EXTENDED REPORT

The unique paired retinal vascular pattern in marsupials: structural, functional and evolutionary perspectives based on observations in a range of species

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Background: In the few marsupial species studied to date that possess a retinal vasculature, the arterial and venous segments, down to the smallest calibre capillaries, have been shown to occur in pairs. It is a pattern seen in the marsupial central nervous system (CNS) but not in other tissues in this group or in any tissues in eutherian mammals. The aim of the present study was to investigate the presence of retinal vessels in a range of non-eutherian mammalian species (marsupials and monotremes) and to determine if the pattern of paired vessels was a widespread phenomenon within this animal group.

Methods: Species studied included a monotreme, the short-billed echidna (*Tachyglossus aculeatus*) and a range of Australian marsupials, the honey possum (*Taripedidae rostratus*), fat-tailed dunnart (*Sminthopsis crassicaudata*), grey-bellied dunnart (*Sminthopsis griseoventer*), numbat (*Myrmecobius fasciatus*), broad-footed marsupial mouse (*Antechinus godmani*) and the North American opossum (*Didelphis virginiana*). Eyes were fixed in glutaraldehyde or paraformaldehyde and retinas were embedded in resin for light and electron microscopic analysis.

Results: Examination revealed that in those species with retinal vessels (fat-tailed dunnart, grey-bellied dunnart, numbat, marsupial mouse, North American opossum) the pattern of vessels differs from the conventional plexus-like arrangement of mammalian retinal vasculature (that is, anastomotic networks of capillaries between arterioles and venules). In marsupials retinal vessels always occur in closely related pairs, with the arteriolar limb usually situated on the vitread aspect. Vessels penetrate the retina and branch to form layers of paired capillaries as far as the outer nuclear layer in some species. The capillaries form blind-ended hairpin loops and display classical morphological features of CNS capillaries.

Conclusion: The phylogenetic relations of this vascular pattern in the marsupial CNS and retina, and in the CNS of a few other classes of non-mammalian vertebrates, suggest that retinal vascularisation may have evolved independently in marsupial and eutherian mammals and that the former may have evolved from a common primitive mammal-like reptilian ancestor which possessed paired vasculature in the CNS. Eutherian mammals may have evolved from an ancestor with anastomotic networks in the CNS or this pattern may have evolved later in eutherian mammal evolutionary radiation. The possible functional and physiological significance of the paired vessels is discussed.

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As blood vessels enter the parenchyma of the central nervous system (CNS) of marsupials they do so in distinctive pairs consisting of an artery and a corresponding vein which branch in unison down to, and including, the finest capillaries until the arterial and venous components of each limb unite forming a terminal arteriovenous hairpin capillary or end loop.^{1–4} The zones of CNS parenchyma supplied by such vascular units overlap little or not at all with neighbouring units and therefore all blood vessels in the marsupial CNS function as true end-arteries.⁵ This differs from the conventional capillary anastomotic networks seen in most other tissues in marsupials and all tissues in eutherian mammals and monotremes.^{3–5}

In some non-mammalian vertebrates, the retina in addition to receiving nourishment from the choroidal vascular bed may also be supplemented by a range of extraretinal or intravitreal vascular structures such as the hyaloid system in amphibians, the pecten in birds or the conus in reptiles.^{6–8} In eutherian and non-eutherian mammals, the temporary hyaloid vasculature which nourishes the developing lens and retina is considered the ontogenic remnant of the intravitreal vascular structures of their non-mammalian ancestors. In adult eutherian mammals (all mammals except monotremes and marsupials) that have evolved more complex retinas and visual function the demand

