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Pedicle and Antler Regeneration Following Antlerogenic Tissue Removal in Red Deer (*Cervus elaphus*)

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ABSTRACT The physiological control mechanisms underlying the histogenesis of the pedicle, which precedes antler growth, from the frontal bones of male deer are poorly understood. The aim of this study was to investigate the extent of pedicle/antler regeneration after removal (for histological evaluation) of the antlerogenic region or pedicle tissue during pedicle development to determine whether the subsequent pattern of regeneration could contribute to the understanding of pedicle histogenesis and the mechanism of the transition between permanent pedicles and deciduous antlers. The contralateral pedicles of six stags were not removed and these data serve as controls. All deer were observed frequently and measurements of regeneration were made in March after all antler growth had ceased for that season. The developmental stage of the pedicle was determined by a combination of pedicle height measurements and histological studies. The results showed that pedicle formation histologically covers three stages: a period of intramembranous ossification (when the pedicle is less than 5 mm in height), a period when the ossification pattern changes (when the pedicle is between 5 and 28 mm in height) and a period of modified endochondral ossification (when the pedicle is over 30 mm in height). In all ossification stages some deer regenerated neither antlers nor pedicles. The pedicles which regenerated following the loss of antlerogenic tissue at the intramembranous ossification stage were shorter than the controls ($P < 0.01$), but longer than the pedicles regenerated after pedicle removal at the transitional stage in the pattern of ossification ($P < 0.01$). No pedicle tissue was regenerated if the pedicles were removed at the endochondral ossification stage and antlers were directly formed from the deer's head. Thus the final height of the regenerated pedicles was closely linked with the histological ossification stage of the original pedicle at removal. Antler regeneration took place at all stages but two deer grew pedicles only when tissue removal took place during the transition period. Overall the results provide evidence that the potential to regenerate a pedicle diminishes as the pedicle increases in height and the necessity for pedicle growth to precede antler growth also decreases. The fact that some deer, whose tissues were removed at the transition period of ossification change, regenerated pedicles but failed to generate antlers highlights the importance of this stage for the transition between the permanent pedicle and the deciduous antler. The results provide evidence for an hypothesis that it is the transition between ossification types which signals the end of pedicle development and the onset of antler development.

Deer pedicles are permanent outgrowths of the frontal bones and antecedents to the formation of antlers. Male deer normally begin to grow pedicles when they approach puberty (Fennessy and Suttie, '85) from the lateral crest periosteum of the antlerogenic region of the frontal bone (Hartwig and Schrudde, '74; Goss and Powel, '85; Goss, '87). Goss and Powel ('85) reported that the antlerogenic region on the frontal bone of the fallow deer before pedicle development covered an area about 1.5 cm in diameter, since the removal of that much periosteum abolished pedicle and antler formation. However, once a pedicle has formed antlerogenesis may not exclusively reside in the pedicle because total pedicle removal from moose (Jaczewski, '54), red deer (Jaczewski, '55), sika deer (Goss, '61) and roe deer (Bubenik and Pavlansky, '65) did not inhibit later antler formation although pedicles did not regenerate. However whether the size of the antlerogenic region varies among deer species before pedicle initiation and whether the potential of the frontal bone to regenerate pedicles after the initial pedicle is removed are not known. Also it is not known why only antler tissue forms without

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pedicle tissue following the removal of a whole pedicle. We have investigated pedicle and antler regeneration after the removal of antlerogenic tissue at different developmental stages from the unpalpable pedicle to the first antler in order to test a hypothesis that the developmental stage of the pedicle at the time of removal influences the extent of subsequent pedicle and antler regeneration. If this is so then the data have strong implications for the understanding of the underlying mechanisms of pedicle and antler formation.

MATERIALS AND METHODS

Animals

All experiments were carried out on red deer (*Cervus elaphus*) which were allocated to one of five groups (Table 1) prior to pedicle growth. The deer were observed weekly and surgery took place when the pedicle had reached the pre-determined height range.

Surgery

The surgery was carried out in the period between 2 April '92 and 30 August '92. Prior to the surgery and following a 24 hr fast, the animals were sedated 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 pedicle height, if appropriate, was measured with a ruler on the medial side of the pedicle. The surgery was carried out using aseptic precautions.

