J. Anat. (1993) 182, pp. 187–195, with 16 figures Printed in Great Britain

Distribution of otic postganglionic and recurrent mandibular nerve fibres to the cavernous sinus plexus in monkeys

G. L. RUSKELL

Applied Vision Research Centre, Department of Optometry and Visual Science, City University, London, UK

(*Accepted 10 December 1992*)

ABSTRACT

The distribution of dorsal rami of the otic ganglion was traced on one or both sides of 1 rhesus and 15 cynomolgus monkeys using interrupted serial sections. From 15 to 24 fine rami containing unmyelinated and small myelinated nerve fibres entered the cranial cavity with the mandibular nerve through the foramen ovale. Most rami contributed to a plexus positioned in the crotch of the mandibular and maxillary nerves adjacent to the trigeminal ganglion. The plexus was augmented by an accessory otic ganglion. Rami then continued dorsally on each side of or through the maxillary nerve and joined the cavernous sinus plexus. The pathway described probably gives otic parasympathetic fibres access to the cerebral arteries and may share a wider distribution in common with other nerves contributing to the cavernous sinus plexus.

INTRODUCTION

Parasympathetic postganglionic fibres of the otic ganglion enter the auriculotemporal branch of the mandibular nerve and terminate in the parotid gland (Williams et al. 1989). Observations suggesting a wider distribution have been reported (Segade et al. 1987) but, until recently, substantive knowledge of other structures in receipt of terminals from the otic ganglion was lacking. For example, branches or rami are known to issue dorsally from the otic ganglion and these presumably do not distribute to the parotid gland. The dorsal rami are seldom described in human anatomical texts and atlases; Clara (1953) and Pernkopf's contribution to Ferner's atlas (1980) are exceptions. The omission may be attributable to an apparent inconstancy and disagreement regarding their distribution. Hovelacque (1927), in a summary of earlier work, referred to 2 dorsal branches, one penetrating the pterygoid canal to join the vidian nerve and the other joining the trigeminal ganglion. They were named the external and internal sphenoidal nerves. Rousset (1922) described only a posterior dorsal branch passing to the middle meningeal artery. Dorsal branches were identified in histological reconstructions of human embryonic tissue by Andres & Kautzky (1956), one passing medial to the trigeminal ganglion and joining a small ganglion in the cavernous sinus region, and another that joined the vidian nerve; the latter junction was inconstant. Dorsal rami were traced, by dissection, to the cavernous sinus in cats and pigs but not in dogs, goats, cattle or a horse (Ohkubo, 1979). They were regarded as sympathetic twigs conducting fibres from the internal carotid plexus to the otic ganglion. No other reference to the dorsal branches in animals could be found.

There is now little doubt that otic ganglion fibres are also distributed to the cerebral vasculature. Various markers applied to the middle cerebral artery were subsequently traced to the otic ganglion in cats (Walters et al. 1986) and rats (Edvinsson et al. 1989; Suzuki et al. 1988, 1990) and vasoactive intestinal polypeptide-containing perivascular nerve fibres of the major cerebral arteries were reduced in number following removal of the otic ganglion in dogs (Uemura et al. 1988). Surprisingly, a similar distribution in monkeys was not found (Hardebo et al. 1991).

While seeking evidence of sensory nerve access to the cerebral arteries in monkeys (Ruskell & Simons, 1987; Simons & Ruskell, 1988), fine nerves were noted passing to the cavernous sinus from a position below the maxillary nerve close to the trigeminal ganglion. Our practical knowledge of the distribution of

Correspondence to Professor G. L. Ruskell, Department of Optometry and Visual Science, City University, 311–321 Goswell Road, London EC1V 7DD, UK.

