

THE MODIFICATION OF THE CLOACA AND TEETH
OF THE ADULT SALAMANDER, *DESMOGNATHUS*,
BY TESTICULAR TRANSPLANTS AND BY
CASTRATION

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(With Four Text-figures and Two Plates.)

IN 1926 de Beaumont showed that some of the secondary sexual characters of the male newt, *Triturus cristatus*, could be produced in the spayed female by testicular transplants. About the same time one of us (Noble, 1926) noted that cloacal glands could be made to arise *de novo* in the glandless cloaca of the female *Desmognathus fuscus fuscus* by the same method. Ponse (1923) with young females, and Welti (1925) with adult females, had previously demonstrated that toads which had been experimentally masculinised would develop nuptial pads. The above investigations were of interest in that they demonstrated, in both Caudata and Salientia, that structures not visible even as rudiments in the female could be made to appear and develop under the influence of the male sex gland.

In 1928 de Beaumont found that in the female *Triton cristatus* 24 months after transplanting the testis both the nephritic tubules and the terminal portion of the Wolffian duct developed secretory activity characteristic of the male. Nakamura (1927) had previously shown that the cloacal papilla of the male *Triturus* develops under the influence of the thyroid and not of the testes, and de Beaumont found that transplanting the testis did not develop this structure in the female *T. cristatus*. Cloacal glands were developed in the masculinised female, and de Beaumont apparently found as Noble had previously described in *Desmognathus* that these arose from the unspecialised epithelium of the cloaca. Some glandular rudiments were present in the posterior part of the female cloaca of *T. cristatus*, and these were modified by testicular influence into abdominal glands characteristic of the male. De Beaumont observed that the spermatheca in the female, after testis transplantation, took on secretory activity and developed into a pelvic gland. Thus de Beaumont, by transplanting a testis into the female, confirmed Noble's findings that the cloacal glands may arise from unspecialised epithelium in a masculinised female salamander. He further showed that the abdominal glands are homologous to gland rudiments at the posterior end of the cloaca of the female newt, and that the pelvic gland was the homologous equivalent of the spermatheca.

The last finding was of special interest in that we had reported in a preliminary communication (Noble and Davis, 1928) that in *Desmognathus*, where the spermatheca is a series of tubules opening into a common duct, the pelvic gland, induced in the adult female by a testicular transplant, arises in part outside the spermatheca from the unspecialised epithelium of the cloacal roof. Hence, the spermatheca is homologous to the whole pelvic gland of *Triturus* and only to part of it in the more specialised *Desmognathus*.

The present paper presents a full report on these induced changes in the cloaca of the adult female salamander *Desmognathus* previously described in the form of a note. It also includes an account of the changes produced in the dentition of the female by testicular transplants and in that of the male by castration. One of us had previously reported (Noble, 1926) that castration of the male *Desmognathus fuscus fuscus* causes the monocuspid premaxillary teeth to be replaced by bicuspid ones characteristic of the female. In the present study we have extended these experiments to another form. The plethodontid salamanders are remarkable among amphibia in the great diversity of dentition found in the various species and in the pronounced sexual dimorphism which often occurs. A discussion of the significance of these differences has been given elsewhere (Noble, 1927).

MATERIAL AND METHODS.

In the present study we have used two races of dusky salamanders: *Desmognathus fuscus fuscus* from the New York region, and *D. f. carolinensis* from the Pisgah-Flat Rock section of North Carolina. As previously noted (Noble, 1927), the two races differ markedly from one another in dentition. Further, specimens of *D. f. carolinensis* from the Great Smokies have a different type of dental modification than that considered here. The subspecific status of these specimens will be considered in another paper.

The salamanders throughout the experiments were kept in separate "Woods Hole" finger bowls of 350 c.c. capacity. The dishes were cleaned and sterilised with lysol or potassium permanganate at frequent intervals. A layer of pebbles or a sheet of Scot Tissue was added to the bottom of the dish and moistened with Great Bear Spring water; these materials were changed for a fresh supply two or three times a week. The dishes were exposed to diffuse daylight at room temperature, and the salamanders were fed approximately twice a week with worms. If they became infected with a growth of fungus they were washed in a weak solution of potassium permanganate.

Before operating, the salamanders were anaesthetised in a 1 to 2000 solution of chloretone. The gonads were removed through a small longitudinal slit made on the right or left side of the body a short distance above the ventral surface. The wound was closed with a few stitches which were removed about ten days after the operation. All the teeth in both the experimentals and controls were taken out by bending them inwards with a blunt-edged instrument until they broke off; the jaws were then scraped with a scalpel or the same instrument, until all

visible tooth rudiments had been removed. The above manipulations were made under a binocular microscope.

The cloacas were fixed in Zenker's fluid and stained in hematoxylin and eosin. The teeth were studied by clearing the whole head in potassium hydroxide after staining in alizarin. Formalin and dilute glycerine were used as retarders and no preliminary fixation in strong alcohol was required. Heads which did not clear readily were treated with concentrated ammonia for a few days and then replaced in the solution of potassium hydroxide.

EFFECT ON THE CLOACA OF TRANSPLANTING A TESTIS INTO THE ADULT FEMALE *DESMOGNATHUS FUSCUS* AFTER SPAYING.

The cloaca of the adult male *Desmognathus fuscus* is lined with three sets of glands (Pl. VIII, fig. 1 a). These are distinguished by the character of their secretion in both the living animal and in the histological preparations of the cloacal region. The secretion of the pelvic gland is creamy white in life. It stains a bright orange in Mallory's and a vivid pink in hematoxylin-eosin preparations. The cloacal glands produce a secretion which is transparent and gelatinous in fresh material and stains pale blue in both Mallory and hematoxylin-eosin slides. The secretion of the abdominal gland is also transparent but is less adhesive than that of the cloacal glands. It stains a purplish colour in Mallory's and a pink in hematoxylin-eosin. Moreover, there are differences in the character of the secretion in fixed and stained material. As pointed out elsewhere (Noble and Weber, 1929) the secretion of the pelvic gland mixes with the spermatozoa to form the head of the spermatophore, while the cloacal gland secretion forms the base of the spermatophore. The abdominal gland secretion probably has a hedonic effect. The pelvic glands open on the roof and upper portions of the sides of the cloaca, usually at the tips of short papillae. On the sides of the cloaca their ducts are carried by longer papillae. Immediately adjacent to the pelvic gland papillae are those which are traversed by the ducts of the cloacal glands. The papillae of the cloacal glands form the greater part of the villous pad on either side of the cloaca. Some cloacal glands open on the roof of the cloaca at its posterior end. The extreme posterior angle of the cloaca is occupied by the abdominal glands. Their larger ducts empty just within the lips of the cloaca.