For groups 1 and 2, a crescent shaped incision was made on the scalp media to the frontal lateral crest where a pedicle is destined to grow. The flap of skin, which was separated from the frontal bone by blunt dissection, was reflected laterally. A 22 mm diameter sterilised hole punch was used to mark out the presumptive antlerogenic region, centred on the frontal lateral crest, on the exposed frontal bone. In this respect the antlerogenic region in fallow deer was reported to be about 15 mm in diameter (Goss and Powel, '85); and as red deer are generally larger than fallow deer a proportionally larger 22 mm diameter disc was removed in red deer. In some cases (n = 14), a 22 mm diameter disc of periosteum only was removed, but in other cases (n = 7, see Table 2) the same size periosteal disc was removed together with a thin layer of underlying bone by shaving with a scalpel. The wound was then closed with 3-0 metric silk sutures spaced at 5 mm intervals. Care was taken to accurately fit the flap of skin with the scalp skin. Three antlerogenic regions from the left sides of group 2 were left intact as controls, but otherwise tissues were removed bilaterally from each deer. A piece of tissue (3 × 5 mm) was taken from the central part (the centre of the antlerogenic tissue) of the periosteum with underlying bone for histological examination to determine the developmental stage.

For all subsequent groups, two incisions were made: the first incision was identical to that for groups 1 and 2, while the second was medially from the apex of the pedicle vertically down to the base, until it met the first incision. The skin was then separated from the pedicle by blunt dissection. The exposed bony column was removed from the base using an embryotomy wire. A slice of tissue about 3 mm in thickness was taken longitudinally from each column for histological examination to determine the developmental stage. The punch was not used in these groups as the wounds left after the pedicle removal were larger than 22 mm in diameter. The skin of the pedicle was trimmed carefully to fit the wound and then the wound was sutured. Three incipient pedicles from the left sides of group 3 were left intact as controls.

Maintenance of the animals

After the surgery all stag calves were kept outdoors on pasture under standard group husbandry procedures so that they could be observed and photographed. The final examination for each group was made in autumn after all animals which developed pedicles had completed antler growth and the antlers were cleaned of velvet. There were two

TABLE 1. Allocation of the experimental animals

Group	n	Age (months)	Pedicle height range (mm)	Mean pedicle height (mm)	Mean liveweight ± S.D. (kg)
1	6	4	< 5	—	41.8 ± 1.48
2	6	5–6	5–9	7	49.9 ± 3.15
3	7	6–8	10–28	19	53.7 ± 5.14
4	3	8–8.5	30–35	33	63.7 ± 6.51
5	3	8–9	55–75[1]	63	68.8 ± 6.51

[1]75 mm = 50 mm pedicle + 25 mm antler

TABLE 2. Influence of the removal of the antlerogenic tissue on pedicle and antler regeneration at the stage when original pedicle is under 10 mm in height

Group	Stag no.	Side of pedicle/antler	Tissue removed	Final antler/pedicle length (mm)
1	346	L	P[1]	390/40
		R	P	340/30
	348	L	P	310/30
		R	P	230/30
	349	L	P	30/30
		R	P+B[2]	0/0
	365	L	P	330/40
		R	P+B	0/0
	369	L	P	345/35
		R	P+B	0/0
	374	L	P	290/40
		R	P+B	0/0
2	31	L	None	440/50
		R	P	0/0
	59	L	None	380/50
		R	P	375/35
	9123	L	None	210/50
		R	P	0/0
	9130	L	P+B	0/0
		R	P	0/0
	9140	L	P+B	0/0
		R	P	0/0
	279	L	P+B	40/20
		R	P	15/25

[1]P, periosteum.
[2]P+B, periosteum plus a sliver of underlying bone.

exceptions (97 left and 9104 right) which showed no sign of growing antlers during the experimental period (Table 3). The length of both pedicles and antlers were measured at the final examination separately. The "pedicle" was defined as the tissue which was not cleaned of skin after velvet antler cleaning.