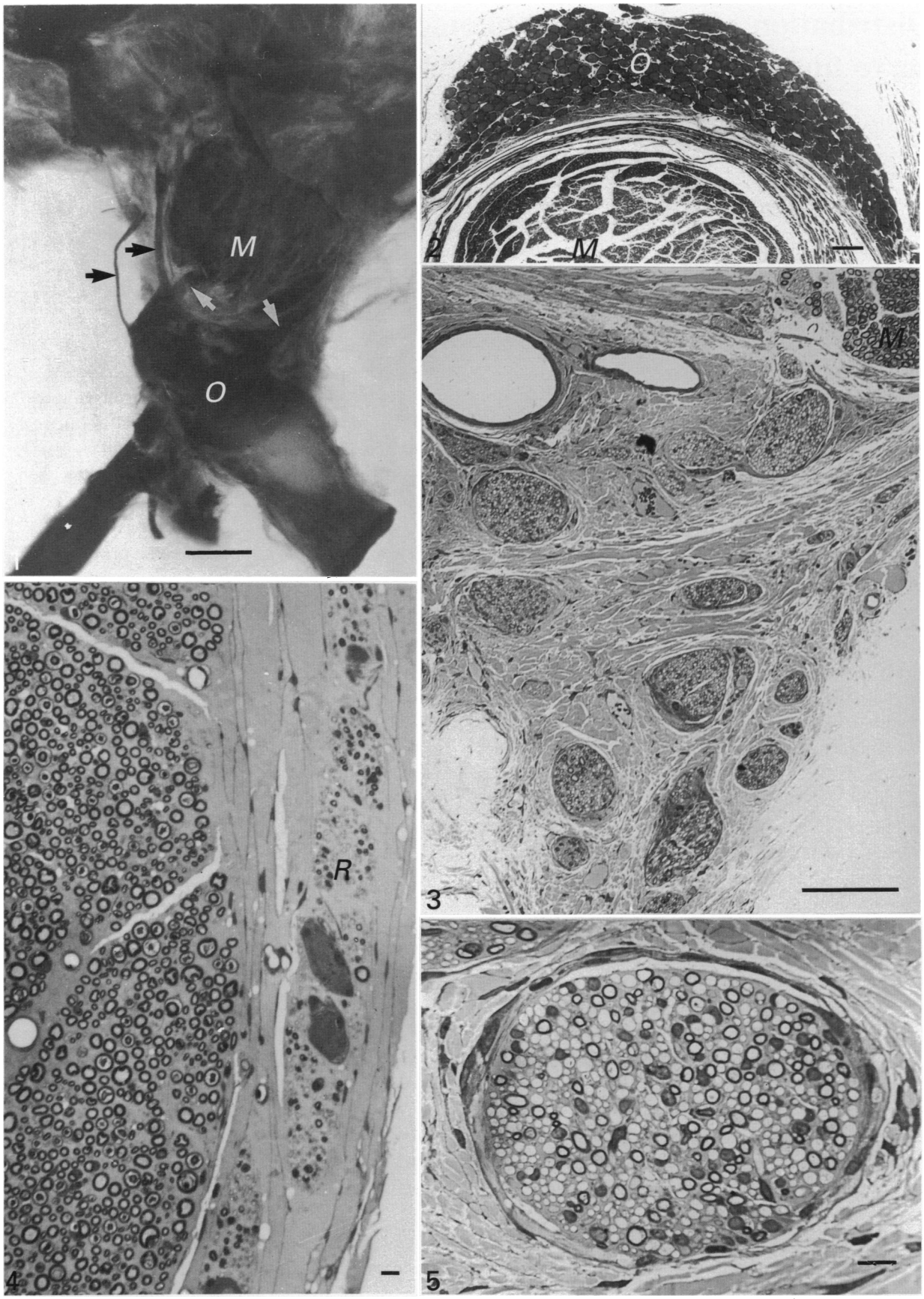

Fig. 1. Medial aspect of the mandibular nerve (*M*) from the right side dissected to reveal the otic ganglion (*O*) and several of its dorsal rami (arrows). The lesser petrosal nerve is not shown. Osmium tetroxide stained. Bar, 1 mm.

Fig. 2. Transverse section through the mandibular nerve (*M*) and the otic ganglion (*O*). Bar, 100 μm.

trigeminal and internal carotid nerve branches and branches from the pterygopalatine ganglion to the cavernous sinus (Ruskell, 1970) could not account for them. Their position pointed to the possibility that they issued from the otic ganglion, which is confirmed in the present study. Moreover, a distribution of trigeminal fibres to the cavernous sinus plexus in fine recurrent mandibular nerve branches was also revealed.

MATERIALS AND METHODS

One young adult rhesus (*Macaca rhesus*) and 15 cynomolgus (*Macaca fascicularis*) monkeys weighing from 3.2–4.1 kg were prepared for study. The rhesus and 9 of the cynomolgus monkeys were female. Fourteen of the animals had been used in experiments, reported earlier, involving unilateral nerve lesions (ophthalmic or maxillary neurotomy, or pterygopalatine ganglion lesion), and 2 were unoperated (Ruskell, 1970; Ruskell & Simons, 1987). All lesions were on the left side and only the right side of these animals was used in the present study; both sides of the unoperated animals were prepared. They were sedated with 2–3 mg kg^{-1} ketamine and anaesthetised with 15–25 mg kg^{-1} Sagatal (sodium pentabarbitone) given via a saphenous vein or intraperitoneally, and given an injection of the anticoagulant heparin sodium (1500 IU). The external jugular veins and the inferior vena cava were cut and 2% glutaraldehyde, 3% paraformaldehyde cacodylate-buffered solution (pH 7.4) was perfused through the left ventricle of the heart. The heads were stored in the fixative at approximately 4 °C and dissected while immersed in a buffered sucrose solution.

The cavernous sinus with its contents was removed in one piece with the trigeminal ganglion attached; the maxillary and mandibular nerves were cut close to the foramen rotundum and just below the otic ganglion respectively. In some preparations the posterior half of the trigeminal ganglion was discarded, and the cavernous sinus divided horizontally into upper and lower halves, and only the latter was used. The nerve of the pterygoid canal, severed at its point of entry into the canal, was retained in all specimens, and the lesser petrosal nerve retained in several of them. Care was taken to ensure that the tissues were free of bone fragments. Most preparations were photographed using a dissecting microscope, either before or after postfixation.

The tissues were postfixed in 1% unbuffered osmium tetroxide, dehydrated in graded solutions of ethanol, embedded in Araldite and sectioned using glass knives. Tissues were oriented to give transverse sections of the mandibular nerve or of the cavernous sinus. Sections (1 μm) were cut and stained with 1% toluidine blue in an equal volume of 2.5% sodium carbonate. The interval between collected sections varied from nil to 200 μm depending on the requirement to permit accurate tracking of nerve paths, which varied with location. Thin sections for electron microscopy of selected areas were prepared from some of the tissues using a diamond knife. They were mounted on unfilmed copper grids, immersed in a saturated solution of uranyl acetate in 70% ethanol for about 20 min, washed and immersed in 0.4% lead citrate in 0.1 N sodium hydroxide for about 15 min.

