THE MAMMARY APPARATUS OF THE MAMMALIA

IN THE LIGHT OF ONTOGENESIS AND PHYLOGENESIS

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WITH 47 ILLUSTRATIONS

METHUEN & CO. LTD.
36 ESSEX STREET W.C.
LONDON

INTRODUCTORY NOTE

THIS volume is based on a course of three lectures on the development of the mammary apparatus of the Mammalia, delivered at University College in March, 1913, under the auspices of the Board of Studies in Zoology, University of London, by Dr. Ernst Bresslau, at that time Professor of Zoology in the University of Strassburg. The proofs were ready for the press in 1914, but the issue of the volume has been delayed until now, owing to the conditions arising out of the war. This delay in publication, I hasten to add, in no way detracts from the value of the volume.

Professor Bresslau is the foremost living authority on the morphology of the mammary organs, and by his detailed and fundamental researches, pursued over a period of some twelve years, he has enormously extended our knowledge of the organogenesis of this characteristically Mammalian system, and more particularly of those accessory structures—*e.g.*, the incubatorium, the marsupium, and the nipples—which have been superadded in the course of evolution to the essential secretory part of the mammary system, the milk glands, with which alone the primitive Mammal was provided, just as is the existing Platypus. Professor Bresslau, moreover, on the basis of his detailed developmental observations, has been led to most interesting and suggestive conclusions as to the first origin of the mammary organs and their evolutionary history in the chief subdivisions of the Mammals.

His principal memoirs on this subject are to be found in Dr. R. Semon's "Forschungsreisen im Australien und dem Malayischen Archipel" (Bd. 4, Lfg. 6, 1907, and Lfg. 7, 1912), a monumental work which, however, is little known outside the ranks of the specialist. The present volume provides the English-speaking student with a résumé of these memoirs, all the more valuable since it has been prepared by their author himself. It should appeal to all who are interested in the fascinating problems of Mammalian evolution.

It is only fair to Professor Bresslau to add that he has had no opportunity of seeing the proofs, the correction of which was undertaken by the publishers.

JAMES P. HILL

February, 1920.

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THE MAMMARY APPARATUS OF THE MAMMALIA

CHAPTER I

THE Mammalia are so called because they present a highly developed organic system for the nourishment of their young—the mammary apparatus—and it might be presumed that this apparatus would be uniformly developed in the whole group like the other principal characteristic, the hair. But that would be a mistake. One finds so many important differences in the development of the separate parts of the mammary apparatus in the various orders of Mammals, that up to the present it has been impossible to compare them properly and to show their relationships one with another.

None of the many attempts to explain the phylogeny of the mammary apparatus, or parts of it, has been able to withstand searching criticism. They have all failed because of the discrepancies between theory and facts which come to light when one follows these speculations to their logical conclusion.

So to-day, taking into consideration all the unsuccessful attempts, some authors have maintained that the phylogeny of the mammary apparatus is still unexplained. It seemed impossible to answer either the question, how the Mammals came into the possession of this apparatus, so necessary for the bringing up of their offspring, or the question, what changes have modified the mammary organs in the various orders of Mammals.

Still, such a pessimistic outlook is not justified. Far-reaching problems like these can only be solved after investigations on a vast material embracing every possible stage and every possible family of Mammalia. For years, it has been my endeavour to bring together such a collection, and the completer it became, the clearer became my conviction that a solution was obtainable. Now that I have finished my work, I hope that my results will afford some explanation of these baffling problems. In dealing with my subject, I propose to describe *seriatim* the development of the mammary apparatus in the three principal groups of the Mammalia, the Monotremata, the Didelphia (Marsupialia), and the Placentalia (Monodelphia), and in so doing I shall always begin by recalling in a few words the typical characteristics of the mammary organs in the adults of these three groups.

The Monotremes comprise, as is well known, only the genera Echidna and Proechidna, both terrestrial, as well as the *Ornithorhynchus anatinus*, which is excellently adapted for an aquatic life. They are forms which in many of their characters recall the reptiles, and which also resemble them in being oviparous. They have on either side of the abdomen a well-developed mammary gland, consisting of about 100-150 separate gland tubes, attaining an average length of 25 millimetres; their secretion serves as nourishment for the young. The individual tubes of the mammary glands are very much like the sweat glands in structure, so much so that Gegenbaur derived them from these glands. The ducts terminate close together on an area, the so-called *gland area*, which in the case of the adult Echidna would measure about 6 millimetres in length and 1½ millimetres in breadth. Each duct opens at the base of a long hair, the *mammary hair*, as I may call it for brevity. Nipples, such as all the other Mammalia show, are absent. As a rule the gland area is nearly on a level with the skin, it may even be sunk a little, or, on the contrary, a little raised.

About the time of pregnancy, the female of the Echidna develops a so-called *incubatorium* on the median line of the abdomen in the form of a little pouch, which has a diameter of about 4 centimetres (Fig. 1, where, however, it is represented much too large). In this pouch, which includes both gland areas, first the egg and then the young are carried for some time by the mother. When the lactation period is over, it disappears completely.

In the case of Ornithorhynchus (Fig. 2), it is only natural in view of the aquatic habits of this creature that the incubatorium should be absent, and this absence, it is important to note, is accompanied by a different development of the skin muscle (panniculus carnosus) of the abdomen from that of Echidna. In the case of Echidna, the cutaneous muscle, which covers nearly the whole surface of the trunk, leaves free an oval area of the abdominal wall, situated between the two mammary glands. This area can accordingly

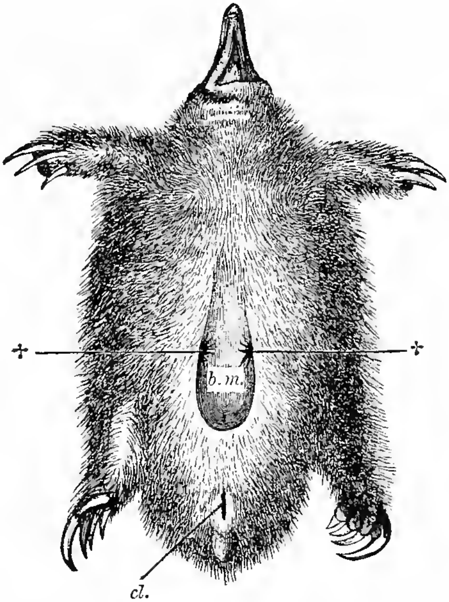

FIG. 1.—ECHIDNA: VENTRAL VIEW OF A BROODING FEMALE, SHOWING THE SO-CALLED INCUBATORIUM SOMEWHAT ENLARGED. (HAACKE.)

+ + The two tufts of hair in the lateral folds of the mammary pouch (*b.m.*), from which the secretion flows; *cl.*, cloaca.

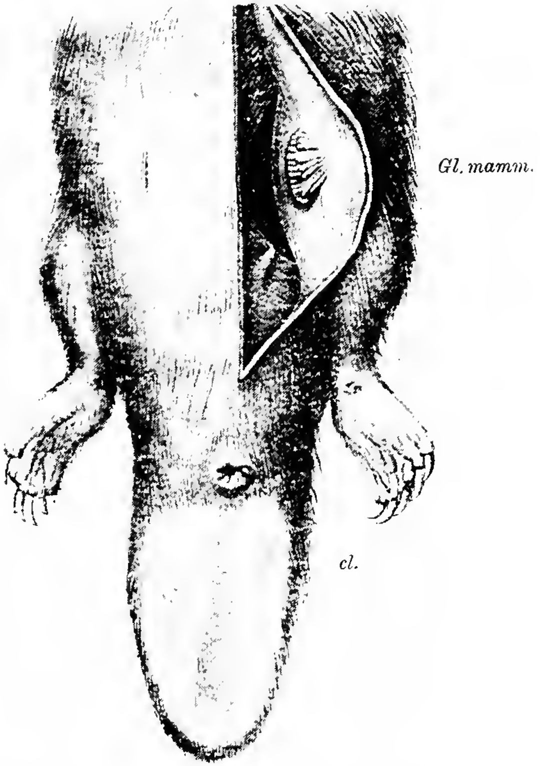

FIG. 2.—ORNITHORHYNCHUS: VENTRAL VIEW, SHOWING THE MAMMARY GLANDS. (AFTER KLAATSCH.)

Gl. mamm., Mammary glands; *cl.*, cloaca.

sink to a pouch, because here there is a place of least resistance. But in the case of Ornithorhynchus there is no such muscle-free area. Only in the immediate region of the mammary glands are there two narrow slits through which the gland-ducts pass.

How under these primitive conditions the young feed themselves has not yet been accurately observed. Even the secretion of the mammary glands has not yet been analyzed, so that we do not know its relation to the milk of the higher Mammalia.

It is of great interest that the male Echidna as well as the male Ornithorhynchus have their mammary glands just as strongly developed as the female, and that the appearance of the panniculus carnosus in both sexes is identical. But in the male Echidna the incubatorium is never found, for physiological reasons, because pregnancy does not occur. As regards this development of the mammary glands in the male, it would be very desirable to know how they behave during the suckling-time of the young. It is very much to be regretted that nothing is known about this as about so many other details of the life-history of these animals.

We are now approaching our particular task of examining how the Monotremes came into possession of these peculiar mammary organs. This is a question which has given rise to much discussion. To begin with, it may be emphasized that up till now it has not been possible to bring the mammary apparatus into connection with any organs of the lower vertebrates from which they could be derived, as is the case with the other characteristics of the Mammals. Leaving aside some vague suggestions, it has been generally held that the mammary apparatus arose as an entirely new formation in the first Mammals. But why should the sweat glands on two particular spots of the abdominal wall—and there only—have developed into milk glands? To this question there can be but one answer, already indicated by Darwin in his "Origin of Species": On those particular spots there must have existed specially intimate relations between the mother and the young, which conditioned the development therefrom of the mammary apparatus. Darwin suggested that these relations were rendered possible by the presence of a marsupium.

The researches of Gegenbaur seemingly confirmed this hypothesis, and since then practically all authorities have agreed that a pouch was already in existence before the sweat glands assumed the function of mammary glands. The incubatorium was therefore regarded as phylogenetically the older organ of the mammary apparatus. The fact that it does not occur in Ornithorhynchus did not constitute a serious objection, for one might suppose that it disappeared with the adoption of the aquatic habit.

With this Darwin-Gegenbaur hypothesis the question of the origin of the mammary apparatus was, of course, not totally answered; since there now arises the question, How did the incubatorium itself originate? Up to the present there have been two conflicting theories —the one promulgated by Gegenbaur and developed by Klaatsch, the other expressed by Ruge.

Gegenbaur and Klaatsch started in their assumptions from Owen's famous description of the mammary apparatus of the Echidna, in which, for the first time, the fact that the nipples are absent was established. Nothing was known then of the incubatorium. Owen said that each gland area was situated in a sort of pouch-like cavity of the integument, the so-called mammary pouch, destined to serve for the reception of the young. At the same time he illustrated these statements with excellent drawings, the most effective of which is reproduced as Fig. 3.

On the basis of this description of the mammary pouches, Gegenbaur and Klaatsch built up an ingenious theory by the help of which they tried to explain the phylogenetic development of the mammary apparatus throughout the whole series of the Mammalia. I shall refer again to this theory in connection with the Didelphia and Monodelphia in the succeeding chapters.

But I must here point out that Klaatsch, on the basis of this theory, thought he could provide the solution of the problem before us—namely, the question of the origin of the incubatorium. He chose Ornithorhynchus as his point of departure, and he assumed that the presence of the two slits in the panniculus muscle which transmit the ducts of the mammary glands was the primary condition. These slits were said to have made it possible for the animal to seize and carry the egg in

FIG. 3.—ECHIDNA: SHOWING THE TWO MAMMARY POUCHES DESCRIBED BY OWEN. (AFTER OWEN.)

case of danger! Further development proceeded by the deepening of these slits, thus producing the mammary pouches. Later these united, forming the incubatorium. In proof of this Klaatsch relied upon observations he had made on the splendid material collected by Professor Semon during his well-known expedition in Australia. He maintained that the mammary pouches were the first parts of the mammary apparatus to appear during ontogenesis (Fig. 4), and, further, that occasionally they even persisted in the adult. Moreover, Klaatsch insisted that every possible transition from the stage of separate mammary pouches to their fusion in a single incubatorium was to be observed. The progress of the phylogenesis, according to Klaatsch, was marked, then, by the following stages: (1) Paired slits; (2) mammary pouches; (3) incubatorium; (4) mammary glands.

Ruge, on the contrary, came to an entirely different conclusion through his researches, which were likewise made on Semon's material. Ruge began by fixing the formation of the incubatorium on that spot of the abdomen occupied during embryonic development by the navel. This coincidence led him to the inference that the position of the last closure of the body wall plays a part in the formation of the incubatorium, inasmuch as that area remains unprovided with muscles, and thus may readily become invaginated to form a pouch-like depression. At all events, according to Ruge, the incubatorium is certainly not developed from paired primordia. What Klaatsch regarded as the paired primordia were simply the lateral halves of the incubatorium temporarily divided in the newly hatched young by the navel-scar. Furthermore, there is no evidence that mammary pouches are present in the embryo. These could not develop until later, when the mammary glands, growing out laterally under the sphincter incubatorii, pro-

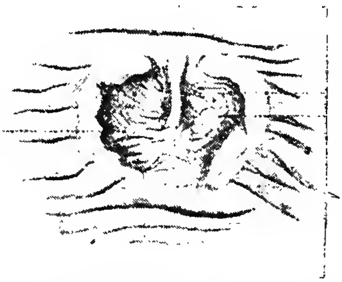

FIG. 4.—ORNITHORHYNCHUS: THE MAMMARY POUCH. (AFTER KLAATSCH.)

duce a drag upon the gland-area and so cause a depression in it. Thus the secretion of the mammary glands can flow into this depression, and can be absorbed more easily by the young. According to Ruge, then, the successive stages in the development of the mammary apparatus are as follows: (1) A single muscle-free area on the umbilical region of the abdominal wall; (2) the incubatorium; (3) the mammary glands; (4) the mammary pouches.