Within the cloaca of the female *D. fuscus* there are no glands, but in the roof there is found the spermatheca which has very much the same form as that reported by Koehring (1925) for *Eurycea bislineata*. The number of tubules in *Desmognathus* varies between five and six (Kingsbury), while in *Eurycea* it varies between seven and sixteen. Typical glands have been reported from the cloaca of various urodeles (Kingsbury, 1895) and it has been assumed by some that they function in the production of the outer gelatinous coat to the egg. However, it has been established that some salamanders which have no cloacal glands nevertheless may have more than one egg-capsule (Noble and Marshall, 1929). In these forms, the oviduct must be differentiated to produce different kinds of secretions in its different

sections. This leaves the question open as to the significance of the cloacal glands in the female *Amblystoma*, *Necturus*, and *Eurycea*. It may be that they are rudimentary male structures retained by the female. In the present study it is important to emphasise that there are no rudiments of any of these glands present in the cloaca of the female (Pl. VIII, fig. 1 *b*).

Transplanting the two testes of a male *D. fuscus* into the body cavity of a female, after removing the ovaries through a small opening in the side of the body, results in the development of glandular structures in the cloacal wall, provided the testes are not later entirely absorbed, that the ovaries have not regenerated to a marked extent, and that sufficient time is allowed after the operation before the cloaca is studied. In the present series there are three females (F. 7, F. 10 and F. 11) in which testes were successfully transplanted after spaying. They lived 220 days before being killed. The transplantations were performed November 10. The condition of the transplants when the specimens were killed on June 17 was as follows: in F. 7 the transplant was attached to the posterior part of the left ovarian mesentery, and the anterior portions of the ovaries were regenerating; in F. 10 two large lobes of the testis were attached to a small remnant of the ovaries; and in F. 11 the transplant was attached to the ovaries which had partly regenerated. As shown in Pl. IX, fig. 2 *b*, all three sets of glands of the male are already well formed in the cloaca of one of the females (F. 10). Of the three glands, the abdominal is the least developed. The pelvic gland is seen to be arising partly from the common duct of the degenerating spermatheca and partly from the roof of the cloaca immediately posterior to the common duct. In another section of the same cloaca, five other ducts of the pelvic gland are found opening on the roof of the cloaca immediately anterior to the common duct. It is thus proved that the spermatheca of the female *D. fuscus* is homologous only to part of the pelvic gland, since, when testes are transplanted and a pelvic gland arises under the influence of these organs, a large part of the pelvic gland develops from undifferentiated epithelium in the roof of the cloaca both anterior and posterior to the common duct.

The other two females of the series have the glands less developed than those found in F. 10 after the same number of days. Nevertheless, their cloacas are instructive in showing an earlier stage in gland formation.

In the 1926 series previously reported by Noble, the earliest appearance of the cloacal glands occurs 50 days after transplantation of the testes into the female. This is shown by specimen D. 19 operated on May 5. Other experiments (D. 1, D. 4 and D. 17) performed the same year were equally successful. D. 1 received parts of four testicular lobes (all from one male); D. 4 also four pieces but these were broken parts of testes; D. 17 was given two whole testicular lobes and two partly broken lobes. The duration of these 1926 experiments was much shorter than in the 1927 series. D. 17 was killed 62 days, D. 1 and D. 4 approximately 80 days after operating. As shown in Pl. IX, fig. 2 *a*, both cloacal and pelvic glands are already well sprouted in D. 17. It is clear from other sections of the cloaca of D. 17, as well as from sections of D. 1 and D. 4, that the pelvic gland arises partly from the common duct of the spermatheca and partly from the roof of the cloaca near

the mouth of the common duct. Thus, both the 1926 and the 1927 series demonstrate that the spermatheca is homologous only to part of the pelvic gland of the male.

In one of the 1927 series (F. 13) we removed only part of the ovary, on November 11, before transplanting a testis. After 154 days the testis graft was found attached to the mesenteries between the remnant of the ovary and the cloaca. Sections of the graft revealed an active spermatogenesis. Nevertheless, no evidence of gland development could be found in the walls of the cloaca. Therefore, it would seem that the ovary had prevented the testicular hormone from inducing the development of glands in the cloaca.

EFFECT OF CASTRATION ON THE TEETH OF *DESMOGNATHUS FUSCUS CAROLINENSIS*; EFFECT OF TESTICULAR TRANSPLANTS ON THE DENTITION OF THE ADULT FEMALE *DESMOGNATHUS FUSCUS FUSCUS*.

As previously reported (Noble, 1926), castration causes the monocuspid, anteriorly directed, premaxillary teeth of the adult male *Desmognathus fuscus fuscus* to be replaced by shorter bicuspid ones characteristic of the female. The best result was obtained in a specimen (D. 2) which was castrated on March 29, the teeth being left intact. After 84 days the premaxillary teeth were distinctly female in appearance.

D. f. fuscus does not exhibit as pronounced a sexual difference of dentition as its subspecies *D. f. carolinensis*, and in repeating these experiments in 1927 we used chiefly the latter form. As shown in Fig. 1 *b* the dentition of the adult male of *D. f. carolinensis* is markedly different from that of the female (Fig. 3 *a*). The premaxillary teeth are monocuspid and directed forward; the maxillary broadened antero-posteriorly, especially the lingual cusp; the dentary teeth are hypertrophied, the inner more than the outer cusp, and are restricted to the anterior part of the jaw; vomerine teeth are lacking. The maxillary bone has a sinuous ventral margin and the dentary is broadened in a manner which makes its dorsal edge roughly correspond to the ventral edge of the maxilla. A comparison of these secondary sexual features with those found in the jaws of other species of *Desmognathus* had previously been made (Noble, 1927), but for the purposes of this paper it should be stressed that the broadest maxillary teeth in *D. f. carolinensis* are found at the most ventral points of the bone; namely, at the extreme anterior end and at a point a short distance from the posterior end. In some cases very broad teeth will be found along the concave section of the margin of the maxillaries (Noble, 1927, Pl. IX, fig. 2 *b*) but usually teeth from this region are smaller and narrower than the teeth lying on the convex edges. There is thus a certain variation in the form of the maxillary teeth, but the teeth are always sufficiently different to be distinguished from the teeth of the female.