RESULTS

The following description applies equally to the cynomolgus monkeys and the single rhesus.

The otic ganglion straddled the mandibular nerve medially, about 3 mm below the foramen ovale. It was commonly shaped like a half or crescent moon with the points or horns directed dorsally (Fig. 1) and curved to conform to the shape of the mandibular nerve (Fig. 2). The cells were small (23.9 ± 4.5 μm in least width), multipolar but predominantly oval in shape. The lesser petrosal nerve joined the otic ganglion posteriorly or on its medial aspect and contained almost exclusively myelinated fibres (diameter 2.34 ± 0.8 μm). Nerves passed inferiorly and anteriorly from the ganglion and shortly entered the substance of mandibular nerve branches; these were studied no further. Another 15–24 fine rami issued dorsally from the ganglion, measuring 10–105 μm in least diameter and usually including one or two extraordinarily broad, thin rami, measuring up to 550 μm in width and a few μm thick (Figs 3, 4). The dorsal rami entered the cranium through the foramen ovale, attached to the medial surface of the mandibular nerve or slightly separated from it anteriorly. An example is shown in Figure 1. One or more lay

Fig. 3. Numerous dorsal rami of the otic ganglion within the foramen ovale. They are buried in the connective tissue plug at the anteromedial rim of the foramen. *M*, Mandibular nerve. Bar, 100 μm.

Fig. 4. Part of a band-shaped dorsal otic ramus (*R*) within the perineurium of the mandibular nerve. There are 3 cell somata in the ramus. Bar, 10 μm.

Fig. 5. Single ramus to show the mixed content of small myelinated and unmyelinated nerve fibres. Bar, 10 μm.

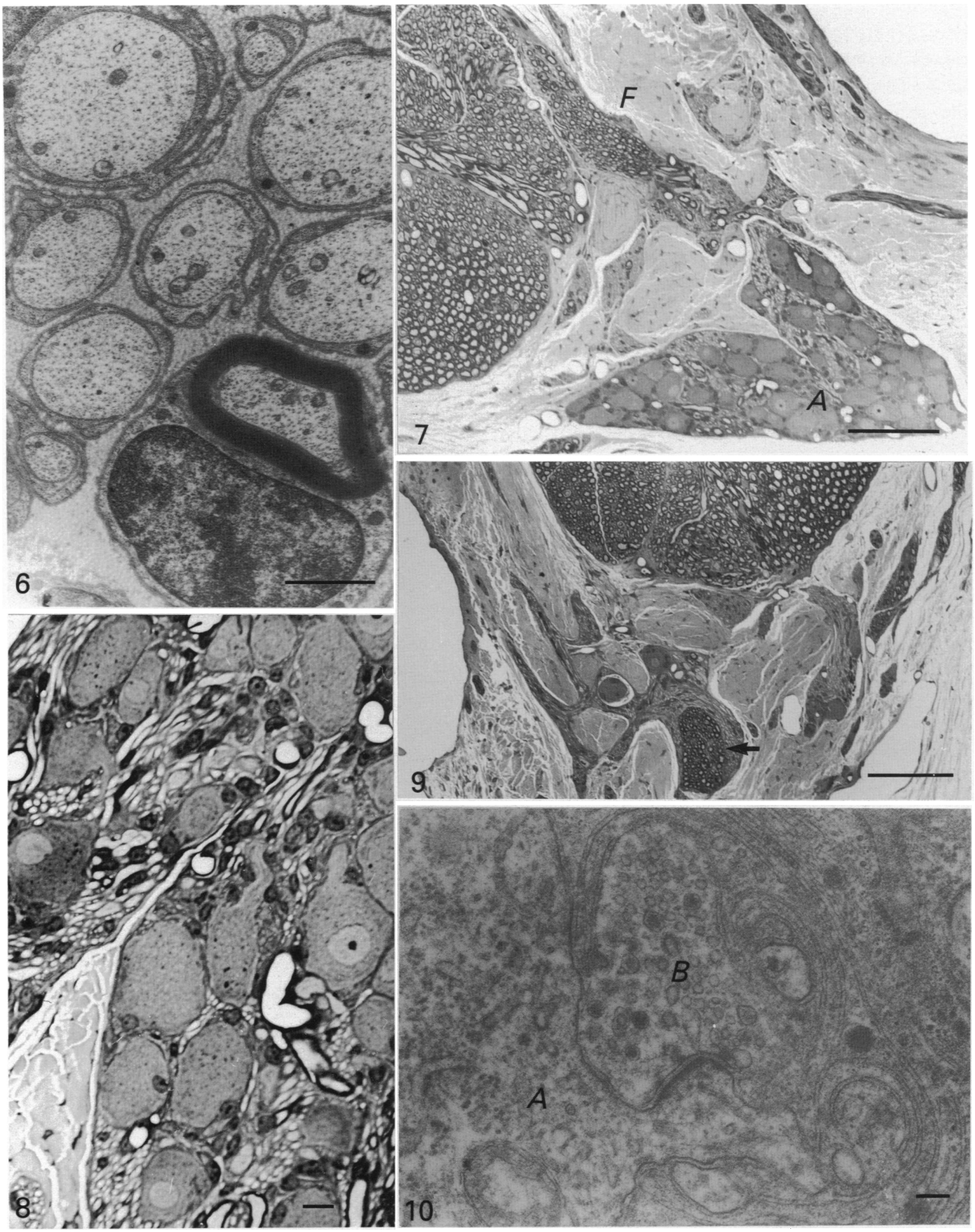

Fig. 6. Detail from a dorsal ramus. Each of the unmyelinated nerve fibre subunits contains a single axon. The axon of the myelinated nerve fibre has a diameter falling within the wide range of unmyelinated fibre diameters. Bar, 1 μm.

