPS
B.

TABLE 2
Comparison of the Periotics of Trichosurins

Feature	*Trichosurus*	*Wyulda*	*Strigocuscus*
Size of internal auditory meatus	small	small	small
Size of subarcuate fossa	large	large	large
Posterodorsal rim of subarcuate fossa	broad	small flap	small flap
Passage in rim for sinus	absent	present	present
Notch between rim and crista petrosa	present	absent	present
Expansion of the crista petrosa	great	great	slight
Curvature of promontorium	none	none	slight
Length of promontorium	long	long	long
Sulcus below internal auditory meatus	none or faint	deep	faint
Aqueductus cochleae	level with rim	level with rim	level with rim
Width of promontorium	wide	wide	narrow
Apex of cupula cochleae	poorly defined	slightly bulbous	poorly defined
Rostral tympanic process	long and well defined	faint	faint
Rostral tympanic process	longitudinal	rounded?	transverse?
Size of FC and FV	large	large	small
Crista promontorii medioventralis	long	short	long

otic in phalangerids (Norris, 1994) is absent, with the exception of a small flap just dorsal to the crus commune. On the left periotic of AMNH 195602, which remained in situ, this flap carried a small circular foramen, which is assumed to be the opening of the prootic sinus. There is a faint ridge between the crus commune and the prefacial commissure, which is sharply depressed. A small aqueductus vestibule is present just ventral to the crus commune. The internal auditory meatus is dominated by the large foramen of the vestibulocochlear nerve, with the small foramen of the facial nerve lying just dorsolateral to it.

From a cerebellar aspect, the promontorium is separated from the remainder of the pars cochlearis by a faint discontinuity, caused by the SIPS crossing the surface of the periotic just rostral to the internal auditory meatus. On the tympanic face, a small, pustular process arises from the ventral surface of the promontorium just caudal to the sulcus of the trigeminal nerve; this structure was not seen in any other phalangerid taxa studied. As in *Trichosurus*, the promontorium itself is long and slender when viewed from both the tympanic and cerebellar aspects. Unlike *Trichosurus*, however, it retains this slender appearance in its squamosal aspect. This is the result of differences in the morphology of the tympanic surface of the pars cochlearis in the two taxa. In *Strigocuscus*, the apex of the cupula cochleae is very small and indistinct (unlike that of *Trichosurus*, which is prominent and well defined), and the rostral tympanic process is small. The squamosal surface of the promontorium is depressed by a narrow trigeminal fossa. The large opening of the hiatus Fallopii lies just posterodorsal to the fossa; just anterior to the fossa, the medial margin of the promontorium is depressed by the SIPS.

Ventrally, the pars cochlearis is bordered by a long CPM. This structure is not nearly as large and ventrally extensive as that seen in *Trichosurus*, where the CPM completely fills the gap between the basioccipital and the tympanic wing of the alisphenoid (Norris, 1994). This is linked, in part, to the development of the ventral portion of the rostral tympanic process in the two taxa. In *Trichosurus* this is a large, well-defined structure, which is greatly expanded ventrally. In *Strigocuscus*, by contrast, the process, though large, is only poorly developed; it is rounded and shows little or no ventral expansion. The lambdoidal face of the pars cochlearis is relatively smooth and lacks the deep sulci seen in a number of extinct and living phalangerid taxa. The acqueductus cochleae is small and has only a very shallow sulcus leading to it.

Further differences between the periotics of *Strigocuscus* and *Trichosurus* can be seen

