

AMERICAN MUSEUM NOVITATES

Number 249

Published by
THE AMERICAN MUSEUM OF NATURAL HISTORY
New York City

Feb. 2, 1927

59.798

THE PLETHODONTID SALAMANDERS; SOME ASPECTS OF THEIR EVOLUTION

BY G. K. NOBLE

During the latter part of September of last year I made a short trip to western North Carolina to collect plethodontid salamanders. It was my good fortune to have at hand during the trip Dr. E. R. Dunn's recent monograph of the group (1926). My brief field work was supplemented by a study in the laboratory. As a result of this work, certain of Dr. Dunn's generalizations in regard to various aspects of the evolution of the group do not appear to me to be well founded. The present paper comprises a record of new facts and interpretations in regard to the habitat preferences, the secondary sexual characters, and the color pattern evolution of those plethodontid salamanders available for study.

I spent two days at Flatrock, N. C., a locality well known through the field studies of Pope (1924), and four days near the summit of Mt. Pisgah (4500-5500 ft.). Two hundred and fifty-seven adult salamanders and about a fourth as many larvæ were captured and brought back to New York alive. Specimens from distinct habitats were kept separate in small containers. In the laboratory the specimens were studied after being anesthetized in chloretone, or in some cases, merely after drying with a towel (to avoid their slipping through one's fingers). It need not be emphasized that the living specimen is far superior to the preserved one in questions of identification. Most of the species encountered I had never seen before in the field and my first impression of the larger forms in their native haunts will long be remembered.

I wish to acknowledge my indebtedness to Mr. George J. Baldwin who placed every facility at my disposal during my stay at his estate, "Mountain Lodge."

HABITAT PREFERENCES

A Northerner visiting the mountains of western North Carolina for the first time is struck at once by the profusion of plant life and the abundance of water supply. Three main types of stream habitats are at once recognized: first, the very large and rocky streams in which *Cryptobranchus* abounds, but only rarely any plethodontids; second,

the smaller rocky streams or cascades of the mountain sides; third, the muddy¹ and moss-grown trickles of both mountain and valley. In crossing such an extensive mountain mass as the Pisgah range one comes successively to many rocky streams and leafy trickles. The plethodontid fauna seems at first to be very different in the two streams. In the rocky streams or trickles *Desmognathus quadra-maculatus* is ubiquitous, while in the leafy trickles *D. phoca* is the dominant salamander. I took two specimens of the striking *Eurycea gutto-lineata* on the muddy banks of a spring-fed stream near Flatrock (Rutledge Estate). It is generally agreed that this species is found chiefly in the muddy stream habitat. How closely are the stream salamanders restricted to one or the other type of stream? And how closely has their evolution been correlated with particular habitats? The problem is best attacked by studying the species in a single genus, such as *Desmognathus*.

Dunn (1926, p. 17) says of *D. phoca*: "Instead of being, like *quadra-maculatus*, an animal of streams, it is a creature of the banks of smaller brooks." He believes (p. 20) that *D. phoca* has arisen from *quadra-maculatus* "by crossing to a different ecologic niche." He conceives (p. 21) that the evolution of the genus represents "a number of major adaptive movements to fit various ecologic niches in the southern Appalachians, together with several minor movements to fit the same ecologic niches outside that region."

A study of the species of *Desmognathus* at Flatrock and on Mt. Pisgah has failed to reveal the clear-cut habitat preferences Dunn seems to imply. I never found an adult *quadra-maculatus* in a muddy trickle or an adult *phoca* in a rocky stream, but the half-grown individuals occur in both types of habitats. Thus, in hunting along one of the small rocky streams which flows into the lake on the Argyle Estate, Flatrock, I secured six half-grown specimens of *phoca* to five of *quadra-maculatus*. Again, in hunting the muddy stream which flows from the north side of Trenholm Mountain across the Rutledge Estate, I captured four half-grown *quadra-maculatus* to eleven adult and half-grown *phoca*. On another occasion a stream in the Argyle Woods yielded four specimens of *phoca* to two *quadra-maculatus*, while the Rutledge stream yielded two of the latter species and eight of the former. This and subsequent indiscriminate collecting on Mt. Pisgah confirmed the conclusion that the half-grown specimens fail to show the habitat preferences of the adults.

What is the reason for this difference in segregation at different ages? It seems clear that the half-grown individuals must move about

¹Referring to the character of the stream bed, not to the water.

more extensively than the adults. It is known from the work of Pope (1924) that the adult *phoca* lays its eggs in muddy streams either on the under surface of rocks or in logs above the surface of the water, while *quadra-maculatus* attaches its eggs to the under surface of the stones in rocky streams. Thus, it is not the larva but the young metamorphosed individual which changes its habitat. Many other salamanders are known to wander about as metamorphosed individuals, returning to particular habitats to breed (*Hemidactylium*, *Triturus*, *Ambystoma*, etc.). The same seems to be true of *D. quadra-maculatus* and *D. phoca*.

What determines that the adult *quadra-maculatus* shall return to rocky and the adult *phoca* to muddy streams? This question cannot be answered definitely, but certain possibilities suggest themselves. An inherited instinct to breed in certain types of streams might predominate; or to be more precise, certain physiological requirements might bring the adults to these situations. Thus, if *quadra-maculatus* demanded cooler and more highly aerated water, it would naturally seek out the rocky streams. However, it is possible that competition alone might tend to bring about the same result. *Phoca* and *quadra-maculatus* are not very different in size (except for the old males of the latter). *Phoca* is certainly not as powerful as the latter and would tend to be crowded out of any habitat the latter selected. It is not unlikely that several factors, breeding site preference, physiological requirements, and competition, have brought about the different adult segregations of the two species.

The habitats in which plethodontids have been captured have been made known from time to time. It is obvious that many species do considerable wandering outside of the breeding season. *Gyrinophilus danielsi* is known to breed in rocky streams, but I caught a specimen in a muddy spring at Flatrock, and two others in a muddy trickle near the Pisgah Forest Inn (5200 ft.), several hundred yards from a rocky stream. *Eurycea bislineata wilderæ* breeds in situations similar to *E. b. bislineata*. At Flatrock I caught an adult half a mile from any stream. Dunn (1926) has cited many other cases of species having been taken far from their breeding habitat. Thus, the impression grows that the species have not evolved by slowly crossing to different ecological niches but rather that it is only the breeding habits which have changed, the species outside of the breeding season occupying other niches in the environment.

Some species, such as *Pseudotriton montanus*, may be so constituted as rarely to move far from their breeding streams. Others, such as *Desmognathus fuscus carolinensis*, may, outside of the breeding season,

compete on the one hand with the terrestrial plethodons and on the other with the juvenile *D. quadra-maculatus*, so great is their tolerance of different conditions. The chief requirements of the latter species seem to be moisture and air. In the moist forests of high altitudes on Mt. Pisgah the species is exceedingly abundant even at long distances from any stream. Further, the individuals move about a great deal. Certain stones near the Mt. Pisgah Inn yielded specimens every day I visited them.

Whether or not the evolution of the species of *Desmognathus* discussed above is so closely correlated with a gradual change in the moisture and oxygen requirements, it seems probable that one or both of these factors played an important part in the evolution of the species of *Plethodon*. At Flatrock both *P. glutinosus* and *P. metcalfi* are found, but the latter only in the dampest woods. My five specimens from this locality were all taken in the wet woods on the north side of Trenholm Mountain. At high altitudes on Mt. Pisgah *glutinosus* is very rare while *metcalfi* is abundant. Here again there is not a clear-cut segregation, for on two occasions I took both species under the same log on Mt. Pisgah (about 5000 ft. elevation).

