

THE LIFE HISTORY OF THE CAVE SALAMANDER, *SPELTERPES MACULICAUDUS* (COPE).

By ARTHUR M. BANTA and WALDO L. MCATEE.

Of the University of Indiana.

During the past two years the senior author has been engaged in a study of the animal ecology of Mayfield's cave, near Bloomington, Indiana. An attempt has been made to work out the distribution, life history, etc., of as many of the species inhabiting that cave as possible. The present paper is an excerpt from the larger one and gives the results of the work on the common cave salamander. It is based largely upon collections made by the authors, but free use has been made of material contained in the United States National Museum.

GENERAL ACCOUNT.

REFERENCES TO LITERATURE.

The cave salamander, *Spelerpes maculicaudus* (Cope), was, until comparatively recently, confounded with its near relative and associate, *Spelerpes longicaudus* (Green). The following references pertain to *maculicaudus* exclusively:

Gyrinophilus maculicaudus COPE, Am. Nat., XXIV, 1890, p. 966, fig.—(Brookville, Indiana).—BUTLER, Journ. Cin. Soc. Nat. Hist., XIV, 1892, p. 172. (Brookville, Indiana; Northeastern Franklin County; Westport, Decatur County.)

Spelerpes maculicaudus HAY, Am. Nat., XXV, 1891, p. 1135 (Brookville, Indiana, p. 1133; Bloomington, Indiana; May's Cave, near Bloomington; Kern's Cave, near Bedford, Indiana); Ann. Rept. Dept. Geol. Ind. (1891), 1892, p. 447, pl. 1, fig. 4. (Brookville, Indiana; Bloomington, Indiana; May's Cave, near Bloomington; Kern's Cave, near Bedford; Decatur County; and small cave, near Wyandotte Cave, Indiana; Barry County, Missouri, p. 448).—GAINES, Am. Nat., XXIX, 1895, p. 55 (Vincennes, Indiana).—COPE, Ann. Rept. Smiths. Inst. (1898), 1900, p. 1213 (Transalleghean district of the Carolinian Faunal area).—EIGENMANN, Trans. Am. Micr. Soc., XXII, 1901, pp. 189-91, pl. xxvii (Rockhouse Cave, Wilson's Cave, and Marble Cave, Missouri; Brookville, Wyandotte Cave, and Bloomington, Indiana).—EIGENMANN and KENNEDY, Biol. Bull., IV, No. 5, 1903, pp. 227-8, fig. 1 (Marble Cave and Rockhouse Cave, Missouri).

Spelerpes maculicauda BLATCHLEY, Ann. Rep. Dept. Geol. Ind., (1896), 1897, pp. 125-183 (Porter's Cave, Owen County, Indiana; Donnehue's Cave, Lawrence County; Clifty Cave, Washington County; Marengo Cave, Wyandotte Cave, Little Wyandotte Cave, Saltpeter Cave, and Sibert's Well Cave, Crawford County; Indian Springs, Martin County; Donnelson's Cave, Lawrence County; May's Cave, Monroe County; Kern's Cave, Lawrence County).—EIGENMANN, Pop. Sci. Mo., LVI, 1899-1900, p. 474, fig. 1 (Caves of Eastern U. S.); Proc. Ind. Ac. Sci. (1899), 1900, pp. 31-3 (Caves of Mississippi Valley); Science, n. s., XI, p. 493 (Caves of Mississippi Valley); Trans. Am. Micr. Soc., XXI (1899), 1900, p. 49 (Caves of Mississippi Valley).

DISTRIBUTION, HABITS, AND HABITAT.

The Cave Salamander^a (fig. 1) is confined to the Mississippi Valley. It has been collected from 2 stations in Tennessee, 1 in West Virginia, 1 in Kentucky, 26 in Indiana, and 5 in Missouri.

All of these localities are within the borders of the Carolinian faunal area (and restricted, obviously, to the Transallegheanian district thereof), a fact which sufficiently attests to the animal's status as a characteristic Carolinian species.

It is most commonly found in caves, and as a rule occurs at no great distance from the mouth, usually barely beyond twilight. Thus in Mayfield's Cave it has been found much oftener near the entrance than farther in, and the same is true of Truitt's Cave, also in Monroe County, Indiana, and the Twin Caves, in Mitchell, Indiana. Doctor Eigemann found it only near the mouths of Wilson's, Marble, and Rock House caves, Missouri. It sometimes ventures into the deeper recesses, however, being reported from a spot $1\frac{1}{2}$ miles within Wyandotte Cave, and it regularly resorts to such places to lay its eggs. The larvæ have been found in the remoter portions of Wyandotte, Mayfield's, and Mammoth caves. The Cave Salamander is likely to be found around springs originating from caves, and indeed at any point along the streams these feed. The nearly mature larvæ particularly are apt to occur in such situations.



FIG. 1.—ADULT SPELERPES MACULICAUDA.

Occasionally *S. maculicauda* is found away from the vicinity of caves. Mr. W. P. Hay writes us as follows concerning this point:

In 1899 and 1900 I found *S. maculicauda* and *S. longicauda* in considerable numbers in West Virginia, both in limestone caverns and in the forest under logs. In

^aIt has also been called the "Hoosier salamander" and the "Spotted-tailed salamander."

the caverns *S. longicaudus* was much more common, while in the woods the two species occurred in about equal numbers.

Blatchley records finding two specimens beneath logs in Monroe County, Indiana, a mile or more from any known cave and half that distance from springs or streams. Its occurrence at Brookville and Vincennes, Indiana, and in Decatur County, localities not in characteristic cave regions, further indicates that it is more or less independent of caves.