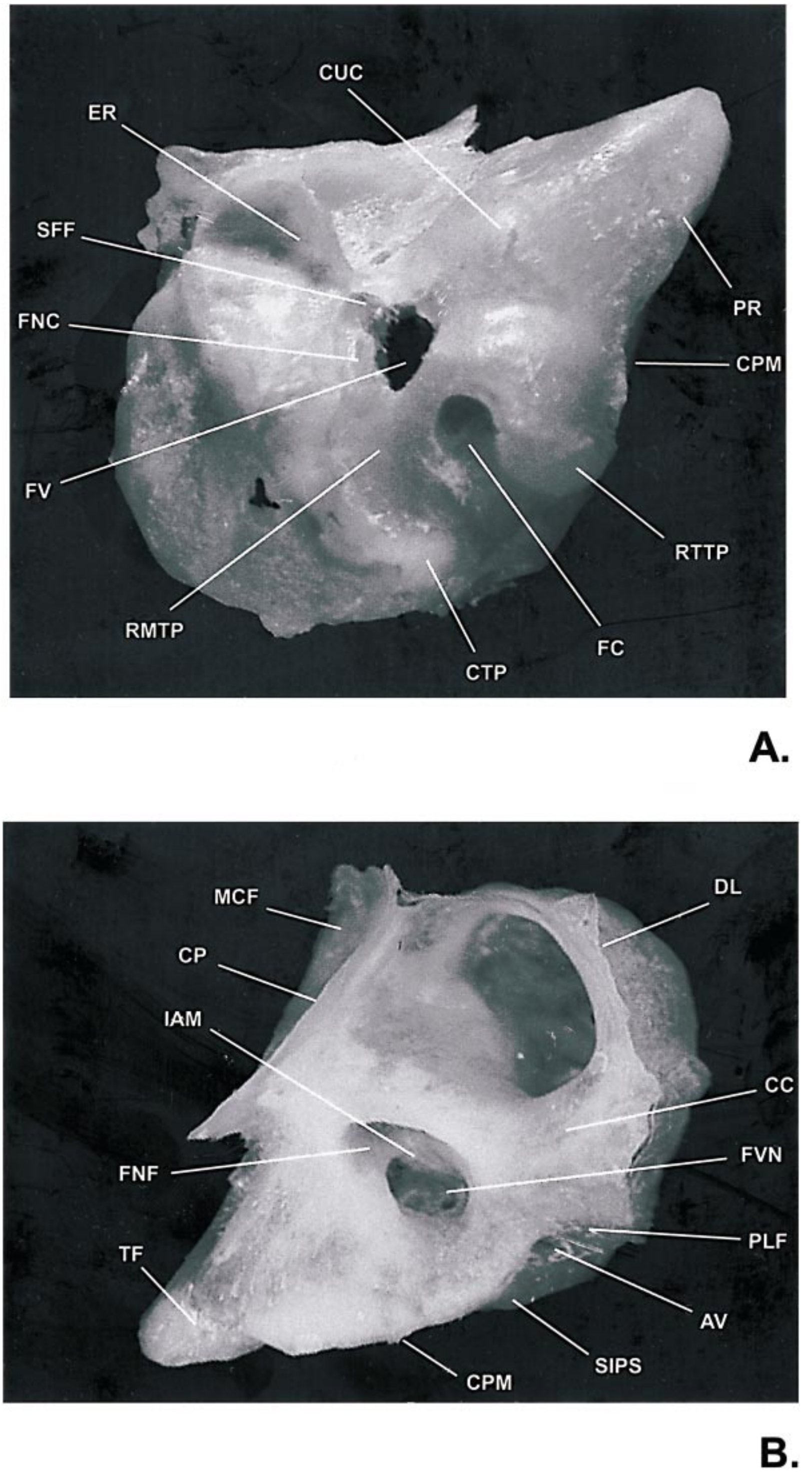

Fig. 3. Periotic of AMNH 196920, *Wyulda squamicaudata*. **A.** Tympanic face. **B.** Cerebellar face. Abbreviations: DL, dorsal lamella; MCF, exposure of periotic in middle cranial fossa. Other abbreviations as for figure 2. Approximately 10× life size.

in the roof of the tympanic sinus. The fenestra cochleae and fenestra vestibulae are much smaller in *Strigocuscus*. The recessus mesotympanicus is curved rather than straight and is bordered by a caudal tympanic process that is only poorly defined. The epitympanic recess is shallow and seems to lack the prominent bordering septa seen in *Trichosurus*: this is reflected in the lack of continuity between the crista petrosa and tegmen tympani in *Strigocuscus*.