for additional supplementary retinal nourishment has resulted in the evolution of true intraretinal vascular networks or retinal vessels such as those seen in humans.^{6–8} In non-eutherian mammals (monotremes and marsupials) both vascular (holangiogenic), partially vascularised (paurangiogenic) and avascular retinas are observed. The diprotodont group of marsupials (koala, wombats, possums, macropods (kangaroos, wallabies)) are generally described as possessing avascular retinas.⁸ The few marsupial species with a retinal vascular supply which have been studied^{3 9–11} belong to orders within the polyprotodont group. The intraretinal vessels in the few species studied to date have been described as being identical to the paired end artery vascular pattern found in the remainder of the marsupial CNS.^{2 3 9–11} Although these unusual paired retinal vessels were first described in the literature over 60 years ago, they have received little attention. Considering the efforts of so much research in the field of ophthalmology is aimed at understanding retinal vascular disease, it is surprising that such a radically different pattern of retinal vasculature has been so poorly described and is even less well understood. The aim of the present study was to provide an updated and more detailed

Abbreviation: CNS, central nervous system

Table 1 Summary of the species investigated in the present study

Species	Weight	Body length	Distribution	Habitat	Diet	Lifestyle	Vascularised retina	Paired vessels
Short-billed echidna (<i>Tachyglossus aculeatus</i>)*	2.5–6 kg	23–35 cm	Australia	Wide variety	Ants, termites, beetles	Nocturnal or diurnal to avoid extremes in heat or cold	No	
Honey possum (<i>Taripedidae rostratus</i>)†	5–10 g	6–8 cm	SW Australia	Heath land	Nectar and pollen	Crepuscular, but sometimes diurnal	No	
Fat-tailed dunnart (<i>Sminthopsis crassicaudata</i>)‡	10–20 g	6–9 cm	Australia	Open grasslands, arid deserts	Insects, invertebrates	Nocturnal/crepuscular	Yes	Yes
Grey-bellied dunnart (<i>Sminthopsis griseoventer</i>)‡	15–25 g	7–9.5 cm	Southwest of Western Australia	Dry arid environments	Insectivore/carnivore	Nocturnal	Yes	Yes
Numbat (<i>Myrmecobius fasciatus</i>)‡	300–715 g	20–27.5 cm	Endangered: restricted areas of SW of Western Australia	Eucalyptus forest	Termites	Diurnal	Yes	Yes
Broad-footed marsupial mouse or Atherton antechinus (<i>Antechinus godmani</i>)‡	55–125 g	9–15 cm	Restricted to a 130 km region of NE Queensland.	Rainforest	Carnivore	Nocturnal/crepuscular	Yes	Yes
North American opossum (<i>Didelphis virginiana</i>)§	2–6 kg	38–51 cm	North America	Woodlands	Omnivorous	Nocturnal	Yes	Yes

Sizes, weight, distribution, habitat and lifestyle based on Menkhorst & Knight.²⁸

*Tissue provided by Dr Adam Lockett, University of Adelaide.

†Tissue provided by Professor Sarah Dunlop, School of Animal Biology, University of Western Australia.

‡Tissue collected in collaboration with Dr Ken Richardson, School of Veterinary Sciences, Murdoch University, WA.

§Tissue collected by Professor William Krause, University of Columbia Missouri, USA.

description of this unusual form of retinal vascularisation in a range of previously undocumented or poorly documented species of non-eutherian mammals. The evolution and functional significance of this pattern of vasculature is discussed.

MATERIALS AND METHODS

Tissues from one monotreme (short-billed echidna, *Tachyglossus aculeatus*) and a range of marsupials were investigated (see table 1). All ocular tissues were collected from animals sacrificed as part of other investigations which conformed to institutional animal ethics committees and wildlife authority regulations. Tissues were fixed in glutaraldehyde or paraformaldehyde. Posterior segments or whole globes were processed and embedded in either Epon or Araldite resin in the standard fashion. Semithin sections (1–2 µm) were stained with toluidine blue. Ultrathin sections (50–70 nm) of selected regions were stained with uranyl acetate and lead citrate and examined using a Philips 410 transmission electron microscope. The methods of investigating the pattern of retinal vessels in *Didelphis virginiana* using vascular filling and wholemount preparations have previously been described.¹⁰ It was not possible to perform vascular filling experiments in the other species due to limited availability and access to live specimens.

