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# BULLETIN of THE UNIVERSITY OF TEXAS

#### NO. 308

ISSUED SIX TIMES A MONTH

SCIENTIFIC SERIES NO. 36

JANUARY 1, 1914

### Development and Histology of the Integument of the Nine-Banded Armadillo

(Tatusia Novemcincta)

BY CHARLIE WOODRUFF WILSON, M. A.



PUBLISHED BY THE UNIVERSITY OF TEXAS, AUSTIN, TEXAS.

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### DEVELOPMENT AND HISTOLOGY OF THE INTEGUMENT OF THE NINE-BANDED ARMADILLO

#### (TATUSIA NOVEMCINCTA\*)

#### INTRODUCTION

The principal point of interest connected with the integument of the armadillo is in the relation of the structure of the integument to studies in heredity. Since the integument is marked off into distinct areas, the question naturally arises, are these areas transmissible? The study of the development of the integument is indispensable in solving that problem. In doing this work, certain points must necessarily be discussed, namely, how is the dermal armor formed, when is it formed, and how nearly is the development of the integument related to that of other forms?

All of the details in the development of the integument are not worked out in this paper; for example, no attempt has been made to trace out the skin glands, but as far as observed they follow Römer's (92a) description. The ossification, too, is as he describes it, but since the material had been prepared before his paper was seen, and since he only gives two figures to show the stages in ossification, this phase of the development has been worked out through the 10 cm. embryo. Besides, the detailed work has been confined to the banded region, because it is more highly differentiated and because the arrangement of its scutes makes the work more simple.

#### REVIEW OF LITERATURE

Some studies have been made on the integument of Dasypidæ, but most of the papers are of a theoretical character, based upon the work of others, or else the material used was too meager to justify the conclusions that have been drawn. Work has also been done on the integument of other Edentates. Weber ('92), working on Manis, states that the scales begin after the outer part

<sup>\*</sup>Contributions from the Zoological Laboratory, University of Texas. No. 116.

is hardened, and that the horny plates, which begin by the raising of the skin, are formed in the epidermis.

Welcher ('64), working on the development and structure of the skin and hairs of Bradypus, found that there was, in the 26.5 cm. embryo, a tight-fitting, sac-like epitrichium which was pushed off by the underlying hairs. Such an epitrichium is absent from Dasypus.

Among the earlier workers on the integument of Dasypus are: Rudolphi ('18), who found that there were bony plates under the epidermis; von Rapp ('43), who tells us that there are bony plates on the upper side of the animal, that these plates have hairs between them, and that there are no plates on the under side of the animal; Meyer ('48), who worked on a piece of dried integument, said that there were bony plates embedded in the cutis, and that there were short hairs between the scales; Leydig ('59), who says that the scales come from the epidermis; and Kerbert ('77), who worked on two Dasypus embryos. He says that the girdles are formed by folds of the skin, that the hairs first arise in the bands, that the exoskeleton is of secondary formation into bands, and that the anlage of a hair is a papilla.

The most detailed work on the armadillo integument is that done by Römer ('92a). He, however, worked only on the later stages of its development. The specimens which he was able to obtain were, of Dasypus novemcinctus, nine embryos of 5, 6, 7, 11, and 12 cm. length; of D. Villosus, six embryos of 10, 11, and 12 cm. length; and an adult D. setosus. His earliest stage is a little later than that shown in figures 21, 22, and 23.

#### MATERIAL AND METHODS

The work presented in this paper was done on the nine-banded armadillo, Tatusia novemcincta. The females were shipped and the embryos removed at laboratory. The embryos used ranged from a very young stage in which the epidermis was undifferentiated and the limb buds barely visible, up to those that breathed when removed, and ranged in size from less than 6 mm. to 100 mm. in length.

The specimens were usually fixed in Zenker's fluid. Some sections were made from a specimen fixed in 95% alcohol. Two of the older specimens, of 6.7 cm. and 7.7 cm. length were fixed in Kleinenberg's picro-sulphuric mixture.