Wyulda squamicaudata

As in *Trichosurus*, the crista petrosa of *Wyulda* is expanded to form a flattened, anteriorly directed, platelike lamella (fig. 3). The prefacial commissure is not especially depressed and instead forms more of a right angle between the crista petrosa and the promontorium. The subarcuate fossa is large and lacks the thickening of the caudal margin seen in *Strigocuscus*, and the internal auditory meatus is relatively large. The most striking feature, however, is the overall morphology of the pars cochlearis, which although almost as long as those of the other two trichosurin taxa, is much broader, especially in its tympanic and squamosal aspects. The ventral edge of the cerebellar face extends downward as a ventrally directed lamella, bordering the inferior petrosal sinus medially and giving the cerebellar surface of the periotic a flattened appearance. This lamella ends rostrally at the point where the inferior petrosal sinus emerges onto, and crosses, the promontorium. The depth of the lamella exaggerates the degree of discontinuity between the promontorium and the remainder of the pars cochlearis. The shallow sulcus of the inferior petrosal sinus is relatively close to the tip of the promontorium and stops part way across the cerebellar face; this is in contrast to the situation seen in the Riversleigh specimens, where the sulcus is deep and runs the entire width of the cerebellar surface of the promontorium (K.C., in prep.).

The breadth of the pars cochlearis is particularly striking when the periotic of *Wyulda* is viewed from its tympanic aspect. The rostral tympanic process is robust, well defined, and ventrally oriented, as in *Trichosurus*. The apex of the cupula cochleae is better defined than in *Strigocuscus*, and the rostral tympanic process is larger. The fenestra cochleae is more ventrally oriented than in either *Trichosurus* or *Strigocuscus*. The epitympanic recess is well defined, with a distinct lamina connecting the crista petrosa to the tegmen tympani. The recessus mesotympanicus is curved, and the caudal tympanic process is small and poorly defined.

From the squamosal aspect, the much greater depth and bulk of the pars cochlearis in *Wyulda* is clearly evident, and it can be seen that this is a function of the size of the rostral tympanic process. The discontinuity between the promontorium and the cerebellar face of the periotic is also very apparent, together with the sulcus of the inferior petrosal sinus that is responsible for the discontinuity. As in *Strigocuscus*, the acqueductus cochleae is small and indistinct. The platelike lamella of the crista petrosa dominates the lambdoidal aspect of the specimen. Expansion of this structure leads to a marked lateral displacement of the sulcus of the prootic sinus, similar to that which is seen in *Trichosurus* (Norris, 1994).

DISCUSSION

In a number of respects, the periotics of *Strigocuscus celebensis* and *Wyulda squamicaudata* are very similar in morphology to those seen in species of *Trichosurus*. These form a tight morphotype when compared to the periotics of species of *Ailurops*, *Phalanger*, and *Spilocuscus* (fig. 4). The morphotype is distinguished primarily by considerable elongation of the promontorium (around

