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Pedicle and Antler Development Following Sectioning of the Sensory Nerves to the Antlerogenic Region of Red Deer (*Cervus elaphus*)

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ABSTRACT Sensory nerves supplying the deer antlerogenic region were sectioned about 60 days prior to pedicle initiation to determine the extent of neural influence on pedicle and first antler growth. Our results from a combination of histological examination and immunohistochemical localization showed that all 12 antlerogenic regions were successfully deprived of sensory nerve supply, but in 10 of 12 cases there was partial regeneration during the experimental period. In the two cases where no sensory reinnervation occurred, pedicle growth did not show any differences compared with partially sensory reinnervated or intact pedicles. With or without reduced sensory nerve supply, first antlers were initiated, grown, cleaned of velvet, cast, and regenerated in the normal way, but they were smaller than controls. Consequently, we conclude that a sensory nerve supply is not necessary for normal pedicle formation and for the first antler cycle, but plays a role in determining antler size.

Pedicles are the permanent bony protuberances of the frontal bone from which antlers grow and cast in deer. Both pedicles and antlers are richly innervated (Suttie, '90). The nerves supplying the pedicles are composed of sensory fibres derived from the zygomaticotemporal and supraorbital branches of the trigeminal nerve (Wislocki and Singer, '46; Adams, '79) and sympathetic fibres originating from the superior cervical ganglion (SCG) (Wika, '80; Rayner and Ewen, '81; Lincoln, '85). Antler nerves are collaterals of sensory fibres from the pedicles (Wislocki and Singer, '46), because the antler normally lacks sympathetic innervation (Wika, '80; Rayner and Ewen, '81).

Deer are not born with pedicles but these develop as secondary sexual characters as the deer approach puberty (Fennessy and Suttie, '85). While nerves are known to be necessary for the full expression of antler growth, they are not required for antler cycles (Suttie, '90) and their role in controlling pedicle growth is not known. Bubenik ('82, '90) and Bubenik and Bubenik ('87) hypothesized that neural input was essential to pedicle development with pedicle formation dependent on a neural connection between the antlerogenic tissue and the central nervous system. However, this hypothesis has not been tested. The aim of the present study was to remove the sensory nerve supply to the antlerogenic region prior to pedicle growth to determine the extent of any influence on pedicle and antler growth.

MATERIALS AND METHODS

Animals

Twelve 4-month-old red deer stag calves were randomly allocated into three groups (n = 4/group) on April 25, 1991: group one was subject to unilateral sensory nerve removal (USX) of the antlerogenic region (left side) (see below for surgery detail), group two was subject to bilateral sensory nerve removal (BSX), and group three remained untreated as a control (CON).

The deer were maintained indoors in two pens (25 m^2, six deer/pen, randomly allocated from the three groups) and fed a concentrate diet and hay ad libitum in the Invermay Flat Deer Yards throughout the study (April 1991–April 1992) and on the day of the surgery (30 April) deer were 46.2 kg ± 5.8 (mean ± S.D.) and none of them had begun to grow pedicles.

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Measurement

The deer were weighed weekly, and the deer liveweight at pedicle initiation was recorded. Pedicle initiation was determined by palpation. After initiation, the pedicle/antler length was measured using a flexible tape biweekly until the antlers had stopped growing. The initiation date of each antler from its pedicle apex was estimated as the event cannot be pinpointed. When the first antler growth was complete and the pedicle diameter was maximal in the growing season, the circumference of the pedicle under the coronet (an enlarged antler base part) was measured and the pedicle volume was calculated.

Surgery

The surgical procedure was similar to that of Suttie and Fennessy ('85). Briefly, the deer were sedated after a 24 hr fast with Rompun (0.75 mg/kg liveweight) (Xylazine, Bayer, Ltd.) i.v., and then anaesthesia was induced with a mixture of halothane, nitrous oxide, and oxygen following intubation. The surgery was carried out with aseptic precautions. An incision was made posterior to the eye and the zygomaticotemporal branch of the trigeminal nerve was exposed, and then it was carefully separated from the adherent branch of the superficial temporal vein using blunt dissection and a 1.0–1.5 cm section of the nerve was removed. The wound was closed with michelle clips. A second incision was made above and slightly dorsal to the eye on the same side and the supraorbital branch of the trigeminal nerve was exposed. This nerve branch is very superficial and not routinely adhered to blood vessels but normally has several tiny branches. Consequently, care was taken to search for all associated nerve fibres. When all the nerves were exposed, they were separated from adherent connective tissues by blunt dissection and 1.0–1.5 cm pieces of the nerves were removed and the wound was closed as above. The removed pieces of tissue were fixed in 10% buffered formalin for subsequent histological examination. Each of the USX stags had the left side denervated only. The animals were given 4 ml Yohimbine (0.9 w/v) (Sigma Chemical Co., St. Louis, MO) to reverse the Rompun anaesthesia and were monitored until fully recovered.