Such, then, was the state of our knowledge when, about eleven years ago, Semon's material, already so often examined, was committed to me for the purpose of further research. I had the advantage of being entrusted with a much more complete set of specimens than any of my predecessors. Only for this reason could the work be brought to completion, and an explanation furnished of the contradictory opinions which I have mentioned. The results were in the highest degree astonishing. I was able to show (1) that no such structures as mammary pouches exist, thus demolishing the theory of Gegenbaur and Klaatsch, and (2) that the incubatorium is *not* the first structure to make its appearance in the development of the mammary apparatus, thus refuting Ruge's views.

Let me now sketch the actual stages in the development of the mammary apparatus in Echidna so far as I could observe them in the material at my disposal.

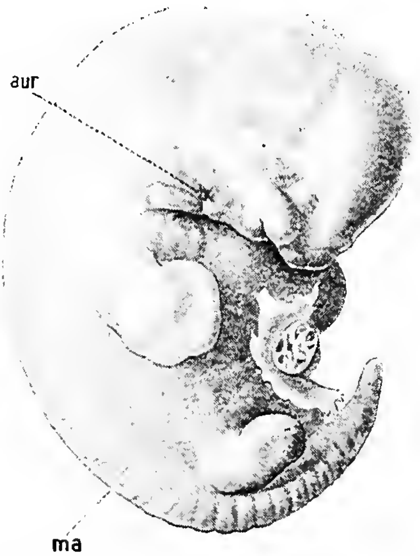

FIG. 5.—ECHIDNA: SEMON'S EMBRYO, STAGE 42.

ma, Primary-primordium ; *aur*, beginnings of the outer ear.

Whereas Klaatsch and Ruge believed that the development of the mammary apparatus began only after the hatching of the young, I was able to show that it begins much earlier, in embryos considerably before the time of hatching.

Fig. 5 is a drawing of Semon's embryo 42, in which I noticed the first primordia of the mammary apparatus. I received the embryo cut in transverse sections, and, on examining the slides, I saw that at this stage the formation of hair and spines had not begun; but

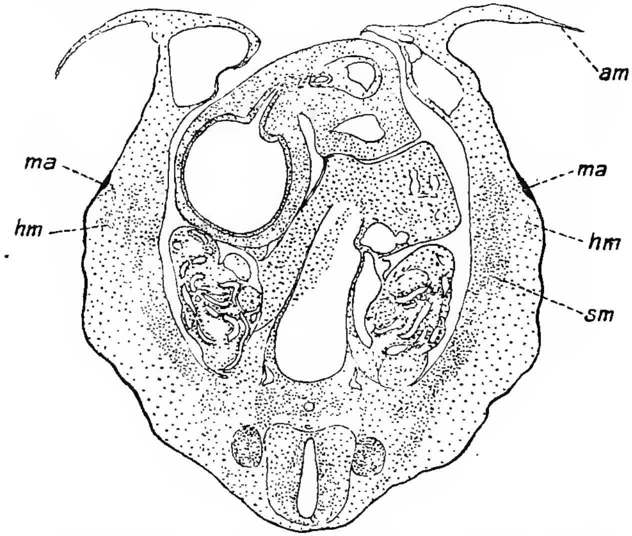

FIG. 6A.—ECHIDNA: TRANSVERSE SECTION OF SEMON'S EMBRYO, SHOWING THE PRIMARY-PRIMORDIA.

ma, Primary-primordia; *hm*, beginning of the skin muscle.

that in the region of the navel at the sides of the body a pair of epidermal thickenings was present (Fig. 6A, *ma*). Each of these extended over a space of perhaps forty sections, and represented altogether a strip three times as long as broad (Fig. 6B). The cutis also underlying these thickenings was specially differentiated, owing to an accumulation of nuclei and

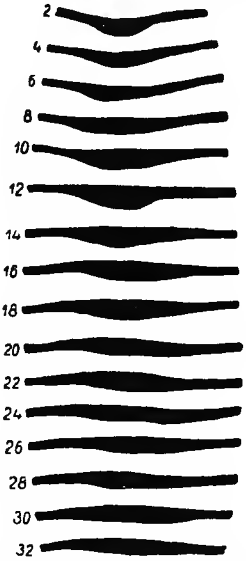

FIG. 6B.—ECHIDNA: SEMON'S EMBRYO. SERIES OF TRANSVERSE SECTIONS THROUGH THE PRIMARY-PRIMORDIA SHOWN IN FIGS. 5 AND 6A.

bloodvessels (Fig. 6c). Internally to the cutis the beginnings of the trunk muscles were distinctly seen. Further, the primordia of the skin muscle were visible as thickenings of the cutis, which extended ventrally on either side as far as the epidermal thickenings.

These formations undoubtedly represent the first primordia of the mammary apparatus, the *primary-primordia* as I call them. It occurred to me that they must have been visible in the entire embryo. This supposition admitted of positive proof, thanks to the care with which Semon had his material illustrated. If you look at the drawing (Fig. 5) you will see on the right side of the trunk a white spot (*ma*), which exactly corresponds to the

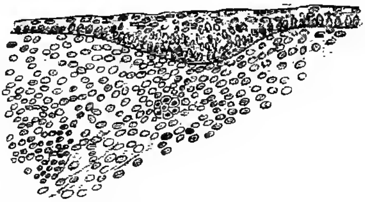

FIG. 6C.—ECHIDNA: SEMON'S EMBRYO. TRANSVERSE SECTION THROUGH THE PRIMARY-PRIMORDIA, SHOWING THE EPIDERMAL THICKENING AND THE UNDERLYING CONDENSED TISSUE OF THE DERMIS.

right primary-primordium, discovered in the sections.

In the following stages you will find, first of all, in connection with the progressive development of the body wall, that a shifting of the primary-primordia, originally situated in the

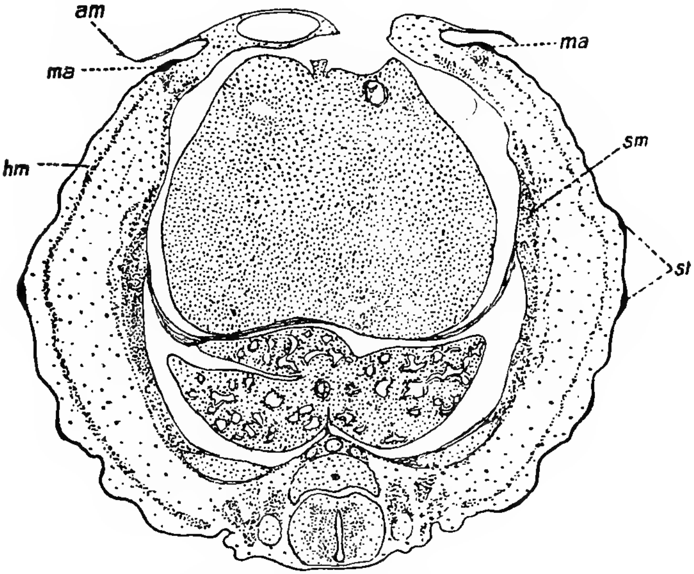

Fig. 7a.—Echidna: Transverse Section of an Older Embryo (Semon's Embryo No. 5), showing the Primary-Primordia shifted in Medioventral Direction, and the Skin Muscular Tissue.

ma, Primary-primordia; *hm*, the skin muscular tissue; *am*, amniotic fold.

lateral region, takes place in a medioventral direction, so that they finally come to lie on either side close to the line of origin of the amniotic folds (Figs. 7A and 7B, *ma*). Processes of growth cause the epidermal thickenings to assume a somewhat lens-shaped form, and to project above the level of the neighbouring skin (Fig. 7C). This condition, however, lasts but a short time, for they soon begin to flatten (Fig. 7D). Thus towards the end of the embryonic period, they form skin areas only slightly thickened and oval in shape, the length being not much greater than the breadth.

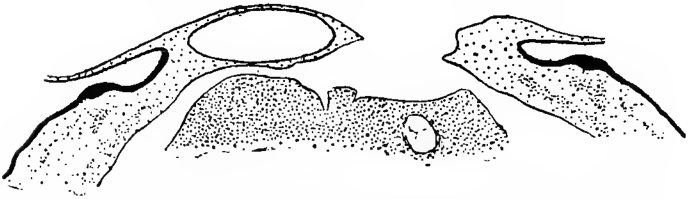

FIG. 7B.—ECHIDNA: SEMON'S EMBRYO NO. 5. ENLARGED VIEW OF VENTRAL PART OF PRECEDING SECTION, SHOWING THE PRIMARY-PRIMORDIA.

In consequence of these transformations, the primary-primordia, in the case of young just hatched, appear as very insignificant and hardly recognizable structures. At this stage, only the cutis part of the primordia is well marked owing to its condensed character and the presence of numerous capillaries (Figs. 8A and 8B). The general topographic features, especially those of the skin muscle, remain unaltered.

Whilst the primary-primordia long persist in this condition, soon after birth other differentiations begin, leading to the formation of the incubatorium. Although this develops quite independently of the primary-primordia, their existence is closely connected with the causes of the formation of the pouch.

FIG. 7C.—ECHIDNA: TRANSVERSE SECTION OF SEMON'S EMBRYO, SHOWING THE PRIMARY-PRIMORDIA WHEN IT FORMS A LENS-SHAPED PROJECTION ON THE SURFACE.

Immediately after the hatching of the young, the skin closes over the navel opening. But the skin-muscle does not grow, because the cutis thickenings of the primary-primordia act as a hindrance to the extension of the panniculus carnosus. That this is so is shown by the sections (Fig. 9); for the edges of the skin-muscle regularly present there a characteristic turning up, already observable in the preceding stage (Figs. 8A and 8B). Thus in the middle of the panniculus, which otherwise spreads uniformly over the ventral side of the trunk, there remains an oval muscle-free area—the incubatorial area—in the anterolateral portions of which the two primary-primordia are situated (in Fig. 9 these are indicated by crosses). The causes which lead to the depression of this incubatorial area have nothing

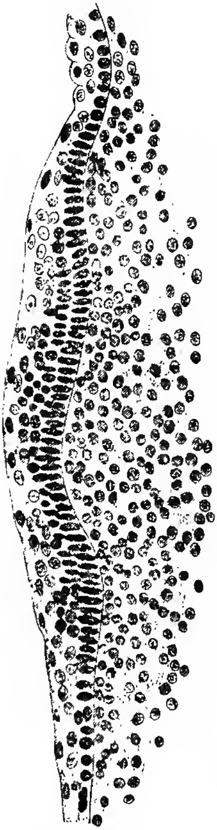
Fig. 7D.—Echidna: Semon's Embryo. Transverse Section of a Later Stage when the Primary-Primordia has Flattened.

to do ontogenetically with the specific organization of the mammary apparatus. When closure of the navel opening takes place a part of the body wall in the caudal portion of the incubatorial area remains connected with the bladder by means of the urachus, and is therefore exposed to a continual pull inwards, which is the more effectual since the muscle-free area

FIG. 8A.

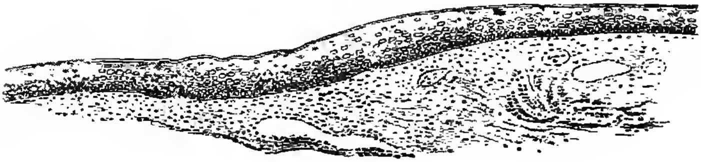

FIG. 8B.

FIGS. 8A AND 8B.—ECHIDNA: TRANSVERSE SECTIONS THROUGH THE PRIMARY-PRIMORDIA OF A STILL LATER EMBRYO (SEMON'S EMBRYO) IN WHICH THE EPIDERMAL THICKENING IS NO LONGER APPARENT, AND ONLY THE CUTIS THICKENING IS DISTINCT.

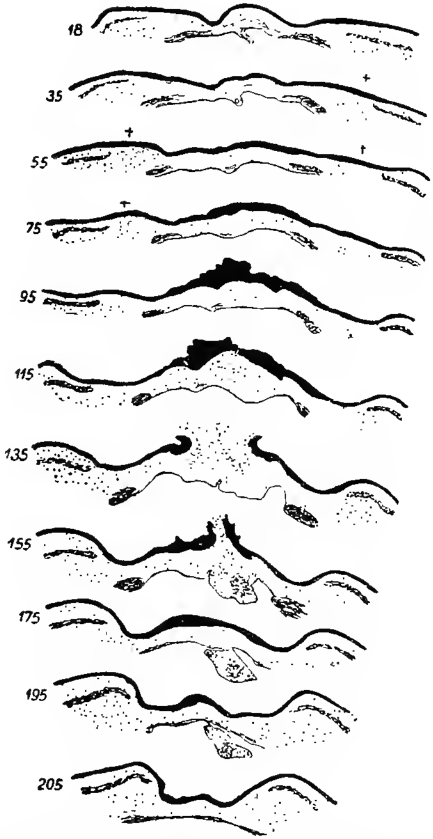

Fig. 9.—Echidna: Semon's Embryo No. 7. Transverse Section through the Primary-Primordia of a Young One shortly after Hatching. These are indicated by Crosses.

of the incubatorium is less resistant than the rest of the abdominal wall.

Through this tension only the caudal part of the incubatorial area becomes depressed at first, while the cranial portion, containing the primary-primordia, remains quite unchanged. It is not until the depression gradually extends in the cranial direction that the primary-primordia are finally drawn into the incubatorium (Fig. 10). The latter is then bounded by the bundles of skin-muscle surrounding the original incubatorial area and crossing each other in front and behind it. This fact justifies their being regarded as forming a sphincter incubatorii, although they are not anatomically distinct. Sometimes the navel-scar, which as a rule quickly disappears, divides the incubatorium into two halves for a short time (Fig. 9). But, of course, as Ruge has already remarked, this is not to be taken as a proof of a paired origin of the incubatorium.