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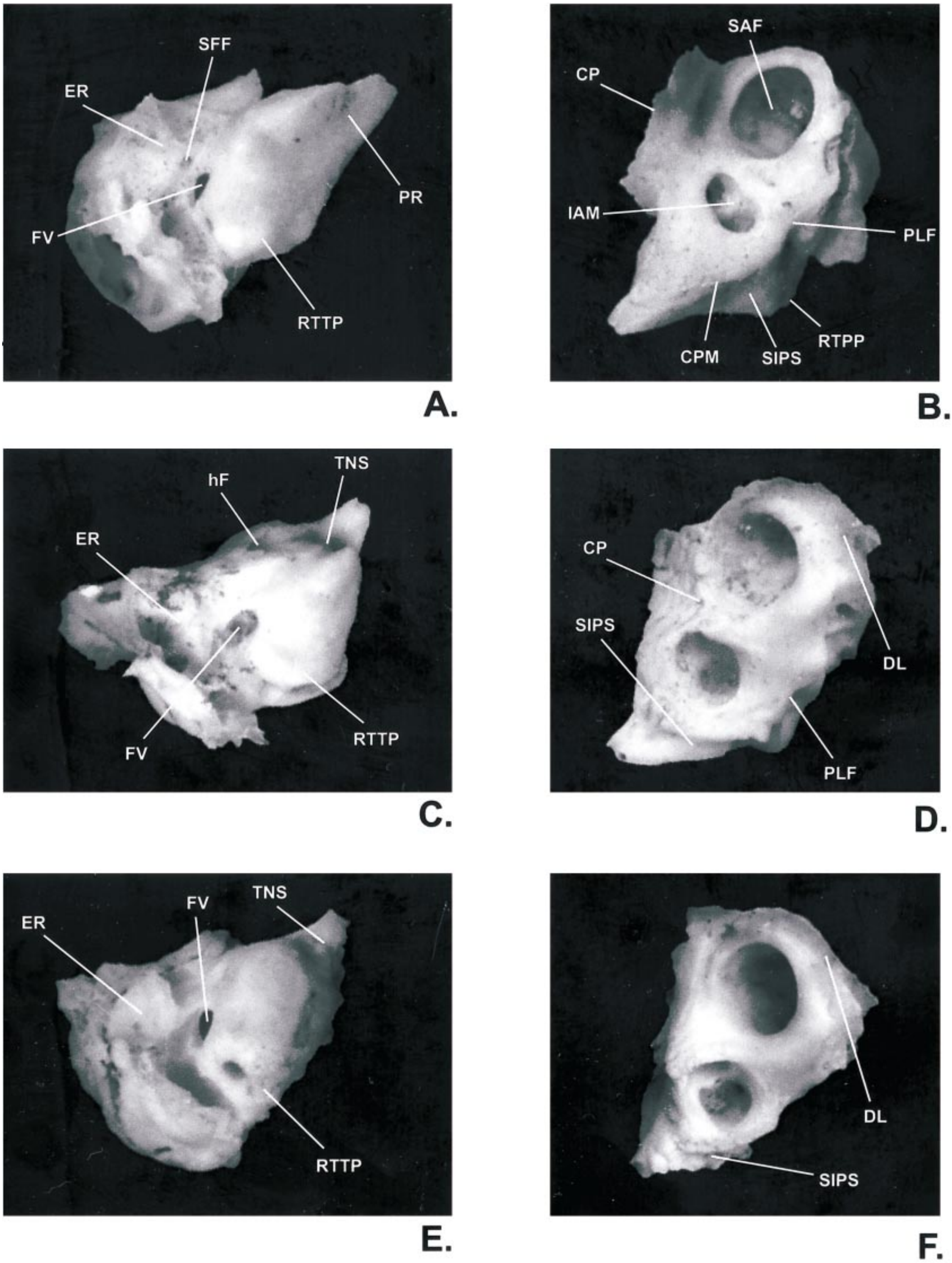
Fig. 4. Periotics of living phalangerids. **A, B,** *Trichosurus vulpecula*; **C, D,** *Phalanger* (*Spilocuscus*) *maculatus;* **E, F,** *Phalanger gymnotis*. A, C, E, tympanic face; B, D, F, cerebellar face. Abbreviations: hF, hiatus Fallopii; TNS, sulcus of the trigeminal nerve. Other abbreviations as for figure 2. Approximately 5× life size.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SIPS
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45% of the total length of the pars cochlearis, compared with 30% in *Ailurops* and the phalangerins). Further features, most notably the extensive expansion of the crista petrosa and the crista promontorii medioventralis, support a closer relationship between *Trichosurus* and *Wyulda* than between either of these taxa and *Strigocuscus*. All three show a more simply built promontorium than that of the phalangerins. In the latter group, a deeply grooved sulcus of the inferior petrosal sinus separates the rostral tympanic process and crista promontorii medioventralis, while the sulcus of the facial nerve cuts deeply into the pars cochlearis anteroventral to the hiatus Fallopii. These two features greatly increase the structural complexity of the promontorium in phalangerins and cause a marked discontinuity between the promontorium and the rest of the pars cochlearis from both cerebellar and tympanic aspects, which is absent in the trichosurins. Finally, while the anteroposterior proportions of both the subarcuate fossa and the internal auditory meatus are fairly consistent across all phalangerid taxa, the dorsoventral axis for the two openings shows consistent differences when the trichosurins are compared to the phalangerins. The subarcuate fossa accounts for around 70% of the dorsoventral axis of the periotic, compared with 55% in the phalangerins, and appears much larger. By contrast, the equivalent axis for the internal auditory meatus in trichosurins accounts for only 50% of the height of the pars cochlearis, compared to 75% in phalangerins, and appears much smaller. These results appear to solidify the relationship between *Trichosurus*, *Wyulda*, and *S. celebensis*, showing that the latter species is definitely a trichosurin, rather than a phalangerin or the sister group of a trichosurin + phalangerin clade.