Although some of these sexual differences of dentition were described by Cope (1889), and others reported by Dunn (1926), all the characters mentioned above were not made known until very recently (Noble, 1927). The characters seem to

be constant in all large adult specimens of *D. f. fuscus* and *D. f. carolinensis*. The teeth which develop in the controls under laboratory conditions are identical to those found in specimens recently captured in the field. Further, there is in the American Museum a large series of preserved specimens of these two races. All males of *D. f. carolinensis* over 27 mm. snout to vent have monocuspid premaxillary teeth, while one male 26.5 mm. snout to vent has bicuspid premaxillary teeth. Of the specimens examined 28 were males. Unfortunately, these specimens were all preserved in June, July and August (with the exception of five that had no dates), and hence are not as good a check as our controls which came from the same

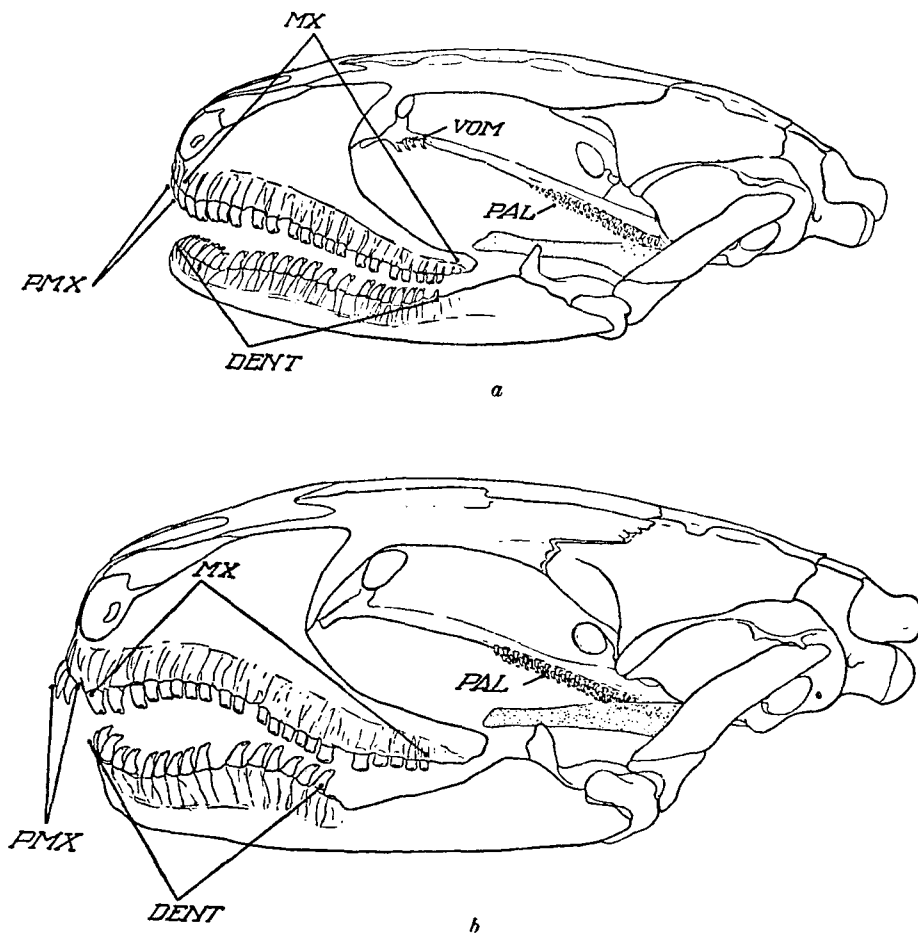


Fig. 1. The skull of the normal female (a) and the normal male (b) *Desmognathus fuscus carolinensis*, drawn to the same scale, illustrating the secondary sexual differences of jaws and teeth. *Dent.* = dentary teeth; *mx.* = maxillary teeth; *pal.* = palatine teeth; *pmx.* = premaxillary teeth; *vom.* = vomarine teeth.

locality and were approximately the same size as our experimental animals. In the case of *D. f. fuscus*, there is a size overlap in the monocuspid and bicuspid series. Adult males, collected in January, April, May, August, October and November have monocuspid premaxillary teeth, while a few males the same size have bicuspid ones. The length from snout to vent of the monocuspid *D. f. fuscus* series (25 specimens) is 60.5 mm. maximum, 29 minimum, 40.1 average; of the bicuspid series (19 specimens), 40 mm. maximum, 28 minimum, 31.7 average. Our laboratory specimens have demonstrated that there is no seasonal change (under laboratory conditions) in the teeth of either race of *D. fuscus*, but the American Museum collection shows that the male of *D. f. fuscus* may reach sexual maturity at various sizes.

It may be stated as a word of warning in using plethodontids for this experimental work that other species may show a pronounced seasonal change in their dentition. For example, the common eastern salamander *Eurycea bislineata bislineata* and the western *E. melanopleura* undergo a remarkable change in their dentition. Adult males have hypertrophied monocuspid teeth in both jaws during the autumn which seems to be the mating season of the former species (Noble and Weber, 1929). Males of these species captured in the late spring have short bicuspid dentary, maxillary and premaxillary teeth. This seasonal variation has not been previously described, and it is obvious that certain published statements in regard to the dentition of plethodontids will be modified as breeding males are made known. For example, large and apparently breeding males of *E. guttolineata* and *E. lucifuga* have the dentary teeth not merely exhibiting a tendency to elongate as already described (Noble, 1927) but are proportionately as long and as spikelike as the teeth of *E. bislineata* and of *E. melanopleura*. It appears likely, therefore, that all species of *Eurycea* will be found to undergo a seasonal fluctuation of teeth in both jaws from a bicuspid to a monocuspid condition.