At the conclusion of the experiment, all deer were slaughtered. Exploratory dissections were carried out on all the operated sites to determine the extent of any nerve regeneration. Pieces of tissue resembling nerve fibres were removed and fixed in 10% buffered formalin for subsequent histological examination.

Antler collection

USX group

The antlers of the deer were kept intact until they totally calcified and cleaned so that the growth of antlers on both sides could be observed. Two weeks after antler cleaning was complete when the deer were 15 months old, they were castrated to induce premature antler casting and new soft velvet antler tissue growth. For castration the animals were sedated with Rompun as above. The scrota were shaved and cleaned. The incision area was sterilised with 70% alcohol and tincture of iodine. Ten ml of 2% Lignocaine was injected subcutaneously at the incision site and also into the testes. A 2–3 cm incision was made at the base of the scrotum. Each testis and epididymis (in turn) was exposed through the incision. The connective tissues, blood vessels, and vas deferens proximal to each testis and epididymis were held with a pair of haemostats and compressed completely. Appositional tearing between the haemostats was continued until the tissues separated. Haemostats were removed and the procedure was repeated for the other testis and epididymis. The wound was left open to allow for good drainage after treatment with topical antibiotic. Sedation was reversed with Yohimbine as above. The length and weight of cast antlers and the date of casting was recorded.

When the brow tines of the new (second growth) antlers were fully divided from their main beams, both antlers were removed immediately above the coronets under local anaesthesia (3 ml Xylacaine/nerve site, Astra Pharmaceuticals, Ltd.), using a medium-toothed meat saw (this is the typical technique for the harvesting of velvet antlers on NZ deer farms). A 0.8 cm thick cross section from each antler was immediately taken from 1.0 cm above the coronet of the antler and immersed in isopentane cooled in liquid nitrogen, and then stored at $-80°C$ for further analysis.

BSX and CON groups

About 60 days after initiation of first antler growth, the left antler of each deer was removed about 1.0 cm below the coronets using the same method as above. A 0.8 cm thick cross section of pedicle from the lower part and a 0.8 cm thick cross section of antler from 5 cm below the growing tip were immediately taken and then stored as above. The opposite pedicles/antlers were left intact for fur-

ther observation. When the antlers of both sides were totally calcified and cleaned, they were removed at 1.0 cm above the coronets. The size, shape, and weight of each antler was recorded.

Immunohistochemical localization

Pieces of antler or pedicle for immunohistochemical localization of neurofilament were prepared for frozen sectioning by placing the tissue in precooled (4°C) OCT compound (Tissue Tek) in an appropriate aluminum foil boat. Antler tissue was sectioned whole, but the large diameter of the pedicle necessitated its division into four sectors for individual processing. The tissue was frozen by partial immersion of the boat in isopentane cooled by liquid nitrogen. Tissue not required immediately was stored at −80°C. Frozen tissue sections were cut at 20 μm in a cryotome and collected on chrome alum-gelatin coated glass microscope slides. Sections were taken from each sector of the divided pedicle tissue. A series of four sections was taken from each tissue block. Sections were air dried at room temperature for 30 min, and then washed in PBS (phosphate buffered saline; NaCl 100 mM, sodium phosphate buffer 20 mM, pH 7.4) for 10 min.

The primary antibody was raised against 200 kD neurofilament polypeptide (mouse anti-pig, Amersham). Primary antibody was diluted in immunodiluent (ID) (PBS with 0.5% bovine serum albumin and 0.2% Triton X100) to a dilution of 1:100. Incubation in primary antibody took place in a humidified chamber at room temperature for 2 hr. Negative control tissues were processed in parallel with the omission of primary antibody from the incubating solution. After incubation tissues were washed twice in PBS (2 × 5 min) and incubated in secondary antibody (biotinylated sheep anti-mouse, Amersham) diluted 1:200 in ID for 1.5 hr at room temperature. Another 2 × 5 minute wash in PBS followed, before incubation in a 1:100 dilution (in ID) of biotin-streptavidin-rhodamine (Amersham) for 45 min at room temperature. After 2 × 5 min washes in PBS the slides were coverslipped with Glycergel (DAKO) and examined using appropriate fluorescence optics on a Zeiss Axioplan fluorescence microscope. Specimens were photographed using Ilford HP5 film rated at ISO 400.

Data analysis

Pedicle and antler growth data were analysed by ANOVA between left and right sides of the USX group and between the BSX and CON groups. Statistical significance was assessed at the 5% level unless otherwise stated.

RESULTS

Effects of sensory nerve removal on pedicle and antler development

Pedicle

For all deer in the USX group, pedicle initiation occurred for the treated and control sides at the same time (mean liveweight = 49.8 kg), while the mean liveweights for the BSX and CON groups were 50.0 and 50.6 (S.E.D. = 3.8) kg, respectively. The date for the treated and the control pedicle initiation all fell in the same period, 148–161 days after birth.