One specimen, an immature female, 135 mm. total length, 70 mm. snout to vent, seems to be exactly intermediate between the two species. It has a pale throat, only a few leucophore spots on the sides, and is not densely pigmented above. Its vomerine teeth are nine on one side and ten on the other. An examination of my series of *glutinosus* from this region (six specimens) shows that the teeth characters Dunn describes (p. 149) do not hold true. Two specimens of this species have as low as eight teeth to a side while three specimens of *metcalfi* run over ten, one male reaching thirteen. Most specimens of *metcalfi* are to be distinguished from *glutinosus* by their slimmer body, larger head, larger eyes and usually paler chin and body tone. No specimens of *metcalfi* in my series (52 specimens) have leucophore spots on the sides. I have referred the apparent intermediate to *glutinosus*. Although it is probable that the specimen is not a true intergrade in the sense of the systematist, it is clear that *metcalfi* is very closely related to *glutinosus*. It is hard to see how the differences which separate the two species can be considered adaptive. Probably the most important difference between them is a physiological one, permitting a greater tolerance to moisture on the part of *metcalfi*.

Segregation into definite habitats is most pronounced throughout the Plethodontidæ during the breeding season. It has been mentioned that

Desmognathus quadra-maculatus does not compete with its derivative *D. phoca*. Nor does *Pseudotriton ruber* compete with *P. montanus*, although outside of the breeding season the former may wander considerably. In the muddy spring stream which flows down the north side of Trenholm Mountain, Flatrock, I found *D. phoca* and *D. f. carolinensis* abundant. This is the same stream in which Pope (1924) collected eggs of both species. On September 25-26 I collected twenty-two egg masses of the latter species, all in a very advanced stage of development and a few already hatched. The remainder hatched before reaching New York (Oct. 1). All of these egg masses were taken among the moss on logs. Usually the eggs were in a little cavity in the mud underlying the moss, but others were entirely surrounded by the moss. Numerous larvæ were found among the moss but none were scooped from the water. It is apparent that the larvæ after hatching remain for a period at least in the moss.

A large series of adult *D. f. carolinensis* were captured in the moss overlying the logs. None were found in the soft earth under the logs. *D. phoca*, on the other hand, was extremely abundant in the latter habitat, and none were found in the moss covering the logs. The latter species, both because of its larger size and its habitat preference, would not compete with the former. It must be largely for this reason that the two closely related species live so well side by side.

It is probable that both size differences and habitat preferences have tended to isolate two closely related species in other regions. Thus *Manculus quadridigitatus* is not closely related to *Eurycea gutto-lineata*, as Dunn believes, but to *Eurycea bislineata cirrigera* with which it agrees very closely in both color and secondary sexual characters. The first species may be considered a dwarf species of the last. In both *Manculus* and *Desmognathus*, a tendency towards terrestriality has accompanied a reduction in size.

It is easy to imagine that every phylogenetic change in the organization of an animal is adaptive. To take a familiar example, in fishes, lizards, and salamanders, there are found numerous cases of elongate forms arising from shorter-bodied types. Dunn (1926, p. 26) says of *Batrachoseps* "Ecologically, this elongate type is a further advance [over *Plethodon*] in terrestrial adaptation and bespeaks a burrowing mode of life." But Storer (1925, p. 97) from whom Dunn quotes extensively assures us that "there is no evidence that *Batrachoseps* actually burrows in the ground. . . ." Whether *Batrachoseps* follows crannies to greater depths than *Plethodon* is an uncertain question. It is far simpler to label

the elongate body of *Batrachoseps* and many other peculiarities of the various Plethodontidæ as "specializations" until they are proved to be adaptations in the usual sense of the word. A close study of the specific or generic characters of the Plethodontidæ will reveal few that are truly adaptive. This implies that salamanders get along with what they have given them by heredity.

There are, to be sure, several peculiarities in the Plethodontidæ which adapt the different genera to various habitats. One of the most remarkable is found in *Desmognathus* and *Leurognathus*. A strong tendinous slip of the temporalis is attached to the atlas. Thus, according to Dunn (1926, p. 45), "the lower jaw is immovably attached to the atlas and the mouth is opened by raising the skull." This statement is not wholly correct. Chloretonized specimens of *D. fuscus* laid on their side will open their jaws for about a third their maximum gape before the skull is bent from its normal axis. The mechanism as a whole, nevertheless, would seem to strengthen the head as Dunn suggests. All species of the genus exhibit great ability in wriggling under stones or through moss or other impediments.

THE SECONDARY SEXUAL CHARACTERS

The Plethodontidæ exhibit a wide range of secondary sexual characters, although most of these are inconspicuous and have usually been overlooked by naturalists. We owe it to Dunn (1926 and earlier papers) for having pointed out that certain peculiarities, namely, the enlarged premaxillary teeth, the sub-nostril cirri, and the lacking vomerine teeth were of this category. He has also brought together a record of the other secondary sexual characters known throughout the family. Of these, the most important are the peculiar dentition and jaws of certain species of *Desmognathus*, the elongated maxillary teeth of *Hydromantes platycephalus*, the "swollen" snout of certain species, the submental gland of *Desmognathus fuscus*, and the different size, tail, and body proportions in the different forms.

Dunn (1926) has not, however, availed himself of the opportunity of making a complete survey of all the secondary sexual characters found in this family. Further, some of his statements are misleading, if not erroneous. Thus, he states (p. 42) that "the normal maxillary teeth are pointed, but they are blunt, with a horizontal cutting edge in some *Desmognathus*." In the males of certain species of the genus the "posterior part of the dentary is without teeth and the hindmost teeth of the row are elongated." In his definition of the genus *Plethodon*, he

states that there is "no marked sexual dimorphism," although in his description of *P. cinereus* he adds "premaxillary teeth enlarged, forward in position, piercing lip." These and certain other statements require either emendation or modification. The following summary of the secondary sexual characters of the Plethodontidæ has been drawn up with a view to supplementing Dunn's account.

The branchiosaur ancestors of both the salamanders and frogs possessed simple, conical teeth. Such teeth are found in the younger larvæ of all urodeles. They are retained in the "more larval" perennibranchs: *Siren*, *Necturus*, and *Typhlomolge*. As most salamanders approach metamorphosis, they acquire bifid teeth, possessing an enamel cap and a breakage plane as in the common frog. Some larvæ retain simple teeth a short time after metamorphosis. There may be great variation in this respect within such species as *Ambystoma tigrinum*. The "more adult" perennibranchs, *Amphiuma*, *Cryptobranchus*, and *Megalobatrachus*, have the bifid teeth of most late larvæ. In the last genus, however, the inner cusp is greatly elongated, obscuring the bifid arrangement of the crown. In all metamorphosed salamanders, bifid teeth occur, except where the teeth have been secondarily elongated (or lost).

The various species of urodeles exhibit many differences in the exact form of the teeth. Most of these differences are due to the elongation of the lingual cusp. In *Gyrinophilus*, for example, the two cusps of each tooth lie on nearly the same plane, while in *Pseudotriton* the inner is elongated. In the species of *Ambystoma* and *Triturus*, the inner cusp exhibits differences which seem to be more or less constant in adults. In short, the elongation of the teeth with the disharmonic growth of the inner cusp is a specific character for many urodeles.

This specific character is taken over as a secondary sexual character and further elaborated in many salamanders. In the male *Eurycea*, there occurs a specialization of the maxillary as well as the premaxillary teeth. The former become elongated, single cusped, and fewer in number. The beginning of such a change is seen in *E. bislineata*, while in *E. gutto-lineata* and *E. lucifuga* (Fig. 1i) the males have the character strongly developed. The dentary teeth do not keep pace with these changes but show a tendency to elongate and lose the posterior ones of the series. The elaboration of a specialized dentition is not merely a matter of size. *Eurycea melanopleura* and *E. longicauda* possess maxillary teeth of the usual form in the adult male although they may attain the size of *E. gutto-lineata*.