Fig. 7. Accessory otic ganglion (*A*) located intracranially at the crotch of mandibular and maxillary nerves. It is joined by a filament (*F*) composed of smaller myelinated fibres of the mandibular nerve. Bar, 100 μm.

Fig. 8. Part of the accessory otic ganglion of Figure 7. Several of the cells reveal their multipolarity. Bar, 10 μm.

Fig. 9. Several dorsal rami and a mandibular filament (arrow) contribute to a small nerve plexus at the anteromedial edge of the mandibular nerve within the cranium. Bar, 100 μm.

Fig. 10. Synapse of a dorsal ramus nerve fibre terminal bouton (*B*) with an accessory ganglion cell (*A*). Bar, 0.1 μm.

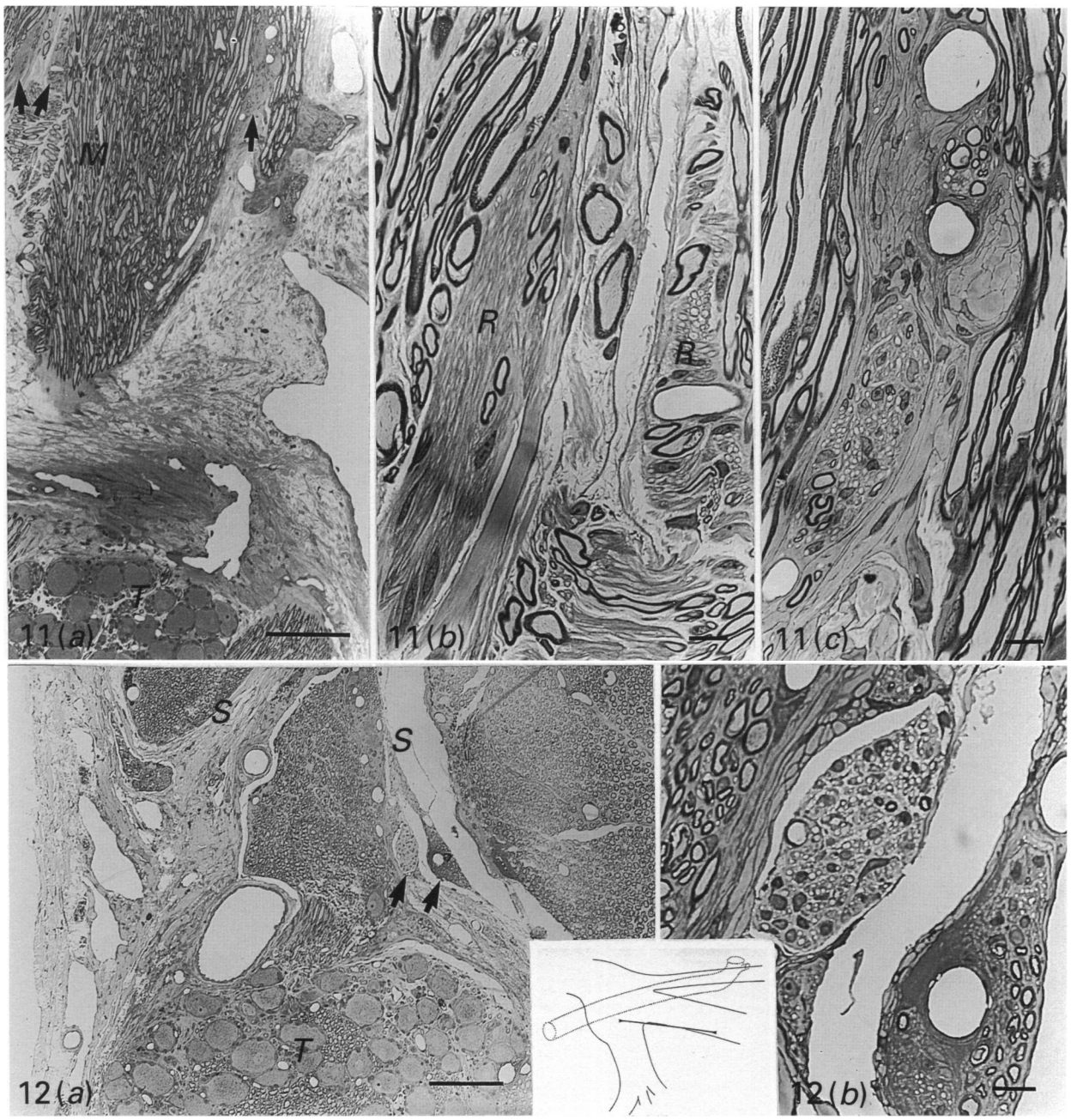

Fig. 11.(*a*) Tangential section through the base of the maxillary nerve (*M*) missing its junction with the trigeminal ganglion (*T*). Arrows indicate the positions of dorsal otic rami entering the nerve from below; those to the left are represented at greater magnification in (*b*) and that to the right in (*c*). Bar, 100 μm. (*b*) Two rami (*R*), one cut obliquely (left) and another cut transversely (right) fuse with the large fibre bundles of the maxillary nerve. Bar, 10 μm. (*c*) The ramus lies in connective tissue separating fascicles of the maxillary nerve. Bar, 10 μm. Fig. 12.(*a*) Another preparation sectioned at a slightly higher level than in Figure 11, showing continuity of the maxillary nerve with the trigeminal ganglion (*T*) and 2 splits (*S*) in the base of the maxillary nerve, each containing dorsal otic rami. Those to the right (arrow) are represented again in (*b*). The inset shows the orientation of the section (bold line) in relation to the trigeminal nerve at the ganglion. Bars, 100 μm and 10 μm.