This account, however, has to do with the species particularly as a cave inhabitant. In Mayfield's Cave it is doubtless fairly common, but is only occasionally seen and then usually not in remote parts of the cavern. Nearly all of the adults seen have occurred between 60 and 150 feet from the mouth. Four, however, were observed in a passage 572 feet back, another at the edge of a shallow pool at 1,200 feet, and a recently matured specimen was collected 1,470 feet from the mouth.

The latter occurrence is readily to be understood because the larvæ are hatched and develop in these deeper fastnesses. Indeed, the whole character of the salamander's distribution in the cave results from this habit. The younger larvæ occur in the remoter parts. After, and even before transformation there is a gradual movement toward the mouth; here the adults—splendid fellows—are most numerous. Depredations of enemies and escape to the outer world regulate their number. That adults are found in the deeper portions of the cave is probably due in most cases to the necessity of laying their eggs in water, of which there is usually none near the entrance. When larvæ are found at the mouth or even outside of the cave it is probable that in most cases they were carried there by freshets.

Within the cave the adults are generally found in a crevice or upon a shelf of the wall. Only three have been observed on the floor. Their favorite resting places, therefore, are to be reached only by climbing. But this is an easy feat for *S. maculicaudus*, as the following will illustrate: At a point 572 feet back two were seen near each other in a cranny near the roof above a 15-foot embankment of earth, while on the opposite side of the passage one had ascended more than 10 feet on a perpendicular surface of stone. In scaling such places they are probably materially assisted by their tails. These are prehensile to quite a degree, enabling the salamander to support itself by the tail alone. The ability of the animals to climb is more severely tested when they are confined in glass jars. Yet they ascend vertical and even overhanging surfaces and usually remain clinging at the highest point.

When thus settled in a comfortable position the salamander is not easily induced to move. In the cave it is not readily disturbed by a light or by an object moving near. While light of itself will rarely

cause it to stir, the heat of a candle or occasionally the near approach of an object will arouse it to action. Its actions when touched are almost galvanic; leaping a foot or more at the first move, it continues to retreat for several feet by a series of leaps and wriggles. Having placed some distance between itself and the cause of its fright it again becomes quiet and is almost as hard to disturb as before.

This apparent apathy even in the glare of a powerful light would seem to indicate poor visual powers, but the eye of *S. maculicaudus* is in nowise degenerate, being as well developed as in the closely related *S. longicaudus*, a species almost entirely epigean. In this respect it differs from all other salamanders known to be true cave dwellers. *Typhlotriton spelæus* of southwestern Missouri has eyes well developed when young, but somewhat degenerate when adult, while *Typhlomolge rathbuni* of the subterranean streams of Texas has exceedingly degenerate eyes, surpassing in this respect even the renowned *Proteus* of Europe.

Returning now to the subject of our sketch, we will continue the discussion of the habits of the adult *S. maculicaudus*. It is not aquatic to any extent; two or three specimens only have been found in shallow water during our collecting. In captivity, where choice is afforded, it always prefers to remain in a damp place whether remote from or near the water, rather than in that element itself.

DEVELOPMENT.

In the breeding season, however, individuals of this species resort to pools of water to deposit their eggs. The process of mating has not been observed nor have the eggs been seen. The larvæ have first been found about February 5, and are at this time slightly under 18 mm. in length. Assuming *Spelerpes maculicaudus* to have about the same rate of growth as some common salamander with which we are familiar, for instance, *Amblystoma opacum*, these larvæ are about one month old. This granted, it follows that the eggs are laid in the early part of January. Small larvæ have been found as late as March 20, indicating a later period of oviposition, but there is no doubt that in Mayfield's Cave the bulk of the eggs of this species are laid at the earlier date.

At 17.5 mm. the larvæ are fairly active. They have a full complement of digits showing that the first larval stages are rapid, and that perfection in larval form is reached comparatively early. The attainment of larger size is, however, a slower process. Twenty-five millimeters is probably the average maximum size reached the first spring. Up to this time the larvæ are fairly uniform in size, but by the succeeding autumn there is a great disparity to be noticed. Larvæ measuring from 31 to 56.5 mm. have been taken in autumn, and some transform at this season. Most of them, however, mature later, twelve to fifteen months after their appearance in the cave.

There is evidence that even a longer period may be passed in the larval state by some individuals, and a longer period than the above seems to be the rule for another member of the genus, *Spelerpes bilineatus*. Concerning this species Wilder^a says: "The larvæ * * * hatch early and continue for a long time in the larval state, probably 2-3 years. * * * The growth must be exceedingly slow and dependent upon the fortune of the individual in securing prey. I have caught all stages from 16-52 mm. at all seasons of the year, and see no indication that those larvæ collected at any one time represent one, two, or three years of definite growth." That slow development is the rule in the genus is further shown by the life history of *Spelerpes ruber*. Small and large larvæ and recently transformed individuals are commonly found together in the same spring.

The small larvæ of *S. maculicaudus* are easily studied in their native pools. They are most often found lying quietly on the bottom, in their position and distribution reminding one of the johnny darters on the creek bed. But the analogy can be carried no further; the darters are the incarnation of irritability and activity, while no mechanical disturbance short of actual poking will cause these larvæ to move. When captured at the first trial the feat seems easy, but when that fails the larvæ are elusive, and by stirring up the sediment cloud the water so that their motions are not easily followed. Their habit of lying openly on the bottom is changed when they are confined in a well-lighted vessel. Here they seem ill at ease except when hiding under some object on the bottom. When disturbed, they swim rapidly, but not for any length of time, as they soon seek the bottom and nose about for a hiding place. This sensitiveness to light agrees with their behavior in the cave. All larvæ are very much more responsive to light stimulus than the adults, the young larvæ more so than the older. The former always swim away from the source of light, while the latter act in a more uncertain way, lowering and raising the head, starting away but stopping immediately only to lower the head and start in another direction. A light held steadily upon them, however, will cause more decided action, a slow movement away from the light resulting.