In *Hydromantes*, the same specialization occurs, but here it may have arisen *de novo*. *H. genei* shows the very beginning of the change, for the inner cusps of the maxillary teeth are only slightly elongated and narrowed. In *H. platycephalus*, according to descriptions, this change is carried to the same extreme found in *Eurycea lucifuga*. *Ædipus*, which may be more closely allied to *Hydromantes* than usually assumed, exhibits a similar modification in at least one species, according to Dunn. Other species of the genus undergo a loss of teeth in the male. This character seems to shift over to both sexes in other species, for, as shown by Dunn (1926), four species in the genus lack maxillary teeth. In this connection it is interesting to note that where the elongation of the teeth appears in both sexes of an amphibian such as *Aneides* (Fig. 4), this character is usually heralded as adaptively correlated with an assumed change of food habits, but where the dentition of the male only is hypertrophied no functional significance is so readily claimed. If the latter character has arisen in evolution without any relation to habit or the external environment, it appears not improbable that the first at the time of its genesis was equally free from the influence of natural selection or of other external factors.

It is instructive to contrast the changes in form of the maxillary with those of the premaxillary teeth. Each set seems to change as a distinct unit. The former exhibit a gradual increase in length in *Eurycea*, *Hydromantes*, and *Ædipus*, while the latter in these genera exhibit practically no changes. The difference, however, is not clear-cut, for the most lateral pair of premaxillary teeth may be intermediate in character between premaxillary and maxillary teeth. The factors which produce changes in the premaxillary teeth are apparently not those which call

Fig. 1. The modification of the teeth as a secondary sexual character in the Plethodontidæ. Drawn to the same scale. Left maxillary teeth of:

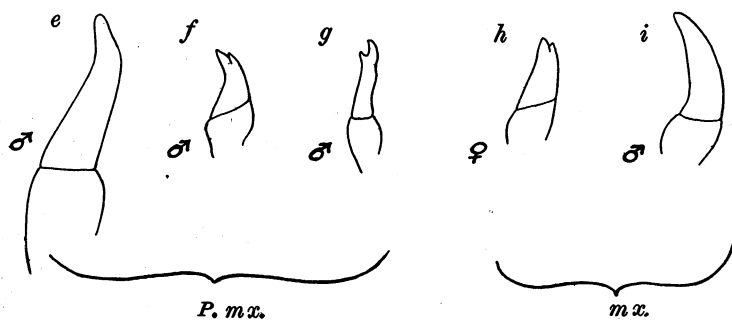
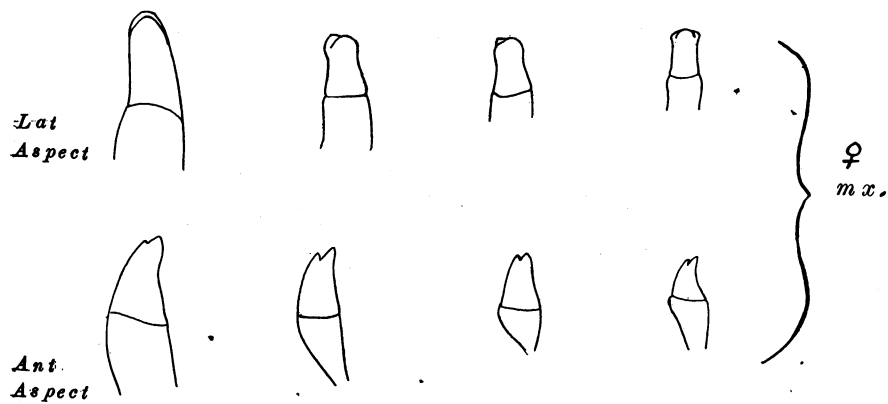
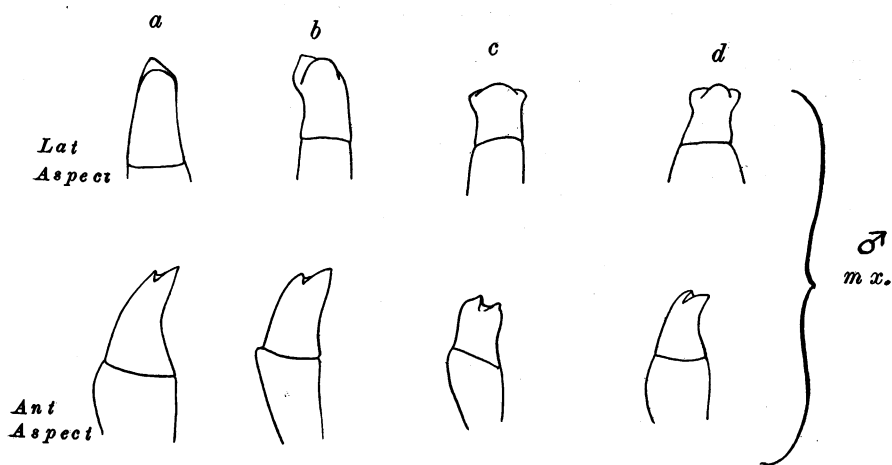
- a. *Desmognathus quadra-maculatus* (Holbrook).
- b. *Desmognathus phoca* (Matthes).
- b. *Desmognathus fuscus fuscus* (Rafinesque).
- d. *Desmognathus fuscus carolinensis* (Dunn).

An orthogenetic change in the teeth of both the male and the female may be noted, the male characters being an exaggeration of those of the female.

In the bottom row the first three figures illustrate the different form of the premaxillary teeth of various adult males (viewed from the side).

- e. *Desmognathus fuscus* (Rafinesque).
- f. *Plethodon metcalfi* Brimley.
- g. *Plethodon cinereus* (Green).

The last two figures (*h* and *i*) show the differences in the male and female maxillary teeth of *Eurycea lucifuga* Rafinesque as viewed posteriorly (left side, in place).



forth changes in the maxillary ones; or, at least, the maxillary and premaxillary teeth are sensitized differently to a hormone action.

It is also interesting to compare the changes in dentition of *Eurycea* with those of *Desmognathus*. In both, the premaxillary teeth are elongated and the dentary teeth somewhat increased in length but reduced in

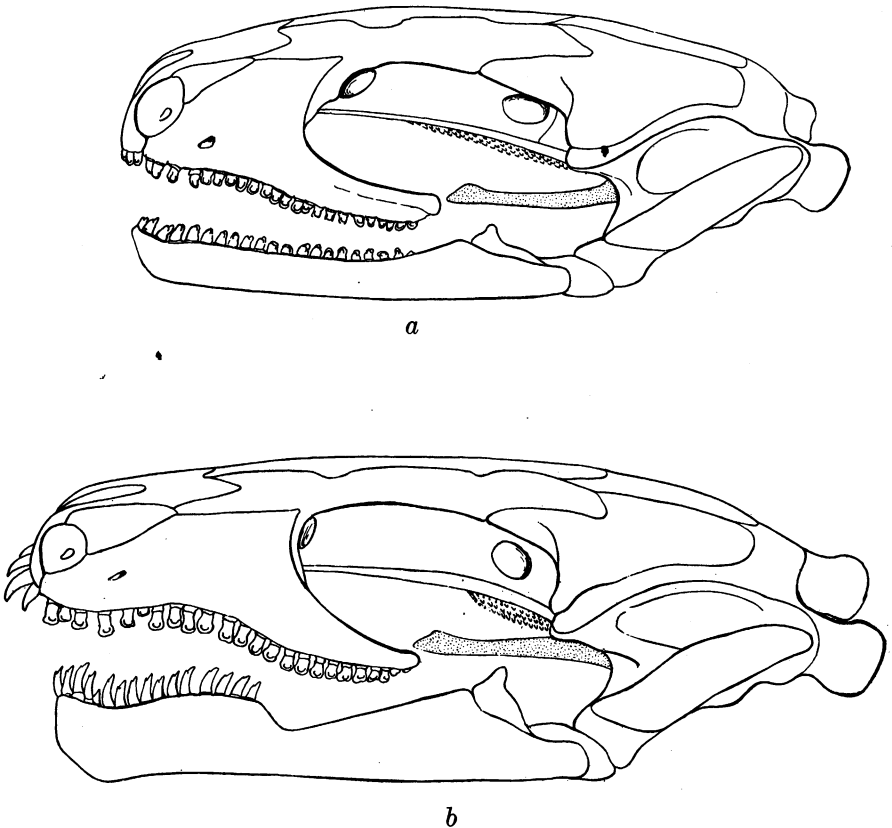


Fig. 2. The skull of the male (b) and the female (a) *Desmognathus fuscus carolinensis* (Dunn), drawn to the same scale, showing the secondary sexual differences of jaws and teeth.