within the mandibular nerve epineurium and others entered the nerve; a few turned around the posterior margin of the nerve to lie laterally. Some rami contained unmyelinated fibres only, but numerous small myelinated fibres (least width 2.41 ± 0.6 μm) were present in others (Figs 3, 5, 6). Cell bodies were disposed singly or in small groups at intervals along the rami (Fig. 4) until close to the trigeminal ganglion where much larger concentrations of cells formed the accessory otic ganglion (Figs 7, 8). The ganglion consisted of 2 or 3 masses of cells disposed on the medial aspect or slightly anterior to the mandibular nerve, each receiving several rami. The cell content of the accessory otic ganglion, estimated from the

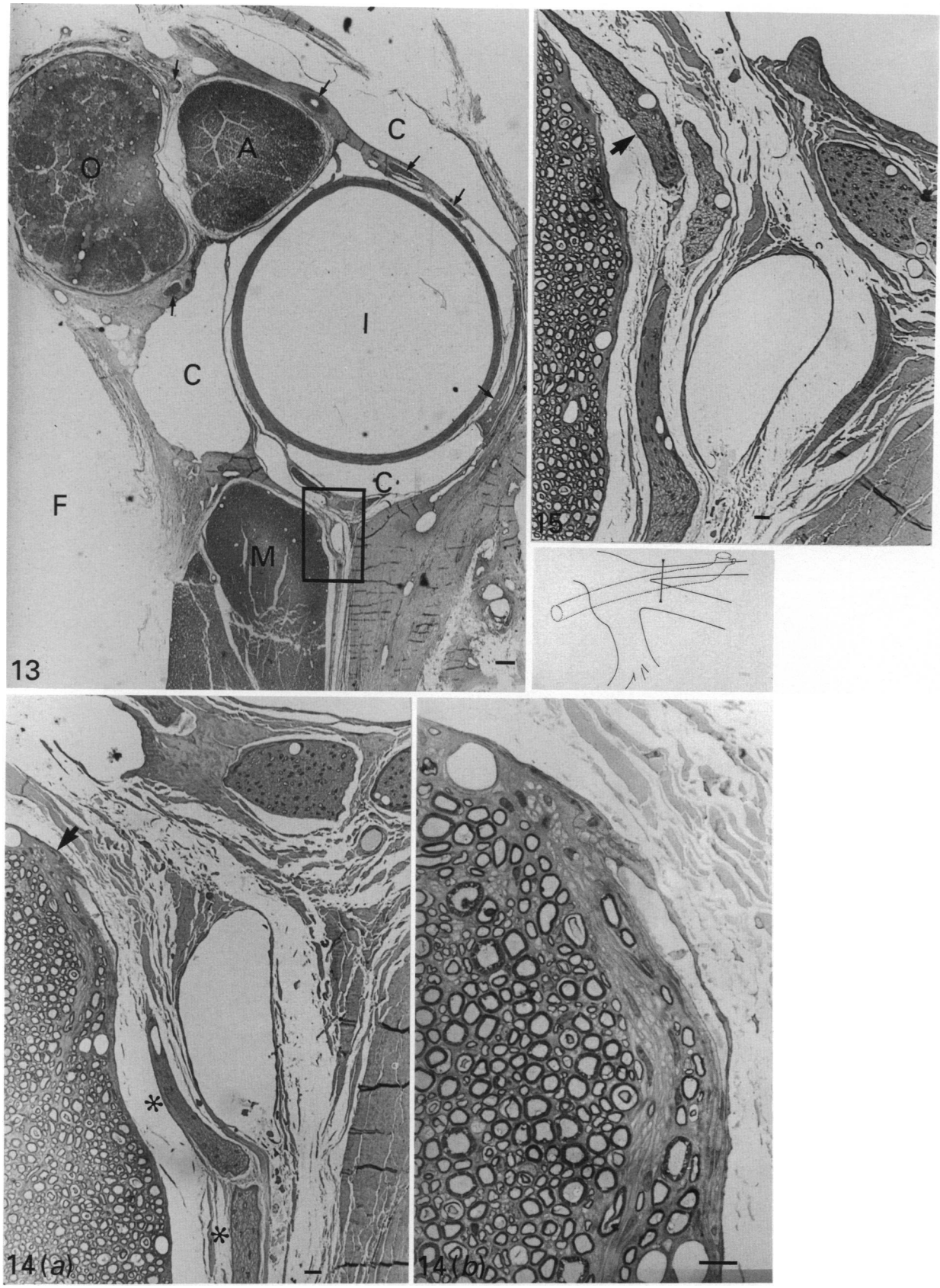

Fig. 13. Transverse section through the cavernous sinus (*C*) distal to the bifurcation of the maxillary (*M*) and ophthalmic (*O*) nerves; the position of the section is represented in the adjacent line drawing (the dotted outline indicates the internal carotid artery). Several filaments of the cavernous sinus plexus are indicated (arrows). *A*, abducent nerve; *F*, middle cranial fossa; *I*, internal carotid artery. Bar, 100 μm.

interrupted serial sections of several preparations, varied from 300–1850; the ganglion was absent from one side of 2 animals.