To show the stages in the development of the bony plates, six sizes of embryos were used, as follows: 5.5 cm., 6.7 cm., 8.5 cm., 8.9 cm., and 10 cm. lengths. These were cleared in a 1% solution of KOH, the method for which was described by Dr. R. L. Moody of the University of Kansas. Since the embryos were large, one of each size was skinned, and the skin cleared, and another of each size, with the eyes and intestines removed, was cleared. It was found that the skin cleared much more satisfactorily than the whole embryos, for the latter went to pieces before all of the muscles and other inner structures cleared up sufficiently. The skins were then removed from the whole specimens and the two sets of skins were hardened and preserved in glycerine.

The stain used for sections was Delafield's Haematoxylin with Orange G for counter stain. In the specimen cleared in KOH, the plate, when it is just beginning to be formed, is more easily differentiated if a stain is used. Safranin is satisfactory for this.

The embryos were measured in the greatest length from head to rump in a line parallel to the dorsal surface.

Most of the figures were drawn with the aid of the camera lucida, either on a Zeiss or on a Spencer microscope. A few were made with the aid of the Bausch and Lomb projecting apparatus.

This work was done under the direction of Dr. Patterson, to whom I am indebted for advice and assistance.

#### THE ADULT INTEGUMENT

In order that the terminology used in connection with the embryonic stages may be clear, a description of the adult integument must be given first. There are present in Tatusia novemcincta five shields described for armadillos, namely: the head, the pectoral, the banded region, the pelvic, and the tail shields. All of these regions are made up of what are termed scutes; and these, in turn, are composed of plates, horny scutes, and associated hair groups.

Since this work is concerned almost entirely with the banded region (Fig. 1), this account is of that region. Each band is made up, on the average, of about sixty-one bony plates, one of which is shown in figure 2. The bony plate is marked off into two distinct regions, an anterior flat portion which is covered by the band just anterior to it, or by the pectoral shield in the case of the plates of the first band, and a posterior portion, which overlaps the band just posterior, or the plates of the pelvic shield in the case of the ninth band. The anterior part of the plate is unmarked except by blood-vessels or nerves, but the posterior part has on its upper surface four rows of markings. The two outer rows represent the places where the roots of the inter-scute hairs are imbedded (Fig. 2, H. P.). It has not been determined as to what is the cause of the inner rows of markings. There are three possible causes, viz: nerves, blood-vessels, and hairs, but no trace has been found of hair development in this region, although the manner of ossification, which is like that in the region of the inter-scute hairs, as well as the form of the prints, would suggest that there are hairs developed in that region.

The number of hair prints, and consequently the number of hairs to the scute, is not always the same. The number of posterior hairs (Fig. 2, P. H. P.) varies from two to four, four being the number which is most often found. When this variation occurs in an individual the scutes with two and three hairs are usually toward the ends of the bands. Sometimes, however, an individual may be found that has, as typical, the three-haired type of scute. This fact has not been brought out in the study of the embryos, because the sections were made from the middle portions of the bands where the three-hair type is not frequent, and because the three-hair type of individual is rare.<sup>1</sup>

The number of inter-scute hairs may also vary in different scutes as well as on the two sides of the same scute. For example in an individual one plate may have four hair prints on one side and five on the other (Fig. 2), another three and four, and still another four and four.

The central part of each plate is covered by a wedge-shaped horny portion which extends between the hair marks and has, therefore, the broad part of the wedge to the posterior. This is termed the primary scute. In between these wedges, and over the seams of the plates, are narrow wedges with the broad part extending to the anterior and showing an indentation over the

<sup>&</sup>lt;sup>1</sup> Newman and Patterson, '11.

plate seam. This wedge is the secondary scute. The part where the bands join is only slightly horny so that the bands have free play.