Likewise no significant differences were found in the mean pedicle growth period, mean pedicle length and volume, and mean pedicle growth rate either between treated and control sides in the USX group, or between the groups of the BSX and the CON (Table 1).

Antler

There were no significant differences in mean deer live weight at antler initiation either between treated and control sides in the USX group (61.3 kg compared to 60.5 kg, S.E.D. = 0.8 kg) or between the groups of the BSX and the CON (69.3 kg compared to 64.8 kg, S.E.D. = 5.3). The date of antler initiation (206–252 days after birth) and the date of commencement of velvet cleaning (334–369 days after birth) of treated and control antlers fell in the same periods, respectively (Table 2).

There were also no significant differences in the growth period between the treated and the control antlers. However, the first hard antler (cast) weight and the length of the USX treated sides were significantly smaller than their control sides (Table 2, Fig. 1), but the growth rate was not significantly different. The antler weight, length and growth rate did not differ significantly between the BSX and

TABLE 1. Mean length, volume, days of growth, and growth rate of treated and control pedicles[1]

Group	Pedicle	Length (cm)	Volume (cm^3)	Days of growth	Growth rate (mm/d)
USX	Treated	4.88	45.3	69.0	0.74
	Control	5.13	51.3	71.3	0.75
	S.E.D.	0.29	3.6	1.8	0.02
BSX		5.19	57.8	81.0	0.66
CON		5.06	52.6	83.6	0.72
	S.E.D.	0.35	10.3	17.9	0.18

[1]Mean, n = 4; S.E.D., standard error of the difference (Volume = Circumference^2/4 π × Height). Growth rate = final length/number of days of growth.
USX, Unilateral sensory ablation; BSX, Bilateral sensory ablation; CON, Control.

TABLE 2. Mean weight, length, days of growth, and growth rate of treated and control antlers[1]

Group	Antler		Weight (g)	Length (cm)	Days of growth	Growth rate (mm/d)
USX	First hard	Treated	199[2]	37.4	109.3	3.6
	(cast)	Control	235	40.9	103.8	4.1
		S.E.D.	6.5	0.3	3.4	0.16
BSX	First velvet		120	21.5	71.5	3.0
CON	(removed)		195	27.2	72.3	4.1
		S.E.D.	87	8.6	5.7	1.6
BSX	First hard		158	31.4	115.3	2.7
CON	(removed)		269	41.9	108.8	3.9
		S.E.D.	102	12.1	17.8	0.9
BSX	Second hard		338	44.7	125	3.6
CON	(removed)		355	47.2	125	3.8
		S.E.D.	95	4.6	0	0.4

[1]Mean, n = 4
[2]One antler lost; S.E.D., standard error of the difference; growth rate = final length/number of days of growth. As before, USX, BSX and CON represent different deer groups.

the CON groups (Table 2), although the treated antlers were smaller than those of controls.

All the regrown antlers, treated or control, had brow tines or exostoses, while the first antlers were all spikes (Fig. 2).

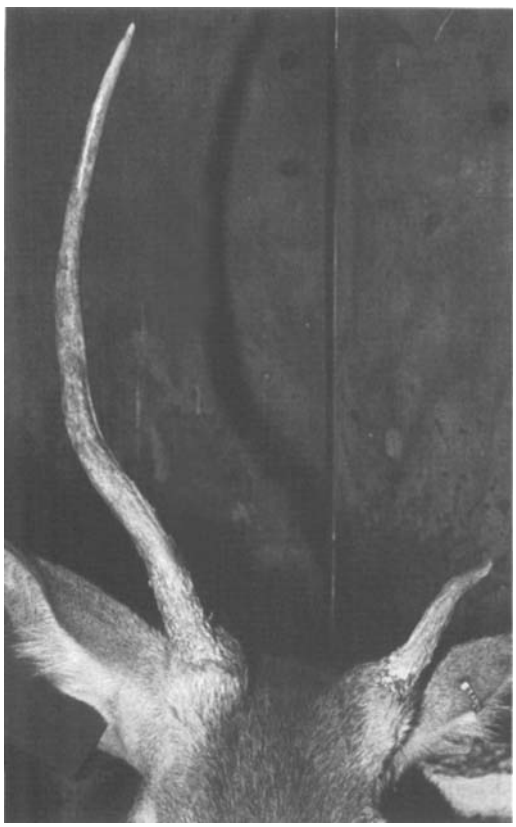


Fig. 1. Pedicles and first hard antlers grown by a stag in the unilateral sensory denervation group. Although the denervated antler is much smaller than the control one, the pedicle length is not different.