In these last stages the primary-primordia become once again easily observable, since they remain entirely free from hairs, which elsewhere develop uniformly all over the skin (Fig. 10). The consequence is that, in surface

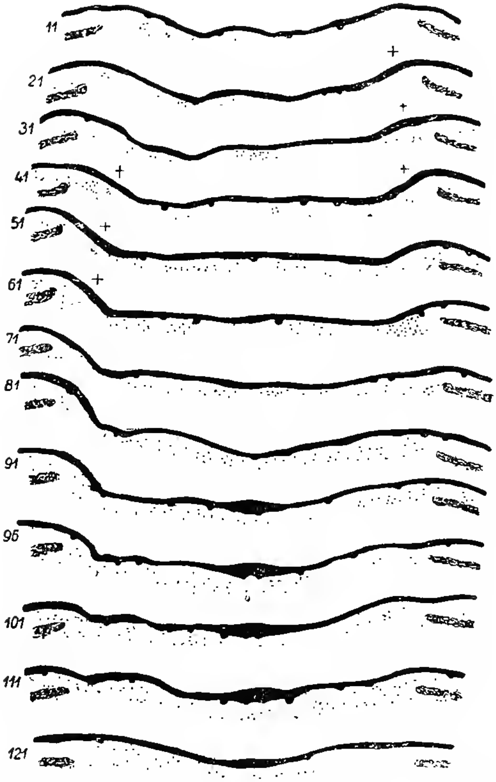

FIG. 10.—ECHIDNA: SEMON'S EMBRYO. TRANSVERSE SECTION OF A STILL OLDER POUCH-YOUNG, SHOWING THE PRIMARY-PRIMORDIA WHICH HAVE AGAIN BECOME DISTINCT. THESE ARE INDICATED BY CROSSES.

examination, these primordia now appear distinctly as circumscribed, oval, bare areas in the anterolateral corners of the hair-clad incubatorial area, as may be seen in Fig. 11A (*Dr*, *De*), representing the appearance of a stained and cleared preparation of the complete incubatorial area.

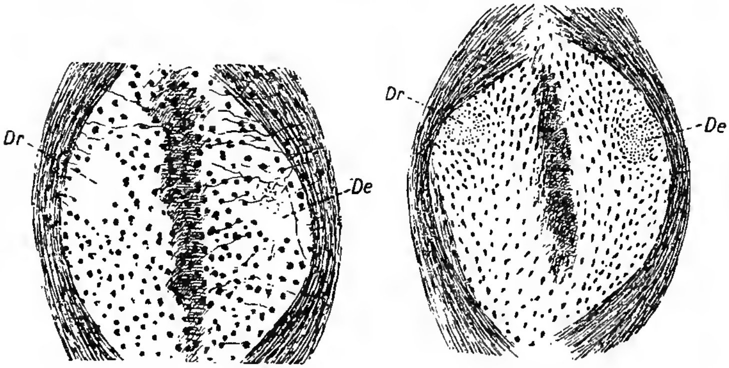

FIG. 11A. FIG. 11B.

FIGS. 11A AND 11B.—ECHIDNA: DRAWINGS OF THE MAMMARY AREAS OF TWO POUCH-YOUNG. SEMON'S STAGES 50 AND 51.

Dr, *De*, Gland areas.

A little later, in Stages 50 and 51 of Semon, the development of hairs begins within the primary-primordia also, and, indeed, all at once, and with a vigour never shown elsewhere in the skin (Fig. 11B, *Dr*, *De*). The number of these hair primordia, which are crowded together and are sometimes concentrically arranged, is over 100 for each primary-primordium, so that they are henceforward characterized by an unusual wealth of hairs, in contradistinction to their former baldness.

The significance of these formations comes out more distinctly still in the following stages, when the hair follicles begin to produce glands. The glandular outgrowths, which appear in the neighbourhood of the primary-primordia, slowly develop into typical sweat glands, the histogenesis of which Eggeling has described in detail. But the glandular outgrowths which arise from the hair follicles in the region of the primary-primordia develop only in their first stages after the manner of sweat glands, and

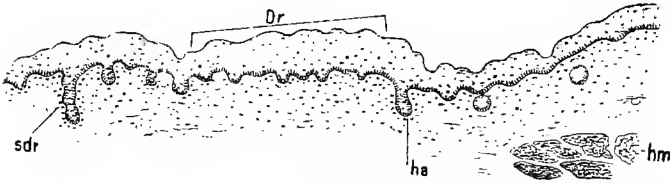

FIG. 12A.—ECHIDNA: TRANSVERSE SECTION THROUGH THE INCUBATORIAL AREA OF SEMON'S EMBRYO, STAGE 51.

Dr, Gland area; *ha*, hair bud; *hm*, skin-muscle; *sdr*, sweat gland.

very soon take their own course. These facts are very clearly illustrated in the series of drawings of successive stages represented in Figs. 12A, 12B, 13A, and 13B.

Fig. 12A represents a section of primary-primordium in Semon's Stage 51, of which Fig. 11B gave a complete view. The hair primordia of the surrounding skin, with the sweat-gland outgrowths now first appearing (*sdr*), and the first hair buds (*ha*) within the primary-primordium, are clearly shown. In Stages 51 and 52 (Fig. 12B) there is a further growth of the hair follicles within as well as without the primary-primordium, and likewise

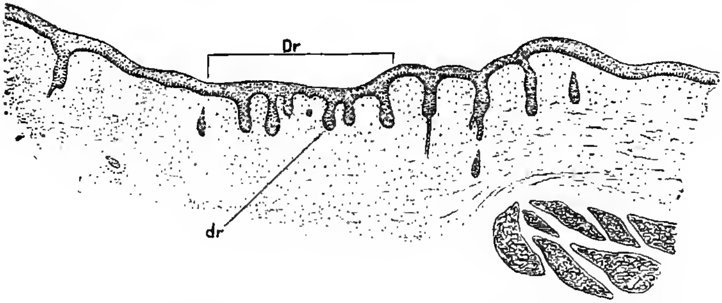

FIG. 12B.—ECHIDNA: TRANSVERSE SECTION THROUGH THE INCUBATORIAL AREA OF SEMON'S EMBRYO, STAGES 51 AND 52.

Dr, Gland area; *dr*, small gland bud.

of the sweat gland buds present in the preceding stage. Now, however, on the hair follicles of the primary-primordia, small gland buds appear (Fig. 12B, *dr*), exactly like the sweat-gland buds of Stage 51 (Fig. 12A, *sdr*).

Passing on to the next stage (Stage 52, Fig. 13A), we observe still further, and, indeed, more marked, progress. The striking feature is the very great development of the gland buds on the hair follicles of the primary-primordia, as compared with the sweat glands of the surrounding skin (Fig. 13A, *dr*).* Finally, in

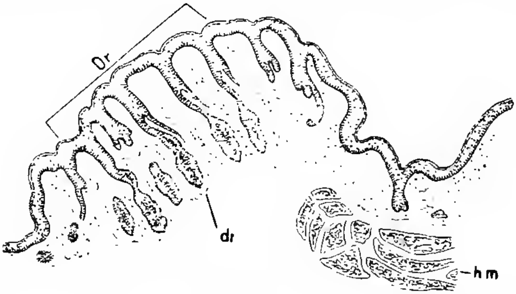

FIG. 13A.—ECHIDNA: TRANSVERSE SECTION THROUGH THE INCUBATORIAL AREA OF SEMON'S EMBRYO, STAGE 52.

Dr, Gland area; *dr*, sweat gland; *hm*, skin-muscle.

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* It should be noted that the piece of skin of which Fig. 13A represents a section was much wrinkled; hence the excessive convexity of the incubatorial area in this figure, which does not correspond to the natural conditions.

Stage 53, these formations, as originally described by Gegenbaur, have grown much larger than the sweat glands (Fig. 13B, *dr*). I was able to examine the incubatorium of Stage 53 *in toto*, and in Fig. 14, it will be seen that the primary-primordia, now distinguishable

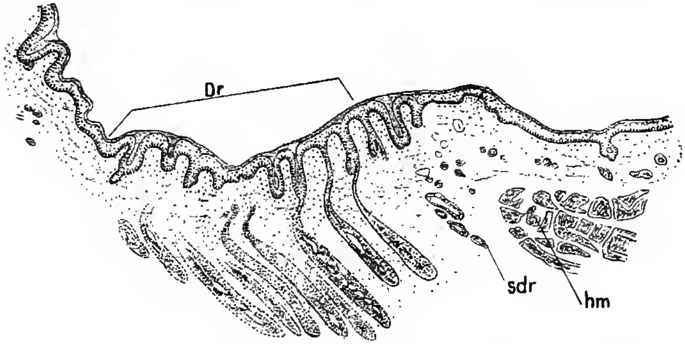

FIG. 13B.—ECHIDNA: TRANSVERSE SECTION THROUGH THE INCUBATORIAL AREA OF SEMON'S EMBRYO, STAGE 53.

Dr, Gland area; *sdr*, sweat gland; *hm*, skin-muscle.

as the definitive gland areas, have just been drawn into the region of the incubatorium, but are still situated quite at the cranial corners of the folds that surround it. Below in the picture is the left gland area, a section of which, still more highly magnified, is shown in Fig. 13B.

It is therefore obvious that the gland areas are the first mammary formations which appear in the course of ontogeny in Echidna. These gland areas, it is true, arise very early in the indifferent form of the primary-primordia. The development of the incubatorium falls in point of time between the first formation of the primary-primordia and their final evolution with the appearance of the mammary glands. In contradistinction, then, to the views held by Klaatsch and Ruge, the organs of the mammary apparatus in the case of Echidna are formed in the following order: (1) primary-primordia —that is to say, gland areas; (2) incubatorium; (3) mammary glands.

FIG. 14.—ECHIDNA: SEMON'S EMBRYO, STAGE 53.

What, then, are Owen's mammary pouches which have hitherto played so great a part in the speculations regarding the evolution of the mammary apparatus? They certainly do not occur in the stages we have so far considered, and, I may add, they do not appear at *any* later stage. In a word, the mammary pouches do not exist, and Owen's statements on the subject are completely wrong.

Owen's mistake is to be explained by the fact that the abdominal wall of the female Echidna he examined had been divided longitudinally with a view to studying the genital apparatus before coming into his hands, as he himself states. He was thus not in a position to recognize the incubatorium, cut up as it was, as a single formation. The unfortunate part is that Owen did not give drawings of the specimen as he saw it, but figured what he supposed to be the true relations (Fig. 3).

The fact that these illustrations of Owen's could be looked upon for forty years as valuable evidence for the existence of the mammary pouches, the appertaining text being wholly ignored, forms, as it seems to me, an interesting chapter in the history of scientific blunders. Their suggestive power was so great that such eminent investigators as Gegenbaur and Ruge did not doubt the correctness of Owen's statements, even though they could find in their own specimens only insignificant remains of the incubatorium, or trifling depressions of the gland areas. And it produced such an effect upon Klaatsch that he fell into the error of describing the different involutionary and evolutionary conditions of the incubatorium in the pauses between the periods of pregnancy as mammary pouches, although the prepared material lying before him was not cut up like the Echidna specimen of Owen. I have had the opportunity myself of studying Klaatsch's interesting material again, and have been able to demonstrate that the supposed mammary pouches are simply parts of the incubatorium more or less reduced.

If we now proceed to draw the phylogenetic conclusions from the facts we have gained from the consideration of the ontogenesis, our point of departure is the established fact that the development of the mammary apparatus does not start with arrangements for the accommodation of the young—that is, with mammary pouches or incubatorium—as nearly all writers since Darwin presumed, but much earlier, with the structures I have termed the primary-primordia. The answer to the question as to the origin of the mammary apparatus depends therefore essentially upon the phylogenetic significance we attach to these formations.

I may perhaps state here that almost a year elapsed between the time when I succeeded in discovering the primary-primordia and *that* later period when I began to have clearer views as to their significance. During this interval I thought constantly about this question before deciding to develop the theory, which I now wish to place before you. I say this because I am now passing from the domain of fact to the domain of speculation.

In weighing the question of the significance of the primary-primordia, the first thing to be considered was, whether from a phylogenetic point of view they were not simply indifferent formations, which had no further meaning than that of providing the material for the gland areas in earlier stages of development—that is to say, whether they had any phylogenetic importance at all.

It seems to me that such an assumption is to be rejected entirely. In the first place it strikes one as very strange that these epidermal growths should appear so early in the embryonic life, while the material so accumulated is not turned to account till very late in the post-embryonic life. Just as little could we understand, on this assumption, the part taken by the cutis in building up the primary-primordia and its relations to the skin-muscle, and the vascular system. Above all, it would be unintelligible why the material once accumulated should at the end of the embryonic period show so retrograde a development that a new budding process should have to take place in the transformation of the primary-primordia into the gland areas. These considerations, it seems to me, contradict such a conception, and have led me to suggest another conclusion—namely, that the primary-primordia represent rudiments of organs which long ago in the ancestors of the Echidna took the place of the later gland areas. The very early appearance of these structures testifies to their phylogenetic age; and that we are dealing with rudiments is indicated by their retrograde metamorphosis during the embryonic development.

If we proceed to inquire as to the nature of those organs of which the primary-primordia may be regarded as the vestiges, it is permissible to suppose that they functioned in some way in relation to the care of the offspring by the parent, and that thus, long before the appearance of the incubatorium and mammary glands, through these organs there existed some connection between the young and the abdomen of the parent animal.

Such considerations led me to regard these formations as organs with which the oviparous ancestors of the recent Mammalia hatched their eggs—*i.e.*, organs analogous in nature to the so-called Brutflecken or brooding-spots, such as are seen in many birds. These brooding-spots lie as paired or unpaired formations on the ventral side of the abdomen, and are fully developed sometimes in the female, sometimes in both sexes, in isolated cases only in the male.

According to the exact investigations of Barkow in 1829, these spots are already clearly differentiated in the young and are distinguished as areas free from cutaneous muscles, but singularly rich in bloodvessels. And now to think that we find in the primary-primordia exactly the same relations to the skin-muscle and the vascular system! It seems to me justifiable, then, in view of these facts, to compare the primary-primordia with these brooding-spots, and indeed to interpret them as vestiges of brooding organs. It must be emphasized that in making this comparison, we are dealing only with physiological analogy, as it is in this way that we may conceive something of the functions of those organs. There can of course be no question of homology between such organs in birds and mammals, and their structural similarity is sufficiently explained on functional grounds.