RESULTS

Intraretinal vessels were present in both species of dunnart, the numbat, the marsupial mouse (or Atherton antechinus) and North American opossum (table 1). The echidna and honey possum did not possess intraretinal vessels (fig 1). Fundus or fluorescein examinations were not performed on these latter two species therefore it was not possible to determine whether there were any vessels at the optic nerve head resembling a conus, a feature which has been described in some other marsupial species (table 2).⁹

Morphological features of the echidna eye, which were reptilian in character included an avascular rod-dominated retina (fig 1A), a keratinised corneal epithelium, an iris sphincter but no dilator or ciliary muscle, and cartilage plates within the sclera similar to that seen in reptiles and birds.²¹ A number of large calibre irregular-shaped vessels with no

Figure 1 (A) Semithin section of the avascular retina of the short-billed echidna (inset). Note the choriocapillaris, which is artefactually separated from Bruch's membrane, consists of wide calibre capillaries within a lightly pigmented choroid. (B) Avascular retina of the honey possum (inset). Note the heavily pigmented choroid and the cones and oil droplets within the retina. (Inset courtesy of Dr Jenny Rodger.)

Table 2 Summary of the presence of double intraretinal vessels in monotremes and marsupials studied to date

Classification	Intraretinal vasculature	Extraretinal vasculature	Reference
Class Mammalia			
Subclass Prototheria (monotremes)			
Family Tachyglossidae			
<i>Tachyglossus aculeatus</i> (echidna)	No	?	Present study
Subclass Marsupialia (marsupials)			
Order Dasyuromorphia (carnivorous marsupials)			
Family Thylacinidae (Thylacine)			
<i>Thylacine cynocephalus</i> (Tasmanian tiger)*	Yes	No	6 13 14
Family Dasyuridae (dasyurids)			
<i>Antechinus godmani</i> (broad-footed marsupial mouse or Atherton antechinus)	Yes	?	Present study
<i>Dasyurus viverrinus</i> (Eastern quoll)	Yes	?	9 15 16
<i>Sacrophilus harrisi</i> (Tasmanian devil)	Yes	No	9 16 17
<i>Sminthopsis crassicaudata</i> (fat-tailed Dunnart)	Yes	?	11; Present study
<i>Sminthopsis griseoventer</i> (grey-bellied Dunnart)	Yes	?	Present study
Family Myrmecobiidae (numbats)			
<i>Myrmecobius fasciatus</i> (numbat)	Yes	?	Present study
Order Didelphimorphia (American marsupials)			
Family Didelphidae			
<i>Didelphis virginiana</i> (North American opossum)	Yes	No	10 18
<i>Marmosa mexicana</i> (Mexican mouse opossum)	Yes	No	6 18
Order Peramelemorphia (bandicoots and bilbies)			
Family Peramelidae (bandicoots)			
<i>Isodon macrourus</i> (Northern brown bandicoot)	No	Yes	19
<i>Isodon obesulus</i> (Southern brown bandicoot)	No	Yes	17 19
<i>Macrotis lagotis</i> (Bilby)	No	Yes	17 19
Order Diprotodontia (kaola, wombats, possums, macropods)			
Family Phalangeridae (brush-tail possums, cuscuses, scaly-tailed possum)			
<i>Trichosurus vulpecula</i> (common brush-tailed possum)	No	Yes	9
Family Tarsipedidae (honey possum)			
<i>Tarsipes rostratus</i> (honey possum)	No	?	Present study
Family Petauridae (striped possum, leadbeaters possum, wrist-winged gliders)			
<i>Petaurus breviceps</i> (sugar glider)	No	?	9 17 20
Family Potoroidae (poteroos and bettongs)			
Family Macropodidae (kangaroos, wallabies, tree kangaroos)	No		16 17 20

*Now extinct.

supporting pericytes or intima or media were noted in the choroid of the echidna (not shown). Unlike other vessels whose lumina were clear as a consequence of the vascular perfusion, the lumina of the irregular vessels contained proteinaceous material. On the basis of the above features these vessels were identified as lymphatics which have so far not been described in the mammalian eye.