Histology

All tissue samples taken for histology were immediately fixed in 10% buffered formalin. After a minimum of 24 hr in fixative, the samples were decalcified in Raymond Lamb "R.D.C." commercial decalcification solution for 4–15 hr and washed in tap water for 2–4 hr. The tissues were then embedded in paraffin wax and sectioned at 5 μm. The sections were stained with Gill's haematoxylin and alcoholic phloxine/eosin, and alcian blue and haematoxylin/eosin. The tissue sections were observed and photographed using a Zeiss Axioplan Microscope. The ossification patterns through which the pedicle was formed were evaluated by comparing them with those occurring in somatic bone (Ham, '69) as well as antler bone formation (Banks and Newbrey, '82a,b). Only the original tissue removed at surgery was examined histologically; no regenerated tissue was examined in this way.

Biometrics

The data were analysed using ANOVA, with each surgery site treated separately.

RESULTS

Histology

The tissue taken at the pre-pedicle stage from group 1 was composed of two portions: an upper antlerogenic periosteum and a lower osseous tissue (Fig. 1). The periosteum consisted of two layers, an outer fibrous layer and an inner cellular layer. The osseous tissue was cancellous bone. Along the interface of the periosteum and subperiosteal bone, active osteoblasts covered the surface of the bony trabeculae and spicules. The subperiosteal bone was formed through typical intramembranous ossification.

The tissue taken at the pedicle initiation stage from group 2 was composed of three portions from distal to proximal: antlerogenic periosteum/perichondrium, osseocartilaginous tissue and osseous tissue (Fig. 2). Compared with group 1, antlerogenic periosteum/perichondrium was more hyperplastic. The osseocartilaginous tissue was a very narrow portion, with some mature chondrocytes appearing in some bony trabeculae in the mid part of the portion underneath the periosteum/perichondrium. The osseous portion was similar to that of group 1. The incipient pedicle was formed by a composite form of intramembraneous and endochondral ossification.

The incipient pedicle taken from group 3 could be divided longitudinally into three portions from distal to proximal: antlerogenic periosteum/perichondrium, osseocartilaginous tissue and osseous tissue (Fig. 3). Compared with group 2, the periosteum/perichondrium was even more hyperplastic. The osseocartilaginous tissue comprised an extensive area in which discrete cartilaginous clusters were scattered in the osseous trabeculae. Toward the distal side, the cartilaginous proportion increased. The osseous tissue was similar to group 2. The pedicle was formed through the same ossification pattern as group 2.

The pedicle or pedicle/antler tissue removed from groups 4 and 5 could be longitudinally divided into four portions from distal to proximal: perichondrium, vascularized cartilaginous tissue, osseocartilaginous tissue and osseous tissue (Fig. 4). The perichondrium, osseocartilaginous tissue and osseous tissue portions were similar to the corre-

TABLE 3. Influence of the removal of the antlerogenic tissue on pedicle and antler regeneration at the stage when original pedicle is over 10 mm in height

Group	Stag no.	Side of pedicle/antler	Original pedicle height at removal (mm)	Final antler/pedicle length (cm)
3	276	L	15[1]	360/50
		R	15	55/30
	60	L	28[1]	510/50
		R	28	365/25
	20	L	25[1]	400/50
		R	25	170/30
	R50	L	20	0/0
		R	22	0/0
	97	L	15	0/30
		R	15	75/25
	9104	L	10	10/20
		R	10	0/20
	271	L	15	0/0
		R	15	0/0
4	G50	L	30	0/0
		R	30	140/0
	30	L	35	80/0
		R	35	0/0
	9127	L	35	0/0
		R	35	0/0
5	273	L	60	0/0
		R	60	10/0
	278	L	55	0/0
		R	55	15/0
	285	L	75 (25 antlers)	0/0
		R	75 (25 antlers)	0/0

[1]Pedicles not removed.