In our few experiments with *Desmognathus fuscus fuscus*, we obtained the same results as in 1926. In experiment F. 16 all the teeth were broken from the upper jaw on November 11, and the animal castrated. After 148 days it was found that bicuspid premaxillary teeth had grown in. After 219 days the animal was killed and at that time the premaxillary teeth were still bicuspid. In F. 12 monocuspid premaxillary teeth had developed in 149 days after castration. An examination of this animal revealed that it had regenerated its testes apparently from rudiments which were inadvertently left behind. The control F. 3 had its premaxillary and maxillary teeth broken on November 9. After 150 days typical male teeth had replaced the broken ones. In neither the 1926 nor the 1927 series did vomerine teeth develop in any of the castrated males of *D. f. fuscus*. The only case in which there was a change in the maxillary teeth was in D. 12 of the 1926 series where they were narrower than in the normal male.

In repeating the experiments with *D. f. carolinensis*, more striking results were obtained. In experiment C. 22 the teeth were left intact and the animal castrated on March 1. After 109 days new premaxillary and maxillary teeth had grown in. The former were short and bicuspid as in the case of the female; the latter were only modified in part. A dissection revealed a partial regeneration of the testes. In Fig. 2 *c* we have shown the maxilla of C. 23 which was treated in the same way as C. 22 and developed the same type of teeth. In only 38 days after castration C. 23 showed two premaxillary teeth that were bicuspid. After 109 days all the premaxillary teeth were bicuspid. There was no regeneration of the testes. As compared with the control C. 3 (Fig. 2 *d*), it will be noted that while the premaxillary are those of a female some of the maxillary are those of a male. The teeth of the control were broken on March 8 and the animal killed 91 days later. In Fig. 2 *a* we have shown the maxilla of a typical female (C. 31) for comparison. The importance of removing the testes entirely, in order that they may not influence the growth of new teeth, is well illustrated by experiment C. 24 in which the male

was castrated but regenerated one large and one small lobe of a new testis. After 109 days, both the premaxillary and maxillary teeth remained those of a male. These experiments were conducted during the spring months, C. 22, C. 23 and C. 24 having been started in March. Three control males which had their premaxillary and maxillary teeth broken in January (C. 3), March (C. 30), and April

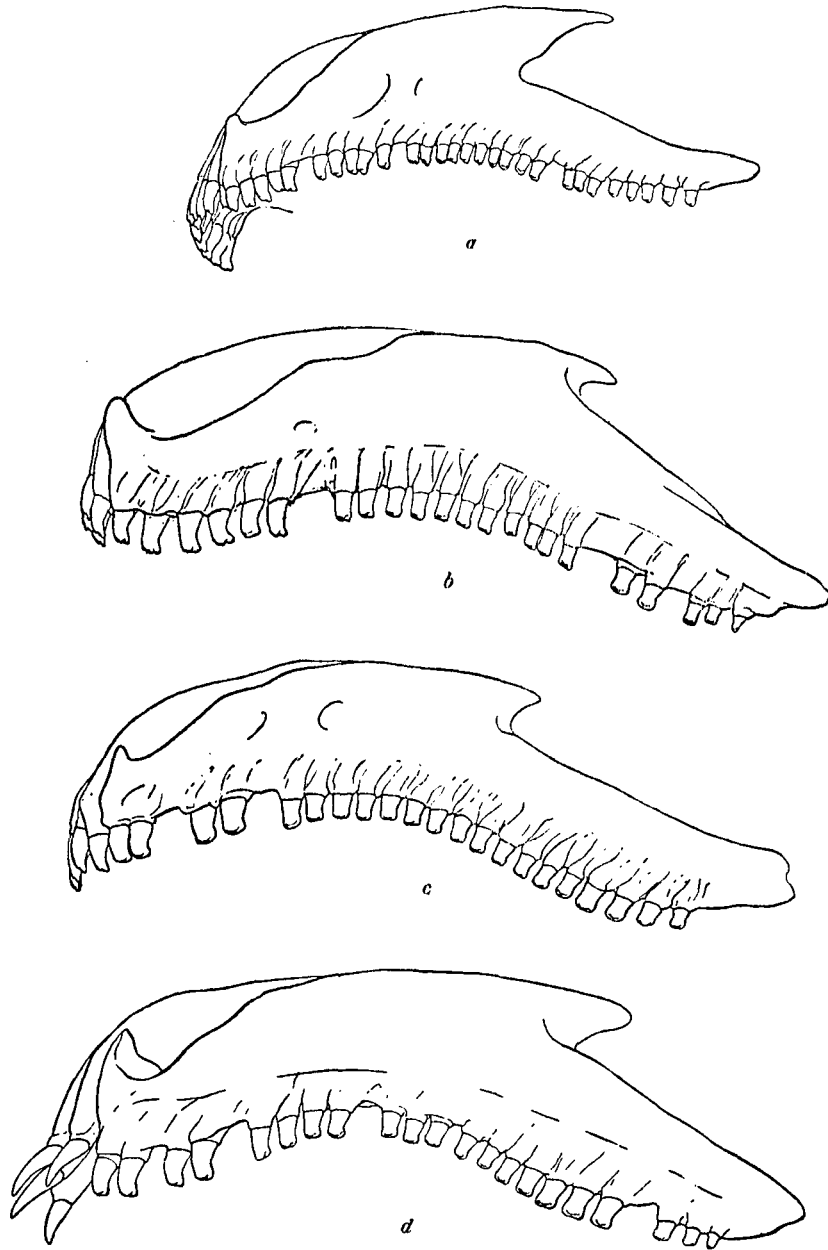


Fig. 2. Effect of castration on the premaxillary and maxillary teeth of *Desmognathus fuscus carolinensis*. (a) An adult female control (C. 31), showing typical female premaxillary and maxillary teeth grown in 91 days after the old teeth were broken off. (b) An adult male (C. 36), showing the female character of the premaxillary and maxillary teeth 79 days after the old teeth were broken off and the animal castrated. (c) An adult male (C. 23), showing the female character of the premaxillary and some of the maxillary teeth, 109 days after castration, the teeth being left intact. There was no regeneration of the testis. (d) An adult male control (C. 3), showing the normal character of the premaxillary and maxillary teeth 94 days after breaking off the old teeth.

(C. 2) grew typical monocuspid premaxillary teeth and broadened bicuspid maxillary teeth. C. 3 was examined after 94 days, C. 30 after 92 days and C. 2 after 216 days.