Corresponding to the hair markings described above for the plate there are hairs. Between the primary and secondary scutes are short, rather fine hairs (Fig. 1, I. H.) which may not be present in the older specimens, though the imprint may be seen in the horn. The posterior hairs (Fig. 1, P. H.) are heavier, more bristly, and longer than the inter-scute hairs. The variation in length in the two kinds of hairs is evidently due to wear.

#### THE EPIDERMIS

In the early stages in the development of the armadillo, there is the undifferentiated ectoderm (Fig. 3). In this stage the nuclei are round or oval. They occur in one layer over the dorsal part of the embryo, but on the sides they are sometimes four deep. Where there is but one layer, the nuclei are usually round, but if elongated the greatest length is parallel to the surface of the ectoderm. When the number of the nuclei increases, the elongation is perpendicular to the surface. When there is more than one layer, all may be round or some round and some elongated. There is a tendency for the inner layer to develop numerous nuclei, and for them to become elongated in a perpendicular direction before nuclei are added as an outer layer.

As is to be expected, there is little cytoplasm, especially in the region where the nuclei are numerous. There are cell walls which may be distinguished at some places better than at others; for example, the cells with perpendicular elongated nuclei have walls that may be easily made out. The same thing is true of the cells that are in a single layer.

After the nuclei which make up the inner layer have become rather numerous, some of them begin to crowd up to the surface. This feature is shown even in the earliest stages which are figured in this paper (Fig. 3, X). When the cells reach the surface both they and their nuclei flatten out and there will be found only an occasional surface cell (Fig. 4, E), but later, enough flatten out to form a continuous layer. Thus we have the two-layered epidermis, the outer layer or epitrichium, and the inner layer or stratum germinativum. The epitrichium consists of cells which are first spindle-shaped then flat, and which have nuclei that appear long and flat in section. The stratum germinativum has elliptical or rounded nuclei. The nuclei of the outer layer stain much more deeply than those of the inner layer (Fig. 5, E).

Further differentiation of the epidermis is brought about by the formation of a layer of cells between the epitrichium and the stratum germinativum and take up a position between the two layers that are already formed (Fig. 6, X). The intermediate layer later becomes best developed at certain points, namely, at the center of the scute primordium, although it is still represented in other regions by an occasional cell (Fig. 9), even as late as the 4.9 cm. embryo. The cells of the intermediate layer increase in number so that the epidermis of this region becomes several layers thick (Figs. 7, 9y, and 15).

The thickening of the epidermis to form the scute takes place first in the posterior part of the band, and it is greatest in the region of the posterior hairs (Fig. 15). The thickening decreases until the anterior part of the band is reached. Here we only find three layers in the 5.5 cm. embryo (Fig. 22) and two layers in the 4.9 cm. one (Fig. 7). More cells are continually added until there is an outer layer of flattened cells, a middle layer of polygonal cells, and a lower layer of columnar cells (Fig. 12). Gradually the cells of the outer layer, which is now several cells thick. become cornified and the nuclei and cytoplasm shrink. The nuclei disappear altogether, especially in the outer layers of the cells in the older stages, as is shown in figures 13, and 14, H, which are from a section of a 7.7 cm. embryo. The cells just beneath the corneous layer are elongated in a direction parallel to the surface and contain granules, from which they get the name, stratum granulosum (Fig. 14, S. G.). The nuclei of these cells, of which there may be several layers, are elongated in the direction with the long axis of the cells. The cells between the stratum and the lowest layer which is of columnar cells, may have elongated nuclei in the cells toward the surface and round nuclei in the inner cells (Fig. 14, I. C.).

#### THE HAIR

The anlage of the hair is found in an early stage in the development of the integument. The hair is formed from the epidermis. Its beginning is characterized by an increase in the number of nuclei in the stratum germinativum. This condition is shown in Fig. 7, which is drawn from a 4.9 cm. embryo. As this thickened area grows down into the corium, it is at first in the form of a bowl, but as further inward growth takes place, a bulb is formed. It is at this last stage that we find the anlage of the papilla, which is a collection of nuclei in the corium at the inner end of the bulb (Fig. 11, P.).