The accessory ganglion was often present in the same horizontally cut sections as the trigeminal ganglion, facilitating comparison between the 2 groups of cells. The largely circular trigeminal cells contained highly contrasted, evenly distributed, fine Nissl granules and the spectrum of cell sizes was large (least diameter 40.0 ± 10.3 μm), whereas the accessory otic ganglion cells were smaller in size and size range (23.9 ± 4.8 μm), and were mostly oval or slightly angular in shape, with poorly contrasted Nissl granules, similar to those of the otic ganglion (Fig. 8). Synapses, revealed electron microscopically, were present only in accessory otic and otic ganglion cells (Fig. 10).

Nerve junctions at the accessory otic ganglion continued above it in the form of a small plexus (Fig. 9). It lay in the dense fibrous connective tissue occupying the crotch of the mandibular and maxillary nerves. Those otic rami that had entered the mandibular nerve now left it to join the plexus and it was also joined by 2 or more fine recurrent branches from the mandibular nerve (Fig. 7). In a few preparations trigeminal cells, associated with the recurrent mandibular branches, were noted.

The plexus lay medial to and slightly below the level of the greater petrosal nerve, close to its junction with the deep petrosal nerve. There were no instances of connection between the plexus or any of its branches with either of these nerves or with the nerve of the pterygoid canal.

The dorsal rami continued beyond the plexus, accompanied by the mandibular branches, on either side of or through the maxillary nerve to the cavernous sinus; 2 or 3 rami took a different course, turning proximally on the medial side of the motor division of the trigeminal nerve and their further course could not be traced. The number of small myelinated fibres was reduced distal to the accessory otic ganglion, presumably because the preganglionic myelinated fibres had terminated in the ganglion. A few otic and mandibular rami fused, producing nerves with a mixed fibre population (Fig. 9). Rami entering the maxillary nerve were dwarfed by its mass of large myelinated fibres (Figs 11, 12), yet they were not particularly difficult to trace because of their differently directed axons and because they mostly lay in small channels of thickened endoneurial connective tissue, often accompanied by blood vessels. However, 1 or 2 rami usually entered maxillary fascicles (Fig. 11*b*). Intramaxillary rami quit the nerve by emerging from its flanks or from its upper surface (Figs 13–15). Sympathetic internal carotid nerve divisions in the wall of the internal carotid artery, first identified in sections cut opposite the proximal part of the trigeminal ganglion, were traced forwards to the position of the rami above the maxillary nerve (Fig. 14*a*). Junctions between the 2 groups of nerves were delayed until both had reached the cavernous sinus. The possibility that some dorsal branch fibres continued forwards in the maxillary nerve cannot be ruled out, but none were identified.

Above the maxillary nerve, otic and mandibular rami passed in the walls and trabeculae of the cavernous sinus and between the abducent, ophthalmic and trochlear nerves and the internal carotid artery and joined other elements of the cavernous sinus plexus (Fig. 16). Tracing the otic contributions proved impractical shortly after they had joined the plexus because of the complexity of the anastomoses and the mixing of various fibre types. Several of the stronger branches of the plexus are visible in Figure 13.

DISCUSSION

A comprehensive account of the nerve pathway from the otic ganglion to the cavernous sinus plexus is presented here for the first time. The otic ganglion is part of the classically accepted cerebral parasympathetic outflow, populated characteristically by cholinergic/VIPergic neurons (Edvinsson et al. 1989; Suzuki et al. 1990). The postganglionic nerves described in this study therefore conduct parasympathetic fibres to the cavernous sinus plexus, and during their passage to the plexus are joined by sensory twigs from the mandibular nerve. It is of interest to consider whether they also receive sympathetic nerves at any point in their course. The first possibility is that the lesser petrosal nerve conducts sympathetic fibres to the otic ganglion, but this is unlikely or, at most, their number would be insubstantial because practically all of its fibres were of the small myelinated variety, typical of a preganglionic

Fig. 14. (*a*) The boxed area of Figure 13 showing 2 dorsal otic rami (asterisks) climbing the medial flank of the maxillary nerve, and another (arrow) emerging from the dorsal edge of the nerve and shown again in (*b*). The nerve and parts of 2 others at the top are sympathetic divisions of the internal carotid nerve. Several of the stronger branches of the cavernous sinus plexus are seen. Bars, 10 μm.

Fig. 15. The same position as displayed in Figure 14*a* represented about 100 μm further forwards. The buried otic ramus (arrow) has fully emerged from the maxillary nerve, and the medial rami have moved dorsally. Bar, 10 μm.