number. In *Eurycea*, the maxillary teeth may gradually increase in length, while in *Desmognathus* they shorten and increase in width (antero-posteriorly). In both cases, it is the inner cusp of each tooth which undergoes the greatest change (Fig. 1). In *Desmognathus*, the smaller species and those most specialized as to life history and structure

possess the most extreme types of sexual dimorphism. In *Eurycea*, there is no such correlation, the large species tending to have just as pronounced sexual characters as some of the small species. Evolution in secondary sexual characters, as in specific ones, may be in some cases gradual and in others discontinuous.

The progressive elaboration of the secondary sexual characters in *Desmognathus* is closely correlated with a progressive change of the specific characters. In the primitive *D. quadra-maculatus*, the dentary and maxillary teeth are bicuspid, as in most Amphibia, and are small and numerous. In *D. phoca*, *D. fuscus*, and *D. f. carolinensis*, the maxillary teeth are shortened and broadened antero-posteriorly, the mesial half being more expanded than the outer half. The dentary teeth are elongated and slightly reduced in number. This is a specific character, for it is found in both sexes. Another specific character is the slight bowing of the maxillary (Fig. 2). In the small species *Desmognathus fuscus carolinensis* and *D. f. ochrophæus*, these three specific characters, the bowing of the maxillary bone, the shortening and broadening of the maxillary teeth, and the elongation (with reduction in number) of the dentary teeth, are seized upon as secondary sexual characters, for they are all exaggerated in the male. These changes in skull and dentition illustrate the general principle that most secondary sexual characters represent an hypertrophy of specific ones and are usually not totally new characters.

Champy (1924) has presented some evidence to show that the sexual hormone acts as a catalyst speeding up disharmonic growths which have begun in many cases as specific characters. In the case of *Desmognathus*, all that we need assume is that this catalyst begins to act at an earlier and earlier period as the species become more specialized. This is quite a different state of affairs than maintains for most disharmonic growths. Champy (1924) has shown the wide application of Lameere's rule that the larger an animal becomes in phylogeny, the more disharmonic will be these growths. In *Desmognathus*, the smallest species have the most pronounced sexual dimorphism.

If secondary sexual characters are merely sex-linked specific ones we would expect them to be of some value as indicators of relationship. Only the Plethodontidæ possess elongated premaxillary teeth (Fig. 3) directed partly forward. This character is not found in the more primitive genera of the family, *Gyrinophilus* and *Pseudotriton*, nor in the derived stocks *Stereochilus* and *Typhlotriton*. It appears fully developed in *Eurycea*. It runs through *Desmognathus* and *Leurognathus*. *Plethodon*,

which is only indirectly related to *Eurycea*, lacks these elongated teeth in all larger species, and so does its close relative *Ensatina*. *Batrachoseps* and *Hemidactylium*, which were very probably directly derived from *Plethodon*, have both redeveloped the character. *Ædipus* and *Ædipina*,

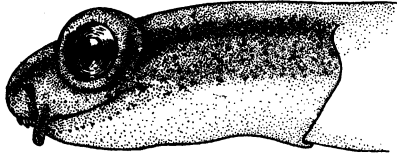


Fig. 3. Head of the adult male *Manculus quadridigitatus* (Holbrook) showing the elongated premaxillary teeth, the swollen snout and the cirri of this sex.

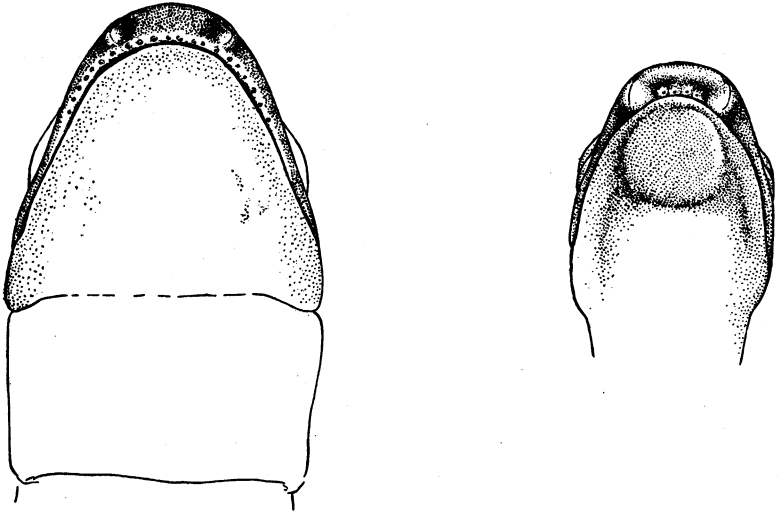


Fig. 4. Elongated teeth as a specific and as a secondary sexual character.

- a. *Aneides lugubris* (Hallowell), female.
- b. *Ædipus adspersus* (Peters), male.

The latter also shows the mental gland and the swollen naso-labial glands of most male plethodontids.

which show close affinity to *Plethodon* in skull structure and to *Eurycea* in tongue form, also possess these teeth (Fig. 4). The elongated premaxillary teeth represent a distinctive plethodontid character but one very irregular in its occurrence. Elongated premaxillary teeth have appeared, disappeared and reappeared again without an obvious relation to the external environment in which the salamanders lived.

It may be objected that the plethodontids with different secondary sexual characters probably have different habits. This objection loses weight when it is realized that species having identical secondary sexual characters may be either aquatic or terrestrial. Very little is known about the mating habits of any plethodontid. But the problem may be attacked by studying the genesis of the characters in a closely related group of species having, so far as known, identical breeding habits. For this purpose I have selected the genus *Plethodon*.

In the large species of *Plethodon* (*glutinosus*, *yonahlossee*, *metcalfi*, *wehrlei*) the maxillary and mandibular teeth of both sexes are alike and of the primitive type. There is no specialization, although the inner (lingual) cusp may be slightly higher in the anterior teeth than in the posterior. This simplicity of dentition is handed on to *Ensatina eschscholtzii*, which is merely a large species of *Plethodon* with a constricted tail base. But in the small species of *Plethodon* a change of dentition begins to appear. In *P. vandykei*, one or two of the premaxillary teeth may possess only a single cusp although the tooth is no longer than its neighbors and is set at the same angle. In *P. intermedius*, which may be considered a dwarf species of *vandykei*, this specialization is elaborated, for all the premaxillary teeth are spike-like and with only a single cusp. These teeth are not, however, directed forward and they are only slightly longer than the adjacent maxillary teeth. In the small *P. cinereus*, the common species of eastern United States, the elaboration is carried farther, but yet does not reach or even parallel that of *Desmognathus*. The outer cusp of the premaxillary teeth is hypertrophied and extends beyond the inner (Fig. 1g); further, each tooth is directed partly forward. This type of tooth is unique among the Amphibia, for in other forms where a cusp is hypertrophied it seems to be invariably the inner. The more specialized species of *Plethodon* parallel *Eurycea*, however, in showing the beginning of an elongation of both maxillary and mandibular teeth and a reduction of their number. *P. cinereus*, which represents the extreme condition, does not approach *E. lucifuga* in the extent of this specialization. It is noteworthy that in *Plethodon*, as in *Desmognathus*, an orthogenetic series of tooth modification may be traced. Further, in direct contrast to the views of Champy (1924), it is the smaller species which exhibit the greatest sexual dimorphism.