If you regard the primary-primordia as rudimentary brooding organs, with which the ancestors of the Mammalia hatched their eggs, then a simple explanation of the origin of the mammary apparatus presents itself. The transformation of the pre-mammalian ancestors* into Mammals brought with it the development of the hairy coat and the skin glands appertaining

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* According to Cope and others, probably Synapsidan reptiles of the stock of the triassic Cynodontia.

thereto. Simultaneously the brooding period grew continually shorter, and the original purpose of the brooding organs—namely, the production of warmth for the young—was lost. And so the rich supply of bloodvessels to these organs favoured the development of the tubular glands in these regions, so that from the very commencement they were able to produce a stronger secretion than the rest of the skin glands. Accordingly, when the primitive mammals attained to that evolutionary phase in which the young, hatching out from the egg in a quite immature condition, required to be fed by the mother, that need could at once be supplied by the gland complexes of the areas of the original brooding organs. Thus, too, in the case of the Prototheria, the first mammary organs sprang from the former brooding organs as circumscribed parts of the abdominal skin, characterized by the possession of strong hairs, the mammary hairs, and by glands opening out of these, strongly developed, and hence well fitted for quicker secretion.

In this form arose the mammary apparatus uniformly in the case of all Prototheria. But in another respect a difference appeared with their separation into two divergent stems, leading to the still extant groups of the Monotremes—the terrestrial Echidna, and the aquatic Ornithorhynchus. In the former, perhaps owing to the greater development of the cutis-thickenings of the brooding organs, the skin-muscle failed to extend over the region between and around the gland areas. The existence of the muscle-free region thus left rendered possible the appearance, during each brooding period, of a median inpushing or depression; a change in itself unimportant, but which gradually led to the formation of a storing-place for the developing egg—that is, an incubatorium. In the aquatic Ornithorhynchus, on the other hand, the skin muscle spread over the whole abdomen, leaving only narrow slits in the places of the brooding organs. Whatever the origin of this difference, there can be no doubt that the absence of an incubatorium in Ornithorhynchus is an adaptive feature. The question whether the Ornithorhynchus condition developed from the Echidna condition, or whether both were derived independently of each other from the conditions in primitive Prototheria, is very difficult to resolve, but for my part I am inclined to give an affirmative answer to the latter alternative.

The great importance, then, of the primary-primordia is that they throw light upon the origin of the mammary apparatus, for they point to a far older relation of the young to the abdominal skin of the parents than that which the appearance of the incubatorium conditioned. We have no longer to suppose that the mammary apparatus of the Mammals arose *de novo* in this highest class of vertebrates, but we now know that it resulted from primitive structures developed in their oviparous ancestors for brooding purposes.

In conclusion, it may be mentioned that this point of view throws a new light upon the much-discussed question of the reasons for the development of the mammary organs in *both* sexes. Although the mammary organs function only in the female, they exist also in the male, and indeed in the male Monotreme are fully developed. It has always been difficult to explain how this came to be without the active participation of the male in lactation. Various, and sometimes very curious, hypotheses have been made to surmount this difficulty. The best known of these assumes that originally only the female possessed the mammary apparatus, and then transferred it to the male by "amphigonous inheritance." The case has been greatly simplified through the possibility, formerly lacking, of referring to the brooding organs of lower forms. It is by no means necessary to assume that the original brooding organs of the pre-mammalian ancestors existed only in the female; they can quite well have been common to both sexes from the beginning, as is the case with many birds, where male and female share in the business of brooding.

With the presence of these brooding organs, a disposition to the development of the mammary apparatus was given to the male as well, especially if, as is not impossible, he took part in brooding during the earliest stages of mammalian history. The mammary apparatus then was not exclusively acquired by the female, but arose quite naturally in both sexes alike, on the ground of inherited disposition, and not until the disappearance of its function in the male did it undergo a retrograde metamorphosis in that sex. This assumption is in agreement with the fact that in the lowest Mammals, the Monotremes, the mammary glands in both sexes show exactly the same development, whilst in the males in the higher orders of Mammals they show a merely rudimentary condition. Had transference from female to male taken place, one would have expected just the reverse.

CHAPTER II

WE pass on next to consider the development of the mammary organs of the Didelphia. But first of all some account of their structure in the adult.

As the name Marsupialia, often used for Didelphia, indicates, their mammary apparatus is distinguished especially by the existence of a marsupium, usually a capacious pouch, surrounded by a strong sphincter muscle, the sphincter marsupii, and enclosing the milk organs. With the exception of the external opening of the pouch, sometimes directed straight down, sometimes towards the head or towards the tail, the marsupium appears similarly formed in most families of the Didelphia, a list of which is given in the table. Greater differences in its structural conditions occur only amongst the lowest families, the Australian Dasyuridæ and the American Didelphyidæ. The modi-

		Number of Nipples.	Pouch.
	I. Family, DIDELPHYIDÆ.		
	Genus, *Marmosa*—		
	(*a*) grisea	19	Absent.
	(*b*) pusilla	11-15	,,
	(*c*) murina	9-15	,,
	(*d*) cinerea	9-11	,,
	Genus, *Peramys*—		
	(*a*) henseli	17-25	,,
	(*b*) tristriata	19	,,
	(*c*) americana	15	,,
	(*d*) domestica	13	,,
	(*e*) sorex	13	,,
	(*f*) brevicaudata	9-11	,,
	Genus, *Caluromys*—		
	(*a*) philander	5-7	Only lateral folds.
	(*b*) lanigera	5-7	,, ,, ,,
	Genus, *Metachirus*—		
	(*a*) crassicaudatus	9	Absent or feebly developed.
	(*b*) nudicaudatus	9	
	(*c*) opossum	7	Well developed.
	Genus, *Didelphys*—		
	(*a*) marsupialis	5-13	,, ,,
	Genus, *Chironectes*—		
	(*a*) minimus	17	,, ,,
	II. Family, DASYURIDÆ.		
Dasyurinæ.	Genus, *Phascologale*—		
	(*a*) penicillata	10	Feebly developed.
	(*b*) flavipes	8-10	,, ,,
	(*c*) minutissima	8-10	Well developed.
	Genus, *Sminthopsis*—		
	(*a*) crassicaudata	10	,, ,,
	(*b*) murina	8	,, ,,
	Genus, *Dasyurus*	6-(8)*	,, ,,
	Genus, *Sarcophilus*	4	,, ,,
	Genus, *Thylacinus*	4	,, ,,
	Genus, *Myrmecobius*	4	,, ,,
	III. Family, PERAMELIDÆ	(6)-8†	,, ,,
	IV. Family, PHALANGERIDÆ	(2)-4‡	,, ,,
	V. Family, PHASCOLARCTIDÆ	2	,, ,,
	VI. Family, MACROPODIDÆ	4	,, ,,

* Eight nipples in *D. hallucatus* alone; other species regularly with six nipples only.

† Thomas mentions in *P. cockerelli* and *longicaudatus* only six nipples; all other Peramelidæ, so far as known, with eight nipples.

‡ The normal number of nipples is four, but single specimens of the genera *Trichosurus*, *Distœchurus*, and *Petaurus*, show sometimes only two nipples.

fications are considerable, especially among the latter, as can readily be seen from a study of the table. It is important to remember that in certain forms, not a complete pouch, but only a pair of lateral folds may exist, and also that in a great number of species the marsupium is missing altogether.

Inside the marsupium are the milk organs, which, unlike those of the Monotremes, have been so perfected that the efferent ducts of the milk glands do not end on a flat gland area, but in a nipple. The nipples of the Marsupialia, however, are distinguished from those of the Placentalia by a very striking feature, the discovery of which we owe to the famous researches of John Morgan in 1833. Morgan stated that the marsupium of the virgin kangaroo does not contain any nipples, but that there are instead in the region in question four small circular apertures, each one leading into a channel at the bottom of which on a small papilla the efferent ducts of the milk glands open (Fig. 15A). This condition remains the same for a long time. Only at the beginning of pregnancy, or shortly before lactation commences, does it experience a change, in that the channels—which we call the nipple-pouches—are everted like the finger of a glove, so that the papilla originally situated at its root now comes to the top of a fairly long nipple (Fig. 15B). The young take this into the mouth, which, as is well known, is especially adapted to this purpose.

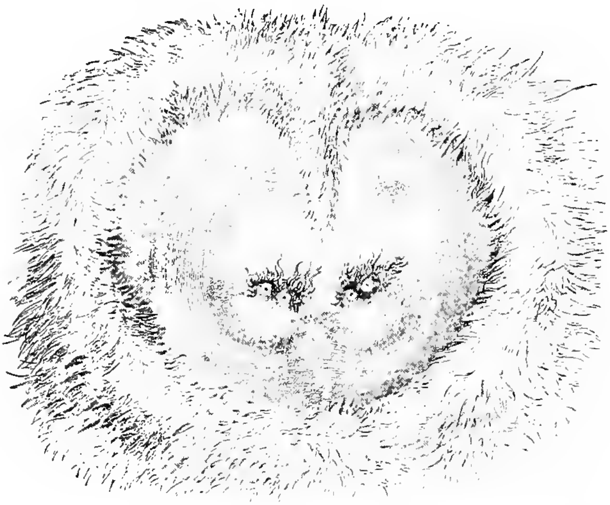


FIG. 15A.—MARSUPIUM OF A YOUNG KANGAROO, SHOWING THE FOUR FOLLICULAR APERTURES THROUGH WHICH THE FUTURE TEATS ARE PROTRUDED. (MORGAN.)

The nipple-pouches, however, are not the only depressions observable within the marsupium. Often there are other recesses, which enclose the nipple-pouches or the everted nipples. Fig. 16 is a reproduction of a photograph of an adult female of *Sminthopsis crassicaudata*, which shows

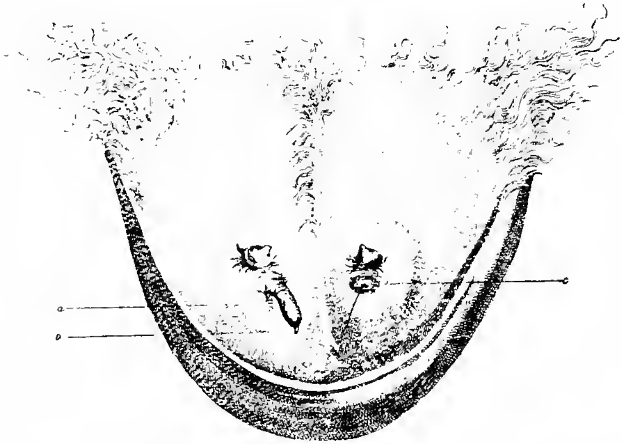


Fig. 15b.—Interior of the Pouch of the Virgin Kangaroo in which the Lower Teat on the Right Side has been Produced by Artificially Everting. (Morgan.)

a, The membranous canal of the mammary gland, and projecting, *b*, its papillary termination ; *c*, the follicular aperture formed by the opening of the canal, and through which the canal with its papilla is pushed and everted.

remarkably clearly the intact marsupium divided into a number of little compartments or *marsupial pockets*, as I may call them, each containing one nipple. I should like to mention here that this specimen belongs to the British Museum, the officials of which

FIG. 16.—THE MARSUPIAL POCKETS OF AN ADULT FEMALE "SMINTHOPSIS CRASSICAUDATA."

were so kind as to place at my disposal a large mass of material. Another case of marsupial pockets is represented in Fig. 18, after a drawing by Klaatsch, taken from a female Trichosurus. In this specimen the marsupium has been opened up and contains two nipples (Fig. 18, P) each surrounded by a marsupial pocket.

The number of nipples varies considerably within the order of Marsupialia, as you will gather from the table. The number two corresponding to the two gland areas of the Monotremes occurs but seldom. Very high numbers are met with in the case of the Didelphyidæ, where the arrangement of the nipples shows, moreover, some peculiar features. The nipples here do not simply occur in pairs, as in the other families, but as their number is odd, a single nipple is to be found in the middle of two lateral rows. Several pouchless species (Fig. 17) show lateral nipple rows stretching over the whole length of the trunk. Still more striking is the fact that sometimes not only one but two nipple rows are placed on either side, as in the case of *Peramys henseli* (Fig. 17).

It has already been mentioned that the efferent ducts of the milk glands end on the apex of the everted nipples, and it only remains to add that mammary hairs are not present in the adult. The number of milk ducts in the individual nipple is, in general, small. The number fifteen, which is said to occur in several species of kangaroo, is—so far as we know—only surpassed in the genus Phascolarctos, in which twenty-four ducts are to be found. Histologically the milk glands of the Marsupialia are very much like those of the

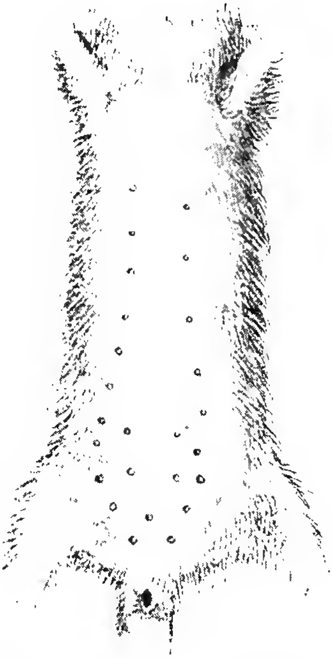


FIG. 17.—"PERAMYS HENSELI," SHOWING ARRANGEMENT OF NIPPLES. (AFTER THOMAS.)

Placentalia, and consequently differ very much from those of the Monotremes.

What, now, have been the prevailing ideas as to these conditions, when viewed in the light of phylogenesis ? The answer to this question is supplied by the famous so-called mammary-pouch theory of Gegenbaur and Klaatsch. To begin with, on the strength of the aforementioned investigations of Morgan, Gegenbaur, in 1876, believed that the nipples of the Marsupialia could be derived from the mammary pouches of Echidna. The nipple-pouches, in his view, corresponded directly to the mammary pouches, and their eversion, he held, was produced as the result of adaptation to the mouth of the suckling young. Gegenbaur was confirmed in this view by observing that the nipples of the Marsupialia first appear as solid, knob-like, epidermal buds, growing into the cutis, and he therefore called them mammary-pouch primordia. The same buds had been observed some years before (1873) by his pupil Huss in the Placentalia.