The first hair formed is the one on the posterior part of the overlapping end of the scute. This hair is developed anterior to the edge of the scute fold, as is shown in Fig. 7. The hair grows further to the anterior, and the integument folds over until in the 7.7 cm. embryo the root of the hair is far to the anterior. although the hair now comes out from the posterior end of the scute (Fig. 13). The next hairs form in order in the scute from posterior to anterior so that we get, in a longitudinal section of a band, as many stages in the development of the hairs as there are hair sections. This is shown in Figs. 22 and 23. Two figures must be used to show this condition, because the hairs are not all in a line perpendicular to the anterior and posterior margins of the band, and a section through the hair region made perpendicular to the margins will not show all of the hairs (Fig. 2). Fig. 23 shows a section of the posterior hair of the region represented in Fig. 22. Numbering the hairs as they occur in order in the section, obviously 3 is a further advanced stage than 1, and 5 is the most highly differentiated stage of all. This same point, namely, that the posterior hairs are far in advance of the other hairs is brought out in the KOH cleared specimens, as well as the fact that the two middle posterior hairs of a scute are formed before the two outer posterior hairs are. The later stages in the development of the hairs follow out the process as it is in other mammals, a fact which Figs. 13 and 14 will suggest; and so the process will not be further described.

#### THE CORIUM

The epidermis, in the early stages of the development of the integument, is not closely connected with the mesenchyme (Fig. 3), but the connection is more intimate later, as is shown in Fig. 4. By the time the limb buds are well formed, nuclei have appeared

close to the eperdimis (Figs. 5 and 6); and by the time the embryo has reached a length of 2.9 cm., the corium is differentiated (Fig. 9). Even as early as the last stage mentioned, the corium is raised in the regions of the primordia of the bands. This thickening increases so that in the 4.9 cm. embryo folds are found (Fig. 7). The folding continues as is shown in Figs. 12, 22, and 13, until finally the definitive condition is reached.

During the process described above for the band, the plate is being formed (1) by a thickening in the corium and (2) by ossification. The raising of the corium to form plates is begun in the posterior region of the band. There is no thickening in the anterior portion of the scute through the stage of the 5.5 cm. embryo, (Fig. 19), which is not true of the 6.7 cm. stage; and there is none in the posterior region even in the 6.7 cm. stage (Figs. 10 and 21). The plate primordia may be found in a 2.9 cm. embryo (Fig. 16), but not in the region where the epidermis is thickest (Fig. 17), which is also the region of the formation of the posterior hairs (Figs. 9 and 7). Fig. 20 shows a later stage, that of the 5.5 cm. embryo, than that of Fig. 16.

The bony formation begins in the pectoral shield about in the center, and later extends backward and to the sides. It next takes place in the banded region and is extended on back finally through the pelvic girdle. In the banded region the ossification takes place first in the center of the first or most anterior bands, it then spreads to the ends of the bands so that in a band where the development has not gone too far we have as many stages of ossification as there are plates. In the later stages, however, the difference in the stages are not so marked, so that the ossification appears to be practically in the same stage in nearly all of the plates.

A description of the ossification regions in the different aged embryos will make the above statements clearer. In the embryos of 5.5 and 6.7 cm. length, no ossification has taken place. In an embryo of 7.7 cm. length, there is no ossification in the pelvic shield, but in the pectoral shield there is a center of ossification which takes in an area that has a diameter equal to about onethird the distance across the shield and which is situated about in the center of the shield. In the banded region, the five anterior bands are ossified nearly to one-sixth of the distance from the ends, bands 6 and 7 are ossified but slightly, and bands 8 and 9 are not ossified at all. Practically the same condition exists in the 8.5 cm. and the 8.9 cm. embryos. In the 10 cm. embryo, however, the ossification has extended into the pelvic shield, but is found only in its center. In the pectoral shield and in the banded region, ossification is found in all except the outermost plates.