The regrown velvet antler weight and length of the treated sides following deer castration were also significantly smaller than those of control sides in the USX group (5.25 g compared to 7.88 g, S.E.D. = 2.48; 4.8 cm compared to 11.2 cm, S.E.D. = 4.8, respectively). The antler casting date of the treated and control sides fell in the same period of 16–21 days following deer castration. All the treated pedicle and antler growth profiles were similar in pattern to those of the Controls (Fig. 3).

Confirmation of sensory denervation

Histology

The results of the histological examination showed that the removal of sensory nerves at initial surgery was successful in all cases, although in one third of the sections, one or two tiny blood vessels were also removed along with nerve fibres.

The final results of the postmortem examination of the operated sites showed that in 4 of 12 zygomaticotemporal sites and 5 of 12 supraorbital sites there was no regeneration beyond the site of nerve transection, and in the other cases there was variable regeneration of fine nerve branches. Only the left antlerogenic regions of two stags had no sensory nerve regeneration from the routine paths of zygomaticotemporal and supraorbital branches of the trigeminal nerve during the period of the experiment.

Immunohistochemical localization

The anti-neurofilament antibody bound strongly and with good specificity to neural tissue in antler and pedicle sections. Neural profiles were clearly visible and background staining and autofluorescence were generally low to moderate. The extent

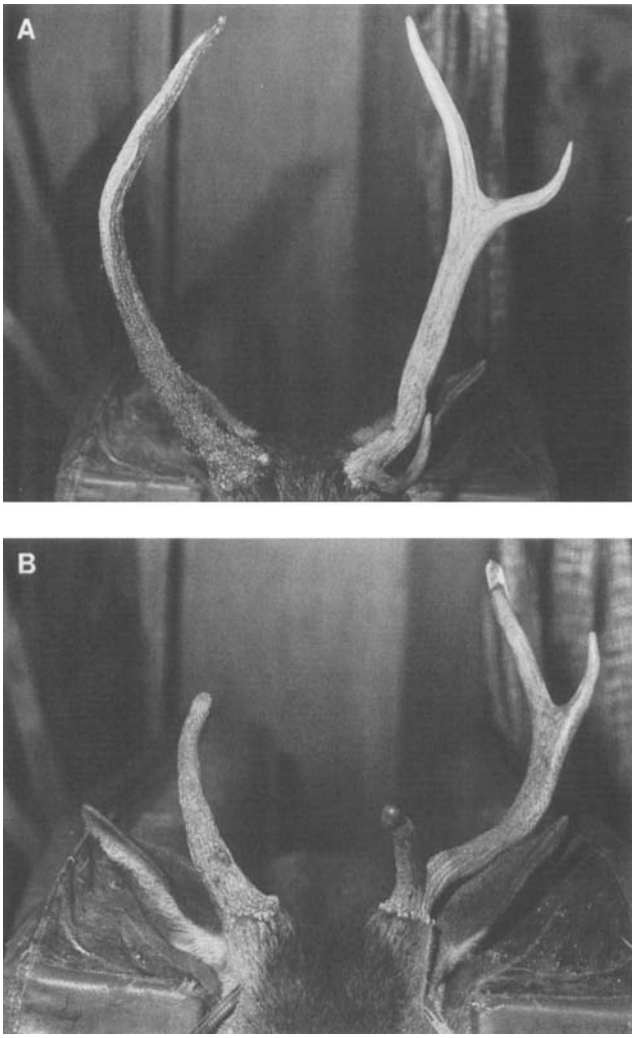


Fig. 2. **A:** Hard antlers grown by a stag in the control group following amputation of the previous left antler. A branched antler has been regenerated from the amputated side. **B:** Hard antlers grown by a stag in the bilateral sensory denervation group following amputation of the previous left antler. A branched antler has been regenerated from the amputated side, which is consistent with the result from control group.

