Experimental Investigations of Morphogenesis in the Growing Antler

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WITH FIVE PLATES

INTRODUCTION

D'Arcy Thompson (1942) described the form of antlers as having developed in a two-dimensional pattern which, during growth, may have become more or less distorted depending on the species. In some (e.g. moose, fallow deer), the antlers may exhibit a palmate configuration; in most deer, however, they are branched structures formed by the repeated two-dimensional bifurcation of the original outgrowth. This process gives rise to a series of tines which vary in number according to age and species. In the sika deer, the first set of antlers, produced in yearlings, are unbranched spikes which may grow as much as 6 inches in length. The following year, these are replaced by branched antlers usually having three points each. Mature bucks ordinarily possess 4 points per antler.

The annual growth cycle of antlers has been thoroughly documented by Waldo & Wislocki (1951), and Wislocki (1956) in the Virginia deer. In the sika deer it is briefly as follows. Shedding of the old antlers occurs in the spring, having been preceded by the local swelling of the skin of the pedicle immediately below the base of the antler. There is reason to believe that the incipient growth of the new antler is somehow instrumental in bringing about the loss of the old. Following autotomy, a scab forms on the stump of the pedicle, and wound healing ensues by the migration of epidermis and subjacent connective tissue from the margins. It is from this undifferentiated tissue derived from the dermis of the pedicle skin that the new antler bud appears to develop. Subsequent invasion and proliferation of such cells results in the formation, within a few weeks, of a rounded knob growing on top of the pedicle. This structure branches dichotomously as it grows throughout the spring and summer, attaining its full size by late August. Growth occurs almost exclusively at the apical end of each branch, where there exists a mass of undifferentiated cells resembling the blastema of regenerating structures in lower vertebrates. In older parts of the growing antler, located progressively more proximal, are zones of chondrification

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and ossification which are honeycombed by numerous small blood-vessels. The whole antler is enveloped in a richly vascularized layer of skin, and is said to be 'in velvet' because of the numerous hair follicles which are formed de novo throughout the growth period (Billingham, Mangold, & Silvers, 1959). Once the ultimate size of the antler is attained and further growth ceases, the entire inner parts of the antler become converted to bone which is solid except for the many small blood-vessels which permeate it. At the end of the summer, apparently due to vascular restrictions, the entire antler dies and the investing layer of desiccated skin is rubbed off by the animal, exposing the bare bony antlers which persist until the following spring when a new cycle is initiated.

It is natural to regard the growing antler as a developing system analogous to certain embryological structures, or comparable to the regenerating appendages encountered among the cold-blooded vertebrates. Inasmuch as the latter systems, during their formative periods, tend to exhibit varying degrees of regulatory capabilities, it was of interest to determine to what extent the antler can adjust its morphogenesis to compensate for various defects surgically inflicted at different periods in the growth cycle. Specifically, the experiments to be described below were devised to provide information concerning (a) the capacity of the antler to exhibit morphogenetic regulation, (b) the degree to which such abilities may be restricted to certain phases of the growth cycle, and (c) the extent of the antler 'territory', i.e. the distribution of tissues potentially capable of participating in antler development.

MATERIALS AND METHODS

All of the experiments in the present account were performed on the sika deer (Cervus nippon), a species which has been bred in captivity for many years and is easier to work with and to obtain than the native Virginia deer. Animals were maintained either in individual enclosures or in small groups confined in larger pens.

In order to anesthetize animals in preparation for operations, equipment manufactured by the Palmer Chemical and Equipment Company, of Atlanta, Georgia, was used. This consisted of a 'Cap-chur' rifle, powered by compressed carbon dioxide, which shoots a projectile designed to inject a drug of choice automatically into the muscle of the deer. In these cases, Anectine (generously donated by Burroughs, Wellcome & Co.) was used in doses of approximately 6 to 8 mg./100 lb. body-weight. Such an intramuscular dose took effect in about 10 minutes and kept the animal unconscious for approximately half an hour. In addition to this general anesthesia, the local area of the pedicle and antler was injected subcutaneously with 1 ml. of 2 per cent. Xylocaine hydrochloride to render the areas to be operated insensitive to pain. Although operations were performed with non-sterile, but clean, instruments and without benefit of antibiotics, no infections occurred. Surgery was accomplished with scalpels in most instances, and with a hacksaw where it was necessary to cut through bone.
Bleeding was often profuse at first, but always subsided within minutes. Wounds resulting from such operations became covered by scabs and healed promptly. All operations were performed on the left antlers only in order to reserve the right antlers as normal controls. Further details of specific operations are presented in the appropriate context below.