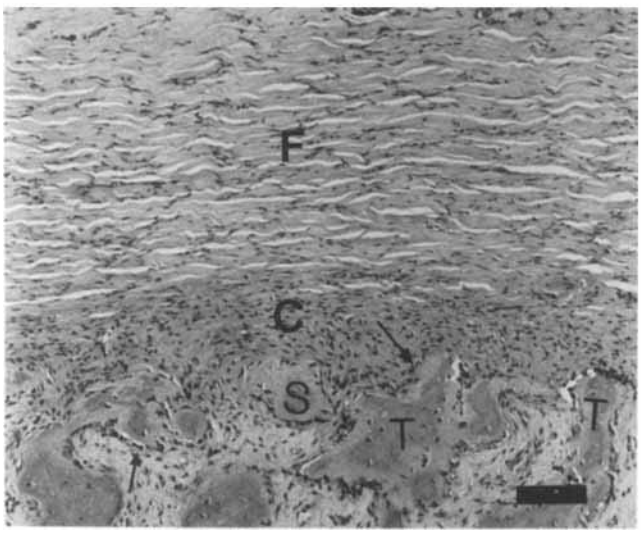

Fig. 1. Longitudinal sections of antlerogenic tissue taken from the left side of the antlerogenic region of a deer (group 1) when its pedicles were under 5 mm in height. The tissue consisted of a fibrous layer (F), a cellular layer (C) and underlying cancellous bone. The spicules (S) and the trabeculae (T) were covered with active osteoblasts (arrows). Bar = 0.1 mm.

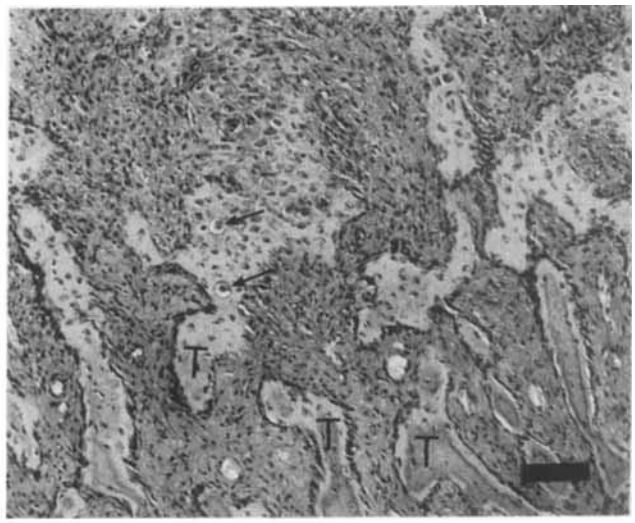

Fig. 2. A longitudinal section of antlerogenic tissue taken from the left side of the original incipient pedicle of a deer from group 2 when its pedicles were about 9 mm in height. Underlying the hyperplastic antlerogenic periosteum/perichondrium, some mature chondrocytes (arrows) appeared in the bony trabeculae (T) which were located in the central part of the pedicle. Bar = 0.1 mm.

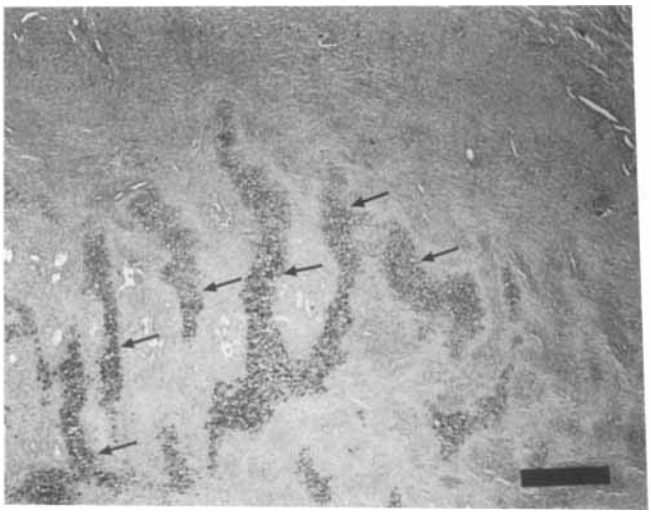

Fig. 3. A longitudinal section of the right side of the original incipient pedicle from a deer from group 3. The osseocartilaginous tissue was underlying the antlerogenic periosteum/perichondrium. The proportion of the cartilaginous tissue (arrows) increased toward the distal end. Bar = 0.5 mm