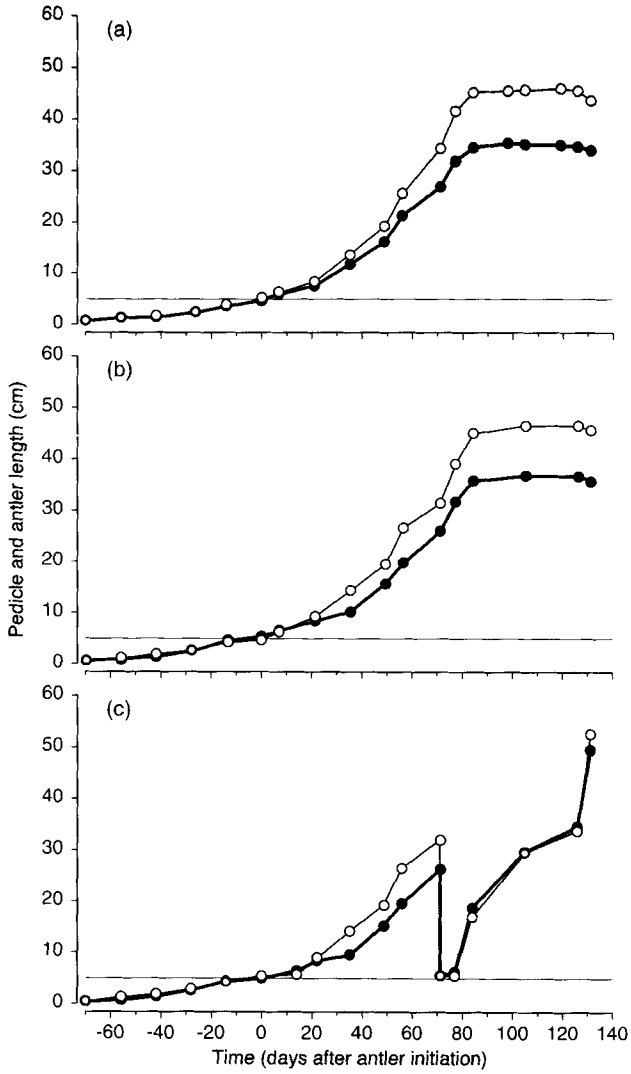


Fig. 3. Pedicle and antler growth profiles. The solid horizontal line refers to the change from pedicle to antler. **a:** Control (○) and denervated antlers (●) from the unilateral sensory denervation group (USX; n = 4). **b:** Comparison between the right pedicles and antlers grown by the Control group (CON ○) and the bilateral denervated group (BXS ○) (n = 4). **c:** As above except the comparison is between the left antlers the previous one of which was amputated after 70 days of growth and a branched antler was regenerated.

of the reduction in neural input was difficult to quantify. We were unable to perform any analysis which yielded reliable estimates of the quantity of neural input to antler or pedicle tissue. For this reason we have provided only qualitative data to demonstrate that neural input is eliminated or substantially reduced in specimens on which neurectomy had been performed.

Pedicle. Neurofilament-positive profiles were found in all pedicles, control and operated. However, it was evident that there was substantially less neural tissue present in denervated specimens (Fig. 4). Neural tissue was most commonly located in the vascular layer between the skin and the periosteum (Fig. 4) but was also represented in the skin (Fig. 5) and in the bone (Fig. 6). Fine nerve branches, presumably of autonomic origin, were often associated with the tunica adventitia of blood vessels.

Antler. As for the pedicles, large bundles of neurofilament positive profiles were found running circumferentially around the antlers in the vascular layer between the velvet and the periosteum in control tissues. No neurofilament-positive profiles were located in the two denervated antlers developed