The plethodontid salamanders possess another set of secondary sexual characters which have been only partly summarized by Dunn (1926). These are the glandular structures which distend the integument over certain regions of the head. The swollen snout which Dunn men-

tions in various genera owes its character to an hypertrophy of the nasolabial glands in the male. In most genera with a swollen snout there appears a conspicuous glandular patch on the chin, although Dunn describes this mental gland only in *Desmognathus* (Fig. 5). The distribution of these secondary sexual characters may be traced in greater detail throughout the family. Both glandular hypertrophies are lacking in *Gyrinophilus* and *Pseudotriton*, which also lack a specialized dentition in the male. They first appear in *Eurycea*. They are present to a greater or less extent in all higher plethodontids, although scarcely distinct in

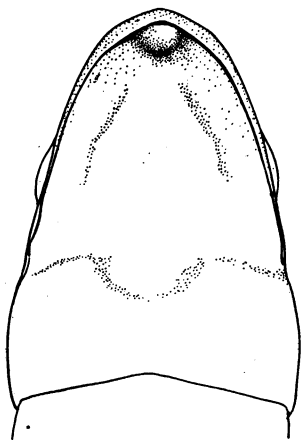


Fig. 5. The mental gland of the male *Desmognathus fuscus* (Rafinesque).

Stereochilus, *Aneides*, and are probably lacking in *Typhlomolge*. They are well developed in such genera as *Plethodon*, *Ensatina*, and *Typhlotriton* which lack (with a few exceptions) a sexual specialization of the dentition. The mental gland is most developed in *Eurycea*, *Oedipus*, and *Hydromantes*. The nasolabial hypertrophy of the male is very marked in these same genera (Fig. 3), but nearly as well in *Typhlotriton*. In *Manculus* and a certain race of *Eurycea*, the glands so extend the lip that the region of the nasolabial groove is extended downward as a sort of proboscis that has been confused by various writers with the tentacles of the cœcilians and of *Xenopus*. When the mental gland is reduced the nasolabial glands are not well developed. Thus, there is some correlation between the hypertrophy of these two glands, but not between the presence of the glands and a specialized dentition.

What can be the function of these glands? The only direct evidence comes from some observations of Mertens (1923), who noted a male *Hydromantes genei* rubbing his chin over a female, presumably to stimulate her. The secretion from the mental gland in *Desmognathus fuscus* is clear and only slightly adhesive. In detailed structure the mental glands of *Desmognathus* and of *Hydromantes* are much the same. Each

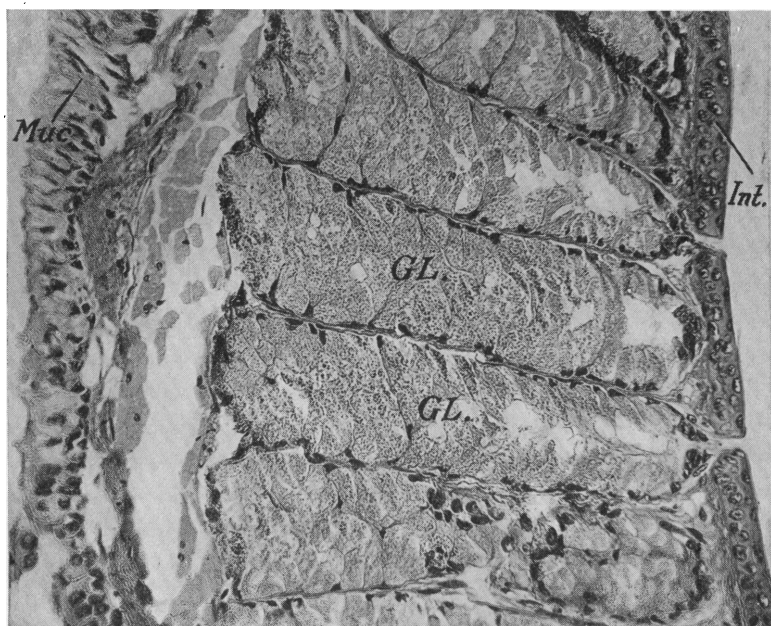


Fig. 6. Sagittal section of the mental gland of *Hydromantes italicus* Dunn. $\times 93$.

GL. = A single gland.

Int. = Integument, epidermis overlying the enlarged gland.

Muc. = Mucosa covering the floor of the mouth, lateral to the tongue.

pad consists of a series of acinous, eosinophilic glands (Fig. 6). The secretion within the lumen of the gland is pasty in appearance, not granular as the poison glands nor stringy like the mature mucus glands. In *Desmognathus*, there are fewer of the individual glands than in *Plethodon* or *Hydromantes*. Further, they are confined to the anterior angle of the jaws. Acinous glands of the same staining reactions and appearance line the pits which occur on each side of the temporal region of the breeding male *Triturus viridescens*. It is well known since the work of Hilton (1902) that these glands serve to intoxicate the female in such a way that

she will pick up the packet of spermatozoa emitted by the male. If these glands play such an important rôle in the breeding of the plethodontids as their histological appearance suggests, it is surprising that no observer has ever seen them functioning. Other glandular hypertrophies occur in the integument of other male salamanders. Mention may be made of the highly glandular process which stands erect on the dorsum of

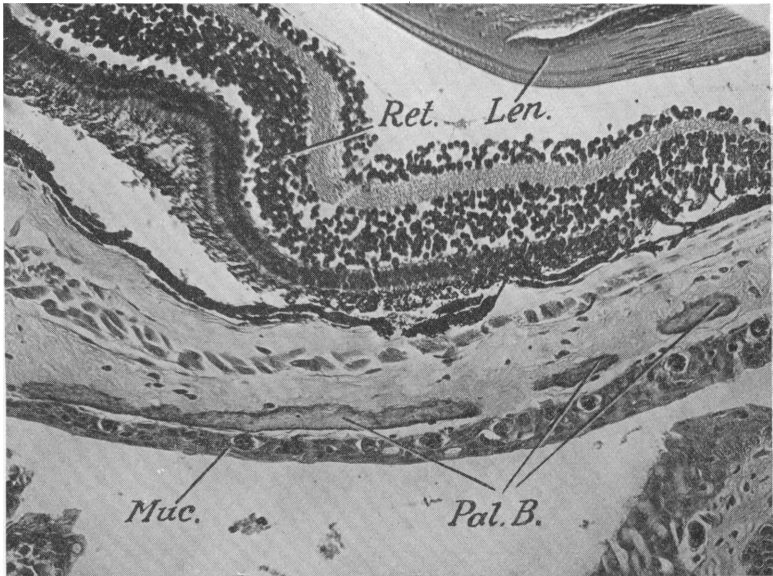


Fig. 7. Cross section of the palate of *Desmognathus fuscus carolinensis* (Dunn) in the region of the eyeball. $\times 93$.

Len. = Lens

Muc. = Mucosa covering the roof of the mouth.

Pal. B. = Nodules of palatal bone.

Ret. = Retina

the tail base in *Salamandra caucasica* and *S. luschani* (Fig. 8). The Japanese newt *Triturus pyrrhogaster* has glandular bunches at the jowls, and in the paratoid and scapular regions of the male. The integument of the male of the European *T. palmatus* is well known to exhibit various glandular hypertrophies. In none of these cases are the glands known to have any specific functions.