One aim of this study was to see what light, if any, the periotics of the modern trichosurin genera could throw on the radiation of phalangerid marsupials in the Tertiary. Two phalangerid species were described by Flannery and Archer (1987) from the Miocene of Riversleigh and assigned to the modern genera *Strigocuscus* and *Trichosurus*. A preliminary look at their associated periotics suggests that these species are more closely related to each other than to either of the modern genera. The distinctive morphology of Miocene phalangerids will be looked at in a separate paper (K.C. in prep.), but a general comparison of the various specimens of periotic from Tertiary phalangerid species with those of modern trichosurins follows.

Periotic morphology of Riversleigh specimens shows more similarities to trichosurins than to phalangerins. Like trichosurins, Riversleigh specimens have an elongate promontorium, small internal auditory meatus, and a large epitympanic recess (fig. 5). However, there are also some striking differences. The Riversleigh specimens lack the expanded crista petrosa that is seen in the trichosurins, and although the crista promontorii medioventralis is expanded ventrally, the space bounded by the edge of the crista, the rostral tympanic process, and the cupula cochleae is concave, rather than smoothly sloping as in the trichosurins. This morphology of the pars cochlearis is also seen in a number of other diprotodontian groups, including pseudocheirids and potoroids and, although absent from the ailuropine petrosal (Norris, 1994), it may be plesiomorphic within phalangerids. All Riversleigh phalangerid taxa show a distinctive discontinuity across the cerebellar face of the periotic formed by the sulcus of the inferior petrosal sinus. This is also seen in *Wyulda*. Unlike *Wyulda*, the Riversleigh periotics are all delicate rather than robust. The promontorium is also quite curved rostrally when compared to the modern trichosurins.

Other features of the periotic in the trichosurins are harder to apportion to individual clades and seem likely to be autapomorphic for the taxa concerned. Most notable here is the shape of the pars cochlearis: slender and elongate in *Strigocuscus*, broad and stocky in

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Fig. 5. Periotics of extinct phalangerids. **A, B,** *Trichosurus dicksoni*. **C, D,** *Strigocuscus reidi*. **E, F,** DSS 23338. A, C, E, tympanic face; B, D, F, cerebellar face. Abbreviations: SMN, stylomastoid notch. Other abbreviations as for figure 2. Approximately 5× life size.