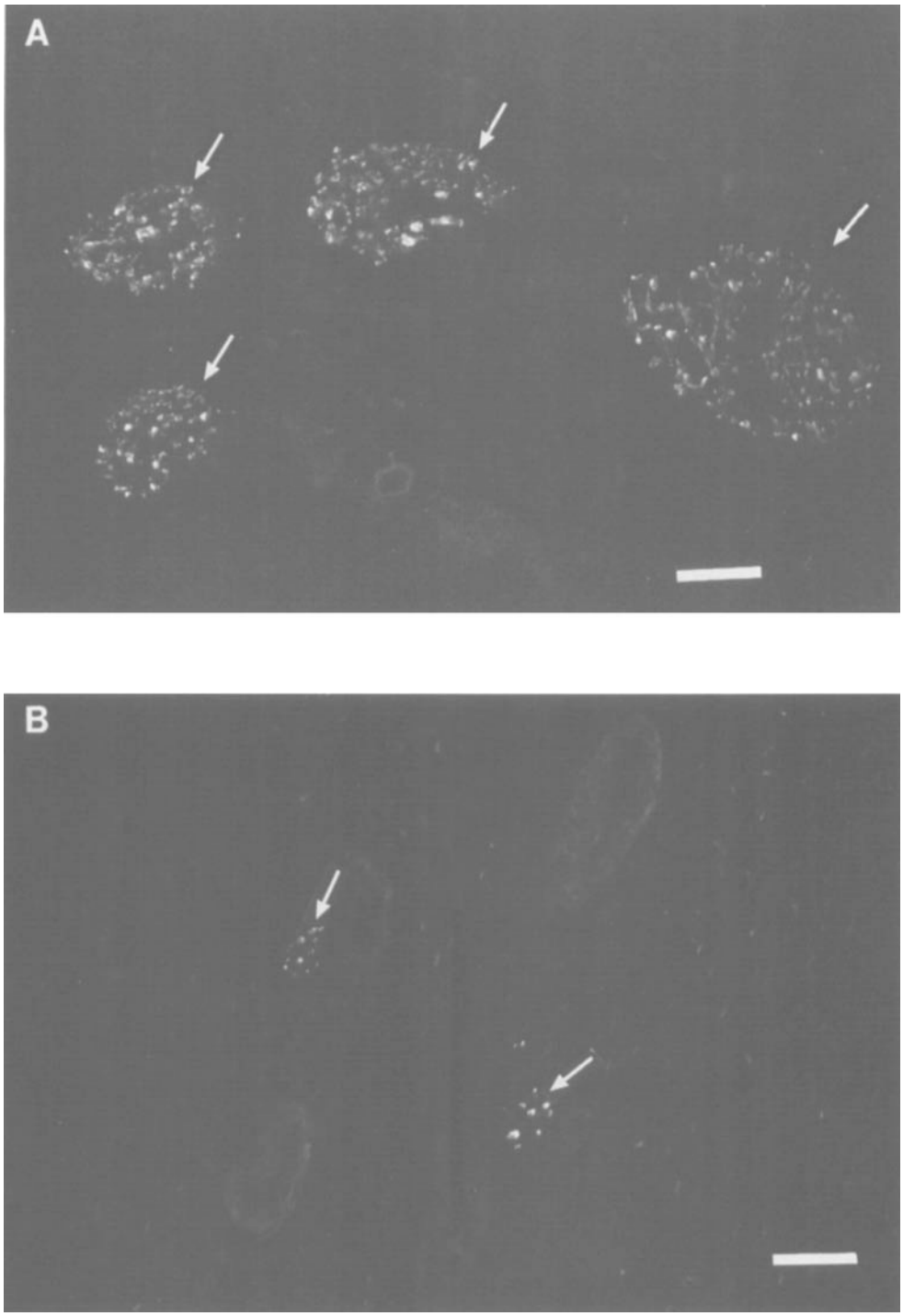
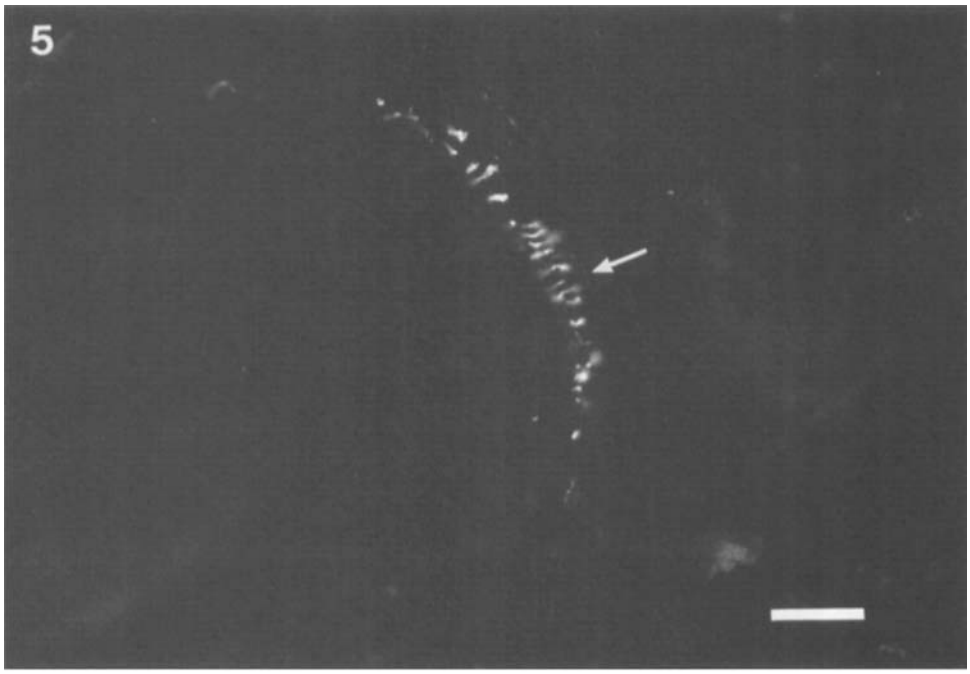


Fig. 4. Neurofilaments in the vascular layer of a pedicle. Arrows point to neurofilaments. **A:** Control pedicle. **B:** Sensory denervated pedicle. Bars, 100 μm.

from the two denervated antlerogenic regions as shown by dissection (see above) and there was once again a substantial obvious reduction in neural tissue present in other operated specimens (Fig. 7). Neural tissue was found associated with blood vessels (Fig. 7).