The distinctive features of the honey possum posterior segment included a heavily pigmented choroid and oil droplets in the cone-rich retina (fig 1B). The retinal thickness in the echidna and honey possum were approximately 110–125 µm.

The retinal vasculature in *Didelphis virginiana* (fig 2A) has been described in detail previously.¹⁰ Briefly, 8–10 large radially arranged pairs of retinal vessels emerge from the optic disc. Each artery is closely paired with a companion vein which usually lies directly beneath or sclerad relative to the artery and is partially obscured in whole mounts viewed from the vitread aspect (fig 2B), except near the optic disc where they may lie side by side for a short distance and also at the terminal capillary end loops where the paired nature of these vessels becomes evident (fig 2C).

Transverse semithin sections of the retina of adult North American opossum, numbat and both species of dunnart were characterised by the distinctive profiles of paired vessels of varying diameters (figs 2D, E, 3, 4) and for the purpose of brevity will be described together except where species-specific differences were noted. The larger retinal vessels in North American opossum (*Didelphis virginiana*) produce prominent elevations on the retinal surface, however in the numbat (*Myrmecobius fasciatus*) (fig 3A) larger calibre vessels were more deeply located in the nerve fibre and ganglion cell layer (fig 3B, C). These larger retinal arteries demonstrated some unchar-

acteristic lamination of the elastic layer or basal lamina of the tunica media (fig 3B, C), a feature not usually present in normal retinal vessels in placental mammals. Vessels penetrating into the depths of the retina only rarely appear in transverse sections but are more apparent in oblique sections (figs 3D, 4C). Paired retinal vessels branch repeatedly as they penetrate from the vitread to the sclerad aspect of the retina (fig 4A–C) and terminate in small capillaries which form hairpin end loops where the arterial and venous limbs become continuous (figs 2C, 4B–D). Thus without exception in the marsupial species investigated which were found to possess retinal vessels, these vessels form a complete system of end vessels that lack anastomoses even at their small capillaries (fig 2B, C).

In whole mount preparations in *Didelphis* and in sections of all the species studied, several levels of capillaries were discernible in the retina (figs 3B, 4A, B, E): one layer in the nerve fibre layer or ganglion cells layer (fig 4A, C, E) and one in the inner plexiform or inner nuclear layer (figs 2, 3, 4B). In *Didelphis*, a distinctive deeper layer is present within the outer nuclear layer extending almost as far as the external limiting membrane layer (fig 2E). In most other species, at each of these levels, the capillaries run parallel to the retinal surface and appear most frequently as paired ovoid/circular profiles (figs 2D, 3E, 4A, B, E). In the grey-bellied dunnart (*Sminthopsis griseoventer*) material examined paired vessels did not penetrate beyond the nerve fibre and ganglion cell layer (fig 4E).

In transverse sections of the species found to have paired vessels, the arterial and venous limbs of the closely apposed capillaries are indistinguishable, each being lined by a continuous thin endothelium and each surrounded by its own distinct basal lamina (fig 2E). In oblique sections, the hairpin loops themselves were occasionally identified (fig 4E). The