The ossification in a plate begins in the anterior half of the part not covered by the plate which is anterior to it (Fig. 13, X). Spots of bone appear between the hairs papillae, and these spots grow and fuse around the roots of the hairs, thus leaving rows of spaces in the early stages (Figs. 24, 25, 26, and 27). In the adult stage, however, the ossification has taken place throughout the corium, so that there are rows of pits marking the position of the hairs (Fig. 2, H. P. and P. H. P.).

#### COMPARISON

We find, then, that the early stages of the development of the integument of the armadillo are very similar to those described for the human integument by Pinkus (Keibel and Mall, '10). The periderm in both has cells which, in section, are spindle-shaped with deeply staining nuclei. These cells later flatten out into a continuous layer. There is also a deeper layer of cells which is at first characterized by broad thick cells with round or oval nuclei, but later is characterized by columnar cells with elongated nuclei. These cells give off an occasional cell between the two layers until finally a continuous layer, the stratum intermedium, is formed. Although the outer cells in both become cornified, the extremely horny scute is peculiar to the armadillo. Just beneath the horny layer are polygonal cells, and lower still, the columnar cells.

The corium in both is developed from the superficial portion of the somites. It has, at first, no very close connection with the epidermis, but as growth takes places, the connection is more intimate. Ridges and folds are produced in the corium of both; in the armadillo to form the plates and bands, in the human, the rete ridges, touch balls, gland ridges, and papillae.

The hairs are also formed in the same way. There is first a local increase of the number of nuclei in the epidermis. These nuclei are higher and more closely packed together than the adjoining ones. A gradual invagination of this thickened area takes place, making at first a columnar papilla which later develops into a bulb. Then connective tissue papilla comes from the corium, and gradually grows up into a concavity in the epidermal papilla. The hair then differentiates into the same layers and parts in both forms.

#### SUMMARY

The band in the adult integument is made up of three elements, (1) the plate, (2) the scute, and (3) the associated hair group.

The number of hairs at both the end and the sides of the plates varies.

The epidermis is early differentiated into two layers, the periderm and the stratum germinativum; and increase in thickness is begun by the addition of a layer of cells, the stratum intermedium, between the first two layers.

In the last stage worked out, the epidermis is composed of an outer horny stratum, which is not nucleated, and an inner germinal stratum, which is made up of a basal row of columnar cells, a region of polygonal cells, and an outer row of granular polygonal cells.

The corium, which comes from the superficial portion of the somite, is thrown into folds and ridges to form the scutes and bands.

Ossification begins in the anterior part of the animal first, and extends back and to the sides.

The ossification centers appear in little patches that grow together around the roots of the hairs, thus leaving rows of pits in the adult plate.

The two middle rows of pits found in the adult plate are not accounted for.

The hair begins as a local increase in the nuclei of the stratum germinativum. The thickened area thus formed invaginates to form the epidermal papilla.

The hairs of the scute develop in order from posterior to anterior, and the posterior hair is far in advance of the others.

The stages in the development of the integument of the armadillo follow very closely those of the human integument. The chief differences being that the armadillo has a very horny epidermis, marked off into definite scutes, and has bony plates in the corium.

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#### EXPLANATION OF PLATES

Sections shown in Figs. 3, 4, 5, and 6 are through the banded region of the embryos.

Plates VII, VIII, and IX are photographs.

#### Plate I

Fig. 1. Portion of band from left side showing, (1) three plates (23, 24, and 25), (2) scute-covered portion of the plate, (3) secondary scute, (4) primary scute, (5) inter-scute hairs, I. H., and (6) posterior hairs, P. H.  $x 2\frac{2}{3}$ .

Fig. 2. Dorsal surface of a plate showing the two regions of the plate; four posterior hair pits, P. H. P.; four inter-scute hair pits on the left side, and five inter-scute hair pits on the right side, H. P.; and two middle rows of pits.  $x 2\frac{2}{3}$ .