DISCUSSION

Although it has been known for some time that the deer pedicle is innervated with sensory and sympathetic nerves (Wika, '80; Rayner and Ewen,



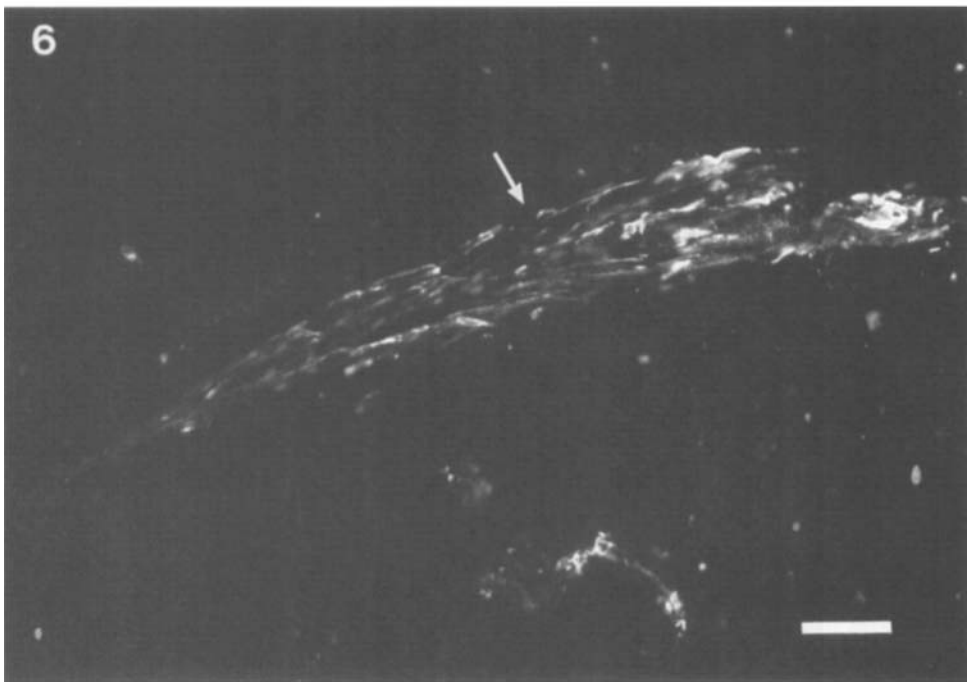


Fig. 5. Distribution of neurofilaments around the hair follicle in the skin of a control pedicle. Arrow points to neurofilaments. Bar, 100 μm.

Fig. 6. A large bundle of neurofilaments in the cancellous bone of a control pedicle. Arrow points to neurofilaments. Bar, 100 μm.