In the very oldest larval stages they are also stimulated by light. A large larva found March 4 seemed annoyed by the light, especially when it was flashed suddenly on and off. This larva was approaching transformation. The gills were quite small, the tail had lost some of its keel, and in the shape of both body and head it resembled an adult. Besides these changes, the larval coloration, while not yet lost, was supplemented by the characteristic spots of the adult. Other habits of larvæ at this stage are of interest and are best known to us from the study of specimens in the laboratory.

^aAm. Nat., XXXIII, 1899, p. 242.

A larva about 45 mm. long was collected in the cave March 15. It showed no signs of transformation and for a long time was content to stay in the water, resting much of the time upon the lower end of a piece of wood placed at such a slant that the larva had choice of varying depths of water. About April 20, more than a month after being brought from the cave, it began resting nearer the surface and remained often with the nose slightly out of water. When disturbed, it dashed to the bottom, but immediately tried to dart up the sides of the jar and get its nose out again. It kept constantly on the move until it again rested in its favorite position on the piece of wood. About May 1 the young salamander began to spend all of its time either on the wood or the side of the jar, with all or nearly all of its body out of the water. At this time its gills had disappeared; they had begun to reduce ten days before. Soon after transformation it escaped from the jar through a slight crevice in the cover. During its period of indoor life it obtained little food and consequently made no growth. This apparently did not retard transformation, which came with a rush, the final changes of form and color seeming almost to occur in a day. At the time this larva escaped it had no tinge of the orange so conspicuous in the adult, although in all other respects it was a perfect miniature of the full grown salamander.

A more detailed account of the final and most interesting stages of larval life is the history of a larva taken among some stones in water December 21. It was 54 mm. long when captured, and showed no signs of transformation. This larva was well fed with small annelids and occasionally bits of meat. Until January 20 it lived contentedly in the water, but on that date it climbed up on a floating mass of water-cress and remained with the nose and part of the upper surface of the head out of water. On January 23 more of the head was projected, but only part of the time was spent in this position. During the remainder it rested on the bottom, usually under cover. On January 26 the gills were noticeably smaller, and on the next day, at 10 o'clock in the morning, the larva was seen on the side of the jar with all of the head and most of the gills out of water. An hour later it had climbed up farther, and was almost clear of the water. It was breathing air, the throat throbbing rapidly. In the afternoon it left the water completely, but turned and remained for some time with the nose thrust in the water, later remaining in a similar position, but wholly out of the water. The larva was now 57 mm. in length and its gills were less than one-fifth their original size. When disturbed, it jumped down and swam frantically about in the aquarium, stopping under the water-cress, but soon crawled up the side until only the tip of the tail dipped in the water. By January 30 it remained out of water all the time, the gills having entirely disappeared. It was, however, able to remain under water for several

minutes, in one instance fifteen, and often chose to stay under water in daytime, remaining under cover. But most of the day it remained above water and at night seemed to do so entirely.

The changes in the size of the gills preceding transformation are the reverse of stages which are passed through during early larval life. These exclusively larval organs are very slightly developed in the young below 18 mm. in length. In a specimen 17.5 mm. (March 20) and in one 18 mm. (February 16) they are very stubby, with short filaments. At 21 mm. (February 16) the filaments are much lengthened, and a corresponding increase is to be noted in larvæ 36 mm. long (November 12). Up to this stage the distal half of the gill is clear and translucent, while the basal part is pigmented. At 48 mm. (September 30) some specimens show a reduction of the gills, but among specimens having them most perfectly developed is one 50 mm. in length (October 7). In these larvæ the gills are pigmented to some extent even on the delicate filaments. Absorption of the gills probably takes place in most cases when the larvæ are between 50 and 55 mm. But we have one larva 56.5 mm. long (October 28) in which the gills are perfect, although this specimen is longer than many of the recently transformed adults. The state of the gills, however, shows that it is a genuine larval form, and although we have observed one longer specimen (57 mm.) with gills reduced and near transformation, it seems certain that the growth of this individual was accomplished under the most favorable conditions and that in it are realized the utmost possibilities of larval development under natural conditions.

The process of absorption of the gills is the reverse of that of growth, in detail as well as in entirety. Whereas the basal stubs are present in early life and from them are budded out the filaments, the latter are the first parts absorbed, the main arches disappearing slowly. After this is completed the place of joining of the edges of the gill-slit is indicated for some time in the young adults by a dark line, which is visible on both the dorsal and ventral surfaces of the side of the neck. Besides the changes in these particular organs of the transforming larvæ the entire body seems to lose in bulk, becoming flattened and undergoing a special reduction in vertical dimension in the tail, which loses all traces of the keel. Further, the neck appears longer and slimmer, making the head more conspicuous, and, finally, the eyes become much more prominent.

The evolution of form is accompanied by as great a change in color. To the naked eye the young larvæ appear uniformly gray, while the adult is flaming orange with conspicuous black spots. The study of the development of the color pattern is of so much importance as an aid in identifying the larval salamanders (a thing still impossible in the case of many common species) that it has been separated from the main account of the life history and treated in greater detail.

DEVELOPMENT OF THE COLOR PATTERN IN THE LARVÆ OF
SPELERPES MACULICAUDUS.

By WALDO L. MCATEE.