Fig. 5. A male deer calf from group 1. When the calf was 4 months old and its pedicles were under 5 mm in height, a 22 mm diameter disc from the left antlerogenic periosteum and a similar sized disc with a layer of underlying bone from the right antlerogenic periosteum were removed. A pedicle and an antler formed from the left surgery site, although the pedicle was shorter than those of normal deer from whom no tissues had been removed. Neither pedicle nor antler was formed from the right surgery site.

sponding portions of group 3. The distinguishing histological feature of the pedicle at this stage was that continuous cartilaginous trabeculae appeared underlying the perichondrium. The pedicle was formed through modified endochondral ossification.

Regeneration

From all group 1 surgery sites where 22 mm diameter discs of antlerogenic periostea only were removed, pedicles and antlers regenerated (Fig. 5), although the mean height of the pedicles (34 ± 5 mm, n = 8) was significantly shorter than the control pedicles (50 ± 0 mm, n = 6) ($P < 0.01$) (Tables 2, 3). However, the surgery sites where the same sized pieces of periostea with underlying bone were removed (n = 4) did not regenerate pedicles or antlers during the experimental period (Fig. 5) (Table 2).

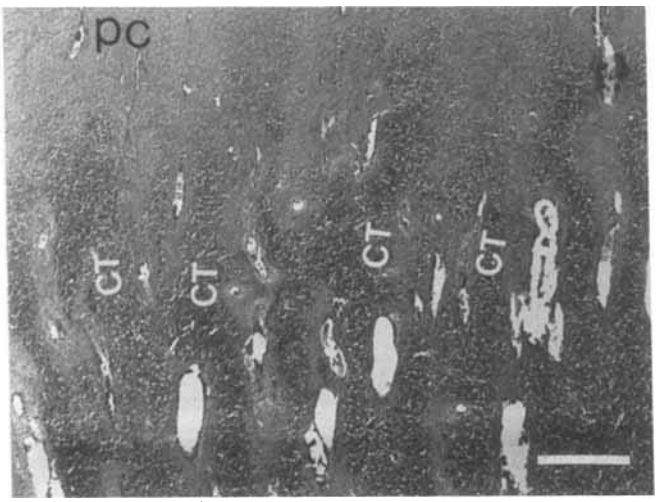

Fig. 4. A longitudinal section of the upper part of the original incipient antler from a deer from group 5. Continuous cartilaginous trabeculae (CT) were formed, underlying the hyperplastic perichondrium (pc). Bar = 0.5 mm.

Of the six surgery sites where 22 mm diameter discs of antlerogenic periostea only were removed from group 2, four did not grow a pedicle or antler during the experimental period while the remaining two regenerated pedicles and antlers. Two of the three surgery sites where 22 mm diameter discs of the periostea together with the underlying bone were removed did not grow a pedicle or antler during the experimental period, while the other formed a pedicle and an antler. However, the pedicles formed (27 ± 8 mm, n = 3) were significantly shorter than the control (50 ± 0 mm, n = 6) ($P < 0.01$) and group 1 (34 ± 5 mm, n = 8) ($P < 0.01$) pedicles (Table 2) (Fig. 6).

Of the 11 surgery sites where the incipient pedicles were removed from group 3, four did not grow any pedicle or antler in the experimental period, two formed only pedicles (Fig. 7A) and five formed pedicles and antlers (Fig. 7B). All pedicles formed in the group (26 ± 5 mm, n = 7) were shorter

Fig. 6. A male deer calf from group 2. When the calf was 6 months old and its pedicles were about 9 mm in height, the same surgical procedure was carried out as in group 1. Neither side formed a pedicle or antler.