Figure 2 (A) Adult and juvenile North American opossums (*Didelphis virginiana*). The retina of this species as seen in whole mounts of carbon filled vascular preparations (B, C), in semithin section (D) and in transmission electron microscopy (E). In B and C, note the branching pattern of one of the eight pairs of retinal vessels, which at low magnification could be mistaken for just one vessel. Higher magnification at the level of the capillaries however reveals that each profile is in fact a pair of vessels whose capillaries terminate in blind-ended loops (C). Note the lack of anastomosis between each set of paired vessels. On transverse section (D, E) the paired capillaries (empty due to cardiac perfusion during fixation) are highly distinctive features of this marsupial retina. Note the proximity of the deeper capillaries to the outer limiting membrane, a feature noted in *Didelphis* but not in other marsupials. Note the tapetum in this species is located within the retinal pigment epithelium, an unusual feature in mammals. (Fig 2A courtesy of Professor Bill Krause.)

retinal vascular endothelial cells are of normal non-fenestrated retinal type with overlapping or mortise cell-cell contact and tight junctions (fig 2E). Numerous pericytes are associated with the paired capillaries but are unusual in that the nuclei are observed most frequently interposed between the two limbs of capillary loops and seldom in other regions of the capillary circumference (figs 2D, 2E, 3E, 4E). The ocular tissue from broad-footed marsupial mouse was poorly fixed and although allowed confirmation of the double vessel pattern did not permit more detailed morphological examination. A summary of the species investigated including their size, distribution, lifestyle, diet and habitat included in table 1.

Vessels of the choroid, as well as those found in other regions of the eye, in all the species examined do not form paired end-loops, but rather form more conventional anastomosing capillary networks or large venous sinuses.

DISCUSSION

Structural and functional considerations

Since the early histological reports of the unusual form of paired vessels in the retina of marsupials^{3 18} little attention has been paid to the structure, function and evolutionary signifi-

cance of this arrangement and whether it is a widespread phenomenon in marsupials. In light of the dearth of information on the vasculature of the marsupial eye, the present study aimed to survey the structure of the retina and supporting tissues in several species of marsupials and one monotreme (short-billed echidna). The investigation revealed that the retinas of the insectivorous short-billed echidna (*Tachyglossus aculeatus*) and nectivorous honey possum (*Taripedidae rostratus*), both of which feed in daylight possess avascular retinas. Intraretinal vessels were present in the fat-tailed dunnart (*Sminthopsis crassicaudata*), grey-bellied dunnart (*Sminthopsis griseoventer*), numbat (*Myrmecobius fasciatus*) and broad-footed marsupial mouse (*Antechinus godmani*) which all belong to orders in the polyprotodont group (that is, orders other than the diprotodontia; table 2). Most of the species predominantly feed at dusk or dawn or are completely nocturnal with the exception of the numbat (table 1). The thickness of the retina in those species possessing retinal vessels in the present study was over 143 μm , the value calculated to be the maximum thickness for avascular retinas which is a function of the diffusion characteristics of oxygen from the choroidal circulation to the retina.^{8 22} Those species with intraretinal vasculature demon-

Figure 3 (A) Adult numbat (*Myrmecobius fasciatus*), (B–E), semithin sections from the retina of this species. (B) Low magnification to show the entire neural retina (detached from retinal pigment epithelium) reveals a pair of large calibre vessels, which at higher magnification in a closely adjacent section (C) is seen to consist of an artery [A] on the vitread aspect a vein [V]. Note the large numbers of layers of smooth muscle cells in the artery wall with intervening layers of elastic lamina or basal lamina (arrow). (D) Note paired vessels penetrating through the retinal layers as longitudinal profiles. (E) In transverse section these deep small calibre paired capillaries are seen to share pericytes (arrows). (Fig A courtesy of Tourism Western Australia.)

strated a pattern of vessels vastly different from the conventional plexus-like arrangement of holangiotic retinas seen in eutherian mammals, such as humans, where there are extensive networks of anastomotic capillaries between arterioles and venules. In marsupials the arteriolar limb and venous limb always occur in closely related pairs, with the former usually situated on the vitread aspect. Vessels penetrate the depths of the retina in this paired arrangement and branch to form layers of paired capillaries which finally terminate in hairpin end loops. The paired units rarely if ever overlap the area supplied by adjacent vascular pairs. These observations confirm and extend the initial observations of Wislocki³ and a limited number of other investigators.^{10–11}