In one experiment (C. 36), begun March 30, on a male *D. f. carolinensis*, the upper jaw was well scraped and the animal castrated. Seventy-nine days later it was found that not only had the premaxillary teeth become bicuspid but most of

the maxillary teeth had become small and narrow, similar to those of a female (Fig. 2 *b*). In neither this, nor any of the preceding experiments with *D. f. carolinensis*, had castration caused the development in teeth on the prevomers or on the posterior part of the dentary. This shows that the form of the teeth is controlled by the presence of a testis, and that the loss of teeth on prevomers and dentaries cannot be replaced by removing the testes.

If the testes have such an important effect in controlling tooth form in the adult salamander, the reverse experiment of developing male teeth in an adult female

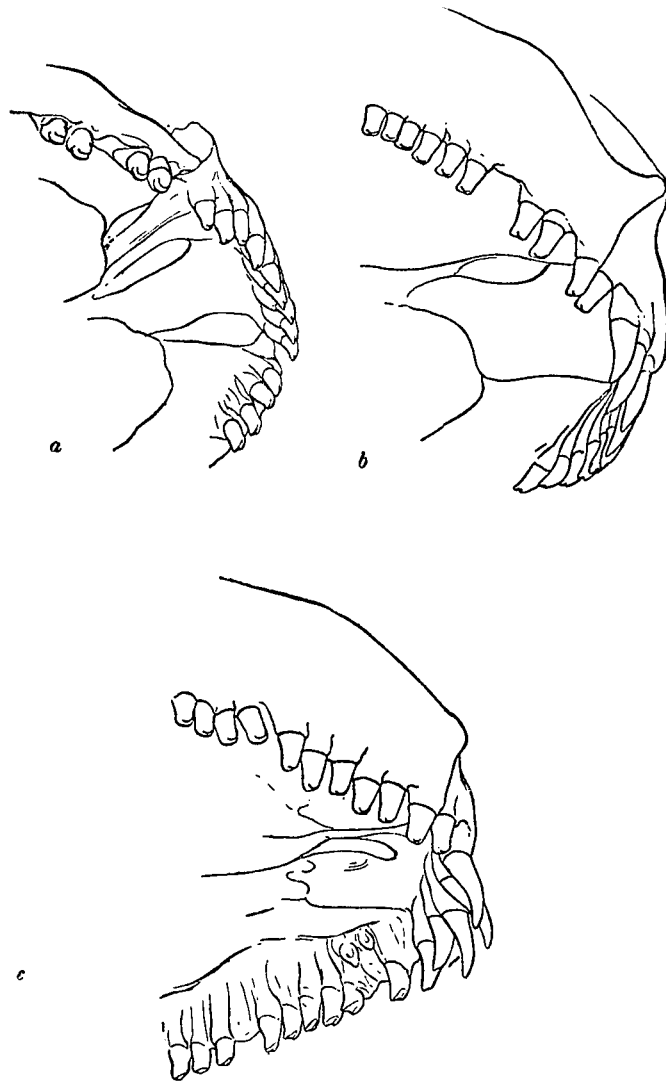


Fig. 3. (*a*) An adult female (F. 7), showing one moncuspid premaxillary tooth grown in 220 days after replacing the ovaries by testes, and breaking the old teeth. The ovaries in this case had partly regenerated. (*b*) An adult female (F. 11), showing a further change in the premaxillary teeth 220 days after transplantation. (*c*) An adult female (F. 10), showing complete transformation of female premaxillary teeth into those characteristic of the male. In this case 220 days after transplantation, there was no regeneration of the ovaries.

salamander seemed to us possible by testicular transplantation. We found some difficulty in making a testicular graft develop, but in three adult females of *D. f. fuscus* (F. 7, F. 10, F. 11) we succeeded, after removing the ovaries and breaking the premaxillary and maxillary teeth, in grafting one or more testes in the body cavity. The experiments were begun in November. After 220 days the animals were killed and the condition of the transplants was as described on page 402. As shown in Fig. 3 *a*, *b* and *c*, 220 days after the transplantations had been made new teeth had grown in, and at least some of the premaxillary teeth were of the

monocuspid type characterising the male. In F. 7 only one monocuspid tooth had grown in, the others being bicuspid and similar to the original female teeth. In F. 11 all but the most lateral premaxillary teeth had changed, but none had become rotated forward in the position characteristic of the breeding male. These lateral teeth are sometimes bicuspid in normal breeding males. In F. 10, which was maintained the same period as the two preceding experiments, but as shown above had retained more testicular and had regenerated less ovarian tissue than the others, all the premaxillary teeth except the most lateral one on each side, had become monocuspid and rotated forward exactly as in the case of an adult male. We have, therefore, demonstrated that the most distinctive secondary sexual modification of the dentition of the male *D. f. fuscus* may be produced in the adult female by testicular transplants. The gradual change of the premaxillary teeth in this series

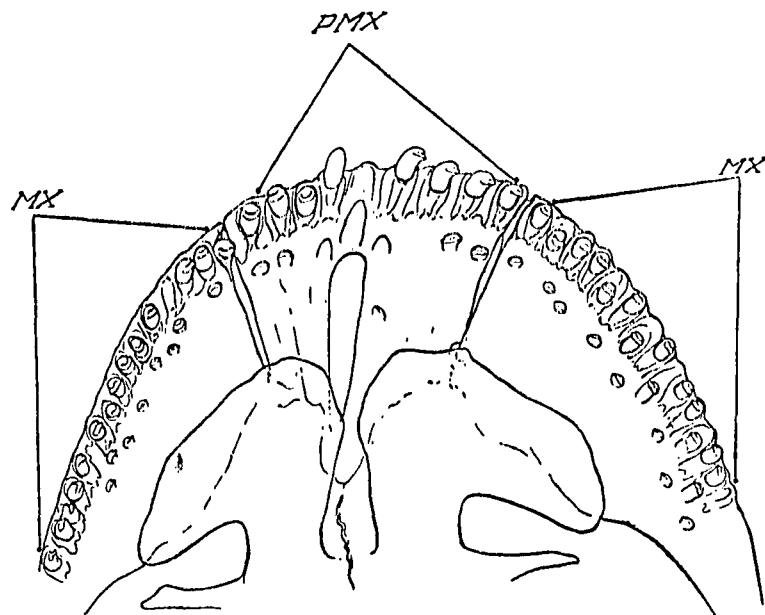


Fig. 4. Palate view of the anterior portion of the upper jaw of an adult female *Desmognathus fuscus* (F. 13), showing the hypertrophy of a single bicuspid premaxillary tooth into a monocuspid one. In this case the ovaries were only partly removed and the remainder apparently prevented any further modification of the teeth in the male direction. *Mx.* = maxillary teeth; *pmx.* = premaxillary teeth.

makes it clear that it is the rudiments of the teeth which would ordinarily have become bicuspid which are hypertrophied by the testicular hormone into monocuspid teeth and then rotated forward out of line with the others.