The progress of experiments on individual animals was recorded periodically by careful examination of anesthetized deer and photographs of the regions under observation. Operations were performed in the springs of 1959 and 1960, and the final results obtained late in the respective summers.

RESULTS

Because of the difficulty and expense involved in acquiring and maintaining deer, it is not always feasible to repeat experiments on numbers of animals. Since most of the various operations described below were performed on single animals, the results obtained cannot be regarded as being as reliable as one might prefer. However, in those cases in which similar experiments were carried out on more than one deer the results were highly consistent, arguing in favor of the validity of other single experiments.

Total transverse amputation

Shedding of the dead antler in the spring may be regarded as an example of autotomy which is followed by the regeneration of a new antler from the pedicle. Obviously, therefore, the greatest antler-producing potential resides in the tissues of the pedicle immediately proximal to the level at which the old antler breaks off. Since this natural case of amputation is followed by the production of a new antler, it is of some interest to explore the antler-producing capacities of other regions, namely, the more proximal parts of the pedicle, as well as the growing antler itself.

Inasmuch as the developing antler appears to elongate by virtue of the growth of an apically located mass of undifferentiated cells, experiments were performed to determine the extent to which the antler can compensate for the loss of this growing tip. In two deer, this part of the antler was amputated transversely about 1 cm. below the apex. In one animal (deer 36), the end of a 6-inch bifurcate antler was removed on June 7 (Plate 1, fig. A). This operation effectively interfered with further development, except for the production of a tapered 2-inch outgrowth formed from the stump (Plate 1, fig. B). The opposite antler became a normal 3-pointed structure nearly twice as long as the operated one. In a younger animal (deer 9) the tip of a growing antler about 1·5 inches long was amputated on July 23 (Plate 1, fig. C). This antler was able to produce only a pointed outgrowth less than 2 inches in length (Plate 1, fig. D), in contrast to the unoperated contralateral antler which had two points and was three times the length of the experimental one. These experiments testify to the importance
of the growing tip in ensuring normal elongation and morphogenesis in the antler. Yet because some growth did occur in both cases despite the removal of the terminal end of the antler, it is apparent that the antler is capable of compensating to a very limited extent for the loss of its growing tip. These results are best explained on the basis of the distribution of undifferentiated, proliferating cells in the growing region of the antler. Largely concentrated at the very apex, significant amounts of such tissue also extend down the sides of the antler. The level of amputation was sufficiently distal to leave behind some of this marginal tissue, which was apparently capable of subsequent reorganization and limited resumption of growth. Indeed, injury to this side of an antler regularly brings about the formation of exostoses, and Bubenik (1959) described the growth of a new side branch in a reindeer antler after the original one had been broken off.

Amputation of the pedicle results in less serious disturbances to the growth of antlers. Normal antler production following loss of both antler and pedicle has been reported in the moose (Jaczewski, 1954) and in the red deer (Jaczewski, 1955). In the present investigation, two deer were subjected to pedicle amputation. One animal (deer 19) was nearly 2 years old and had short, 1-inch spike antlers which had not yet been shed. Amputation was performed by sawing through the middle of the left pedicle on 18 March, which was 77 days before the right antler was normally shed (June 3). The operated pedicle failed to heal until after the opposite antler was lost. Thus, for nearly 3 months the severed pedicle bone protruded as a bare stump, although the skin on the sides of the pedicle exhibited the usual tumescence characteristic of the preparatory changes in that region prior to actual antler growth (Plate 1, fig. E). After shedding of the old antler on the right side, healing of the pedicle occurred normally on both sides, and identical normal antlers developed from both pedicles (Plate 1, fig. F).