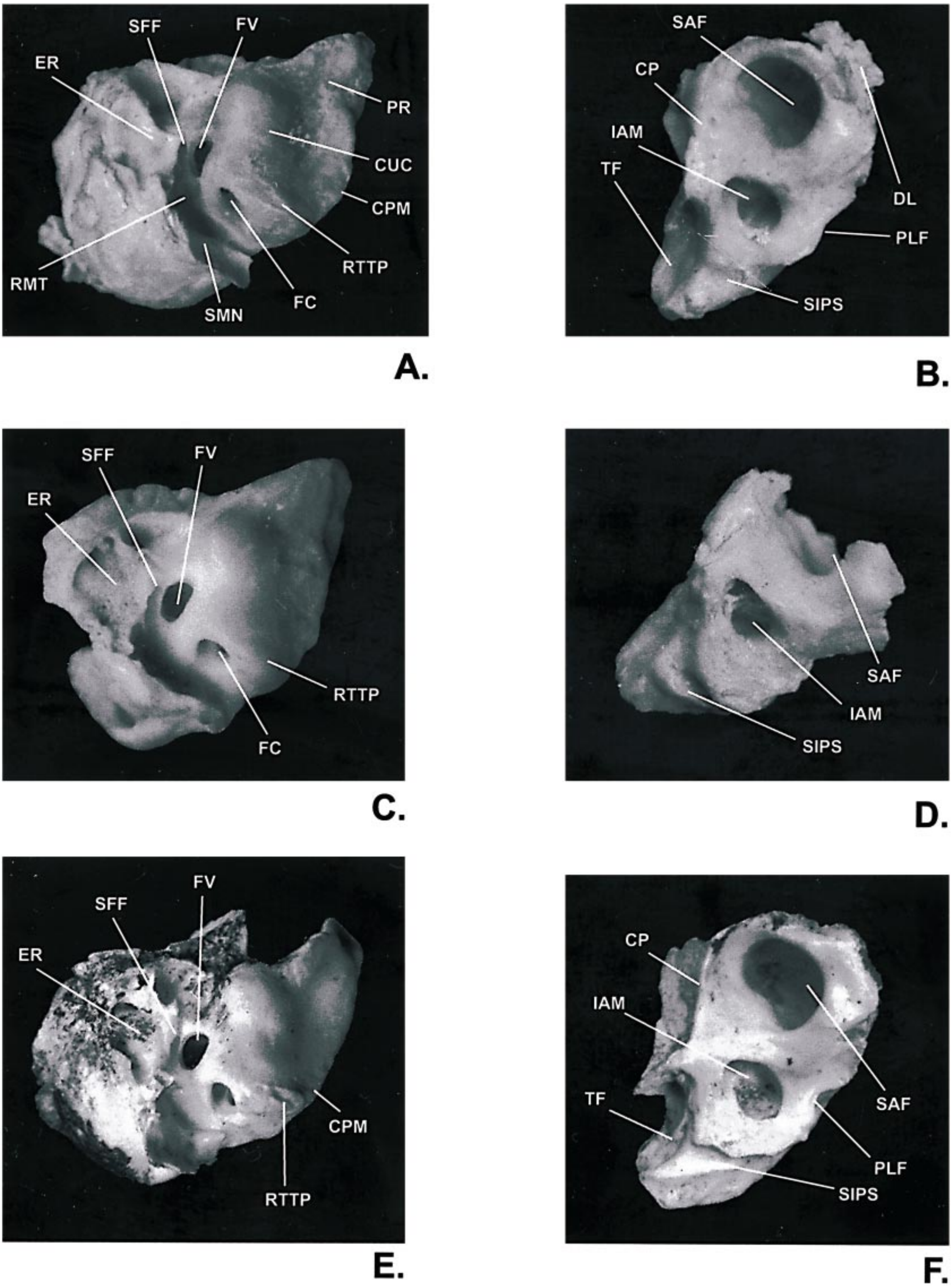
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TABLE 3

Synapomorphies of the Trichosurini (sensu Flannery et al., 1987)

Synapomorphies of the Trichosurini

1. Lacrimal retracted from the face and barely extends beyond the orbital rim.
2. The rostrum is relatively narrowed.
3. The ventral rim of the orbit overhangs the cheektooth row such that when viewed from below, the rim of the orbit is clearly visible.
4. The ectotympanic is almost totally excluded from the anterior face of the postglenoid process (this character may be partly ontogenetic).
5. The P3 is set at a more oblique angle relative to the molar row (the obliqueness of the P3 is quite variable within the genus *Phalanger*).

Synapomorphies of *Trichosurus* + *Wyulda*

1. The metaconid of the m1 is posteriorly displaced and the protoconid-metaconid crest is lengthened.
2. The alisphenoid extends far posteriorly on the basicranium.
3. The ventral portion of the periotic is extremely elongate.
4. The squamosal overlaps the anterior part of the ectotympanic.
5. The squamosal forms the medial side of the hypotympanic sinus.
6. The hypotympanic sinus is expanded, and the lamina of the bone medial to the glenoid fossa is more vertically oriented.
7. The midlink of the upper molars and the cristid obliqua of the lower molars are extremely well developed and are not interrupted by a fissure at their lowest point.
8. The striated pads of the plantar surface of the pes are separated into hallucal, digital, and marginal pads.

Synapomorphies of the Phalangerini

1. M1 preprotocrista does not contact the parastyle.
2. Crenulated molars.
3. Expanded caudal rim of the subarcuate fossa.
4. Short pars cochlearis (i.e., short between internal auditory meatus and tip of promontorium).
5. Recessus mesotympanicus curved.
6. Ectotympanic recess medium in size.
7. Surface of the pars cochlearis (tympanic face) bulges.
8. Incudal fossa enclosed by crista Fascialis petrosi.
9. Sigmoid sinus runs lateral to the margin of the subarcuate fossa.
10. Crista promontorii medioventralis short (also seen in some Riversleigh taxa).