In this F. series the new maxillary teeth of the adult females were altered during growth by the testicular transplants. This is clearly shown in F. 7 where both the asymmetrical female teeth (Noble, 1927, Fig. 1c) and the broader symmetrical male teeth are present. In F. 10 and F. 11 there are more male teeth and these average broader than in F. 7; thus, there is an agreement with the premaxillary teeth in extent of effect by the transplant, but the change of dentition is far more striking in the premaxillary than in the maxillary teeth.

In experiment F. 13, where the ovary was only partly removed before transplanting the testes and where no cloacal glands developed after 154 days, although the transplant was in a good state of development (attached to the mesentery lateral to the digestive tract and posterior to the ovary near the cloacal region), the most

median premaxillary teeth alone (Fig. 4) were hypertrophied into the monocuspid type. It would seem from this one experiment that the teeth were more susceptible to the influence of the testicular graft than the cloaca, for the latter showed no evidence of glandular growth.

DISCUSSION.

The most detailed study of the spermatheca of American urodeles has been made by Kingsbury (1895). His observations led him to believe that the spermathecal tubules were not homologous to any glands in the cloaca of the male. He concluded in part:

“Blanchard regarded the tubules which have been seen to function as reservoirs for the zoösperms as homologous with the pelvic gland of the male, as likewise does Fischer, and Jordan, though very guardedly. As before stated, I do not believe a homology can safely be declared between any of the cloacal glands of the male and female, which are so evidently dependent on their function for their existence, which is again clearly different in the two sexes. In regard to the spermathecas, difficulties occur in *Amblystoma* and *Necturus* in the presence of other tubules in the dorsal wall of the cloaca, which are again so different in the two genera. With Jordan, I regard the question as a barren one.”

An experimental analysis of the problem has shown the question far from “barren.” De Beaumont (1928) has shown in *Triturus cristatus* that the glandular rudiments in the posterior part of the cloaca of the female hypertrophied into abdominal glands, and the spermathecal tubules into a pelvic gland. We have shown above that in the more specialised *Desmognathus*, transplanting a testis causes the common duct of the spermathecal tubules to sprout glands, while glands indistinguishable from these arise from the roof of the cloaca both anterior and posterior to the common duct outlet. It is clear that the spermatheca of *Desmognathus* is homologous only to part of the pelvic gland of the male.

De Beaumont (1928) describes the spermatheca of the female *T. cristatus* as merely taking on a secretory activity in the presence of the male transplant. This is noteworthy because Noble and Weber (1929) showed that the spermatheca of *Eurycea bislineata* during the breeding season normally developed a secretory activity in the female and the secretion apparently served to attract the migratory spermatozoa into its tubules. De Beaumont's observations have been published in the form of a note, and it is assumed that he has found characters which distinguish this modified secretory activity of the masculinised female from that which it probably normally exhibits during the breeding season.

Our work on *Desmognathus* is of interest, for we find tubular glands replacing the old spermathecal tubules. The spermathecal tubules do not take over new functions under the influence of the testicular transplant as de Beaumont described in *Triturus*, but rather there is a complete replacement (Pl. IX, fig. 2 *b*) of the old tubules by new tubules sprouting from the walls of the common duct or from the cloacal roof. In the case of *Triturus*, if de Beaumont's observations are correct, the

spermathecal tubules are directly homologous with pelvic gland tubules, but in *Desmognathus* the pelvic gland would seem to be homologous with merely potencies for gland formation residing partly in and partly out of the spermatheca. This kind of homology is more frequent in vertebrates than is usually recognised. Thus Smith (1920) found that in the transformation of the hyobranchial apparatus of *E. bislineata* new parts were built out of indifferent tissue although these parts are usually considered homologous to larval structures. In the same broad sense the spermatheca of the female *Desmognathus* is homologous to part of the pelvic gland of the male.

It has long been recognised that there are various kinds of homology. A comparison of the modification of the dentition throughout the Plethodontidae will show that it is generally the inner or lingual cusp which is hypertrophied at the expense of the outer (Noble, 1927). It is interesting to note that the monocuspid premaxillary teeth which are permanent throughout the year in *Desmognathus* have the power of regenerating the more primitive bicuspid teeth if the hormone influence which makes them monocuspid is removed. This raises the question as to whether highly specialised carnassial or dagger teeth in other vertebrates might not revert by replacement to a more primitive type if the physiology of the animal were altered. Amphibia and fishes offer ideal material for the experimental analysis of this question.

CONCLUSIONS.

1. Castration of the adult *Desmognathus fuscus carolinensis* results in the replacement of both premaxillary and maxillary teeth characteristic of the adult male throughout the year by those characteristic of the female. It does not result in a development of teeth on the posterior part of the dentary or on the prevomers where they occur in females, but not in males.
2. Transplantation of the testis into the adult female *D. fuscus* after spaying results in the replacement of the original short, bicuspid premaxillary teeth by elongate, forwardly directed, monocuspid ones characteristic of the adult male. Intermediate types of teeth occur, showing that the bicuspid tooth rudiments are hypertrophied into monocuspid teeth.
3. Testicular transplants in the adult female cause the development of pelvic, abdominal and cloacal glands. Part of the pelvic gland develops from the spermatheca, the remainder from the cloacal epithelium near the duct of the spermatheca. Hence, the spermatheca in *Desmognathus* is homologous only to part of the pelvic gland.
4. Where the ovary of *D. fuscus* was replaced in part by two testes, only the median premaxillary teeth, and not the cloaca, was affected. This suggests an antagonism between the glands, and a sensitivity to hormone action greater in the teeth than in the cloaca.