The assertion of Rein, directed against this hypothesis, that Gegenbaur's supposed mammary-pouch primordia were actually the first milk-gland buds, led to Klaatsch's further development of the views of the great Heidelberg anatomist.

In 1883 Klaatsch, completely refuting Rein's theory, succeeded in showing from observations on a large number of marsupial young that the nipple-pouches actually spring from the knob-shaped primordia, and that it is from the bottom of these pouches that the milk glands bud out. In a second work (1891) he tried also to explain the genesis of the marsupium by means of the mammary-pouch theory. He found that in the case of the fully developed Trichosurus female, the two nipples were situated in pouch-shaped depressions, the lateral edges of which coincided with the edges of the marsupium (Fig. 18). These pouches are the structures which we have distinguished (*antea,* p. 17) as marsupial pockets. Klaatsch made the mistake of taking them for nipple or mammary pouches, an almost inconceivable mistake, since in the female the nipples were already present, and it was, of course, impossible that nipple pouches should exist after they had been everted. But he came to this conclusion, because it fitted in excellently with his previous ideas, and because it explained the marsupium as having developed from the fusion of the mammary pouches in the same way as the incubatorium of Echidna. Thus Gegenbaur and Klaatsch believed that they could trace back the mammary apparatus of the Marsupialia to conditions existing in the Echidna. The glands, however, which provide the nutritive fluid for the young were, in their view, of diphyletic origin, because the mammary glands of the Monotremes, they held, had developed from the sweat glands, whilst the milk glands of the rest of the Mammals, in their view, developed from the sebaceous glands of the hairs of the bottom of the mammary pouches.

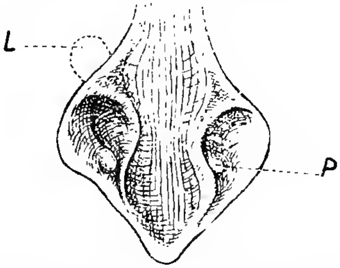


FIG. 18.—MARSUPIUM OF FULLY DEVELOPED TRICHOSURUS, SHOWING THE TWO NIPPLES, *P*, EACH SURROUNDED BY A MARSUPIAL POCKET.

After what has been written in the preceding chapter, a criticism of these views is scarcely necessary. For it is evident that nothing can be more fatal to a mammary-pouch theory than the proof of the non-existence of mammary pouches ! Eliminate mammary pouches from the cleverly combined ideas of Gegenbaur and Klaatsch and it is seen at once that they rest upon no firm basis of observation. And if we wish to replace the Gegenbaur-Klaatsch theory by a new and better established one, we must start by carefully examining the development of the mammary apparatus of the Marsupialia at every stage and in as many different forms as possible.

My thanks are due to the authorities of many public and private collections, in and out of Germany, for providing me with a very rich material for this purpose, comprising nearly 400 specimens of the young of the various families of marsupials. And yet for a long time I was not able to come to a conclusion, because of the absence from my material of uterine embryos, which alone would have enabled me to observe how the development of the mammary apparatus begins. I owe the possibility of filling up these gaps to the kindness of Professor Hill, and if I have succeeded in completing my work, the results will be in great measure due to him.

When I came to London to study Professor Hill's preparations in University College, I had definite hopes of being able to discover the first primordia of the mammary apparatus. But I had not expected that this discovery would be so simple as it turned out to be.

FIG. 19A.—SIX-DAYS-OLD EMBRYO OF "DIDELPHYS MARSUPIALIS." (AFTER HILL.)

ma, Primary-primordium.

My first successful observation was made upon an embryo of *Didelphys marsupialis*, perhaps six days old. Upon examining the sections of the region of the trunk, which probably contained the primordia of the mammary apparatus, I at once saw that here exactly the same primary-primordia were present as exist in Echidna—viz., little circumscribed areas of the abdominal wall, characterized by thickened epidermis and an underlying cutis thickening, penetrated by numerous blood-vessels, and down to which the primordia of the trunk muscles reached (Fig. 19B, *ma*, and 19C).

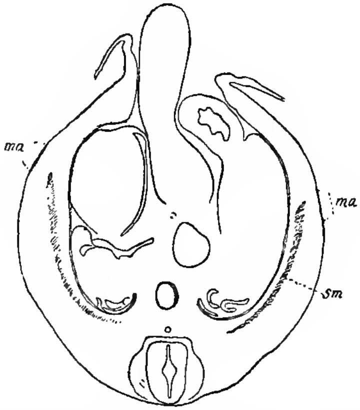


FIG. 19B.—TRANSVERSE SECTION OF SIX-DAYS-OLD EMBRYO OF "DIDELPHYS MARSUPIALIS."

ma, Primary-primordia of mammary apparatus; *sm*, primordium of trunk musculature.

The thickening of the epidermis in the sections through the primary-primordia was not everywhere uniformly distributed. In a number of sections taken from the caudal region the thickening was lens-shaped (Fig. 19c, lower figure), just as we shall see later is the case in the first primordia of the single nipples. Towards the cranial region the area in question was on the whole less convex, sometimes thinner, sometimes thicker; but it was not possible to distinguish individual primordia from each other. The whole behaviour suggested that the common blastema, represented by the primary-primordia, had just begun to differentiate into a number of small individual primordia.

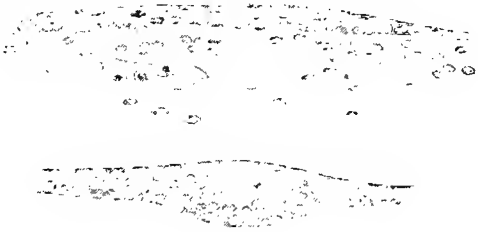


FIG. 19C.—TRANSVERSE SECTION OF PRIMARY-PRIMORDIUM OF MAMMARY APPARATUS OF SIX-DAYS-OLD EMBRYO OF "DIDELPHYS MARSUPIALIS."

After the examination of the sections had led to the discovery of these primary-primordia, it was, of course, interesting to know if they had also been macroscopically visible. Professor Hill's custom of photographing his objects before cutting them made it possible to decide this. We were both surprised to see in the photograph of the Didelphys embryo the right primary-primordium clearly appearing as a whitish spot on the abdomen (Fig. 19A, *ma*). Once having noted the primary-primordia, I could then ascertain their appearance in sections of Dasyurus, Phascolarctos, and Phascolomys, and in a well-preserved, entire embryo of Perameles (Fig. 20). In Petaurus and Æpyprymnus too, although the earliest stages were lacking, formations were found which could be nothing else but remains of the primary-primordia. Thus it may be regarded as an established fact that in the Marsupials, as well as in the Monotremes, the development of the mammary apparatus begins with the formation of the primary-primordia.

In the following stages, just as in the Monotremes, the primary-primordia move from the lateral position they occupy at first (Figs. 19A and 20), and, with the disappearance of the membrana reuniens inferior, approach each other in a medioventral direction. But while in the Echidna they remain passive until the formation of the mammary hairs and glands, in the Marsupialia the differentiating processes,

FIG. 20.—EMBRYO OF PERAMELES. (AFTER HILL.)

already started in the Didelphys embryo, go steadily forwards, so that even before birth the primary-primordia have entirely disappeared as such, and their place is taken by a number of small separate epidermal thickenings, which constitute the primordia of the individual nipples. These at first appear in the form of biconvex, lens-shaped thickenings, as seen already in the caudal part of the primary-primordia (Fig. 19c). But shortly before or after birth they begin to grow further, and finally present the knob-shaped form described by Gegenbaur. They remain in this stage for a long time after birth ; in the case of the opossum young, indeed, during the whole period it is attached to the nipple. Meantime other interesting developmental processes are going on, which lead to the appearance of the marsupium. But before considering these processes we have to pay attention to the mode of arrangement of the nipples peculiar to the Didelphyidæ, to which I referred at the beginning of this chapter. How can such an arrangement, characterized by an unpaired median nipple, arise when symmetrical, paired primary-primordia form the starting-point of the nipple primordia ?

We are provided with an answer to this question if we examine Fig. 21, representing the abdominal wall of one of three new-born opossum young belonging to Semon's collection, and measuring in dorsal contour length 2·15 centimetres. In all the three female young the same condition was clearly observable. Right and left run two bloodvessels, cutaneous branches of the vasa epigastrica. These in the caudal region flank an area enclosed by the fibres of the sphincter marsupii, just beginning to develop. In the centre of the area is the transverse section of the navel with its three vessels, and you can count on the right six, on the left five, dark spots corresponding to so many nipple primordia. In the middle behind the navel, where the primordium of the unpaired median nipple would be expected, you find instead a pair of them.

FIG. 21.—ABDOMINAL WALL OF NEW-BORN OPOSSUM. (SEMON COLLECTION.)

Micro-photograph 12 diameters.

In spite of the fact that the piece of skin had to be stretched out flat in order to obtain this preparation and so pulled out of shape, you can gather from the figure how far originally the primary-primordia extended, and how each of the elongated oval primary areas has produced one of the primordia of the central pair. Observe now in Fig. 21, taken at a magnification of twelve diameters, how far the lateral rows of nipple primordia are separated from each other, and compare with this Fig. 22 of a young one, 3·65 centimetres long, taken at a magnification of eighteen diameters. In

FIG. 22.—ABDOMINAL WALL OF YOUNG DIDELPHYS. (BRESSLAU.)

Micro-photograph 18 diameters.

this figure it will be noticed that there is now no trace of the navel-scar in the region of the linea alba. On the other hand, and in spite of the higher magnification, the two lateral rows of nipple primordia lie much nearer to each other than in the preceding preparation ; but the single primordia are more separated from each other in a longitudinal direction. Further, at the spot occupied in Fig. 21 by the two central paired primordia, there is present only the typical unpaired primordium. There is no doubt as to the explanation of this. At the closing of the navel-scar, the areas of the two primary-primordia became approximated by rather more, indeed, than the distance between the two central nipple primordia, as I ascertained by exact measurement. These primordia in consequence became pressed together, and finally fused completely—a phenomenon quite similar to that observable in the group of the placentalia in the case of the nipple primordia of the horse and ass, as long ago known.

Thus the central nipple of the Didelphia is only apparently an unpaired formation, having, in fact, sprung from paired primordia, just as we should presume from the paired appearance of the primary-primordia. Consideration of this evidence leads us to a series of conclusions, which further throw an unexpected light on the conditions of the nipple arrangement in the Didelphyidæ.

Let us make these conclusions clear with the help of the diagrams (Fig. 23, *a*, *b*, *c*). Our point of departure is the primary-primordia, which, as we saw in the Didelphys embryo, formed two oval areas on the lateral parts of the abdomen. Projected on to a plane, we can draw them as two ellipses, whose long axes converge in a caudal direction. Suppose now that the nipple primordia differentiate within these areas, there would be a waste of space were all the primordia to arrange themselves in a single row behind one another. The fact is that the primary-primordia leave space in breadth as well as in length for the differentiation of individual nipple primordia. We can therefore represent their arrangement as you see in Fig. 23A, where eight nipple primordia, partly unpaired (*a* and *e*), partly in two rows ($b\beta$, $c\gamma$, $d\delta$), are indicated in each primary-primordium.

Through the disappearance of the membrana reuniens, the areas of the two primary-primordia, in the course of further development, get gradually pressed nearer together towards the middle of the abdomen. In consequence, the nipple primordia of the right and left side become approximated, and finally the primordia β, which have shifted nearest together,

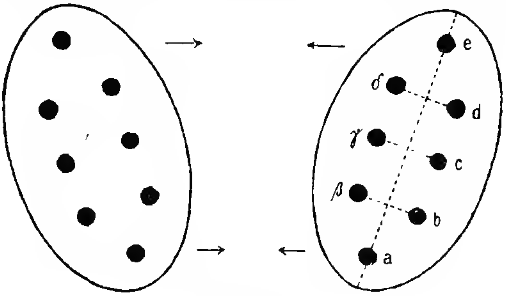


Fig. 23A.

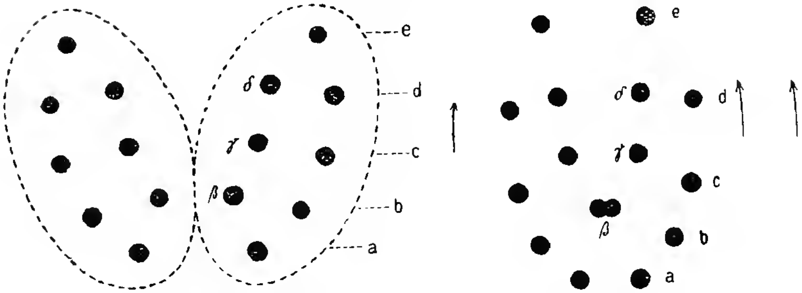


Fig. 23B. Fig. 23C.

Figs. 23A, 23B, and 23C.—Diagrams showing the Genesis of the Double Row of Nipples in the Didelphia. (Bresslau.)

touch and undergo fusion. At the same time, as the young ones grow in length, the individual nipple primordia are pulled somewhat apart in a longitudinal direction, as shown by the arrows (Fig. 23c). Thus results an arrangement of the nipple primordia, from which we can derive all the different types met with in the Didelphyidæ.

And first you see at once that here, there is a four-rowed arrangement of the nipple primordia, a complex of five central nipples being shut in by five on either side, corresponding to the nipple formula 5-5-5, as usually written.

In nature this condition is exactly realized in *Peramys americana*, as is seen in the description given of it by Oldfield Thomas in his excellent catalogue of Marsupialia. He says: "Mammæ 5-5-5, the outer series placed in such a curve, that the anterior pair are in line with those of the inner set, and might almost be reckoned as belonging to them." With increase of the number of nipples, in front of the primordia a single row of nipple primordia differentiates on each side without affecting the inner nipple complex, as in *Peramys henseli*. If, in the reverse case, a reduction of the number of nipples occurs—as is characteristic of many of the Didelphyidæ—it always happens through the disappearance of the more cranial nipples, and the outer as well as the inner rows may be affected. In the latter case, if the primordia δ and γ are suppressed, there would result only two simple rows of nipples, enclosing between them an unpaired central nipple. In the other eventuality, when the primordia *d* and *e* are suppressed, we have actually four rows of nipples, which, however, are so arranged as to appear like two.