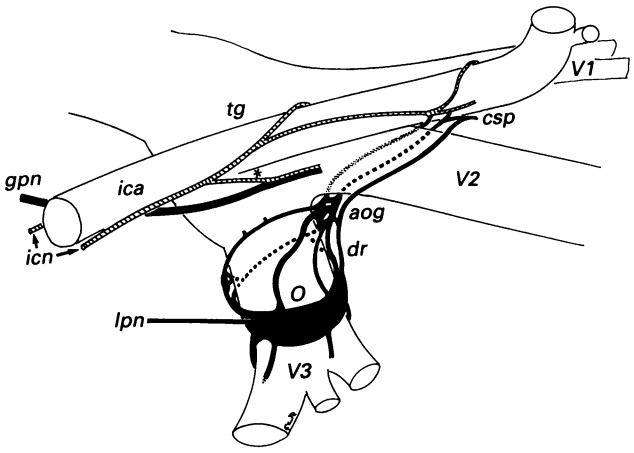

Fig. 16. Drawing of the trigeminal nerve, the otic ganglion and a representative sample of its dorsal rami viewed from the medial aspect. The solid, broken and shaded lines crossing the maxillary nerve (*V2*) are dorsal otic rami passing medial to, through and lateral to the nerve. *aog*, Accessory otic ganglion; *csp*, cavernous sinus plexus; *dr*, dorsal rami; *gpn*, greater petrosal nerve; *ica*, internal carotid artery; *icn*, internal carotid nerve branches; *lpn*, lesser petrosal nerve; *o*, otic ganglion; *tg*, trigeminal ganglion; *V1, V2, V3*, ophthalmic, maxillary and mandibular nerves. The asterisk indicates the junction of the deep petrosal and greater petrosal nerves to form the nerve of the pterygoid canal—the nerve is cut at its point of entry into the canal.

parasympathetic ganglion. This observation finds a parallel in histochemical studies of dogs in which neither adrenergic neurons were found within the ganglion nor adrenergic fibres passing through it (Sano et al. 1969).

In view of the complexity of neural interconnections at the crotch of the mandibular and maxillary nerves it cannot be claimed with confidence that sympathetic fibres do not join the dorsal otic rami in this position, but there was no evidence that they do so. An obvious opportunity for the introduction of sympathetic nerve fibres was presented by the proximity of the deep petrosal nerve and the nerve of the pterygoid canal but, contrary to observations made in man (Andres & Kautzky, 1956), no connections were found. Consequently, the rami ascending from the plexus through or around the maxillary nerve are composed of otic parasympathetic and mandibular fibres and their anastomosis with sympathetic and other nerves is probably delayed until they reach the cavernous sinus plexus as shown in Figure 16. Although appropriate counts were not made, the total number of otic parasympathetic fibres entering the cavernous sinus plexus was clearly substantially less than the sympathetic fibres; an impression of the disparity can be gained from Figures 13–15.

The cavernous sinus plexus branches are known to use the internal carotid artery wall and the intracavernous somatic nerves as conduits to a variety of structures (Ruskell & Simons, 1987; Ruskell, 1988; Hardebo et al. 1991). Their presence in the cavernous sinus plexus offers a variety of potential targets for otic parasympathetic nerves. Intracranial targets are the most obvious and to these can be added intraorbital structures, because the cavernous venous plexus is continuous with the retro-orbital plexus which is known to be a source of autonomic fibres to the eye and its appendages (Ruskell, 1985).

There is evidence that postganglionic otic fibres terminate on cerebral arteries. Subsequent to the application of the retrograde tracers, horseradish peroxidase, wheat germ agglutinin or True Blue to the middle cerebral artery in cats and rats, they appear in the otic ganglion (Walters et al. 1986; Suzuki et al. 1988, 1990; Edvinsson et al. 1989). Were the same true of monkeys, there would be little doubt that the nerve fibres taking up the tracers are distributed via the cavernous sinus plexus and the wall of the internal carotid artery. Yet, following the same procedure in monkeys, otic ganglion cells were not marked (Hardebo et al. 1991). This surprising result is open to question for, as the authors point out, negative findings should be interpreted with caution when a single application site for the tracer along the vascular tree is used. The present results indicate the need for further study.

Despite the penetration of the maxillary nerve by some of the otic rami, none appeared to be distributed peripherally with the nerve. They were all seen to leave the nerve and continue dorsally to join the cavernous sinus plexus. Results indicating the absence of otic ganglion fibres from the distal maxillary nerve had also been reported in guinea pigs; application of the retrograde marker True Blue to the cut maxillary nerve failed to label the otic ganglion (Segade et al. 1987). Presumably the application was made well forward of the trigeminal ganglion, otherwise label may have been found in the otic ganglion.

Identification of recurrent branches of the mandibular nerve close to its origin appears to be a novel observation. Their contribution to the cavernous sinus plexus implies that they also may contribute to the innervation of the cerebral arteries. This would explain the sparing of many of the myelinated fibres in cerebral vascular nerves following ophthalmic or combined ophthalmic and maxillary neurotomies in monkeys (Simons & Ruskell, 1988). Otherwise the literature offers no encouragement to this suggestion. For example, Tsai et al. (1988) reported ipsilateral elimination of calcitonin gene-related polypeptide-reactive cerebral vascular innervation following unilateral ophthalmic nerve transection in rats, but

innervation density was undiminished following transection of the maxillary and mandibular divisions of the trigeminal nerve. Again, the results of applying retrograde tracers to the wall of the middle cerebral artery in monkeys fail to support cerebral vascular innervation by the mandibular nerve, as only trigeminal neurons in the ophthalmic and maxillary regions of the ganglion were labelled (Hardebo et al. 1991). Further experimentation is called for if these inconsistencies are to be resolved.