The similarity in the pattern of paired vessels to those in the brain and their shared structural characteristics is not surprising considering the embryological link between the eye and the brain.²³ Experimentally induced emboli in the marsupial brain result in well-circumscribed ischaemic zones which reflect the territory of individual capillary loops.⁵ Thus marsupial CNS capillaries are end arteries both anatomically and functionally, whereas in eutherian mammals although anastomoses exist in the capillary bed of the CNS they are still considered functionally (as are retinal vessels) to be end arteries. Various theories have been proposed to explain the possible functional and physiological basis for this unusual paired vascular pattern in the marsupial brain and retina. Possibilities include a

countercurrent exchange system for thermoregulation or as a means of optimising retinal oxygen tensions.^{18–24} It has also been speculated that the paired arrangement may serve to conserve space occupied in the retina by vessels and thus minimise their interference with visual acuity, which seems unlikely because when viewed from the vitread aspect they create a similar profile to the vessels of eutherian holangiotic retinas.

More recently, on the basis of studies of retinal development in the fat-tailed dunnart Rodger and co-workers¹¹ have proposed the paired vascular pattern may simply be related to the precocious development of marsupials which are required to interact—independent of maternal physiological support—with their environment much earlier than placental mammals. These authors demonstrated that retinal vessels in the dunnart develop as paired end artery loops that are patent “ab initio” and therefore can meet the immediate metabolic demands of the functional developing retina. In contrast to the events during retinal development in placental mammals the developing vasculature of marsupials does not have to undergo remodelling to become functionally patent.¹¹ Thus a vasculature that functions as it grows would allow a young marsupial brain to regulate breathing, locomotion and navigate via olfaction to reach the pouch where it must suckle. This is a more attractive hypothesis than the previously discussed thermoregulation or space-conserving theories.

Figure 4 Paired vessels in the retina of the fat-tailed dunnart (inset, A) (A–D) and grey-bellied dunnart (E). Note the highly vascular nature of the retina in the fat-tailed dunnart with numerous vessels clearly visible penetrating as far as the outer plexiform layer (A, B). Note large superficial vessels branching in pairs (C) and the profile of an individual capillary terminal loop (D, arrow). Note the unusual large calibre venous sinuses in the choroid of this species (A, arrow). In the grey-bellied dunnart paired vessels were restricted to the nerve fibre layer and ganglion cell layer (E).

Evolutionary perspective

The unusual paired vessels as seen in marsupial CNS tissue, including the retina, are present in the CNS of a few invertebrates including earthworms,²⁵ lampreys but not other cyclostomes such as hagfish,¹² almost no fish except possibly lungfish, a limited number of amphibians (newts, salamanders) and in a few reptiles including some lizards and sphenedon.^{12 26 27} Interestingly, some reptiles appear to have a mixture of paired vessels and anastomotic networks or intermediate forms in their CNS.²⁴ Paired vessels are not however present in the CNS of any birds, monotremes or eutherian mammals. This pattern of occurrence in the non-vertebrates and non-mammalian vertebrates suggests that one vascular pattern has evolved from the other several times in evolution.²⁴