The youngest larvæ of the species are nearly uniformly pigmented, while the adults are marked with separate, sharply defined spots. The development of the color pattern, therefore, is the change from even distribution of pigment cells on the smaller animal to their concentration in restricted areas on the larger.

At 17.5 mm. (fig. 1, Plates VIII and IX) the pigment^a cells are abundant and about evenly distributed over the whole body, with the exception of certain invariably pigmentless areas which form the most conspicuous and characteristic feature of the larval coloration. The least important of these (that is, the one which for all practical purposes is identical in adult and larva) is the ventral area and its history may as well be completed at once. This ventral area extends from the gular fold or from slightly in front of it to the cloaca, often being prolonged in a narrow line on the tail, and includes the inner surfaces of the limbs with which it may or may not be connected. It is generally bridged by a band of pigment cells over the pubic region and in cases where it extends anterior to the gular fold, by a narrower band along the gill slits. In younger larvæ the latter condition exists, as the lower surface of the head is not so completely pigmented as in older larvæ and adults. In the later larval stages the anterior bridge of pigment may separate in the median line or it may persist, leaving thus a small separate pigmentless area. In the adult, however, the head is entirely pigmented on the underside back to the gular fold.

In larvæ above 30 mm. in length the ventral area is liable to be encroached upon by pigment in various places, but the middle line at least remains spotless until transformation. In the adult, while the lower side of the tail loses the marbling which it generally possesses in the larva, it retains some pigment; in fact there is no considerable area on any part of the body free from pigment dots. The dots can be made out with close scrutiny by the unaided eye, but are more easily studied with a lens.

Thus while the presence of pigment cells over the whole ventral surface is exclusively an adult character of the species, and demands consideration in a discussion of the development of the color pattern, this area, with the exception of the lower surface of the head, may, for the purpose of ordinary description, as before mentioned, be considered immaculate in the adult as it actually is in the larva.

The other conspicuous pigmentless areas of the larva are arranged in three longitudinal series on each side, and together with the pigment around them play the major part in the evolution of the color pattern.

^a The term pigment as used here refers to the apparently black color spots only.

These areas are roughly circular to oblong, and are most prominently developed between the levels of the root of the fore limb and of the cloaca, although each series may be traced more or less distinctly on both the head and tail. Counting from the insertion of the fore leg to the region which may be overlapped by the hind one, there are in the upper (first) series of areas about ten, in the middle or second series, thirteen to fifteen, and in the lowest or third series from seven to thirteen.

The upper series is near the mid-dorsal line and in larvæ from 17.5 to 21 mm. (fig. 2, Plates VIII and IX), is the most conspicuous of the three, being made up of the largest areas. This series is first to disappear in the development of the color pattern. The second series is situated just above the middle of the side, being visible from above. It is the longest lived of the series, sometimes remaining quite perfect after transformation. The third and lowest series begins under the fore leg and extends along the side toward the hind leg, sometimes falling short of that point, sometimes surpassing it. This series is the most variable and is not of much importance in the production of the adult coloration. It is none the less an important larval character. In some salamanders, notably various species of *Amblystoma*, this series exhibits metallic color.

Returning now to the smallest of the larval stages (17.5 mm.) we will trace the fate of the pigmentless areas and also of the abundant pigment cells so uniformly covering the surface of the larvæ of this age. Besides the above-mentioned conspicuous immaculate areas, the interstices of the pigment spots form a reticulation over the whole body, which with the former makes the ground color of the larva. In the stage at present under discussion this is light yellow.^a

The ventral area in this as well as succeeding stages is pale. The legs are covered above with a coarse network of pigment, generally with an open space over the base of the toes, which is also a persistent character in the larva. The particular feature to be noticed about this larva, however, is the uniformity of coloration, especially of the dorsal surface (fig. 1, Plate IX). At 21 mm. (fig. 2, Plates VIII and IX), the principal differences to be noted are those due to growth. As a result the only change in color is a general paling, due to the widening of the spaces between the pigment spots. It is possible that this is just a little more conspicuous in the area between the mid-dorsal line and the first series of larval spots, beginning the most important change of the next stage.

At 31 mm. (not figured), the pigment on the dorsal surface on either side of the mid-dorsal line begins to collect, forming nuclei for the future spots. In this first stage of analysis the mid-dorsal region retains its reticulated pigmentation. The 36.5 mm. larva (fig. 3, Plates

^a In formalin.

VIII and IX) shows the same process; the migration of pigment cells from the borders of the upper series of larval areas, destroying them as such, and merging them into the now lightly pigmented dorso-lateral areas. The pigment on the head shows a tendency to concentrate, making this part of the dorsal surface lighter. At this stage the ground color is clear yellow. The second and third series of larval areas, and the pigment spots of the legs and tail, maintain their previous arrangement.

When the larva is 48 mm. in length (Fig. 4, Plates VIII and IX), the lightness of the dorsal area is emphasized, most of the primary pigment reticulum having aggregated into the now distinct spots. The spots on top of the head are further intensified, reaching a stage of development in which they remain until or after transformation. The pigment-cells move away from areas on both the lower and upper parts of the tail at the base of the keel, marking the proportion of this that will be absorbed and forming for the tail dorso-lateral areas similar to those shown in the last stage on the dorsal surface of the body proper.

The pigment blotches on the legs and on the side of tail, head, and body are more widely separated, but the lower two rows of larval areas remain intact. The ground color is possibly a shade more yellowish at this stage.

The principal change in the next stage (51.7 mm., fig. 5, Plates VIII and IX) is the further development of the dorsal spots. They are probably as conspicuous in the specimens figured as they ever are before transformation. From the same figures it will be seen that all the other features are about the same as in the preceding stage and that the pattern of the legs and the second and third series of larval areas are in practically the same condition as in the 17.5 mm. larva.