If now we pass from these theoretical possibilities to the examination of the specimens themselves, the significance of the above considerations at once becomes clear. For we learn that in all genera of the Didelphyidæ, a four-rowed arrangement of nipples exists, although hitherto it has not been recognized.

Fig. 24A and Fig. 24B illustrate the nipple arrangement in a *Marmosa murina*, belonging to the British Museum. According to the usual conception, the nipple formula here is 5-1-5, in spite of the peculiar position of the cranial nipples not fully everted out of their pouches (Fig. 24A). But if we compare now the diagram (Fig. 24B) with the previous scheme (Fig. 23), we see that this is not the right view of the case. The dotted line at the right shows you that the five lateral nipples do not form a continuous row, as would be the case if they corresponded to the nipples *a-e.* But as the dotted line on the left indicates, the two cranial pairs of nipples belong to the inner nipple complex, and so must be called γ and δ instead of *d* and *e.* The nipple arrangement here, then, is only apparently two-rowed. In

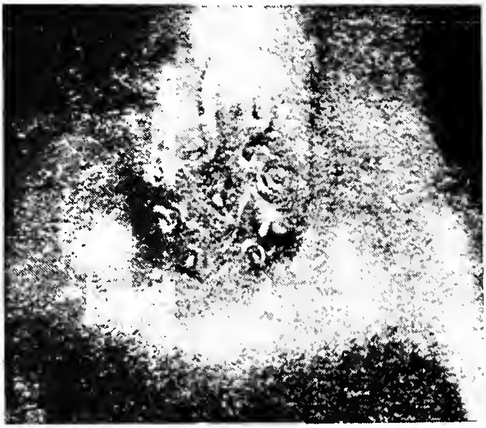


FIG. 24A.

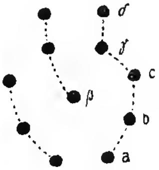


FIG. 24B.

FIGS. 24A AND 24B.—NIPPLE ARRANGEMENT IN "MARMOSA MURINA." (BRESSLAU.)

reality there are four rows of nipples, and the formula to be used is 3-5-3, and not 5-1-5.

The same four-rowed arrangement is quite obvious in many other species of Didelphyidæ. In others it is sometimes more or less obscured, as, for example, in *Didelphys marsupialis*, as the result of secondary displacements or of reduction in number of the nipples. In young specimens, however, of this species, the four-rowed arrangement is perfectly distinct.

We now return to follow the further development of the mammary apparatus, and more especially the mode of formation of the pouch, and, as our point of departure, we may take the stage in Didelphys represented in Fig. 22. The individual nipple primordia have become differentiated, and have reached the knob-shaped stage. The marsupium is non-existent as yet, but the darker stained areas in the neighbourhood of the three caudal pairs of nipples indicate the beginning of its development. If we look now at sections of the abdominal skin in the region of those nipple primordia (Fig. 25), we find in the case of young 3·55 centimetres long that only these primordia project into the cutis as knob-shaped buds of the epidermis. In the stage 3·8 centimetres long, corresponding to the dark tones in Fig. 22, there are now present on either side of the nipple primordia well-marked ingrowths of the epidermis. These then extend inwards so rapidly that at the stage 4·4 centimetres they are much larger than the nipple primordia, and, as a sectional reconstruction shows, they surround the latter in the form of continuous

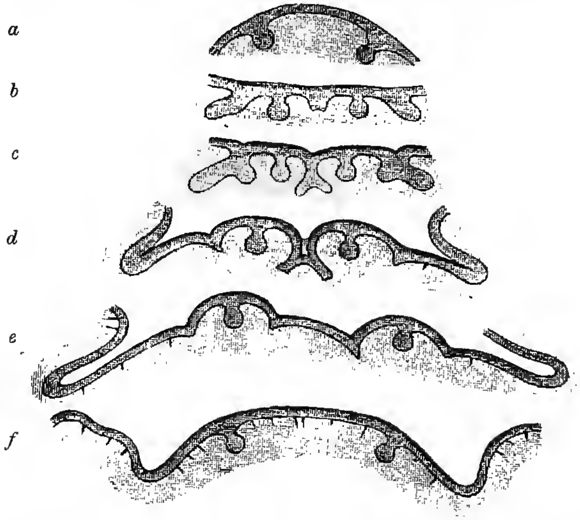


FIG. 25.—TRANSVERSE SECTION OF ABDOMINAL SKIN IN THE REGION OF THE NIPPLE PRIMORDIA OF "DIDELPHYS MARSUPIALIS." SUCCESSIVE STAGES. (BRESSLAU.)

ring-shaped walls partly in contact with each other.

This structural condition, which leads to the formation of the marsupial pockets, is very clearly seen in preparations of the mammary region made from these and the following stages (Figs. 26, 27, 28). In Fig. 26 is illustrated the condition of the mammary apparatus in the stage of 4·4 centimetres, where, in correspondence with the last sections, there was as yet no external pouch. The ring-shaped epidermal ingrowths surrounding the three

FIG. 26.—ABDOMINAL WALL OF YOUNG DIDELPHYS. (BRESSLAU.)

Micro-photograph, 18 diameters.

caudal pairs of nipple primordia are clearly seen. Round the central primordium and the fourth pair, however, they are only beginning to develop. These primordia obviously belong to the inner series of the four-rowed arrangement that we have already recognized. I would especially emphasize that these ring-shaped ingrowths are to be regarded as individual formations, and as a proof of this, one can see in the figure that their lateral walls form distinct convex projections.

FIG. 27.—ABDOMINAL WALL OF YOUNG DIDELPHYS. (BRESSLAU.)

Micro-photograph, 12 diameters.

But this condition does not last long. In young only slightly larger than the last stage

—namely, 4·6 centimetres long—we find that the lateral margins of the three pairs of caudal rings have straightened out to form a continuous horseshoe-shaped fold bounding a slightly depressed area. This area represents the future pouch, and the fold its wall. The way in which the originally solid ingrowths are changed into folds is explained by diagrammatic sections (Fig. 25, *a-f*). They show that within the ingrowths there sets in a process of cornification, as the result of which they gradually become hollowed out. Fig. 25, *c*, representing the stage

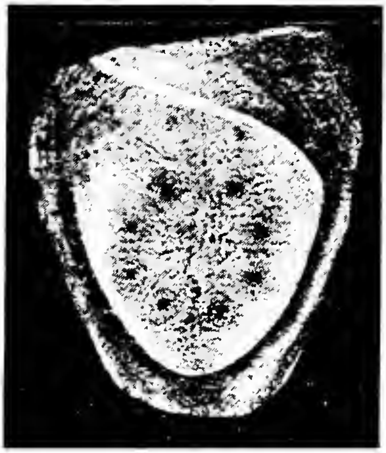


FIG. 28.—ABDOMINAL WALL OF YOUNG DIDELPHYS. (BRESSLAU.)

illustrated in Fig. 26, shows the beginning of this process; Fig. 25, *d*, a further advanced stage, in which the original ingrowths are already hollowed out into regular folds, which are deepest laterally. Thus, in photographs representing the stage 5·5 centimetres, in place of the earlier solid primordia we get deep lateral pouch folds, and in connection ring folds surrounding the nipple primordia (Fig. 27). It is therefore clear that the ring-shaped epidermal ingrowths are nothing else than the primordia of the marsupial pockets, of which we have already spoken, whose value for the pouch formation was so justly recognized by Klaatsch, but whose phylogenetic significance he entirely misunderstood.

In the course of further development, the pouch folds and marsupial pockets get completely hollowed out. At the same time they flatten, so that the pouch area increases considerably (Fig. 25, *e*, *f*). Meantime, marsupial pockets have been formed round the cranial nipple primordia (Fig. 27), but these, owing to the four-rowed arrangement of the nipple primordia, take no part in the formation of the pouch folds.

In the next stages, the marsupial pockets and their remains gradually disappear through the continuation of the flattening process; thus the lateral walls of these pockets alone persist as the wall of the marsupium. This leads us to the condition seen in the 6·4 centimetres stage, where only feeble remains of the marsupial pockets are to be observed. But these also are finally lost, no traces of them being found in the almost completely developed marsupium of, for example, a young one 8·7 centimetres long (Fig. 28). The inner surface of the pouch, now much increased in area, is perfectly smooth with the exception of the nipple primordia, and the last indication of the previous existence of the marsupial pockets is seen in faint wrinkles and in the arrangement of the hair primordia, which have in the meantime begun to develop. The great increase in size resulting from the flattening of the inner folds is even more clearly seen if one compares the figures of sections from three successive stages (Fig. 25, *d*, *e*, *f*), *d* and *e* taken at the same magnification, *f* at one-quarter less. It should be noted that the nipple primordia remain unchanged at the knob-shaped stage during the whole time of the pouch development, and have nothing to do with its formation, as Klaatsch presumed.

As regards the development of the pouch in the other families of the Marsupialia, it need only be mentioned that in the Dasyuridæ, as in the Didelphyidæ, the pouch is formed at the expense of a number of marsupial pockets, and that in the remaining families also its development is always connected with their appearance. Accordingly, it may be concluded that the marsupial pockets in general represent the starting-point of the pouch development, even though in the higher marsupial families modifications have taken place, adapted to bring about a further enlargement of the simple marsupium originally derived from the marsupial pockets alone. Fig. 29, Fig. 30A, and Fig. 30B demonstrate the presence of the marsupial pockets in Trichosurus, and it is of interest to notice that in this and other genera they do not appear only as folds, but also as solid epidermal ingrowths, which later become hollowed out.

An extremely important conclusion follows from our observations — that is, that the marsupium can in no way be compared with the incubatorium.

The incubatorium is an unpaired single formation; the marsupium, on the other hand, a complex. As we have seen, the genesis of the incubatorium is conditioned by the behaviour of the skin muscle, in so far as primarily a muscle-free area of the abdominal wall, surrounded by the sphincter incubatorii, is formed, and then becomes invaginated by a tension from within. In the Marsupialia, on the other hand, the sphincter marsupii takes not the slightest part in the genesis of the pouch. The marsupium here arises as the result of formative processes in the epidermis, leading to the development of marsupial pockets, wholly unrepresented in Echidna.

FIG. 29.—MARSUPIAL POCKETS IN TRICHOSURUS. (BRESSLAU.)

There can, therefore, be no question of homology between the incubatorium of the Monotremes and the marsupium of the Didelphia.

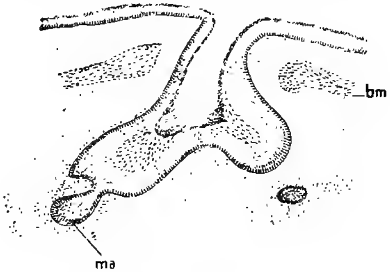


FIG. 30A.—TRANSVERSE SECTION OF TRICHOSURUS. × 60.

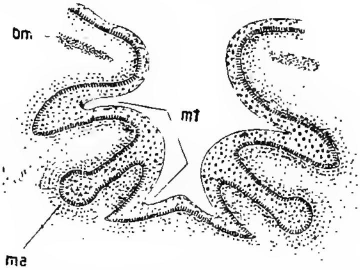


FIG. 30B.—TRANSVERSE SECTION OF "TRICHOSURUS VULPECULA." × 45. (BRESSLAU.)

ma, Primary-primordia; *mt*, marsupial pocket; *bm*, pouch muscle.

If, hitherto, such an assumption has always been made as a matter of course, the explanation is to be found in the great apparent similarity of these two organs in the adult animals. But this similarity rests solely on convergence.

With the establishment of these facts two old misapprehensions naturally fall to the ground. We have first of all to give up the idea that the marsupium represents a formation inherited from the Monotremes; and, in the second place, we can no longer hold that all Didelphia originally possessed a marsupium, and that in all those forms where it is now absent the pouch has been secondarily lost. Forms certainly do exist where the marsupium has secondarily disappeared, as, for example, Myrmecobius amongst the Dasyuridæ, where, during ontogenesis, the primordia of the marsupial pockets and of a typical marsupium are to be observed, though they disappear relatively early. Moreover, in spite of this, a sphincter marsupii is formed, and persists in the adult. On the other hand, when we proceed now to examine the pouchless Didelphyidæ, we find in development, so far as known, no rudiments of a pouch, whilst the sphincter marsupii is also absent, even in the adult. We have therefore every reason to suppose that they have never possessed a pouch, and we are justified in coming to the conclusion that the marsupium first originated within the limits of the marsupial series itself.

We may now return to the consideration of the nipple primordia, whose development we traced to the knob-shaped stage, and which have not materially altered during the development of the marsupium. It is only after the completion of the latter that they become transformed into the definitive organs.

If we again take *Didelphys marsupialis* as our type, it is to be noted that the processes of nipple development apparently do not agree with those observed by Morgan in the kangaroo. The knob-shaped nipple primordia, instead of developing into nipple pouches, gradually become reduced, so that in young ones about 15 centimetres long there are only insignificant remains of them, corresponding to the bases of the original knob-shaped buds. During this reduction there grow out from them eight epithelial sprouts, and each primary sprout produces one secondary and a pair of tertiary outgrowths.

The primary sprouts represent the primordia of the mammary hairs; the tertiary those of the sebaceous glands. The secondary give rise to the milk glands, which in their first stages are quite similar to the primordia of the sweat glands in the rest of the skin (Fig. 31). At first the remains of the nipple primordia are only slightly raised above the level of the surrounding skin. But in the following stages the so-called "cutis wall"—as Klaatsch has named the part of the integument surrounding the nipple primordia, coloured black in the figures—grows gradually, and so brings about the elevation of the nipples. These, then, are produced essentially by the cutis wall, their apical portions only being derived from the original knob-shaped primordia. During the development of the nipples the mammary hairs and the appertaining sebaceous glands become reduced, so that finally only the milk glands open on the fully formed nipples.