In examining cleared specimens of a large series of *Desmognathus* a secondary sexual character of a totally new type was found. This character is of especial interest for it affords one more example of a specific

character of one species carried over to another as a sex-linked character having almost certainly no rôle in the breeding process. In the large and primitive *D. quadra-maculatus*, both sexes possess a cluster of bony or calcareous nodules in the palate underlying each eyeball (Fig. 9). This cluster of ossifications is not in the sclerotic membrane but in the connective tissue underlying the mucosa of the palate (Fig. 7). The larger nodules resemble true bone histologically. They take the haematoxylin and the alizarin stains in the same way. The smaller appear to be calcifications, although they differ only slightly from the larger nodules. They both would seem to function in protecting the eyeball or possibly in acting as a crushing plate on each side of the dentigerous para-

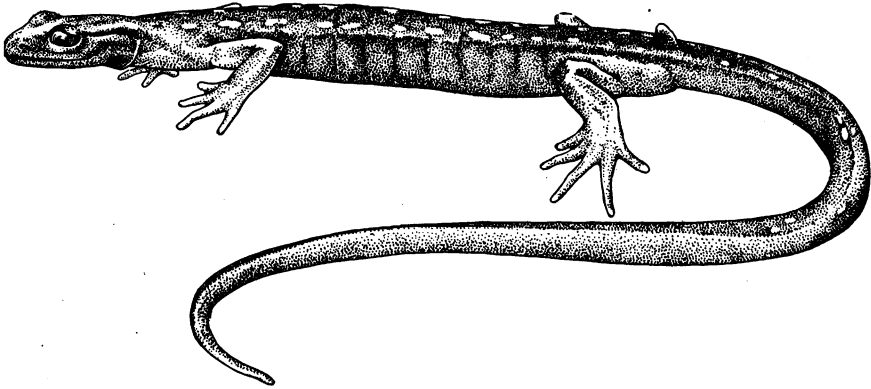


Fig. 8. Male *Salamandra caucasica* (Waga) showing the glandular process at the base of the tail.

sphenoid. I have not found similar ossifications in any other species of *Desmognathus* except *D. fuscus carolinensis*, where they are best developed in the male. In some specimens they form a single plate surrounded by nodules. I have examined eleven cleared specimens of this species, five males and six females, also serial sections of the heads of two males. One male has the ossifications better developed than any female. Two females were without any indication of the ossifications. Two of them had from one to ten small nodules under each eyeball while the remainder had larger ossified areas. No males lacked the ossifications. If these palatal ossifications can be considered a secondary sexual difference, they represent at best not a very constant difference, for, while no males lack the structures, some males do not have them as well developed as some females.

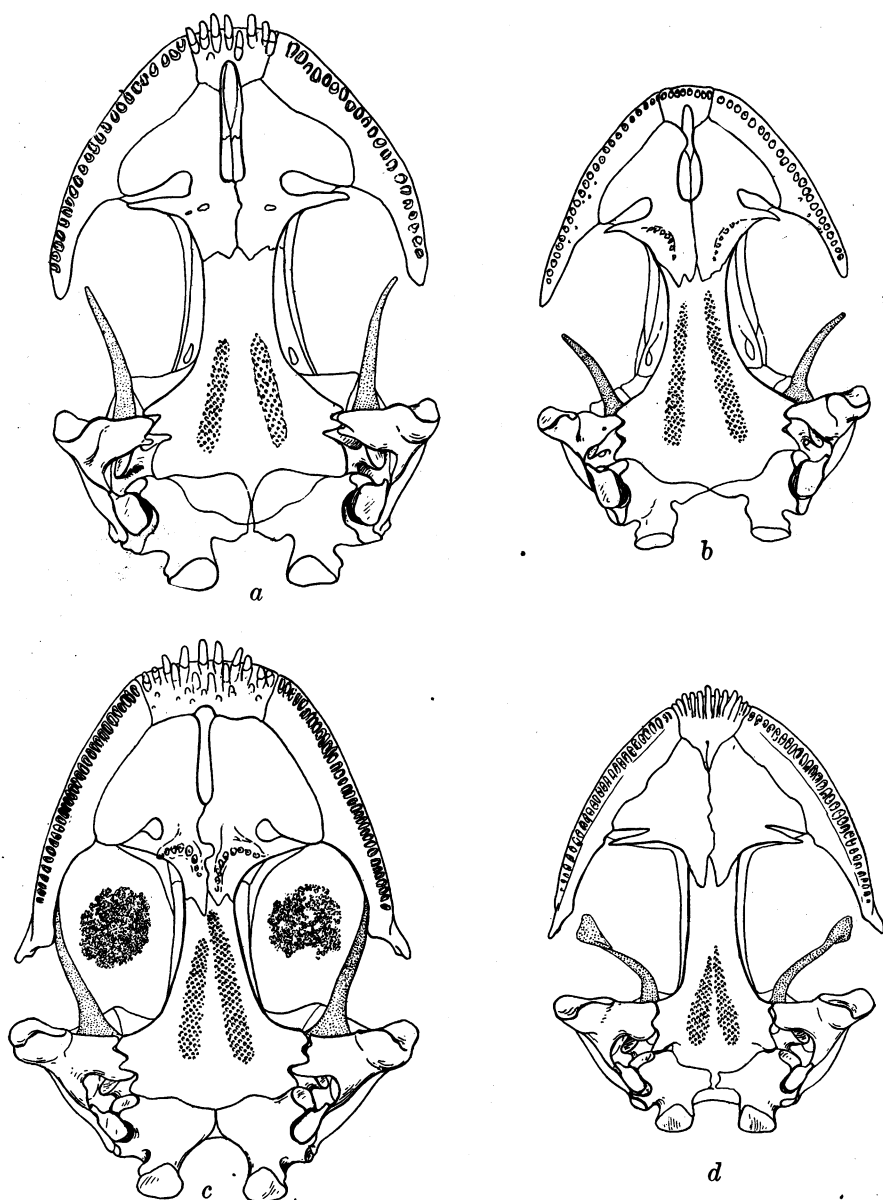


Fig. 9. Palates of *Desmognathus* and *Leurognathus* showing the secondary sexual characters of premaxillary teeth, vomerine teeth and palatal nodules (in the eyeball region of fig. c.).

- a. *Desmognathus fuscus fuscus* (Rafinesque), male.
- b. Same species, female.
- c. *Desmognathus quadramaculatus* (Holbrook), male.
- d. *Leurognathus marmorata* Moore, male.

Whatever might be the immediate function of the palatal plates, it is interesting to speculate in regard to their phylogenetic origin. No other urodeles are known to possess such palatal plates, but in the salamandrid ancestors of the plethodontids a number were provided with a secondary deposit of bone over the roof of the skull. The palatal ossifications have the form of a secondary deposit in that they consist of clusters of nodules. They differ from most secondary bony deposits in that they are not connected with any skull elements, and seem to have arisen *de novo* in the palate.

It may be emphasized again that many secondary sexual characters in the Amphibia are merely specific characters which have been taken over and often elaborated by the male sex of other species. In the genus *Desmognathus*, mention has been made of the bowing of the maxilla and the broadening of the maxillary teeth. Dunn was the first to show clearly that the reverse process has occurred in the case of another secondary sexual character. In the evolution of the genus *Desmognathus* from the large *D. quadra-maculatus* to the small *D. fuscus ochrophæus*, the male exhibits a greater and greater tendency to lose its vomerine teeth and to reduce the anterior part of the parasphenoid teeth patches. In *Leurognathus marmorata*, which has been directly evolved from *D. quadra-maculatus*, both sexes when fully adult exhibit similar losses. It is very difficult to understand how the loss of the vomerine teeth could have any particular function (Fig. 9).