What does the presence of double vessels in the various marsupials tell us about their evolution? The mammalia include three major subclasses, the monotremes (Prototheria), marsupials (Marsupialia) and placental (Eutheria) mammals. Approximately 180 million years ago Pangea, the last supercontinent, began

separating into two landmasses, Laurasia and Gondwanaland. That separation coincided with the last common ancestor of the mammalian clades (clade: a lineage of animals with a common genealogy). Continental drift would eventually isolate marsupials to Gondwanaland, especially Australia, Antarctica and South America. Once isolated on South America and Australia, around 30 million years ago by the submersion of the last dry land bridges linking Antarctica to Tasmania, monotremes and particularly marsupials continued to radiate and evolve into several different orders.²⁸ Seven such orders are extant, three found in the new world: Didelphimorphia (common opossums); Microbiotheria (only one extant representative, the Monito del Monte ("little mountain monkey", *Dromiciops gliroides*)), and Paucituberculata (shrew opossums). Four orders exist in Australia: the Dasyuromorphia (carnivorous marsupials such as dasyurids—for example, quolls, dunnarts, Tasmanian devils, and numbats), the Peramelemorphia (bandicoots and bilbies), the Notoryctemorphia (marsupial voles) and lastly Diprotodontia (koala, wombats, possums and macropods (kangaroos and wallabies)).²⁸

Having inherited the double vessel pattern in the CNS from an early marsupial ancestor this pattern has been retained in all subsequent marsupial descendants. In marsupials that radiated into different niches and developed increasingly complex visual functions requiring a separate intraretinal vasculature, those vessels developed as paired vessels.^{10 11} Thus, meeting the functional needs of a more metabolically demanding inner retina with a true intraretinal plexus, rather than intravitreal vessels, such as a conus or pecten found in reptiles and birds, has led to the evolution of retinal blood vessels within marsupials in an almost identical manner to that which evolved independently in eutherian mammals. This illustrates that the imperative for such vascularisation was not a unique feature of eutherian mammal evolution. The evolution of intraretinal vessels is considered a more recent evolutionary adaptation associated with the radiation of mammal groups, including primates.⁸ To the author's knowledge, paired intraretinal vessels are present only in Dasyuromorphia and Didelphimorphia (table 2). A large number of Australasian marsupials belonging to the order Diprotodontia, which includes kangaroos, wombats, the koala and most possums, have avascular retinas^{16 17 20} and are believed to have evolved from the didelphid-dasyurid clade.²⁹ This would suggest that retinal vessels may have been lost during the evolution of the diprotodonts as well as the bandicoots. The latter group, despite being classified with the polyprotodonts, lack true vascular retinas and instead exhibit a conus-like vascular structure in the vitreous.¹⁹

In summary, regardless of whether marsupials independently evolved the paired end artery system in the CNS or have retained it from a primitive ancestral line, it is clear that marsupial groups that evolved higher visual functional requirements, and therefore required supplementary retinal nutrition, were destined to develop paired vessels typical of the remaining marsupial CNS.