Didelphys marsupialis, so far as I have observed hitherto, stands alone amongst the Marsupials in possessing nipples of this kind, which may be termed "proliferation nipples" (Fig. 31, *f* and *g*).

In all the other species the nipples arise from the nipple pouches discovered by Morgan, and therefore form "eversion nipples," as we may term them (Fig. 31, *b*-*d*). In all Australian Marsupialia their development proceeds as follows: The knob-shaped primordia are con-

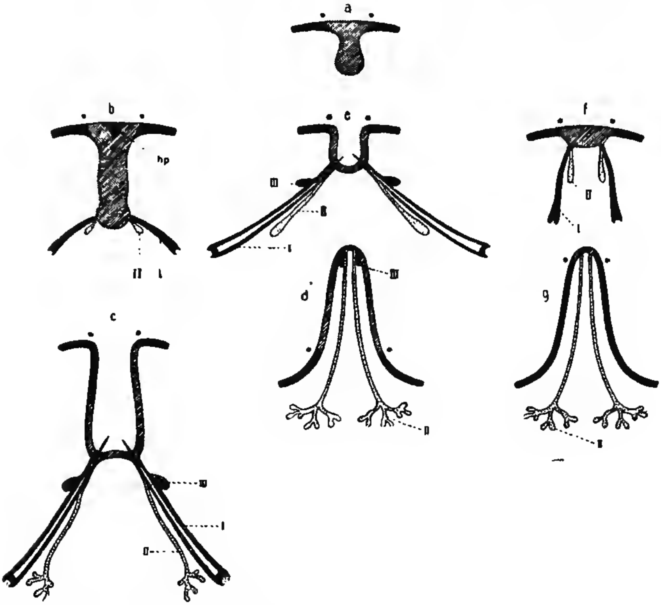


FIG. 31.—NIPPLE DEVELOPMENT OF THE MARSUPIALS. (BRESSLAU.)

I. Primary sprouts (primordia of mammary hairs).
II. Secondary sprouts which give rise to milk glands.
III. Tertiary sprouts (primordia of sebaceous glands).

a, Nipple primordium; *b*-*d*, stages of eversion nipples; *e*, transition between eversion nipples and proliferation nipples; *f*-*g*, stages of proliferation nipples.

siderably lengthened through the growth of the neck of the knob, and then, by a process of cornification, are hollowed out into nipple pouches, whilst at their bases the primordia of the mammary hairs, of the milk and sebaceous glands, appear just as in the proliferation nipples. These nipple pouches then continue for a shorter or longer time, until the final nipples appear through the eversion of the pouches. The epithelial covering of these nipples is thus for the most part furnished by the nipple pouches—that is, by the original knob-shaped primordia. The cutis wall only enters into the formation of the basal part of the nipple, if at all (Fig. 31, *b-d*).

The transition between these very distinct types of nipples (proliferation and eversion) is afforded by the conditions met with in certain Didelphyidæ—namely, the pouchless species, as, for example, *Marmosa murina*, and others. Here, in the development of the nipples (Fig. 31, *e*), the knob-shaped primordia are not reduced as in *Didelphys marsupialis*, nor are they so considerably lengthened as in the Australian forms, but are directly hollowed out into nipple pouches, characterized especially by their small size. It is evident that from this nipple type both the actual eversion nipples of the Australian Marsupials, as well as the proliferation nipples, can be derived—the one through progressive development, the other through involution of the nipple-pouch stage.

Thus, study of nipple development, like that of pouch development, leads us to the conclusion that the pouchless Didelphyidæ exhibit the most primitive conditions of the mammary apparatus in the Marsupialia. Now, Winge and Bensley, as the result of their investigations on the foot structure and teeth of the Marsupialia, have placed just those pouchless forms—namely, Marmosa and Peramys—at the very base of the marsupial series. We have here, then, quite a striking confirmation of the conclusions reached above from the evidence of the mammary apparatus alone.

If we now proceed to consider the phylogeny of the mammary organs in the Marsupialia, it is clear that we must ignore the old theory of Darwin and Gegenbaur, according to which nipples and milk glands were superadded to a previously existing pouch. For, as we have seen, the most primitive Marsupials completely lack a pouch. Moreover, in those forms where a pouch exists, it does not commence to develop until long after the appearance of the nipple primordia.*

We have therefore to start with the primary-primordia, which here, as in the Monotremes, constitute the primordia of the mammary apparatus. Here, as there, we have to trace the origin of the mammary organs to the same source—namely, to the brooding organs with which the pre-mammalian ancestors were provided.

Whilst in the Monotremes the two primary-primordia give rise only to the two gland areas, in the Marsupials they produce typically several nipple primordia—indeed, fifteen and more in the lowest Didelphyidæ. This circumstance precludes the possibility of deriving the nipple primordia directly from the gland areas, as hitherto has mostly been done. Their relation to each other becomes clear, when we remember

* In the Dasyurus, for example, the first primordia of the marsupial pockets, leading to the formation of the pouch, do not appear until fourteen days after the development of the nipple primordia, according to Professor Hill's exact statements as to the age of the young ones examined.

that the Monotremes have at most one or two young ones, but the most primitive Marsupials, on the other hand, a much greater number, ten and more.

In the Monotremes, therefore, the two gland areas sufficiently provide for the needs of the one or two young. But in forms producing a much larger number of offspring, such a simple arrangement of mammary organs was obviously not satisfactory. Accordingly we find in the Marsupialia that the primordia of the mammary apparatus, given in the original brooding organs, take another developmental course : (1) the area of the primary-primordia has become divided up into several separate parts (the nipple primordia), corresponding approximately to the number of the young ; (2) the surface of these separate primordia has become increased by way of invagination.

This last indeed happens very frequently in gland-bearing regions of the integument in numerous classes of the animal kingdom, invertebrate as well as vertebrate. Sometimes these glandular invaginations can be everted, as is the case, for example, with the so-called dorsal gland of the Peccary (*Dicotyles* *torquatus*), which is quite similar, structurally and developmentally, to the nipple-pouches.

We therefore can picture to ourselves the development of nipple primordia, nipple-pouches, and nipples from the primary-primordia without any direct reference to the gland areas. In correspondence with the higher number of young in the Marsupials, we find that here the area of the primary-primordia was utilized to the greatest possible extent. Thus we see a four-rowed arrangement of the nipple primordia in all Didelphyidæ and also in several species of the more primitive Dasyuridæ, which possess a high number of nipples. Fig. 32 shows the nipple arrangement in *Phascologale flavipes*, which would exactly correspond to the Didelphyd condition, if an unpaired central nipple were present.

The fact that the area of the original primary-primordium is divided into a number of separate nipple primordia explains why there develops in connection with each of these primordia only a relatively small number of mammary hairs and glands. In *Didelphys marsupialis* there are, for example, only eight, as already mentioned. But if we multiply that number by the number of nipples (thirteen or fifteen), we get a total which approximates to the number of mammary hairs and glands in the gland areas of the Monotremes.

A further result of this subdivision is that the relatively few milk glands in connection with each nipple, if they are to produce the amount

FIG. 32.—NIPPLE ARRANGEMENT IN "PHASCOLOGALE FLAVIPES." (BRESSLAU.)

of nourishment necessary for the young, must attain to a far higher degree of development than the mammary glands of the Monotremes. Thus we obtain a rational explanation of the remarkable diversity between the mammary glands of the Monotremes and the milk glands of the Marsupials. In my view these glands are neither so completely homologous, as many authors assume to-day, nor yet of so heterogeneous a nature as to necessitate the association of the one with the sweat glands and the other with the sebaceous glands as Gegenbaur asserted. Both represent rather two forms of development from an indifferent type of skin gland, from which also are derived the sweat glands.

The fact that the mammary hairs, unlike those of the Monotremes, have only a temporary existence is no doubt connected with the formation of the nipples. Whilst these hairs in the Monotremes probably serve as paths for the conveyance of the mammary secretion, there can be no question of such a function in the Marsupialia. Indeed, it is obvious that their existence on the adult nipple would be none other than a nuisance. As a matter of fact they are always shed early, usually before the eversion of the nipple pouches. It is only in the Phascolarctidæ and perhaps also in the Phalangeridæ, where the eversion of the nipple pouches is very precocious, that it is possible for the mammary hairs to occur for a short time at the apex of the nipple, as may be seen in Fig. 33. This figure represents the pouch opened up, and shows clearly the remains of the marsupial pockets and the nipples, which have just emerged from their pouches, each carrying on its tip a pencil-like tuft of mammary hairs.

Primary-primordia, nipple primordia, nipple pouches with their appertaining hair and gland buds, and finally the nipples—this is the order of developmental succession of the mammary organs in the lowest pouchless Didelphyidæ. In the higher forms we find, in addition, the marsupium. How, then, is the appearance of this organ to be explained ?

FIG. 33.—NIPPLE OF PHASCOLARCTOS, SHOWING MAMMARY HAIRS.

In order to answer this question we must bear in mind that even in the pouchless

Didelphyidæ the young ones are carried about by the mother attached to the nipples, as is shown in Owen's figure of a female *Marmosa murina* (Fig. 34). Such an arrangement is obviously very primitive, and any variation which tended towards fixing the young more

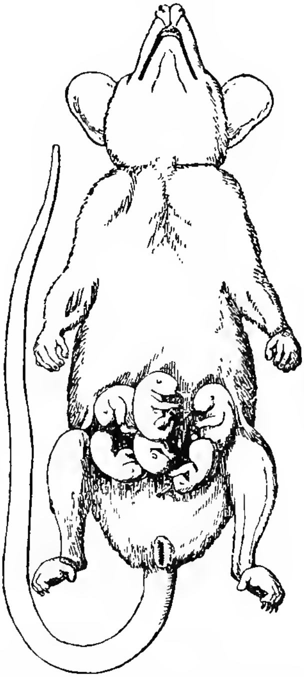


FIG. 34.—FEMALE "MARMOSA MURINA," WITH YOUNG ONES ATTACHED TO THE NIPPLES. (OWEN.)

securely would be preserved, even though at first it had nothing to do with a pouch. It would suffice if folds were to appear in the neighbourhood of the individual nipples, which afforded additional support to the young by clasping round their snouts. In this way we can picture to ourselves the beginning of the marsupial pockets. Indeed, I have observed in some cases—for instance, in the female Sminthopsis, already referred to—how by means of such folds the head of the young one is more firmly fixed to the mother's abdomen (Fig. 35).

FIG. 35.—YOUNG OF SMINTHOPSIS ATTACHED BY POUCH. (BRESSLAU.)

The acquisition of such marsupial pockets, however, was not necessarily followed by the evolution of the marsupium. If the nipples were widely distributed—as is, for example, the case in the genus Peramys—the marsupial pockets, even if they have already appeared here, remain isolated. If, on the other hand, the nipples are so close together that the walls of the surrounding marsupial pockets come into contact, the possibility arises for the fusion of their lateral parts to form the folds of the marsupium. From the lateral pouch folds so arising it is quite easy to derive the different types of the pouch by variations in their mode of union.

In the fusion of the lateral walls of the marsupial pockets into the pouch folds, the pockets themselves did not necessarily cease to exist. They mostly do so by flattening out, with resulting increase of the marsupial area, as we have seen in *Didelphys marsupialis*. But in other cases they have persisted perhaps because they aided in the fixation of the young.

Such, then, is my idea of the phylogeny of the mammary apparatus in the Marsupialia—certainly a very different one from that put forward by Gegenbaur and Klaatsch. I am well aware that my views in respect of certain details still require confirmation. It is above all necessary to obtain further material for the study of the ontogeny of the mammary apparatus in the pouchless Didelphyidæ. If, as the result of such study, my views here and there may require modification, I nevertheless hope that in the main they will prove to be correct.

CHAPTER III

WE come now to the discussion of the organization of the mammary apparatus in the highest order of Mammals—namely, the Placentalia (Monodelphia, Eutheria). Its relations are here very materially influenced by the fact that owing to the lengthening of the intra-uterine period of development the young are born in a far more advanced state than in the Marsupialia. In correlation therewith marsupial pockets and marsupium are absent, and the mammary apparatus consists solely of the nipples and milk glands, the latter being quite similar to those of the Marsupials.

The number and likewise the arrangement of the nipples in the Placentalia varies still more considerably than in the Marsupialia. The maximum number of nipples—namely, twenty-two—reached by the primitive insectivore *Centetes ecaudatus* parallels that met with amongst the Marsupialia in the genera Peramys and Marmosa, but unpaired nipples and the four-rowed arrangement are never met with. Very frequently the nipples are arranged in single rows all along the abdomen, from the axilla to the inguinal region—as, for example, in the pig and the dog. In many cases the middle region of the abdomen is free from nipples, as in *Mus musculus*, where there are three pairs of nipples on the breast, and two pairs in the inguinal region. Often only the caudal parts of the nipple rows are developed, most conspicuously in the ruminants and the Perissodactyls, where the nipples of the right and left sides are situated together on the so-called udders. On the other hand, the nipples are often found only on the breast, as, for instance, in man, the anthropoid and catarrhine monkeys and also in elephants, many of the Edentata, bats, etc. The nipples of many South American rodents are very singularly placed, those, for instance, of the Coypu (Myopotamus), Viscacha (Lagostomus), and Chinchilla, being situated a little above a line drawn between the origins of the fore and hind limbs (Fig. 36). In the hippopotamus the nipples occupy a similar dorso-lateral position, and it is asserted that the young, sitting on the back of the swimming mothers, can in this way get their food in comfort.

Further, it has long been remarked that there is not always a constant number of nipples in individuals of the same species. In many species the number of nipples has a wide range of variation—for example, in the pig, where they vary between eight and eighteen, 30-40 per cent. possessing twelve. This phenomenon, which is also observable in some of the lower Didelphyidæ, I have termed

Fig. 36.—Dorso-Lateral Arrangement of Nipples as in Myopotamus Sp. (Embryo).