However the ventral fin of the tail has been absorbed and nearly all of the pigment-cells have migrated from the dorsal keel and are collected with the rest in a dense reticulation over the surface of what will be the adult tail. The cells remaining in the keel later form the few spots that exist on the mid-dorsal line of the tail in the adult. In all larvæ 50 mm. or more in length the ground color has deepened and is noticeably yellow.

The changes in form of the body at transformation are much greater than those in its color, but the latter are important. In a specimen 55 mm. long representing the most recently transformed stage we have (Fig. 6, Plates VIII and IX) the ground color can scarcely have changed from that of the last stage, but the dorsal spots of both body and tail have attained the perfect size and definition. The color pattern of the head and legs remains about as in the last stage. Both the second and third series of pigmentless areas are breaking up, however, anastomosing with each other and with the adjoining lighter

areas. The pigment forming the lower border of the first series and the upper margin of the second now collects into the most conspicuous series of spots on the lateral surface. The pigment on the sides of the tail is also beginning to form spots.

It is possible that stages of the various components of the color pattern presented by this specimen may be omitted by some at transformation, and on the other hand they may be prolonged, in other cases for some time afterward. *Spelerpes bilineatus* seems especially liable to such vagaries at transformation, and this suggests the possibility of a parallel case in the present species. However, the larva is undoubtedly intermediate in age between the preceding and succeeding examples making the color stage valid for our series if it is not for every one.

The next stage (55.5 mm. fig. 7, Plates VIII and IX) is a typical newly-transformed cave salamander. The ground color is lemon yellow, the spots are distinct with but few traces of the primitive pigment reticulation. The pigment on the legs is now for the first time collected in spots. The head is more plainly spotted, approaching nearly to the adult condition. The spotting on the sides of the tail is definite though not yet perfect, and of the series of immaculate larval areas only one, the second, is traceable. On each side of this series of clear areas the bands of pigment cells are collected into dense bars, which now break up to form two rows of spots, which are very conspicuous in the adult salamander. The third and lowest series of larval areas is no longer present. The nebulous pigment surrounding them forms irregularly distributed blotches on the lower sides of the salamander and contributes many cells to the ventral area, which now becomes entirely, if sparsely, pigmented. In a salamander of this age, with the second series of larval areas almost intact, the original position of the three series of clear areas and the fate of their accompanying pigment masses is not difficult to trace. But in the fully grown adult, at first blush, it does not appear that the grouping of the blotches is the result of even a fairly definite system. The influence of their origin upon their arrangement becomes apparent at once, however, when compared with newly transformed specimens, such as the one just described.

The scattered pigment cells at this stage are more abundant than in the full grown adult, and the pigment blotches less distinct. As the animal grows the scattered pigment collects more and more in the blotches, which grow larger and at the same time more dense. Stages in this aggregative process may be seen about the edges of the blotches on any adult. Approaching and newly united pigment cells form a fringe about most of them.

Few other changes occur in the pigment beyond the stage just described (55.5 mm.). In many adults the chaining of blotches along

the sides gives way to separate spots (Fig. 2, Plate X), but this is not an essential change as some specimens show a nearly continuous bar from back of the eye to the middle of the tail. The ground color, however, gradually deepens, becoming vermilion in highly colored specimens.

The development of the color pattern may be summed up as follows: Originally pigment cells are evenly distributed except for a ventral and three lateral series of pigmentless areas. In later development these acquire pigment by influx from adjoining parts thus causing a dilution of pigment. Otherwise the keynote of the entire process is concentration.

The pigment of the head, legs, and tail moves little, simply crowding together in blotches. The concentration of the pigment cells of the tail presents one notable feature, namely, that a few cells remaining in the keel are laid down as median spots when that portion is absorbed, forming the only noticeable group of so located spots on any part of the animal.

The movements of pigment cells on the body proper are more complex. The spots on the dorsal surface are formed of pigment from the immediate vicinity and also from the border of the upper series of immaculate areas. The fact that the first spots originating here are lateral probably accounts for the scarcity of true median spots. The large amount of pigment paralleling the second series of pigmentless areas on each side collects into the two series of distinct blotches on the side of the adult. The pigment of the third series forms many small scattered spots on the flanks of the adult and contributes to the pigmentation of the ventral area.

While in the development of the pigment pattern there seems to be no increase in the number of cells, the change of the ground color from buff to orange and vermilion is accomplished wholly by the addition of coloring matter.

MELANISTIC SPECIMENS.

A point that arises in connection with the matter of the addition of pigment is whether the so-called melanistic specimens really have an extra amount of pigment, or whether their peculiar coloration may not be explained in another way. Dr. C. H. Eigenmann gives an account of two specimens of the cave salamander which have more than the usual proportion of the surface pigmented. In one from Rock House Cave, Missouri, there is a lateral streak "broad enough to cover the sides with a mottled pattern." Another specimen among twelve from Marble Cave, Missouri, is described at length:^a

The lower surface of the head is more densely pigmented than in the other specimens. The sides are more uniformly pigmented than in the melanistic individual from Rock House. The sides of the head, body, the arms, and anterior surface of

^aBiological Bulletin, IV, 1903, pp. 227-8, fig. 1.

the legs are uniformly pigmented, except a few small blotches or spots. The pigmentation is not as intense as in the dorsal spots. The most striking deviation is found on the dorsal surface. The usual spots are present, rather smaller than in the other specimens. The intervening spaces are more densely covered with pigment cells than in the normal specimens, and in several places, notably the head, the nape, and one or two places on the back, the spots seem to have "run," their closely compacted pigment cells having been distributed in a thinner coat over a wider area and form, with the similarly distributed pigment of other spots, diffuse, evenly pigmented blotches. In life the specimen suggested that the inhibitory force which kept these color cells from spreading, or the positive tropism which kept them together, was dissolved and the cells scattered evenly in a single layer over the surrounding region. The centers of distribution are still distinguishable as darker areas at the margin of or in the blotches.