In deer 38 the left pedicle was completely removed at the level of its basal attachment to the skull on 7 June (Plate 1, fig. G), which was less than 1 week after the old antlers had been shed. The wound healed normally and then proceeded to give rise to an antler which appeared normal except that its development lagged behind that of the normal right antler. By 26 August, when the right antler had attained its full size and form (3 points), the left antler had achieved a length equal to half that of the control, and exhibited every indication of still being in an active state of growth (Plate 1, fig. H). At its tip it was rounded and soft, and was beginning to branch. Further growth resulted in a terminal bifurcation. On 24 September it was in the process of shedding its skin, several weeks after the control antler had done so.

Partial excision of antler tissues

In order to investigate the possibility of morphogenetic regulation in the antler following surgically inflicted defects, a series of experiments was performed in which portions of pedicles or of antler buds were removed at various
times before or after shedding and initiation of antler growth. Future development was observed to determine the extent to which the morphology of the resultant antler reflected the effects of the original operation.

In one group of animals the posterior half of the antler bud or pedicle was extirpated. When the posterior half of a young antler about 1 inch in height was removed on 23 April (deer 4: Plate 2, fig. A), growth continued anteriorly to produce a normal brow tine, but the development of the rest of the antler was seriously disturbed. By 21 May, when the main branch of the control antler was elongating rapidly (having attained a length of about 6 inches), the operated antler had produced an abortive outgrowth directed posteriorly (Plate 2, fig. B). This structure continued to grow throughout the summer at a very slow rate, eventually becoming about 3 inches long (Plate 2, fig. C). On the opposite side, a large normal 3-point antler was formed. A similar operation on another younger animal (deer 32) was performed at the same stage of development. The posterior part of the young bud was excised on 3 June. In this case, less tissue was removed than in the previous example (cf. Plate 2, figs. A and D). Two weeks later the brow tine had elongated considerably, but there were no longer indications of growth of the rest of the antler from the posterior region (Plate 2, fig. E). At the end of the summer, only a very small (1-inch) spur had formed posteriorly, while the anterior brow tine had grown to a length of some 6 inches (Plate 2, fig. F), nearly twice as long as the corresponding tine on the opposite normal 3-point antler.

Removal of the posterior half of an even younger antler primordium was performed on deer 22. The left antler had been shed less than 1 week previously and the pedicle stump had healed over but was still flattened on the end. Only the soft tissues of the incipient antler plus part of the adjacent pedicle skin were removed on 20 April (Plate 3, fig. A). Healing of the wound was followed by the posteriorly directed growth of the remaining anterior part of the antler bud (Plate 3, fig. B). After 1 month, a large rounded mass of tissue had formed which proceeded to become elevated posteriorly (Plate 3, fig. C). There were no indications of the formation of a brow tine, but this was also lacking in the opposite control antler, except for an extremely diminutive protuberance. The posterior outgrowth from the left antler had become nearly 2 inches long 6 weeks after the operation (Plate 3, fig. D) and continued to grow throughout the summer. It eventually grew to a length of approximately 5 inches (Plate 3, fig. E), which was about one-third the length of the control antler.

A final experiment in this series involved the removal of the distal, posterior half of the left pedicle of deer 25 on 29 April, about 3 weeks prior to shedding. Wound healing occurred normally after the operation (Plate 3, fig. F) as well as after shedding. The antler bud formed on the experimental side (Plate 3, fig. G) was originally semicircular in shape but gradually assumed a more symmetrical outline as tissue invaded what had once been the posterior side of the pedicle. It then grew into a normal 3-point antler during the course of the summer (Plate 3,
fig. H). Thus, with respect to the posterior half of the antler, it would appear that the earlier the defect is inflicted, the more complete is the morphogenetic regulation.

Additional studies of the regulatory capacities of the pedicle were conducted on 3 deer. In one animal (deer 31), the anterior half of the pedicle was removed on the day (21 May) that the old antler was shed (Plate 4, fig. A). The right antler had been lost the day before. After 2 weeks, wound healing had taken place and a rudimentary antler had formed. Four weeks after the operation the young antler had become about 2 inches long and had partly filled in the missing anterior half of the pedicle (Plate 4, fig. B). Subsequent growth resulted in the production of a nearly normal antler (Plate 4, fig. C). Although it lacked a brow tine, and was slightly shorter than the control at its branched end, it is clear that the absence of the anterior half of the pedicle causes only minor disturbances in the development of the antler. In deer 28 the median half of the pedicle was ablated (21 May) a few days after shedding of the old antler (Plate 4, fig. D). From this deficient pedicle there developed a 3-point antler of normal size and proportions (Plate 4, fig. F). The brow tine was absent, but in this particular animal the control antler also lacked this branch.