Evolution is usually believed to be progressive and continuous, changing only in its course as the environment changes. It is enlightening to study the secondary sexual characters for they are so haphazard in their occurrence. A great many in both urodeles and Salientia have apparently arisen suddenly in different groups of Amphibia and afford examples of parallel evolution under different environmental conditions. Conversely, closely related forms in the same habitat may have strikingly different secondary sexual characters. It follows that many of these characters may have no particular function but, as Morgan (1919, p. 94) has expressed it, may "be only by-products of genes whose important function lies in some other direction."

THE COLOR PATTERN

The plethodontid salamanders, being of small size and of secretive and usually nocturnal habits, would not be expected to exhibit a highly protective coloration. It might be expected that they would exhibit an evolution of color pattern irrespective of the colors of their habitat.

Dunn (1926) sees in this evolution a highly orthogenetic process, one of the most striking ever described in the Amphibia. The essential features of Dunn's theory may be given in his own words (p. 49):

The color pattern of the mountain-brook forms is based largely on the development of three rows of unpigmented areas on each side of the larva, a dorsal set, a lateral set and a ventro-lateral set, the last running from arm to leg. These unpigmented areas as shown by Banta and McAtee (1906) for *Eurycea lucifuga* attract black pigment cells. With transformation a general pigmentation of either red or yellow appears in places where the black pigment is absent.

The history of the color pattern in various forms is the history of the varying development and fate of these unpigmented areas and their relative success in attracting pigment. . . .

This process is gone through in its entirety by every individual of *Desmognathus fuscus fuscus* or *Eurycea bislineata bislineata*, so that a description of the color pattern of either of these species is practically a description of nearly every form of pattern found in the entire family and no easy matter. Fortunately the adult and permanent pattern is fairly definitive for different species, which stop at one stage or another in the general scheme outlined above.

An examination of the large series of plethodontids, both larvæ and adults, in the American Museum has failed to reveal any evidence to support the theses advocated by Dunn. On the other hand, considerable evidence has come to light which disproves the facts on which Dunn's conclusions are based. It seems clear from a study of this material: (1) that there is no actual attraction of pigment by the pigmentless areas; (2) that the pigmentless stripes of the adults of certain species have not arisen by an extension of the pigmentless areas of its larvæ; and (3) that the adult color patterns of the various mountain brook plethodontids cannot be considered arrested stages in the ontogeny of *Eurycea bislineata*.

The late embryo of *D. fuscus* and of *E. bislineata* as well as that of most plethodontids tends to be uniformly pigmented above with stellate melanophores. The multiplication of the melanophores does not keep up with the growth of the body. Disturbing factors enter in to prevent a uniform pigmentation above. The chief disturbing elements of the early larva are the lateral line organs. In *E. bislineata* and certain other species each lateral line organ becomes surrounded by a pigmentless area. The lateral line organs are in three rows on each side of the body, and the color pattern of the early larva is determined by the distribution of these organs (Fig. 10). This power of the lateral line organs to repel pigment in *E. bislineata* is probably due to some mechanical difficulties which are overcome in other species. In *Desmognathus phoca*, each lateral

line organ of the dorsal series is surrounded by a pigmentless area while the organs in the median row are nearly obscured by the pigment which uniformly covers this region.

The evolution of the color pattern within a genus is not determined by the expansion or contraction of the pigmentless areas surrounding the lateral line organs. In the larva of *E. bislineata*, the relation of pigmentless areas to the lateral line organs is conspicuous. In the larvæ of *Eurycea gutto-lineata* of the same size, a stripe of black pigment runs the length of the middle row of lateral line organs and another the length of the ventral row either obscuring the organs completely or leaving a narrow ring of unpigmented epidermis around each organ.

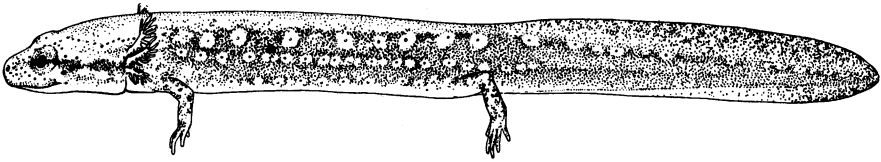


Fig. 10. The early larva of *Eurycea bislineata bislineata* (Green) showing the relation of the early color pattern to the lateral line organs (the small circles within the light areas).

A study of the development of the color pattern in such forms as *E. bislineata*, *E. gutto-lineata*, and *D. phoca* gives the impression that there is during ontogeny a shift of pigment to sides of the body, although some may remain on the dorsum to form the basis of the dorsal color pattern. On the body the color pattern may be influenced but not controlled by the neuromasts. On the head and frequently on the tail a melanophore, even in the early larva, may lay immediately adjacent to a neuromast, showing that there is nothing in the organ itself which repels pigment. In both *D. phoca* and *D. quadra-maculatus*, the pigmentless areas around the dorsal neuromasts are large, while they are practically nonexistent around the organs of the middle row. Any theory which attempts to explain the evolution of the color pattern in the Plethodontidæ should take into consideration these facts.

The literature dealing with the coloration of the Amphibia is enormous, but very few suggestions have been made as to the origin of the color pattern (for the literature see Biedermann, 1926, and Fuchs, 1914). The integumentary melanophores are well known to lie usually in the vicinity of capillaries. But, as the latter form a net between epidermis and derm over the entire surface of the body (see Noble, 1925, Figs.

20-24), the question remains, why are melanophores more abundant in some regions than in others? In certain minnow embryos where an artery and vein were close together, only the artery was found by Loeb (1898) to be covered by pigment cells. This suggested that the response was chemotactic rather than thigmotactic. On the other hand, Zenneck (1894) has shown that in a European snake (*Natrix*) pigment first appears on the surface in the vicinity of the larger veins. Many plethodontids show a tendency toward the development of a pair of lateral stripes. The largest superficial vein in the Plethodontidæ, namely, the *Vena cutanea magna* and its ventral branches, lies directly under this stripe, as I have determined by injecting specimens of *Plethodon vandykei*. In these species, at least, there is a correlation between the distribution of the large superficial veins and the largest masses of melanophores.

The striping which occurs so frequently in salamanders, frogs, lizards, and snakes apparently owes its existence to the distribution of the large superficial veins. Not all reptiles and amphibians are striped, for, due to a rapid secondary development of pigment, the early striped pattern may be obscured. Uniformly colored salamanders may be primitive or specialized, for the secondary development of pigment is a very haphazard phenomenon even within the genus *Desmognathus*.

A detailed study of the relation of the veins to the color pattern within the Plethodontidæ has not been made. The work of Zenneck and the observations reported here make it seem highly probable that a very close relationship will be found throughout. The following conclusions may be expressed as a tentative hypothesis. The early plethodontid larvæ tend to be uniformly pigmented above. In certain species, as in *Eurycea bislineata*, the lateral line organs on the body present mechanical difficulties and pigment is not formed around them. In other species, such as *Desmognathus phoca*, only the neuromasts in the dorsal row have this effect. As development proceeds, the pigment, at least in most brook species, tends to withdraw from the dorsal surface of the back, although some may be retained in the midline. Pigment cells increase along and perhaps migrate towards the sides of the body. The greatest pigmentation occurs in the derm lying near the largest superficial veins (excluding those of the ventral surface). This approximation of melanophores and veins may be due to chemotaxis, for respiratory interchanges occur in the vicinity of the veins; but it is more likely due to some mechanical relationship, the wandering melanophores escaping more readily or in greater numbers through the walls of the large vessels. The striped pattern is the basal pattern of salamanders, frogs, lizards, and snakes,

although it may be realized only here and there throughout the series. The phylogeny of the color pattern in the Plethodontidæ is not a repetition of certain stages in the ontogeny of *Eurycea bislineata*. Disturbing factors may obscure or modify the striped pattern at any point in the phylogenetic series. Self-colored forms may be primitive or specialized.