The "centers of *distribution*" are more probably the original spots where the *collection* of pigment began. In fact all points in con-

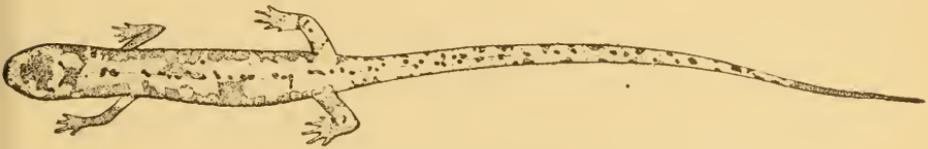


FIG. 2.—MELANISTIC SPELERPES MACULICAUDUS. (DORSAL VIEW.)

nection with these specimens suggest that they represent, not modified adult stages but inhibited larval conditions. The lateral color pattern of the Marble Cave specimen, as shown by the figure (fig. 3), could be easily produced by the cessation of pigment aggregation at the stage represented by fig. 5, Plates VIII and IX (51.7 mm.), plus the uniform distribution of isolated pigment cells over the clear lateral areas, which process always occurs in the ordinary adult. On the dorsal surface there are not many spots, indicating that a few of the earliest centers attracted all the pigment. The diffuse condition of these blotches and

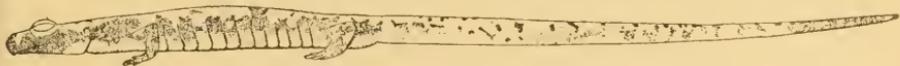


FIG. 3.—MELANISTIC SPELERPES MACULICAUDUS. (LATERAL VIEW.)

the connection of many of them with the lateral pigment band is a further indication of the cessation of concentration at some larval stage. The Rock House Cave specimen with its mottled pattern on the sides is probably almost a copy, as far as coloration goes, of the larval stage to which we have just referred.

IDENTIFICATION OF LARVÆ.

Now that we have considered in detail the color pattern of the larvæ of *Speleperes maculicaudus*, and have many characters to identify them as such, it will be of interest to know how they may be distinguished from larvæ of other species with which they may be associated.

Speleperes larvæ may be easily separated from those of *Amblystoma* by their more slender form. The latter always have broad heads,

their general appearance in the water suggesting a small catfish. Larvæ of *Diemyctylus* are maculate at an early age, have a dark line through the eye, and when of fair size show the red lateral spots, all of which characters the larvæ of the cave salamander lack. In one larva of the newt examined, the upper series of larval areas is 6 in number, the middle, 12, and the lower series obsolete. *Desmognathus* larvæ are characterized by an upper series of 10 to 11 large clear areas which are distinctly dorsal in position and run together on the tail. (The number given includes only those anterior to the point of union.) As this series of areas is distinctly lateral in *maculicaudus*, the separation of the larvæ of these two species will not be difficult.

In the genus *Spelerpes* itself, the differentiation is as easy in the case of the species we have studied. Not a sufficient number of *longicaudus* larvæ have been seen to warrant a definition. This is particularly unfortunate, as there is no doubt that it is most closely related to the present species. In one large larva of *longicaudus* the upper series of clear areas had disappeared, the middle one had about 16 to 18 spots, and the lowest series 12. If these numbers are constant they furnish a means of distinguishing these nearly related larvæ. In larvæ of *longicaudus* that have attained fair size the vertical bars on the tail are apparent, thus making this character available for identifying larvæ as well as adults.

Only large larvæ of *guttolineatus* have been seen. These are conspicuously marked. In the upper series of clear areas there are four, and the middle and lower series form continuous light bands on the sides of the animal. The belly is longitudinally striped, this character serving to separate these larvæ from any others of the genus here considered.

The young larvæ of *bilineatus* have the upper series of larval areas very conspicuous and the lower two series not evident. The upper of these is developed to some extent later. Also *bilineatus* larvæ have the dorsal area light in very early as well as later stages, and there are never as many nor as prominent blotches on it as in *maculicaudus*. *Spelerpes ruber* is easily distinguished in all stages. The older larvæ are, up to the time of transformation, almost uniformly vermiculated with pigment, while the young larvæ, in addition to practical uniformity of color, have a decided character in the great number of areas in the middle series, namely, 28. These resemble the stitching of a sewing machine, so close together are they, and appear as a finely dotted line on the side of the larvæ. In this series it will be remembered *maculicaudus* has only 13 to 15. These series of immaculate areas on the side of the larval salamanders seem to form a good character for the determination of species. Therefore we offer tentatively a table embodying the results of the study of a few species as a further aid in distinguishing the larvæ of the cave salamander.

Tabulation of the immaculate areas on the sides of larval salamanders.

Name.	Upper row.	Middle row.	Lower row.
<i>Spelerpes maculicaudus</i>	10	13-15	7-13
<i>Spelerpes bilineatus</i>	14	^a indistinct.	indistinct.
<i>Spelerpes ruber</i>	13	28	do.
<i>Spelerpes longicaudus</i>	^b unknown.	16-18	12
<i>Spelerpes guttolineatus</i>	^c 4	continuous.	continuous.
<i>Diemyctylus viridescens</i>	^d 6	12	indistinct.
<i>Desmognathus fuscus</i>	10-11	11	10
<i>Amblystoma opacum</i>	5	9	12

^a See notes above.