Although excision of the anterior, posterior, and median halves of the pedicle had little or no effect on the final outcome of antler development, removal of the lateral half of the pedicle was responsible for the complete failure of antler renewal. In deer 30, which had lost its left antler less than a week before, the lateral half of the incipient antler bud, along with the pedicle, was removed on 21 May (Plate 4, fig. G). Although healing occurred as in previously described cases, the residual tissues of the early antler bud failed to grow any farther, and at the end of the summer only a rounded remnant of the bud persisted on the pedicle (Plate 4, fig. H). From this result it would appear that the lateral portion of the antler bud and/or pedicle is particularly important for the production of a normal antler, a conclusion which is substantiated by the experiment described below.

To learn to what extent a young antler bud is morphogenetically determined, an anterior-posterior wedge of tissue was excised from the middle of a bud 1 inch high (deer 5, operated 23 April). Although this antler bud was thus split into median and lateral halves (Plate 5, fig. E), an antler grew only from the lateral half. The other side of the original bud remained only as a small excrescence on the median basal region of the otherwise normal 4-point antler (Plate 5, fig. F). This experiment demonstrates that the lateral half of the young antler bud is capable of giving rise to a complete antler, but that the median half is not. It had been expected that if the bud were split into two halves, there would grow a set of double antlers. Since this did not occur the first time, the experiment was repeated on another animal (deer 27) the following year. This time the anterior-posterior cleft in the 1-inch high antler bud was made just lateral to the mid-line on 6 May (Plate 5, fig. A). A week later healing was
complete and the median and lateral halves of the divided antler were developing independently (Plate 5, fig. B). Already, however, bifurcation was evident in the lateral half, while the median portion was deficient in this regard. After 4 weeks (Plate 5, fig. C), the two antlers had grown to a height of approximately 6 inches, and by the end of the summer (Plate 5, fig. D) they had become almost as long as the normal 4-point antler produced on the right side. Neither the left median nor the left lateral antler had become branched at their upper ends, a result possibly attributable to the mutual reduction in the total amount of formative material available to each half. Although both sets of antlers were abnormal, it is noteworthy that the lateral one was the more complete inasmuch as it had a brow tine. This again emphasizes the dominant nature of the lateral portion of the young antler bud.

A final experiment along similar lines involved the cleavage of an antler bud in the median-lateral direction (Plate 5, fig. G). This operation was performed on deer 35 on June 7, and served to emphasize precociously the natural bifurcation which normally gives rise to the brow tine anteriorly and the rest of the antler posteriorly. Thus, this kind of a defect had no observable effect on the future development of the antler. In this deer, both left and right sides produced normal and equal 3-point antlers (Plate 5, fig. H). Similar experiments on roe bucks by Bubenik & Pavlansky (1959), however, yielded duplicate, albeit abnormal, antlers.

DISCUSSION

The experimental results herein related demonstrate that the developing antler is capable of morphogenetic regulation following injury, but that this is profoundly affected by the stage of antler development at the time of operation as well as the location of the defect. Well-developed antlers in which growth is still in progress are especially susceptible to injury and incapable of compensating for loss of the growing tip. Nevertheless, if part of the undifferentiated apex of an antler remains (as was the case in the present studies), it is able to continue growth but to a very limited extent. In this respect, it would be of interest to remove just half of the tip of an advanced antler to determine if this would affect subsequent morphogenesis in the same way that excision of parts of the young antler bud does. In the latter instance, removal of the posterior half of the early antler bud (1 inch long) resulted in serious deficiencies in the future growth of the antler. Regulation at this stage is practically absent. The comparable experiment performed on an even younger bud which had not yet become rounded, however, was followed by a significant degree of morphogenetic adjustment. Indeed, when the posterior half of the pedicle itself is excised before loss of the old antler, there develops a completely normal antler. Similarly, removal of the anterior or median halves of pedicles around the time of antler shedding does not have serious consequences on the future course of antler development.
TEXT-FIG. 1. Illustrative summary of certain of the experiments and their results described more fully in text. Blackened areas on left designate portions of antlers and/or pedicles removed. On the right are diagrammatically illustrated the resulting extents of antler growth and development in relation to normal control antler structures (broken lines).
Thus, with the exception to be noted below, the antler pedicle is capable of considerable regulatory potentialities before shedding or during the very early phases of antler growth. How long after this it retains such capacities has not been determined as yet. The incipient antler can likewise compensate for experimental injuries, but as growth proceeds this capacity rapidly diminishes.