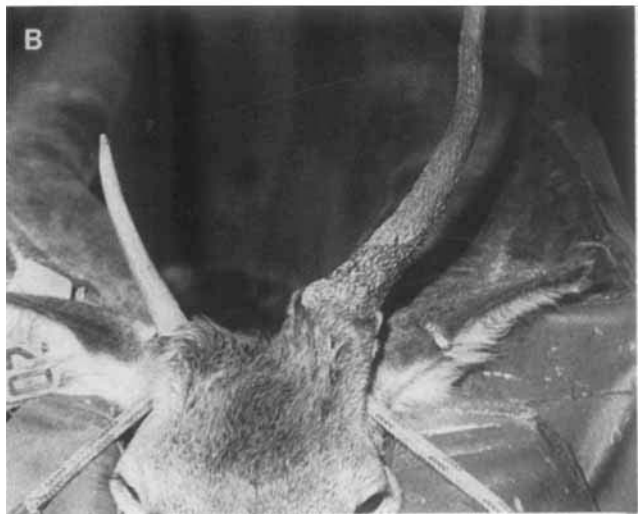

Fig. 7. Two male deer calves from group 3. When the calves were 8 months old and their pedicles were about 25 mm and 15 mm in height, they were operated as follows: **A:** The incipient pedicles from both sides of one calf (with 15 mm high pedicle) were removed at their bases. A pedicle and an antler formed from the left side, but only a short pedicle formed from the right side in the growing season. **B:** The right side of the incipient pedicle of one calf (with 25 mm high pedicle) was removed at its base. A pedicle and an antler formed from the surgery site, but the pedicle was shorter than the control contralateral side, which was unmanipulated.

than the control ($P < 0.01$) and group 1 ($P < 0.01$), but were not significantly different compared with group 2 ($P > 0.05$) (Table 3).

Of the 12 surgery sites where the pedicles were removed from groups 4 and 5, four formed only antlers, while the others grew neither pedicle nor antler in the experimental period (Table 3) (Fig. 8).

DISCUSSION

We have a comprehensive understanding of the histological structure of growing antlers (Banks and Newbrey, '82a), but the histogenesis of the pedicle, from which antler initiates, has not been studied. Our results show that pedicle formation histologically covers three stages: a period of intramembranous ossification, a transitional period of ossification pattern change and a period of modified endochondral ossification. Through the intramembranous ossification stage, the height of the deer frontal lateral crest/pedicle increases. The emergence of the chondrocytes in the bony trabeculae when the pedicle is about 7 mm long signifies the beginning of the ossification pattern change stage, through which the pedicle elongates to 30 mm, which is about half the height of the completely formed pedicle in red deer. After this, continuous vascularized cartilage begins to form exclusively under the apex of pedicle, which initiates the modified endochondral ossification stage, which continues until the pedicle completes its final development to antler.

In all five groups there were surgery sites from which no regeneration took place after tissue removal during the study. It is considered that, in these cases, all cells with the potential to become pedicles or antlers were lost at the time of surgery. Goss et al. ('64) found that removal of the bony pedicle rudiment prevented further pedicle or antler growth in each of five white-tailed deer (*Odocoileus virginianus*) fawns. In a further study Goss and Powel ('85) found in young fallow deer (*Dama dama*) that the number of surgery sites which developed pedicles or antlers after removal

Fig. 8. A male deer calf from group 5. When the calf was 9 months old and antlers about 25 mm high had grown from the tips of the pedicles, both pedicles were removed at their bases. An antler regenerated only from the left site.

of the antlerogenic periosteum was inversely proportional to the diameter of the tissue removal, but some sites still developed even after a 15 mm diameter disc was removed. In the present study a 22 mm disc of periosteum or the entire pedicle, if present, was removed, so that the potential to regenerate was independent of the amount of tissue removed at surgery. In group 1 pedicle and antler growth was prevented only in those surgery sites where a thin slice of underlying bone was removed as well as the periosteum. It is possible that either the periosteum was so closely attached to the bone that some cells remained after surgery or there may be an important interaction between the bone and the periosteum such that cells from both must be removed to ablate pedicle and antler growth. In view of the fact that the periosteum was tightly adherent to the bone in group 1 animals, it is most likely that a few periosteal cells remained after surgery. In contrast, in group 2 animals, the periosteum detached readily from the bone so that complete removal was easier. So although an interaction between the periosteum and the underlying bone cannot be completely precluded because bony trabeculae lined with osteoblasts penetrated the periosteum in group 1, it seems more likely that if all antlerogenic cells are removed no regeneration can take place.