Fig. 3. Section showing undifferentiated ectoderm. x 840.

#### Plate II

Fig. 4. Cells in epidermis beginning to flatten out at the surface; E, flattened cell; X, cell beginning to flatten. x 1066.

Fig. 5. Two-layered condition of epidermis. E, epitrichium; S. G., stratum germinativum. x 520.

Fig. 6. Beginning of the intermediate layer at x. E, epitrichium; S. G., stratum germinativum. x 520.

#### Plate III

Fig. 7. A longitudinal section of the integument of a 4.9 cm. embryo to show the folding to form the band, and the beginning of the hair.  $x 77\frac{1}{4}$ .

Fig. 8. High power drawing of longitudinal section from a 2.7 cm. embryo to show the thickening of the epidermis. x 375.

#### Plate IV

Fig. 9. Longitudinal section from a 2.9 cm. embryo to show the thickening of the epidermis. G. L., germinal layer; E, epitrichium; Y, beginning of scute. x 200.

Fig. 10. A cross section from a 6.7 cm. embryo through the posterior end of the scute showing at the top two hairs of one scute, and at the bottom, three of the next. x 177.

#### Plate V

Fig. 11. High power drawing of the second hair follocle of Fig. 10. P, the dermal papilla. x 568.

Fig. 12. A longitudinal section of one plate and a portion of the two adjoining ones, showing folding and stage of development of the posterior hair of a 6.7 cm. embryo. x  $46\frac{2}{3}$ .

#### Plate VI

Fig. 13. A longitudinal section from a 7.7 cm. embryo showing folding, formation of plates at x; and layers of the skin.  $x \ 463^{\circ}$ .

Fig. 14. High power drawing from the section of Fig. 13 through the epidermis in the region of the root of the hair. H, horny layer; S. G. stratum granulosum; I. C. intermediate cells; C. C. columnar cells; C, corium; H, hair. x 233.

#### Plate VII

Fig. 15. A longitudinal section from a 2.7 cm. embryo showing a stage between that of Fig. 9 and Fig. 7. x 100. Fig. 16. A transverse section of a band to show the thickening of the corium in the region of three primary and three secondary scutes in a 2.9 cm. embryo. x 102.

Fig. 17. Section from the same embryos that on Fig. 16 to show that the corium is not thickened in the region of greatest scute formation. x 92.

#### Plate VIII

Fig. 18. A longitudinal section of a 4.4 cm. embryo showing a slightly later stage than that in Fig. 7. x 82.

Fig. 19. A transverse section from the anterior region of a scute showing that there is no thickening of the corium. From a 5.5 cm. embryo. x 61.

Fig. 20. A transverse section of a band of the same embryo as that shown in Fig. 19 to show thickening of the corium in the region of the anterior hairs. x 51.

#### Plate IX

Fig. 21. A transverse section from the same embryo as shown in Figs. 19 and 20, showing the four posterior hairs of one plate. x 53.

Fig. 22. A longitudinal section from the same embryo showing the stages of development of the interscute hairs. x 53.

Fig. 23. The posterior hair of the plate shown in Fig. 22. x 64.

#### Plate X.

Fig. 24. Two plates from a KOH-cleared specimen to show early plate formation. From the region  $\frac{1}{4}$  the distance from the left and of the first band of a 8.9 cm. embryo. x 24.75.

Fig. 25. The middle region of the same band as that in Fig. 24 to show further development. x 24.75.

Fig. 26. Three plates from a KOH-cleared specimen to show later plate formation and posterior hairs. From the end of the first band of a 10 cm. embryo. x 12.

Fig. 27. Two plates from the center of the same band as that shown in Fig. 26. The holes in the bone are where the roots of the hairs are.  $\times 11.25$ .

PLATE I



PLATE II







PLATE V



PLATE VI



PLATE VII





PLATE IX



PLATE X