The lateral side of the pedicle appears to be particularly important in antler production. Perhaps this is related to the fact that antlers normally grow at a laterally directed angle from the head of the deer. Not only can the lateral half of the pedicle alone give rise to a complete and normal antler, as already mentioned above, but also the lateral half of the 1-inch antler bud can develop into an entire structure, something which the anterior half cannot do. Conversely, if the lateral half of the pedicle is removed, no antler develops. Removal of the posterior, anterior, or median halves of pedicles permits typical antler growth. Judging from these results, the greatest morphogenetic potential of the pedicle and the antler bud is concentrated in the lateral region. Nevertheless, this area is capable of being subdivided, for double antlers can be produced experimentally by longitudinally cleaving the antler bud lateral to the centre. Naturally occurring instances of antler duplication have been reported in the literature. Bland-Sutton (1890) mentioned a case of dichotomy in moose antlers, and Kitchener (1954) described an antler of a Malayan Sambar deer which possessed a double brow tine. When duplication of a structure is possible, the opposite phenomenon of unification may also occur. Thus, Dove (1936) was able to produce an artificial unicorn in an Ayrshire bull by fusing horn buds in the calf. Tegner (1954), Fooks (1955), and Whitehead (1955a) described partially coalesced antlers in roe deer. Inasmuch as duplication and fusion have been shown to occur, it would appear that antlers (and horns) develop under the influence of morphogenetic fields.

The primary site of antler production resides in the pedicle. Under normal circumstances the distal region of the pedicle provides the requisite materials for antler formation. This usually follows loss of the old antler, but antler renewal will occur even if the shedding of the old one is delayed. In this eventuality, growth occurs to the side of the persistent old antler, usually in a lateral direction. Accessory antler production from the side of the pedicle has occasionally been reported (Gadow, 1902; Rhumbler, 1916; Whitehead, 1955b), and is probably the result of injury to the pedicle. Even removal of the entire pedicle is not sufficient to preclude antler production. The limits of the 'antler territory' have not yet been determined.

The regeneration of the antler is somewhat unique since the structure formed is not always an exact replica of that which is replaced. As the deer matures, successive sets of antlers may develop to increasingly elaborate extents, from a single spike in the young buck to repeatedly branched racks in mature stags. It is of interest to correlate several sets of facts related to this phenomenon. The larger the animal, for example, the more highly branched are its antlers. This is
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correlated with the greater diameter of the pedicle supporting such antlers. These large antlers are shed earlier than are smaller antlers in young deer. This early loss of the larger antlers is followed by the precocious initiation of new antler development and a longer growing season which is required for the production of such a massive amount of tissue. From these observations it is tempting to speculate that the degree of morphological development of the antler (i.e. the number of branches) may be solely related to the amount of tissue initially available in the young, undifferentiated antler bud. This, in turn, is obviously related to the diameter of the pedicle and the age of the animal. As development progresses and bifurcation occurs, the sizes of the growing apices diminish and further branching is correspondingly reduced. When the young antler bud is bisected (as in deer 27) double antlers are produced which fail to branch terminally. Perhaps this is due to the mutual reduction in the amount of formative material in the two halves. Further experiments designed to test the possible relation between mass of available tissue and degree of morphogenetic expression are in order.

SUMMARY

1. Investigations of the morphogenesis of antler growth have been undertaken in the sika deer (Cervus nippon). Operations were performed on the left antlers, while the intact right antlers served as controls.

2. Amputation of the terminal centimetre of growing antlers seriously impedes further development except for the production of an abortive outgrowth from the stump. By contrast, transverse amputation through the middle of the pedicle is followed by normal antler formation. Removal of the entire pedicle permits antler development to occur, although at a retarded rate. Therefore, antler-forming potentiality resides in the growing tips of the elongating antler as well as in the tissues of the entire pedicle.