In all five groups there were surgery sites from which regeneration took place during the study, presumably from residual cells. However, the extent (size) and pattern (pedicle only, pedicle and antler, antler only) of regeneration varied with the height of the pedicle, and consequently ossification type, at the time of removal surgery. In groups 1 and 2 (pedicles <10 mm in height and where bone growth was due to intramembranous ossification) both pedicle and antler regenerated. In group 3, (20–30 mm pedicles and transitional ossification type) the pedicle and antler or pedicle alone regenerated. In groups 4 and 5, (pedicles >30 mm where bone formation occurs by endochondral ossification) only the antler regenerated. The height of the regenerated pedicle tended to reduce from group 1 to group 3 and was non-existent in groups 4 and 5, but some antler regeneration took place in all groups. Thus the pattern of regeneration of pedicle and antler was consistent neither among groups nor ossification types. An hypothesis to explain these findings is advanced below. In groups 1 and 2, in the intramembranous ossification stage the cells remaining following periosteal tissue removal (with or without a slice of bone) could have the full potential to develop pedicles, which could transform into antlers. Because the great majority of cells were removed the size of this regeneration would be less than unoperated controls. In group 3 during the transition stage between the ossification types the regeneration could be dependent on the precise point in the transition; pedicles could develop which could or could not develop antlers. If a pedicle only forms then the transition stage could have been incomplete because a pedicle is still required prior to antler transformation, but the pedicles are in some way deficient. This stage is analogous to the situation with castrate stags induced to develop pedicles due to testosterone treatment but which do not form antlers (Jaczewski, '82). Finally, in groups 4 and 5 undergoing endochondral ossification the residual cells may have completely transformed to antlerogenic and consequently no pedicle need develop to permit full antlerogenesis. Thus there is a strong link between the type of ossification and the regeneration patterns of the residual cells. The transition period is seen as critical; in this period a great variation in pattern of regeneration (both within and between animals) was found, presumably reflecting a rapidly changing ossification environment. What could be "deficient" about the pedicles which do not form antler is open to speculation. Conceivably they could be simply too small, but group 2 pedicles of similar size produced antlers. More likely the transition stage was incomplete; the potential of the pedicle to transform was lost but the potential of the cells to directly produce antlers had not been gained. It could be argued that the study did not extend long enough to allow for ultimate development of antlers from the pedicles. Nonethe-

less the fact that velvet antler growth from these pedicles was delayed compared with pedicles from groups 1 and 2 and indeed some from group 3 is reason enough to speculate on the causes.

We have used the pattern/extent of regeneration of residual cells following tissue removal to speculate on the histogenesis of the pedicle and antler. This has highlighted the ossification type change as a potentially critical stage in development. The pedicle is initially indispensable for normal antler development but this factor becomes progressively less critical and eventually pedicle cells seem to lose their ability to form antlers, but after this phase, antler cells can form spontaneously without pedicles. It is still unclear from which cells in the pedicle the antler forms; it seems what is more important is that these cells are forming tissue via endochondral ossification. Inasmuch as the steroid status of the young stag controls pedicle and early antler growth, stimulatory for the former and inhibitory for the latter (Suttie et al., '91), it is possible that the steroid status may be, in part, the underlying mechanism controlling this transformation, although the precise mechanism needs further study. In castrate stags whose pedicles are induced exogenously with steroids, trauma can mimic this effect (Jaczewski, '82). Nerves are not required for the transition from pedicle to antler (Li et al., '93) in contrast to Bubenik's ('90) speculation. it may be that growth factors released locally by the cartilage are responsible for ultimate antler growth.

If the hypothesis that the ossification type change is indeed responsible for the transition between the pedicle and the antler then it is interesting that this occurs when the pedicle is only one third to one half grown (red deer). This means that two thirds of visible pedicle growth is, in fact, antler growth, but the skin/hair take longer to transform from pedicle type to antler type than the bone. The fact that only the true antler skin peels off at velvet antler cleaning to hard antler is evidence that a transition in skin type also takes place. Why the bone and skin transformation are not simultaneous is not known but could point to a relationship between the skin and bone having some mutual relevance in histogenesis.

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