^b Only 1 large larva at hand.

^c Only large larvæ seen.

^d Only one specimen examined.

Using the table in connection with the remarks above there should be no difficulty in separating the species treated.

SYNOPSIS OF THE PRINTED RECORDS OF THE OCCURRENCE OF
SPELERPES MACULICAUDUS.

Indiana:

- Brookville, Franklin County.
- Northeastern Franklin County.
- Decatur County.
- Westport, Decatur County.
- Monroe County.
- Bloomington, Monroe County.
- May's Cave.
- Vincennes, Knox County.
- Indian Springs, Martin County.
- Porter's Cave, Owen County.
- Donnehue's Cave, Lawrence County.
- Donnelson's Cave, Lawrence County.
- Kern's Cave, Lawrence County.
- Clifty Cave, Washington County.
- Wyandotte Cave, Crawford County.
- Little Wyandotte Cave, Crawford County.
- Small cave near Wyandotte, Crawford County.
- Marengo Cave, Crawford County.
- Salt peter Cave, Crawford County.
- Sibert's Well Cave, Crawford County.

Missouri:

- Barry County.
- Rockhouse Cave.
- Wilson's Cave.
- Marble Cave.

ADDITIONAL RECORDS.

Besides the stations given above, the following localities are represented by specimens in the United States National Museum: Barger's Spring, near Hinton, West Virginia; Union County and Winehouse Cave, Tennessee; Mammoth Cave, Kentucky, and Jefferson County, Missouri. The following localities may now be added to the Indiana list: Mayfield's and Truitt's caves, Stony and Leonard's springs and Griffey Creek, Monroe County; and Twin Caves, Lawrence County.

BIBLIOGRAPHY.

- BLATCHLEY, W. S., Indiana caves and their fauna. Ann. Rep. Dept. Geol. Ind., 1896 (1897), pp. 121-122, pls. IV-XIII, figs. Habits and distribution.
- BUTLER, A. W., Contributions to Indiana Herpetology, No. 3. Journ. Cin. Soc. Nat. Hist., XIV, 1891-2, pp. 169-179. Sums up existing knowledge of the species.
- COPE, E. D., On a new species of Salamander from Indiana. Am. Nat., XXIV, 1890, pp. 966-7, figs. (*Gyrinophilus maculicaudus*.)
- Geographical Distribution, pp. 1199-1234 in The Crocodilians, Lizards, and Snakes of North America. Ann. Rep. Smith. Inst., 1898 (1900), 1294 pp., 36 pls., figs. The portion on distribution includes batrachia.
- EIGENMANN, C. H., Degeneration in the eyes of the cold-blooded vertebrates of the North American caves. Proc. Ind. Ac. Sci., 1899 (1900), pp. 31-46.
- Degeneration in the eyes of the cold-blooded vertebrates of the North American caves. Science, N. S., XL, 1900, pp. 492-503. A reprint of the above.
- The Blind Fishes of North America. Pop. Sci. Mo., LVI, 1899-1900, pp. 473-486, figs. Refers to and figures *S. maculicaudus*.
- The eyes of the blind vertebrates of North America, II. The eyes of *Typhlomolge rathbuni* Stejneger. Trans. Am. Micr. Soc., XXI, 1899, pp. 49-56, pls. III and IV. Refers to *S. maculicaudus* and figures the eye.
- Description of a new cave salamander, *Spelerpes stejneri*, from the caves of southwestern Missouri. Trans. Am. Micr. Soc., XXII, 1901, pp. 189-192, pls. XXVII-XXVIII. Refers to and figures *S. maculicaudus*.
- EIGENMANN, C. H., and KENNEDY, C., Variation notes. Biol. Bull., IV, 5, April, 1903, pp. 227-30, figs. Description and figures of a melanistic *S. maculicaudus*. The figures are reprinted on page 131 of "Indiana University, 1820-1904." Roy. Svo. Bloomington, Ind., 1904.
- GAINES, ANGUS. Batrachia of Vincennes, Indiana. Am. Nat., XXIX, 1895, pp. 53-6.
- HAY, O. P., Note on *Gyrinophilus maculicaudus* Cope. Am. Nat., XXV, 1891, pp. 1133-5. Points out inapplicability of *Gyrinophilus*. *Spelerpes* must be substituted.
- The Batrachians and Reptiles of the State of Indiana. Ann. Rep. Dept. Geol. Ind., 1891, pp. 409-602, pls. I-III. Habits and distribution.

EXPLANATION OF PLATES.

PLATE VIII.

Spelerpes maculicaudus (Cope).

- Fig. 1. Larva, 17.5 mm. long x 4. Lateral view.
 2. Larva, 21 mm. long x 4. Lateral view.
 3. Larva, 36.5 mm. long x 2. Lateral view.
 4. Larva, 48 mm. long x 2. Lateral view.
 5. Larva, 51.7 mm. long x 2. Lateral view.
 6. Young adult, 55 mm. long x 2. Lateral view.
 7. Young adult, 55.5 mm. long x 2. Lateral view.

PLATE IX.

Spelerpes maculicaudus (Cope).

- Fig. 1. Larva, 17.5 mm. long x 4. Dorsal view.
2. Larva, 21 mm. long x 4. Dorsal view.
3. Larva, 36.5 mm. long x 2. Dorsal view.
4. Larva, 48 mm. long x 2. Dorsal view.
5. Larva, 51.7 mm. long x 2. Dorsal view.
6. Young adult, 55 mm. long x 2. Dorsal view.
7. Young adult, 55.5 mm. long x 2. Dorsal view.