3. The extent of morphogenetic regulation for defects surgically inflicted on the antler bud or pedicle depends on the age of the antler and the location of the injury. Excision of the posterior halves of 1-inch antler buds results in corresponding deficiencies in the antlers produced. The same injury to an extremely rudimentary bud, however, is followed by considerable regulation, and removal of the posterior half of the pedicle prior to shedding of the old antler has no effect on the normal development of the resulting antler. Ablation of anterior or median halves of pedicles likewise causes no morphogenetic abnormality, but if the lateral half of the pedicle is removed no antler develops. The importance of the lateral half of the antler-forming structure is further illustrated by the fact that a complete and normal antler can grow from just the lateral half of a pedicle or of a 1-inch antler bud.

4. The morphogenetic field of the antler can give rise to double antlers if bisected longitudinally; transverse subdivision, however, does not alter subsequent normal production of a single antler. It is proposed that a relationship
between the initial mass of antler-forming material and the degree of morphogenetic expression may possibly exist.

RÉSUMÉ

Recherches expérimentales sur la morphogenèse des bois du Cerf en cours de croissance

1. Des recherches sur la morphogenèse et la croissance des bois ont été entreprises chez le Cerf Sika (*Cervus nippon*). Les opérations ont été réalisées sur les bois gauches, ceux de droite, intacts, servant de témoins.

2. L'amputation du centimètre terminal des bois en cours de croissance empêche leur développement ultérieur, excepté en ce qui concerne la formation d'une excroissance abortive à partir du moignon. Par contraste, l'amputation transversale au milieu de la tige est suivie de la formation d'un bois normal. L'ablation de la tige entière permet le développement du bois, mais à un rythme ralenti. Ainsi, la potentialité formatrice du bois réside dans l'extrémité en croissance de celui-ci aussi bien que dans les tissus de la tige entière.

3. L'étendue de la régulation morphogénétique des blessures infligées chirurgicalement au bourgeon ou à la tige du bois dépend de l'âge de ce dernier et de l'emplacement de la blessure. L'excision des moitiés postérieures de bourgeons de 25 mm. provoque des déficiences corrélatives dans les bois produits. Néanmoins, la même blessure infligée à un bourgeon très rudimentaire est suivie d'une régulation considérable et l'ablation de la moitié postérieure de la tige, avant la chute du vieux bois, n'a pas d'effet sur le développement normal du bois suivant. De même, l'ablation des moitiés antérieure ou médiane des tiges ne provoque pas d'anomalies morphogénétiques, mais il ne se développe pas de bois si on ôte la moitié latérale de la tige. L'importance de cette moitié latérale est encore soulignée par le fait qu'un bois complet et normal peut croître à partir de la seule moitié latérale d'une tige ou d'un bourgeon de 25 mm.

4. Le champ morphogénétique du bois peut donner naissance à des bois doubles s'il est sectionné en deux longitudinalement. Une subdivision transversale, néanmoins, n'altère pas la formation ultérieure normale d'un bois unique. On suggère l'existence possible d'un rapport entre la quantité initiale de matériel formateur du bois et le degré de son expression morphogénétique.

ACKNOWLEDGEMENTS

The indispensable technical assistance of Miss Marsha Rankin is gratefully acknowledged. The author is also indebted to Mr. Robert Bolinder, of the Dama Dama Game Farm, Middleborough, Massachusetts, for his co-operation in caring for the experimental animals.

These investigations have been supported by a research grant (B–923) from the National Institute of Neurological Diseases and Blindness of the National Institutes of Health.
REFERENCES


EXPLANATIONS OF PLATES

Plate 1

Fig. A. Photograph of left antler of deer 36 on 7 June, the day the apex was amputated at the leve indicated by the transverse line.

Fig. B. Same antler on 26 August, showing the abortive terminal point.

Fig. C. Left antler of deer 9, showing level of amputation of its tip on 23 July.

Fig. D. Same antler on 25 September. A short, tapered point has grown from the stump.

Fig. E. Deer 19, on 29 April, 42 days after the distal half of the left pedicle had been amputated, and 35 days before shedding of the right antler. In the absence of wound healing, the pedicle bone has remained exposed.