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REFERENCES

- 1 **Wislocki GB**, Campbell ACP. The unusual manner of vascularization of the brain of the opossum (*Didelphis virginiana*). *Anat Rec* 1937;**67**:177–91.
- 2 **Craigie EH**. The blood vessels in the central nervous system of the kangaroo. *Science* 1938a;**88**:359–60.
- 3 **Wislocki GB**. Peculiarities of the cerebral blood vessels of the opossum: diencephalon, area postrema and retina. *Anat Rec* 1940;**78**:119–31.
- 4 **Sunderland S**. The vascular pattern in the central nervous system of the monotremes and Australian marsupials. *J Comp Neurol* 1941;**75**:123–9.
- 5 **Scharrer E**. The functional significance of the capillary bed in the brain of the opossum. *Anat Rec* 1939;**75**:319–40.
- 6 **Walls GL**. *The vertebrate eye and its adaptive radiation*. Cranbrook Institute of Science, Bloomfield Hills, Hafner, New York, 1942 (reprinted in 1967).
- 7 **Duke-Elder S**. The eye in evolution. In: *System of ophthalmology*. London: Henry Kimpton, 1958:438–41.
- 8 **Chase J**. The evolution of retinal vascularization in mammals: a comparison of vascular and avascular retinæ. *Ophthalmology* 1982;**89**:1518–25.
- 9 **Buttery RG**, Haight JR, Bell K. Vascular and avascular retinæ in mammals. A fundusoscopic and fluorescein angiographic study. *Brain Behav Evol* 1990;**35**:156–75.
- 10 **McMenamin PG**, Krause WJ. Ultrastructural observations on the unique paired capillaries of the opossum retina. *Cell and Tissue Research* 1993;**271**:461–8.
- 11 **Rodger J**, Dunlop SA, Beaver R, et al. The development and mature organization of the end-artery retinal vasculature in a marsupial, the dunnart *Sminthopsis crassicaudata*. *Vision Research* 2001;**41**:13–21.
- 12 **Craigie EH**. The comparative anatomy and embryology of the capillary bed of the central nervous system. *Res Publ Ass Nerv Ment Dis* 1938b;**18**:3–28.
- 13 **Franz V**. *Lehrbuch der vergleichenden mikroskopischen Anatomie der Wirbeltiere*. Jena: Schorpan Verlag, 1913.
- 14 **Franz V**. Anatomie des Wirbeltierauges. In: *Hanbuch der vergleichenden anatomie der wirbeltiere*, Bd 2 Abt 3, Kap 1. Berlin u Wien: Urban u Schwarzenberg, 1934.
- 15 **O'Day K**. The retina of the Australian marsupial. *Med J Australia* 1938;**1**:326–8.
- 16 **Tancred E**. The number and distribution of ganglion cells in the retinas of five Australian marsupials. *J Comp Neurol* 1981;**196**:585–603.
- 17 **Johnson GL**. Contributions to the comparative anatomy of the mammalian eye, chiefly based on ophthalmoscopic examination. *Phil Trans R Soc Lond B* 1901;**197**:1–82.
- 18 **Walls GL**. Notes on the retinæ of two opossum genera. *J Morph* 1939;**64**:67–87.
- 19 **Chase J**, Graydon ML. The eye of the northern brown bandicoot, *Isodon macrourus*. In: *Bandicoots and bilbies*. In: Seebeck JH, Brown PR, Wallis RL, Kemper CM, eds. Sydney, Australia: Surrey Beatty and Sons, 1990:117–22.
- 20 **Johnson GL**. Ophthalmoscopic studies on the eyes of mammals. *Phil Trans R Soc Lond B* 1968;**254**:207–20.
- 21 **Schwab I**, McMenamin PG. Echidna: How do eye fit in? *Tachyglossus aculeatus*. *Br J Ophthalmol* 2005;**89**:129–30.
- 22 **Dollery CT**, Bulpitt CJ, Kohner EM. Oxygen supply to the retina and choroidal circulation at normal and increased oxygen tensions. *Invest Ophthalmol* 1969;**8**:588–94.
- 23 **Forrester JV**, Dick A, McMenamin PG, et al. *The eye: basic sciences in practice*, Second edition. London: WB Saunders, 2002.
- 24 **Craigie EH**. The architecture of the cerebral capillary bed. *Biol Rev* 1945;**20**:133–46.
- 25 **Sharrer E**. The capillary bed of the central nervous system of certain invertebrates. *Biol Bull* 1944;**87**:52–58.
- 26 **Schöbl J**. Ueber eine eigenthümliche schleifenbildung der blutgefäße im gehirn und rückenmark der saurier. *Arch Mikr Anat*, Bd 1878;**15**:S60–63.
- 27 **Sterzi G**. Die blutgefäße des rückenmarks. Untersuchungen über ihre vergleichende anatomie und entwicklungsgeschichte. *Anat Hefte I Abt*, Bd 1904;**24**:S1–361.
- 28 **Menkhorst P**, Knight F. *A field guide to the mammals of Australia*. Oxford: Oxford University Press, 2004.
- 29 **Kirsch JAW**. The classification of marsupials, with special reference to karyotypes and serum proteins. In: Hunsker D, ed. *The biology of marsupials*. New York: Academic Press, 1977:1–50.

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