PLATE X.

Spelerpes maculicaudus (Cope).

- Fig. 1. Half-grown adult, 88 mm. long x 2. Dorsal view.
2. Half-grown adult, 88 mm. long x 2. Lateral view.



1



2



3



4



5



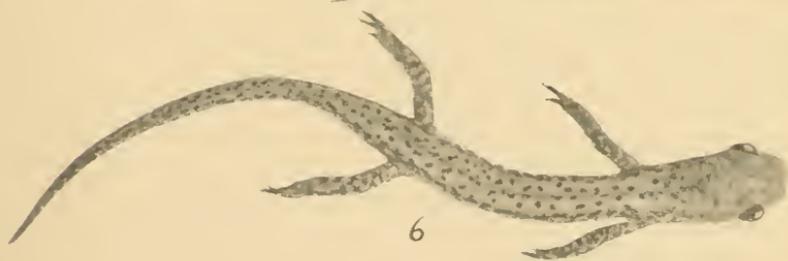
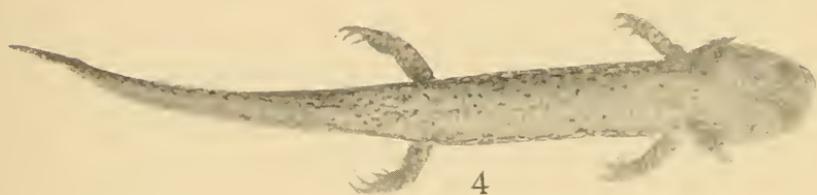
6



7

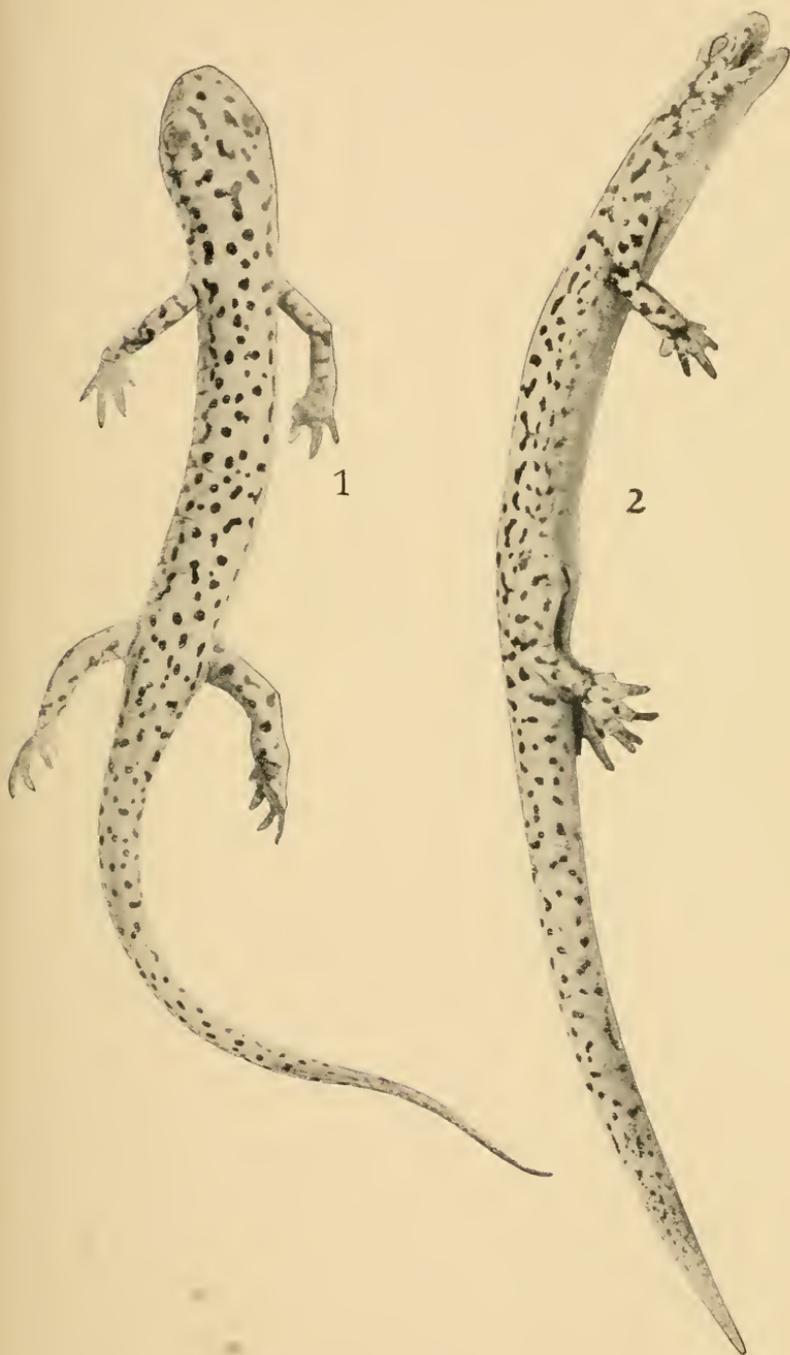
LARVÆ AND YOUNG ADULTS OF SPELERPES MACULICAUDUS.

FOR EXPLANATION OF PLATE SEE PAGE 82.



LARVÆ AND YOUNG ADULTS OF SPELERPES MACULICAUDUS.

FOR EXPLANATION OF PLATE SEE PAGE 83.



ADULT OF SPELERPES MACULICAUDUS.

FOR EXPLANATION OF PLATE SEE PAGE 83.