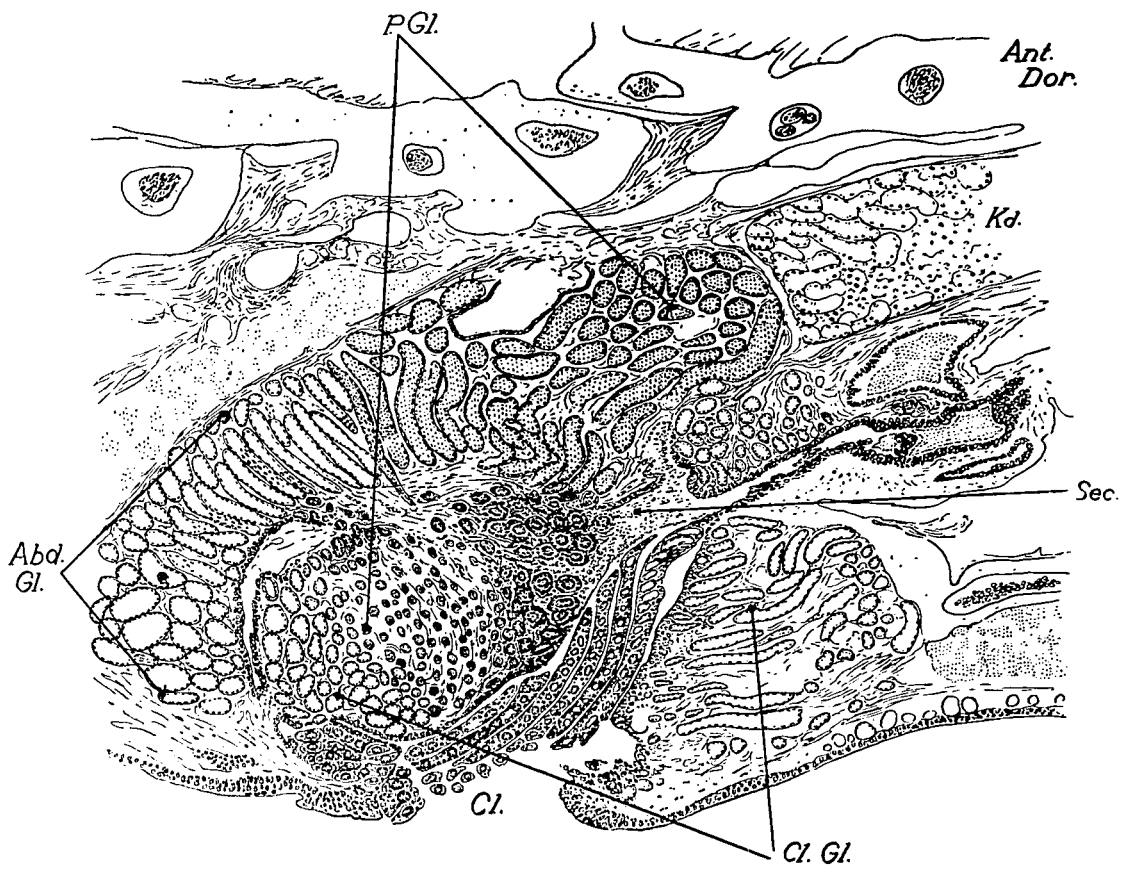


Fig. 1 a

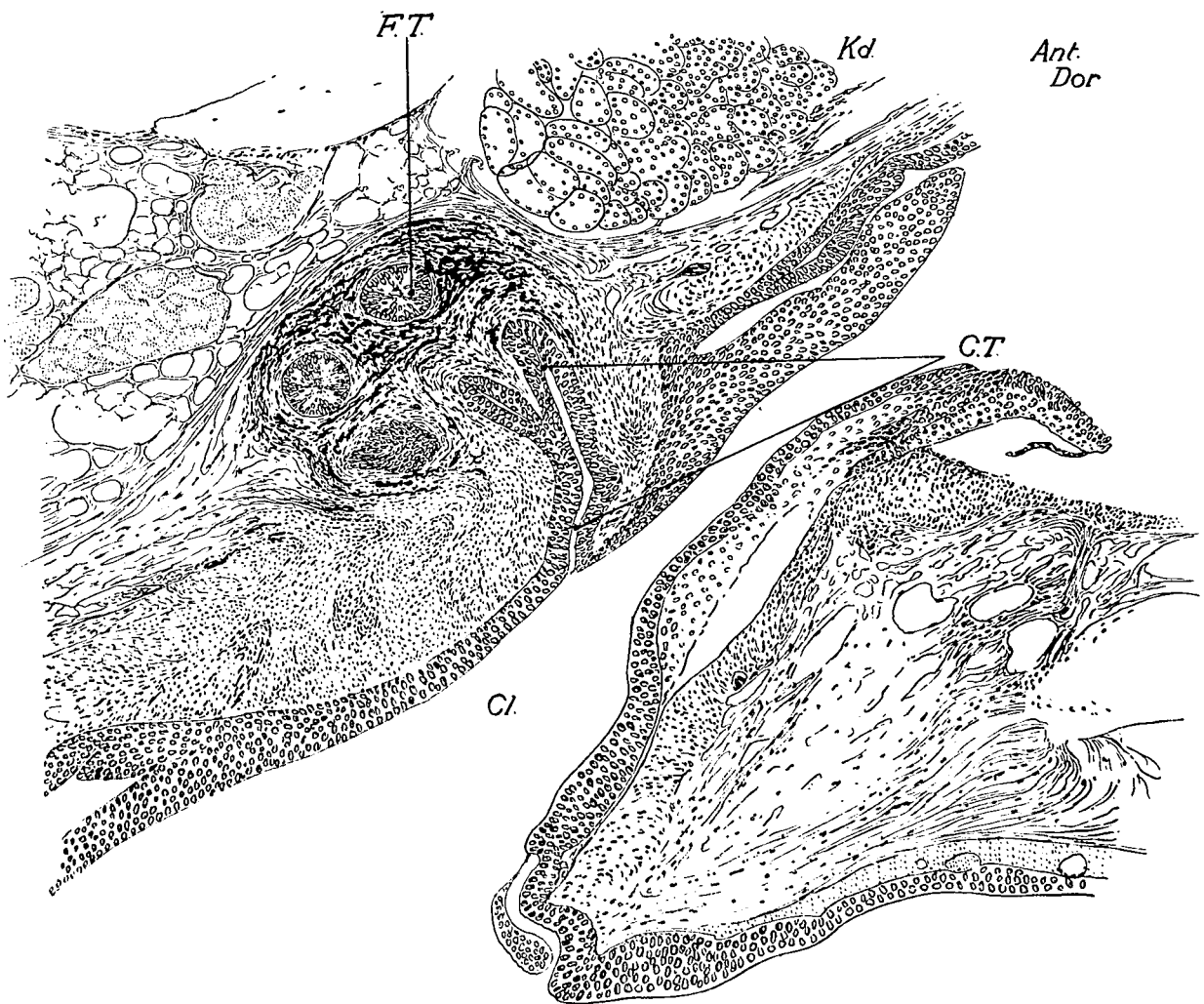


Fig. 1 b

NOBLE AND POPE—TESTICULAR TRANSPLANTATION IN *DESMOGNATHUS*

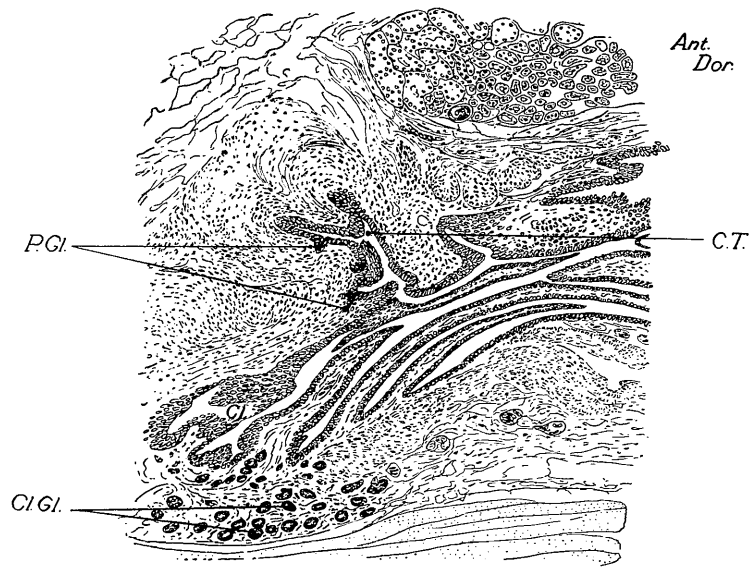


Fig. 2 a

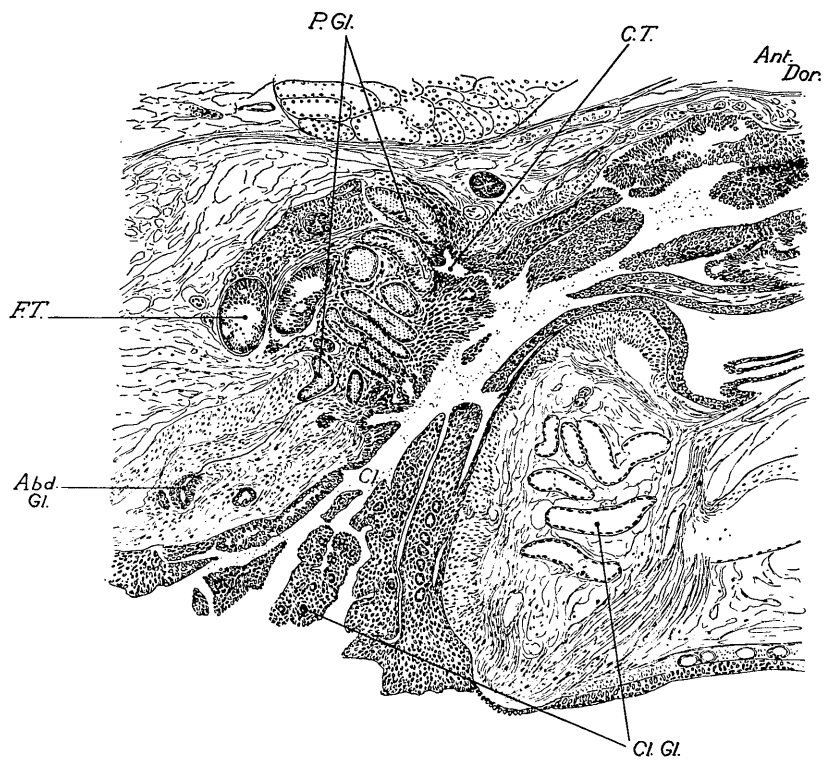


Fig. 2 b

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DESCRIPTION OF PLATES VIII AND IX.

PLATE VIII.

Fig. 1 *a*. Sagittal section of the cloaca of a normal adult male *Desmognathus fuscus fuscus* showing the three series of glands present in this sex. ($\times 18.5$) *Abd. gl.* = abdominal gland; *ant. dor.* = antero-dorsal corner; *cl.* = cloaca; *cl. gl.* = cloacal gland; *kd.* = kidney; *p. gl.* = pelvic gland; *sec.* = glandular secretion.

Fig. 1 *b*. Sagittal section of the cloaca of a normal adult female *Desmognathus fuscus fuscus* showing the absence of glands, but the presence of the spermatheca. ($\times 62.5$) *Ant. dor.* = antero-dorsal corner; *cl.* = cloaca; *c. t.* = common tube or duct; *f. t.* = flask tubule; *kd.* = kidney.

PLATE IX.

Fig. 2 *a*. Para-sagittal section of the cloaca of an adult female *Desmognathus fuscus fuscus* (D. 17) 62 days after spaying and transplantation of two whole testicular lobes and two partly broken ones into the body cavity. Pelvic and cloacal glands are beginning to form. ($\times 49.5$) *Ant. dor.* = antero-dorsal corner; *cl.* = cloaca; *cl. gl.* = cloacal gland; *c. t.* = common tube or duct; *p. gl.* = pelvic gland.

Fig. 2 *b*. Sagittal section of the cloaca of an adult female *Desmognathus fuscus fuscus* (F. 10) 220 days after spaying and the transplantation of testes. Pelvic, cloacal and abdominal glands are well formed. ($\times 49.5$) *Abd. gl.* = abdominal gland; *ant. dor.* = antero-dorsal corner; *cl.* = cloaca; *cl. gl.* = cloacal gland; *c. t.* = common tube or duct; *f. t.* = flask tubule; *p. gl.* = pelvic gland.