The species of *Desmognathus* may be readily recognized in the field at all stages during their life as metamorphosed individuals. The color pattern changes considerably during this period. The pigment surrounding the dorsal neuromasts usually fades and melanophores usually increase along the upper part of the sides. Old individuals tend to darken the ground tone and obscure the pattern. The small species are usually not as dark above as the large species. As the species grade from large to small there is an orthogenetic sequence of color pattern within the genus. But the series is not a very exact one. The small *D. f. carolinensis* varies considerably and many specimens are darker above than the mature *D. phoca*.

There are a number of cases in the Plethodontidæ where a small species will retain the juvenile coloration of a larger species. These are examples of "arrested development," and usually indicate a specialized rather than a primitive stock. Dunn, however, has interpreted some of these cases in exactly the opposite way. For example, he remarks concerning *Pseudotriton ruber nitidus*, the red salamander of the northern half of the southern Blue Ridge: "This appears the most primitive of the three races of *ruber*. Its general adult coloration is nearest that of the young of all three." Dunn names no other characters which testify to the primitiveness of this race. In most species of Amphibia where a race occupies a small range within that of a wide ranging form (compare Dunn, 1926, map 40), the former usually proves to be a derivative of the latter. Again, many known derived stocks, such as *Leurognathus*, retain a more juvenile coloration than their ancestral stock. There is no *a priori* reason for considering a juvenile coloration primitive, although Dunn considers it such in his sketch of the relationships of several of the species.

The occurrence in phylogeny of certain pigment masses is extremely erratic. Mention may be made of the leucophores which fleck the sides of several species of *Desmognathus*, form distinct blotches in *Plethodon glutinosus*, and then disappear entirely in its close relative *P. metcalfi*. The black coloring of the ventral surface of *Desmognathus quadramaculatus* may reappear in the old male *D. f. carolinensis*. It is difficult to

see how these pigmented areas could have any survival value. And what could be their functional use? In the present state of our knowledge it is most reasonable to assume that they, like many secondary sexual characters, are merely "by-products" of genes which have other functions.

CONCLUSIONS

Habitat Preferences

1.—In the North Carolina mountains the rocky and the muddy stream habitats usually possess different salamander faunas.

2.—The adult *Desmognathus quadra-maculatus* is the dominant form of the first, the adult *D. phoca* of the second habitat. Juveniles of these species may occur in either habitat.

3.—Many other plethodontids wander through various ecological niches outside of the breeding season, but closely related forms tend to occupy different habitats at the time of egg laying.

4.—*Desmognathus phoca* and *D. f. carolinensis* live during the breeding season in the same muddy streams, but the former is found under and the latter upon the logs, thus avoiding competition.

5.—Competition between some closely related species (as *Plethodon*) is avoided by their preferences for habitats of different humidities, in others (as *Pseudotriton*) by preferences for different types of streams, at least during the breeding season.

Secondary Sexual Characters

1.—The secondary sexual characters of the Amphibia are usually specific characters which are further modified by the male sex.

2.—In *Desmognathus* there is an orthogenetic change of the maxillary tooth form in both sexes and a less obvious change in the dentary teeth. These changes are exaggerated in the males of the smaller species.

3.—An elongation of the maxillary teeth occurs as a secondary sexual character in *Eurycea*, reaching its extreme in *E. lucifuga* and *E. gutto-lineatus*. A similar progressive change is found within the genus *Hydromantes*.

4.—The premaxillary teeth are modified as a unit distinct from the maxillary ones. The elongation of the premaxillary teeth as a character has appeared, disappeared and reappeared again in phylogeny without relation to the environment. This involves the change of bicuspid teeth to monocuspid ones and the reverse.

5.—In *Plethodon* there is a gradual change in form of the premaxillary teeth of the male, the smaller species having the extreme type and one different from that of other plethodontids.

6.—Most plethodontids possess a prominent mental gland in the male which in histological structure agrees with that of the temporal glands of *Triturus viridescens* and which may function in stimulating the female. An enlargement of this gland is usually associated with an hypertrophy of the naso-labial glands, but not always with an elongation of the premaxillary teeth.

7.—In the submucosa of the palate underlying each eyeball there is found in *Desmognathus quadra-maculatus* a cluster of bony nodules. In *D. f. carolinensis* these are well developed in the male, usually less developed and sometimes absent in the female.

8.—The evolution of the secondary sexual characters is usually not progressive and continuous but haphazard and often parallel in not closely related stocks.

The Color Pattern

1.—The early plethodontid larva tends to be uniformly pigmented above, but certain disturbing elements usually prevent this from being accomplished.

2.—The first pattern of most brook plethodontids is determined by the lateral line organs which frequently prevent melanophores from taking up a position near them.

3.—The next pattern during ontogeny is controlled by the distribution of the large superficial veins near which pigment accumulates. The resulting striped pattern may be considered the most fundamental pattern of plethodontids. Its wide occurrence in both reptiles and amphibians is noteworthy. Disturbing factors may prevent the striped pattern from appearing or it may be covered over by a secondary pigmentation at any of the later stages of ontogeny. Self-colored forms may be primitive or specialized.

4.—The color pattern of most plethodontids is not concealing nor directly correlated with the colors of specific environments.

LITERATURE CITED

- BANTA, ARTHUR M. AND McATEE, WALDO L. 1906. 'The life history of the cave salamander, *Spelerpes maculicaudus* (Cope).' Proc. U. S. Nat. Mus., XXX, pp. 67-83, Pls. VIII-IX.
- BIEDERMANN, W. 1926. 'Vergleichende Physiologie des Integuments der Wirbeltiere.' Ergeb. d. Biol., I, pp. 1-342.

- CHAMPY, CH. 1924. 'Les caractères sexuels considérés comme phénomènes de développement et dans leurs rapports avec l'hormone sexuelle.' Paris.
- DUNN, EMMETT REID. 1926. 'The salamanders of the family Plethodontidae.' Northampton, Mass.
- FUCHS, R. F. 1914. 'Der Farbenwechsel und die chromatische Hautfunktion der Tiere.' In Winterstein, Handbuch der Vergl. Phys., III, pp. 1189-1656.
- HILTON, W. A. 1902. 'A structural feature connected with the mating of *Diemictylus viridescens*. Amer. Nat., XXXVI, pp. 643-651.
- LOEB, JACQUES, 1899. 'On the heredity of the marking in fish embryos.' Biol. Lectures, Woods Hole, for 1898, pp. 227-234.
- MERTENS, ROBERT. 1923. 'Zur Biologie des Höhlenmolches, *Spelerpes fuscus* Bonaparte.' Bl. f. Aquar. Terr.-kunde, XXXIV, pp. 1-4.
- MORGAN, T. H. 1919. 'The genetic and operative evidence relating to secondary sexual characters.' Carnegie Inst. Wash. Publ. 285.
- NOBLE, G. K. 1925. 'The integumentary, pulmonary and cardiac modifications correlated with increased cutaneous respiration in the Amphibia: a solution of the "hairy frog" problem.' Journ. Morph. Phys., XL, pp. 341-416.
- POPE, CLIFFORD, H. 1924. 'Notes on North Carolina salamanders with especial reference to the egg laying habits of *Leurognathus* and *Desmognathus*.' Amer. Mus. Novitates, No. 153.
- STORER, TRACY I. 1925. 'A synopsis of the Amphibia of California.' U. of Calif., Publ. Zool., XXVII, pp. 1-342, Pls. I-XVIII.
- ZENNECK, J. 1894. 'Die Anlage der Zeichnung und deren physiologische Ursachen bei Ringelnatterembryonen.' Zeitsch. f. wiss. Zool., LVIII, pp. 364-393, Pl. XXIII.