Wyulda, or with a prominent, ventrally directed "blade" in *Trichosurus*.

Although a broader examination of craniodental morphology in the Trichosurini is outside the scope of this particular study (but is the subject of ongoing work by K.C.), it is worth making a brief overview of the situation in order to put the anatomy of the periotic into a wider context. Flannery et al. (1987) listed a set of five synapomorphies defining the tribe Trichosurini and a further eight defining the clade *Trichosurus* + *Wyulda* (table 3). Subsequent investigation by a number of authors (Springer et al., 1990; Norris, 1992, 1994; Hamilton and Springer, 1999), drawing on both molecular and morphological evidence, has led to a number of these characters being discarded as cases of homoplasy between the trichosurins and certain members of the phalangerin radiation, but have also produced new characters, most notably in the otic region. A revised list of diagnostic characters for the Trichosurini is given in table 4. When combined with the results of our study of periotic anatomy, we think that this character set provides a sufficient basis for support of a monophyletic Trichosurini including *S. celebensis*.

One outstanding issue concerning the Trichosurini is the phylogenetic position of *Phalanger pelengensis*, which is still uncertain. This species was originally considered a subspecies of *Strigocuscus celebensis* (Tate, 1945). Flannery et al.. (1987) suggested that the species might be a plesiomorphic sister taxon to both *Phalanger* and *Spilocus-*

TABLE 4

Revised Diagnostic Characters of the Tribe Trichosaurini

Trichosurini and Riversleigh characters

1. Lacrimal retracted from the face, and barely extends beyond the orbital rim.
2. The rostrum is relatively narrowed.
3. The ventral rim of the orbit overhangs the cheektooth row such that when viewed from below, the rim of the orbit is clearly visible.
4. Very large epitympanic recess.
5. Small internal auditory meatus.

Trichosurini (excluding Riversleigh)

1. The striated pads of the plantar surface of the pes are separated into hallucal, digital, and marginal pads (see Bensley, 1903; Flannery, 1994).
2. Notch in the subarcuate fossa.
3. The promontorium is extremely elongate.
4. Expanded crista petrosa.

Trichosurus and *Wyulda*

1. The metaconid of the m1 is posteriorly displaced and the protoconid-metaconid crest is lengthened.
2. The alisphenoid extends far posteriorly on the basicranium.
3. The ventral portion of the periotic is extremely elongate.
4. The squamosal overlaps the anterior part of the ectotympanic.
5. The squamosal forms the medial side of the hypotympanic sinus.
6. The hypotympanic sinus is expanded, and the lamina of the bone medial to the glenoid fossa is more vertically oriented.
7. The midlink of the upper molars and the cristid obliqua of the lower molars are extremely well developed and are not interrupted by a fissure at their lowest point.
8. Development of the diastema between I3 and C1.
9. Extremely expanded crista petrosa.

cus, but left the species as ‘‘*Phalanger*’’. George (1987) also kept *P. pelengensis* in *Phalanger* rather than following *S. celebensis* to *Strigocuscus*. Groves (1987) maintained the close relationship with *S. celebensis*, but kept both in *Phalanger*. Flannery (1994, 1995) also maintained this relationship, but used the genus *Strigocuscus*. However, preliminary study of skull morphology by the authors suggests that, despite the outward similarity of these species, the skull of *Phalanger pelengensis* is much more similar to phalangerins than to trichosurins (including *S. celebensis*): the periotic of *P. pelengensis* lacks the elongate promontorium and expanded crista petrosa seen in the trichosurin possums; there is no I3-C1 diastema; the ventral surface of the orbits shows only a limited overhang of the cheek tooth row; and the molars are slightly crenulate. It is possible that the taxonomic affinities of this species may lie with the endemic cuscuses of the neighboring Moluccan archipelago, *P. alexandrae*, *P. ornatus*, and *P. rothschildi*: this hypothesis is still under study, and will be explored in detail in a future paper (Crosby and Norris, in prep.).

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