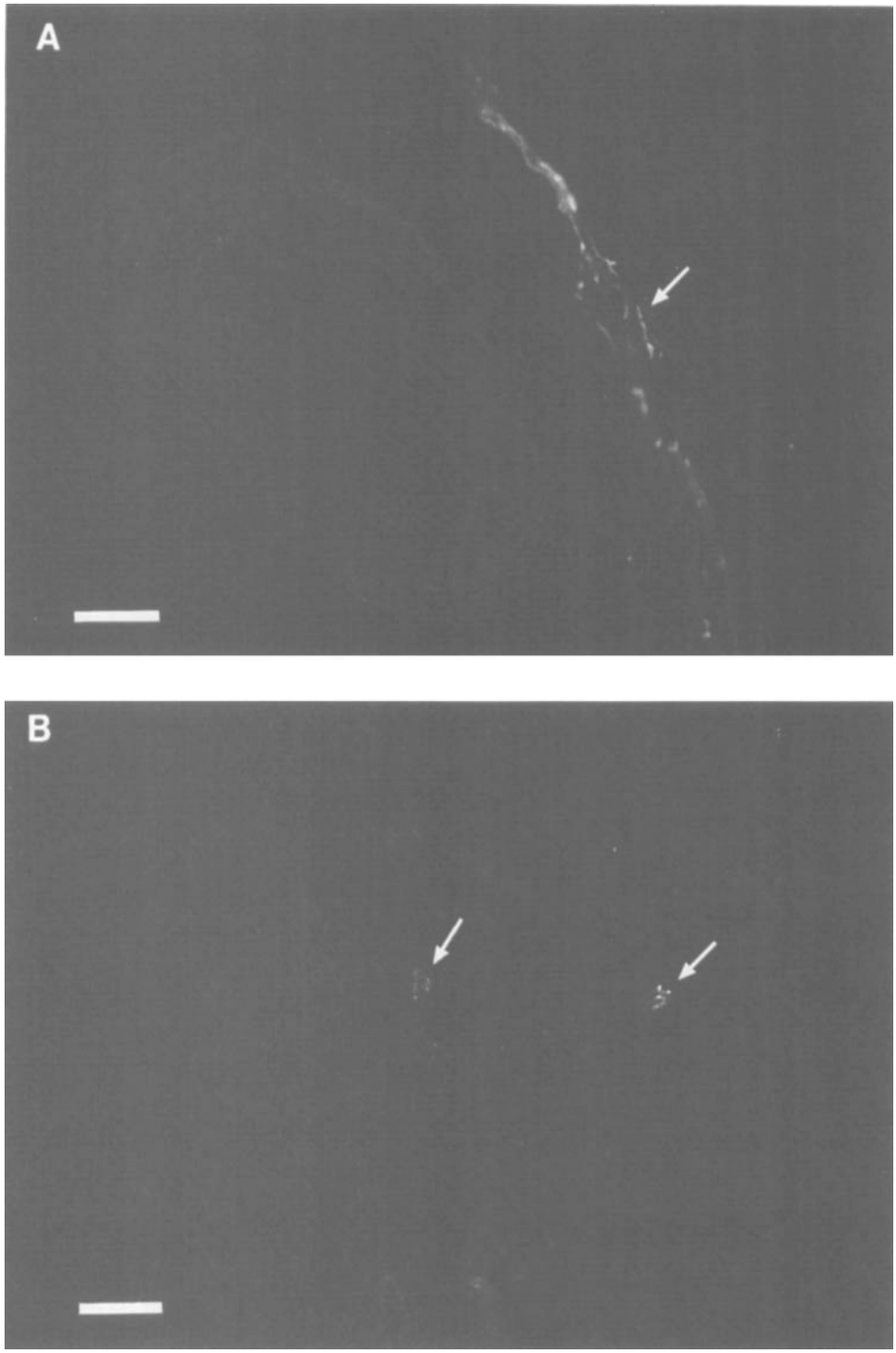


Fig. 7. Neurofilaments in the vascular layer of the antler. Arrows point to neurofilaments. **A:** Control antler. **B:** Sensory denervated antler. Bar, 100 μm.

'81), antlers are normally supplied only with sensory nerves (Wislocki and Singer, '46; Adams, '79), and the nerve supply affects the size and shape, but not the cycle of regenerated antlers (Suttie and Fennessy, '85). The influences of the nerve supply on the pedicle and the first antler development have not, to our knowledge, been experimentally studied so far. Our results, from a combination of his-

tological examination of the tissues, from exploratory dissections on the operated sites and immunohistochemical localization of neurofilaments on the cross sections of antler confirmed that in two deer the antlerogenic regions were successfully deprived completely of sensory nerve supply about 60 days prior to pedicle initiation. No reinnervation occurred until 60 days after the pedicle and antler had formed. Therefore, the pedicle initiation, growth, and first antler formation cannot be affected by the sensory nerve supply. Also, without a sensory nerve supply, the pedicle growth did not show any differences compared with partially sensory reinnervated and intact pedicles. Under conditions of reduced or absent nerve supply, the first antlers can initiate, grow, clean velvet, cast, and regenerate normally, but they are smaller (although there were no significant differences between the treated and control antlers in the present study due to high variability and the limited sample numbers) than controls, which is consistent with the results from regenerated antlers (Suttie and Fennessy, '85). Consequently, we conclude that a sensory nerve supply is not necessary for normal pedicle formation and for the first antler initiation, growth, cleaning or casting, but plays a role in determining the size of the first antler.

Aro et al. ('81) suggested that innervation might not play a role in the initiation of periosteal cell proliferation, as callus formation of a fracture began in the classical way in denervated bones. Likewise innervation of the antlerogenic region might not be necessary for pedicle and antler formation since pedicle tissue is also initiated by periosteal cell proliferation from the antlerogenic region and antler tissue is formed by proliferation of perichondrial cells which are derived from periosteal cells in the antlerogenic region (Hartwig and Schrudde, '72; Goss and Powel, '85; Banks and Newbrey, '82; and our unpublished observations).

Suttie and Fennessy ('85) thought the reason that denervated antlers were smaller than control antlers was through the loss of influence from the sensory nerves, but they did not explain why the antler might be smaller after losing the influence. It has been reported that sensory nerves possess a trophic function, which is likely mediated by the synthesis in the cell body of a trophic substance, its transport along the axon, and its release from sensory nerve endings. Interference with the supply of trophic substances during development could result in a reduction in the size of a peripheral structure or loss of specific peripheral organelles (reviewed by Guth, '71; Jacobson, '91). Singh et al. ('82) found that osteoblastic activity in bone significantly decreased following sensory denervation. Consequently antler size reduction following sensory denervation might be caused by the loss of trophic influences on osteoblastic activity. However, sensory denervation did not show any influence on the pedicle size. The reason for this may be either the sensory nerves do not exert their trophic function on pedicle growth, or the sympathetic nerves provide some trophic support when the pedicle loses its sensory nerve supply, because unlike antler which is innervated only with sensory nerves, the pedicle is supplied with sensory as well as sympathetic nerves. Whether or not pedicle development is totally independent of sensory nerve supply is a question awaiting further study.

Corbin and Hinsey ('39) suggested that innervation of bone, whether sensory or autonomic, is clearly not the major regulator of osteogenic activity in view of the fact that the skeleton can be maintained even when completely denervated. Likewise, nerves supplying the antlerogenic region may only exert auxiliary function on pedicle and antler growth and development.

Unlike the desensitized velvet antlers of the deer in the experiment of Wislocki and Singer ('46), the denervated velvet antlers in the experiment were not subject to visible injuries. The possible reasons might be that the deer were very tame and deer were maintained in pens with smooth plywood walls.

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