The impressive histological reconstructions of otic and other cranial autonomic ganglion distributions in human embryos by Andres and Kautzky (1955, 1956) revealed a pathway from the ganglion to the cavernous sinus plexus similar to the one described here. But, in contrast to the profusion of dorsal rami in monkeys, they found only 2, and, unlike monkeys, 1 of them joined the greater petrosal nerve. But in the present context, it is the sinus distribution that is of interest and, assuming that the connection is not transient during development in man, a projection from the plexus to the cerebral arteries appears highly likely.

REFERENCES

Andres KH, Kautzky R (1955) Die Frühentwicklung der vegetativen Hals- und Kopfganglien des Menschen. *Zeitschrift für Anatomie und Entwicklungsgeschichte* **119**, 55–84.

Andres KH, Kautzky R (1956) Kleine vegetative Ganglien in Bereich der Schädelbasis des Menschen. *Deutsche Zeitschrift für Nervenheilkunde* **174**, 272–282.

Clara M (1953) *Das Nervensystem des Menschen*, 2nd edn, p. 366. Leipzig: Johan Ambrosius Barth.

Edvinsson L, Hara H, Uddman R (1989) Retrograde tracing of nerve fibers to the rat middle cerebral artery with true blue: colocalization with different peptides. *Journal of Cerebral Blood Flow and Metabolism* **9**, 212–218.

Hardebo JE, Arbab M, Suzuki N, Svendgaard NA (1991) Pathways of parasympathetic and sensory cerebrovascular nerves in monkeys. *Stroke* **22**, 331–342.

Hovelacque A (1927) *Anatomie des Nerfs Craniens et Rachidiens et du Système Grande Sympathique Chez l'Homme*, p. 668. Paris: Doin.

Ohkubo M (1979) Macroscopic study of the otic ganglion in domestic animals (in Japanese). *Acta Anatomica Nippon* **54**, 322–333.

Pernkopf E (1980) *Head and Neck. Atlas of Topographical and Applied Human Anatomy*, Vol. 1 (ed. H. Ferner, translated by H. Monsen), p. 75. Baltimore, Munich: Urban and Schwarzenberg.

Rousset J (1922) Anomalies du ganglion sphéno-palatine, du ganglion otique et du nerf péristaphylin externe. *Bulletin et Mémoires de la Société Anatomique de Paris* **7**, 333–336.

Ruskell GL (1970) The orbital branches of the pterygopalatine ganglion and their relationship with internal carotid nerve branches in primates. *Journal of Anatomy* **106**, 195–203.

Ruskell GL (1985) Facial nerve distribution to the eye. *American Journal of Optometry and Physiological Optics* **62**, 793–798.

Ruskell GL (1988) The tentorial nerve in monkeys is a branch of the cavernous plexus. *Journal of Anatomy* **157**, 67–77.

Ruskell GL, Simons T (1987) Trigeminal nerve pathways to the cerebral arteries in monkeys. *Journal of Anatomy* **155**, 23–37.

Sano Y, Yoshikawa H, Konishi M, Ochi J (1969) Fluorescence microscopic findings on the otic and pterygopalatine ganglia of the dog. *Archives Histologica Japonica* **30**, 315–320.

Segade LAG, Quintanilla DS, Nuñez JMS (1987) The postganglionic parasympathetic fibres originating in the otic ganglion are distributed in several branches of the trigeminal mandibular nerve; an HRP study in the guinea pig. *Brain Research* **411**, 386–390.

Simons T, Ruskell GL (1988) Distribution and termination of trigeminal nerves to the cerebral arteries in monkeys. *Journal of Anatomy* **159**, 57–71.

Suzuki N, Hardebo JE, Owman C (1988) Origins and pathways of cerebrovascular vasoactive intestinal polypeptide-positive nerves in the rat. *Journal of Cerebral Blood Flow and Metabolism* **8**, 697–712.

Suzuki N, Hardebo JE, Kåhrström J, Owman C (1990) Neuropeptide Y co-exists with vasoactive intestinal polypeptide and acetylcholine in parasympathetic cerebrovascular nerves originating in the sphenopalatine, otic, and internal carotid ganglia in the rat. *Neuroscience* **36**, 507–519.

Tsai S-H, Tew JM, McLean JH, Shipley MT (1988) Cerebral artery innervation by nerve fibers containing calcitonin gene-related peptide (CGRP): I. Distribution and origin of CGRP perivascular innervation in the rat. *Journal of Comparative Neurology* **271**, 435–444.

Uemura Y, Sugimoto T, Kikuchi H, Mizuno N (1988) Possible origins of cerebrovascular nerve fibers showing vasoactive polypeptide-like immunoreactivity; an immunohistochemical study in the dog. *Brain Research* **448**, 98–105.

Walters BB, Gillespie SA, Moskowitz MA (1986) Cerebrovascular projections from the sphenopalatine and otic ganglia to the middle cerebral artery of the cat. *Stroke* **17**, 488–494.

Williams PL, Warwick R, Dyson M, Bannister LH (1989) *Gray's Anatomy*, p. 1113. Edinburgh: Churchill Livingstone.