Fig. F. Normal antler (26 August) produced from the left pedicle of deer 19.

Fig. G. Appearance of deer 38 on 7 June, when its left pedicle was totally removed at the level of the skull.

Fig. H. Same animal on 26 August. The left antler, though retarded, is otherwise normal.

Plate 2

Fig. A. Deer 4, on 23 April, showing the amount of tissue removed from the posterior portion of the young antler bud.

Fig. B. Four weeks later, this antler has formed a typical brow tine, but is abnormal posteriorly.

Fig. C. Same antler on 24 September. The final configuration of the antler indicates that the development of the main branch of the antler was seriously impeded by excision of the posterior half of the young bud.

Fig. D. Deer 32, on 3 June when part of the posterior region of the left antler bud was amputated at the level indicated.

Fig. E. Same antler on 18 June. The brow tine is growing normally, but no growth has occurred from the posterior part of the antler.

Fig. F. The final form of the left antler of deer 32 (26 August) is represented by an elongate brow tine.
FIG. A. Deer 22 immediately after operation on 20 April. All soft tissues of the incipient antler bud were removed posterior to the level indicated by the arrow.

FIG. B. Same animal 16 days later (6 May). Wound healing has occurred and growth of the remaining anterior part of the antler is in progress.

FIG. C. Same antler on 21 May. The originally defective antler bud has become reconstituted and is beginning to elongate.

FIG. D. Same antler on 3 June. Though considerably retarded with respect to the opposite control antler, growth in the normal direction is occurring.

FIG. E. Final appearance of the left antler of deer 22 (26 August). It reached a length about one-third that of the control.

FIG. F. Appearance of left pedicle of deer 25 on 14 May, 2 weeks after excision of its posterior half. The base of the old antler, most of which had previously been cut off, remained attached to the pedicle for about another week.

FIG. G. Two-week-old antler bud (3 June) formed on anterior half of the same pedicle. Antler-forming tissue is invading the posterior region of the pedicle.

FIG. H. Same antler on 26 August, illustrating the normal appearance of the antler produced from the anterior half of the pedicle.

FIG. A. Deer 31 on 21 May after removal of the anterior half of the left pedicle (arrow). The old antler was shed on the same day.

FIG. B. Same animal on 18 June. The anterior region of the pedicle has been partly filled in, and elongation of the antler is proceeding normally.

FIG. C. Appearance of the same antler on 26 August when the full extent of its growth had been achieved. It departed from the control only in its slightly shorter length and in the absence of the brow tine.

FIG. D. Deer 28 on 21 May after excision of the median half of the left pedicle (several days after shedding of the old antler).

FIG. E. Same animal 4 weeks after operation. A normal antler is forming.

FIG. F. Appearance of deer 28 on 26 August. The animal's left experimental antler is identical with the control.

FIG. G. Front view of deer 30 on 21 May when the lateral half of the left pedicle was removed less than a week after shedding of the old antler.

FIG. H. Same animal on 26 August, showing the presence of only a rudimentary mass of tissue on the operated side (arrow) in contrast with the normal antler produced on the right side.

FIG. A. Appearance of deer 27 following removal of a segment of tissue slightly lateral to the mid-line of the left antler bud (May 6).

FIG. B. Front view of same antler on May 14, showing continued but separate growth of the two parts of the antler. The lateral portion has bifurcated.

FIG. C. Same antler on June 3. Further growth of the double antler.

FIG. D. Final form of the same antler in lateral view (August 26). The two components of the double antler have elongated considerable, but have failed to branch at their ends.

FIG. E. Deer 5 after excision of an antero-posterior wedge of tissue dividing the antler bud into median and lateral halves.

FIG. F. Median view of same antler after the final normal form had been attained. The antler grew entirely from the lateral half, while the median half gave rise only to a diminutive outgrowth (arrow). Remnants of the original scar can still be seen.

FIG. G. Deer 35 following bisection of the young antler into anterior and posterior halves (June 7).

FIG. H. The same animal, on August 26, had developed a normal pair of identical antlers, indicating the inefficacy of the original operation.

(Manuscript received 1 : xii : 1960)
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Plate 4