Eurythely. But even in forms where the number is normally constant (Stenothely), sometimes accessory nipples or mammæ are found. It is a well-known fact that these anomalies, which are usually called cases of hyperthely or hypermasty (polythely or polymasty) also occur in a percentage of human beings. The most detailed statistics we have on this subject relate to the Japanese, and show that 1½ per cent. in males and about 5 per cent. in females possess accessory nipples. We have so far no exact statistics relating to Europeans, but in any case the percentage would appear to be lower.

All these diverse conditions in number and arrangement of nipples in the Placentalia received, twenty years ago, an explanation, which, in its essentials, we can still accept. This explanation is based upon the fundamental discovery of O. Schultze in 1892, that the development of the mammary apparatus of the Placentals begins with the appearance of the so-called "milk-line," which in early embryos is distinctly recognizable macroscopically as an epidermal ridge extending on each side along the lateral aspect of the trunk, from the axilla to the inguinal region (Fig. 37A). Very soon there appear along this milk-line a series of small swellings ("Milchhügel"), the first primordia of the individual nipples (Fig. 37B). These next become completely separated from each other by the gradual disappearance of the connecting parts of the milk-line (Fig. 37C). At the same time the nipple primordia become transformed into lens-shaped thickenings projecting into the cutis, and these finally assume the characteristic knob-shaped form.

Milk-lines not only occur where the nipples in the adult extend over the whole length of the trunk, but also where they are limited to a restricted region. Accordingly the conclusion is justified that originally the Placentalia possessed an elongated row of nipples on either side, and that all deviations from this arrangement are due to processes of reduction. Thus the accessory milk organs could be explained as atavistic structures inherited from ancestors provided with a greater number of nipples and milk glands. This explanation of the phenomena of hyperthely and hypermasty has completely displaced those older views, according to which the accessory nipples were

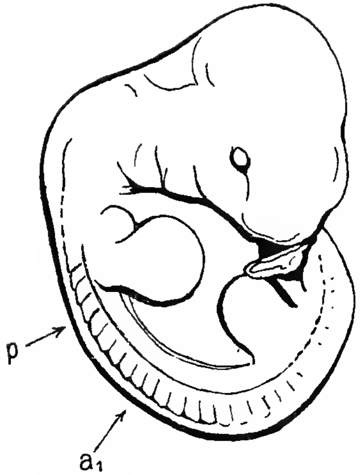


Fig. 37a.—Embryo No. 1.

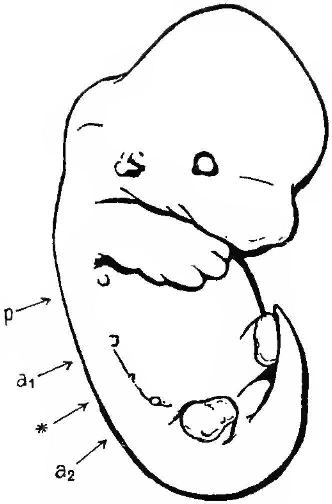


Fig. 37b.—Embryo No. 2.

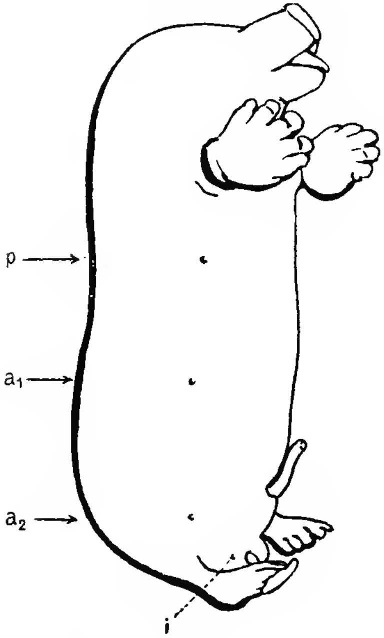


Fig. 37c.—Embryo No. 5.

Figs. 37a, 37b, and 37c.—"Talpa europæa." (Bresslau.)

p, Pectoral primary-primordium; a_1, first abdominal primary-primordium; a_2, second abdominal primary-primordium; *i*, inguinal primary-primordium; *, surplus primordia.

Fig. 37a shows the so-called "milk-line" from axilla to inguinal region.

Fig. 37b shows the appearance of primary-primordia of individual nipples.

Fig. 37c shows separation of nipples by disappearance of "milk-line."

regarded as pathological formations, resulting from the dismemberment of milk ducts, or from the displacement or splitting or doubling of the primordia of the mammæ.

But much as the discovery of the milk-line contributed to an increased understanding of the mammary apparatus of the Placentals themselves, it introduced at the same time a great difficulty from the point of view of phylogeny. For now, naturally, arose the question, What is the meaning of the milk-line ? Hitherto all attempts to answer this question have proved unsatisfactory. It is obvious that it is not possible to trace back the milk-line to the lateral line of fishes or Urodela, and to the glandular structures connected therewith, and Wiedersheim, though he at one time accepted this idea, following O. Schultze, soon dropped it. Klaatsch and I met with just as little success in attempting to discover the starting-point of the milk-line in Marsupials. Klaatsch believed he could explain the milk-lines as rudiments of the pouch folds. He started from the supposition, which we now know to be false, that the marsupium arose through the fusion of the nipple or mammary pouches.

Naturally the conclusion drawn from this false supposition was untenable. I then suggested the derivation of the milk-line from the fusion of the marsupial pockets, such fusion producing in certain species solid epidermal ridges, as, for example, is the case in Myrmecobius. But this supposition could not be correct, because the marsupial pockets (the suggested milk-lines) succeed, in point of time, the nipple primordia, whilst in the Placentals just the reverse holds true, the milk lines appearing before the nipple primordia.

The difficulty of tracing any homologue of the milk-line led other workers to do away with the problem altogether, by simply denying to the milk-line any phylogenetic significance at all. Thus Beard, in 1898, explained the milk-line as a mere "developmental structure, which, first appearing as a distinct line or ridge, afterwards becomes broken up into a number of separate entities." Shortly afterwards Profé, and more recently Brouha and Pinkus, following Beard's suggestion, placed the milk-line in the same category with the neural crest and the dental lamina and other transitory epithelial ridges only met with during embryonal development.

The genesis of these ridges was, according to Profé, the result of an endeavour of the organism to lay down in advance, by a single process of differentiation, the material for the formation of a series of homologous organs. This developmental principle, he believed, was of special importance just in the formation of the mammary apparatus, because the ridge-like form of the milk-line would prevent the displacement of the nipples, the arrangement of which in rows he regarded as necessary for the preservation of the young, and therefore of the species.

This reasoning certainly sounds somewhat plausible, but it will not hold. First of all it is unintelligible how the arrangement of the nipples in exact rows can tend to the preservation of the young, especially in view of the fact that in the Marsupials practically all possible arrangements occur from the serial to the apparently completely circular. Further, if the above-mentioned principle of development, which, according to Profé, is so important for the mammary apparatus, possessed any actual value, its working should be observable in those marsupials furnished with rows of nipples. In other words, we should expect to find in these forms milk-lines. But this is not the case, as we know.

We have seen, however, in the foregoing chapter, that there are *other* formations in the Marsupials—namely, the primary-primordia, which represent the common starting-point for the differentiation of the nipples on either side of the body.

The recognition of this fact reveals to us a noteworthy parallelism between the first processes in the development of the mammary apparatus of the Marsupials and Placentals, and leads us at once to consider whether the milk-lines of the Placentals do not correspond to the primary-primordia of the Marsupials, and whether such a comparison might not afford the basis for a new explanation of the nature of the milk-lines?

This question, however, is not so easily solved. For comparison of the primary-primordia and the milk-lines is confronted by the difficulty that the two formations are so different in appearance. In face of this morphological diversity we are not justified in at once homologizing them.

The difficulty here indicated directs our attention to a fact which, although known more than fifteen years, has so far been entirely left out of account in the discussions as to the significance of the milk-line. And that is the fact that the milk-lines in no wise represent the first primordia of the mammary apparatus of the Placentals, but, as numerous investigators have shown, are differentiated secondarily from other formations, usually called "milk-streaks" (Fig. 38). These milk-streaks appear in early embryos in the region of the later milk-lines as two comparatively broad zones of the integument, characterized by higher epithelium and by a condensation of the mesenchyme cells of the cutis, penetrated by numerous capillaries. It is not till later that the central region of each streak becomes elevated to form the milk-line, while the rest of it disappears. This being ascertained, two conclusions follow: First, it follows that those investigators were in the wrong who, like Beard, Profé, and others, compared the milk-lines with formations such as the neural crest and the dental lamina, which actually represent nothing but developmental structures, and which are not preceded by any primordia corresponding to the milk-streak. Secondly, it follows that when we trace back the mammary apparatus of the Placentals, we have to compare the primary-primordia, not with the milk-lines, but with the milk-streaks. And indeed this comparison presents no difficulty.

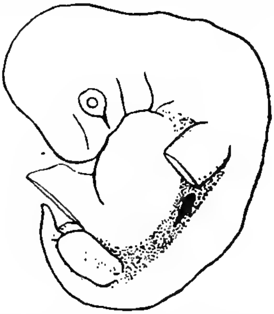


FIG. 38.—HUMAN EMBRYO, SHOWING "MILK-STREAK" AND CENTRAL REGION BECOMING ELEVATED TO FORM "MILK-LINE." (SCHMITT.)

11·5 mm.

It is clear, then, from the above statements that the primary-primordia and the milk-streaks are entirely similar in structure. In both formations we recognize (1) an area of thickened epidermis; (2) an underlying zone of condensed and richly vascularized cutis. Topographically, also, both harmonize fully.

We have seen that in the Monotremes as well as in the Marsupials, the primary-primordia originate in a dorso-lateral position, and that with the disappearance of the membrana reuniens inferior they shift towards each other in a medio-ventral direction to take up their final abdominal position. Exactly the same ventral shifting is shown by the milk-streaks and milk-lines of the Placentalia. Further, in all three orders of Mammals, the skin-muscle plate of the early embryo reaches invariably as far as the cutis thickenings below the first primordia of the mammary apparatus, whether they be primary-primordia or milk-streaks.

It is true that in Echidna and in those marsupial species investigated so far, the primary-primordia form areas of quite small extent, situated on the caudal part of the abdomen, and only 3-5 times longer than broad. The milk-streaks, on the other hand, typically extend over the whole length of the trunk. But that is doubtless only a difference of secondary importance, and may be due to the great forward extension of the nipple rows in the Placentals. Occasionally, however, in forms where this extension of the nipple rows does not exist, conditions are observable which are very similar to those in the Marsupials, as, for instance, in the Ungulates, whose milk streaks and lines do not reach cranially beyond the region of the navel. On the other hand, it is not impossible that the primary-primordia of those species of Peramys and Marmosa amongst the Marsupials, having long rows of nipples, may be found to be similar, as regards their extension, to the milk-streaks of the Placentalia.

The importance which hitherto has been attached to the milk-lines in discussions concerning the genesis of the mammary apparatus must now accordingly be transferred to the milk-streaks. The milk-lines are merely secondary, ridge-like differentiations within the milk-streaks, for the understanding of which this fact is perhaps of importance—namely, that the disposition to form such ridge-like structures already exists within the primary-primordia of Echidna and the Marsupials.

It now becomes clear that in all three orders of Mammals, the first indifferent primordia of the mammary apparatus, from which the later milk organs spring, are homologous—that is, the primary-primordia of the Monotremes and Marsupials, and the milk-streaks of the Placentals. In the milk-streaks of the Placentalia, therefore, we have preserved a last reminiscence of the primitive brooding organs, which formed the basis of the development of the mammary apparatus.

If, then, the milk-streaks are homologous with the primary-primordia of the Marsupials, it is not astonishing that the milk organs derived from them should show essentially the same development in the two orders. Accordingly we find in both, nipples and milk glands so similarly constructed, that—even without any knowledge of the original primordium common to both—one would have assumed that genetically they were nearly related. As a matter of fact, the older authors all agreed in regarding the milk organs of the Marsupials and Placentals as identical formations.

But when Gegenbaur and his school took up the investigation of this subject, especially the study of the relations of the nipples in the different orders of Placentals, they came to quite another conclusion. They maintained that it was necessary to distinguish at least four types of nipples among the Placentals, each of which was regarded as having arisen independently of the others out of the conditions existing in the different stages of the development of the eversion nipples of the Marsupials.

Gegenbaur and Klaatsch thought they could find the nearest link to the Marsupials in the Muridæ amongst the Rodents, which possess deep sheaths, in which the nipples are for a long time enclosed, and from which they only emerge when the period of lactation begins (Fig. 39). These sheaths, therefore, were regarded as being derived from knob-shaped primordia surrounded by a cutis wall, just like the nipple pouches in the kangaroo, and it was held that the nipples arose in a similar way as there through eversion. In a second type, represented in the Prosimiæ and Primates, including man, a nipple pouch, somewhat shallower, was also said to develop in the same way. But this pouch only partially became raised to a nipple, whilst the rest of it, adjacent to the original cutis wall, remained as the so-called areola mammæ. The nipples of the Carnivora represent a third type, the nipple pouch here being early reduced, and forming only the tip of the nipple. The greater part of the latter was held to be formed by the cutis wall. Finally, a fourth type of nipple was said to be characteristic of the Ruminants. Here the nipple pouches were regarded as persisting in their original condition without eversion or reduction—as so-called "Strichkanäle"—in the interior of the nipples, here derived exclusively from the cutis wall.

It is evident at once, assuming these views to be correct, that the nipples of the Placentalia, in spite of their external similarity, must represent totally heterogeneous formations, which could only have sprung from the nipples of the Marsupials along different lines. The mammary pouch of Echidna was to have served "as a common starting-point, as a condition of perfect indifference" (Klaatsch, 1884, p. 378).

We see here, again, how much the unfortunate mammary-pouch theory has influenced the views of the scientific world. For, in spite of the fact that the observations of Gegenbaur and his pupils have repeatedly been shown to be incorrect, we still find these views reproduced in almost all textbooks of zoology and comparative anatomy at the present time. In particular, it is constantly repeated (*cf.*, for example, Wiedersheim) that the nipples of the Ruminants are pseudo-nipples, fundamentally

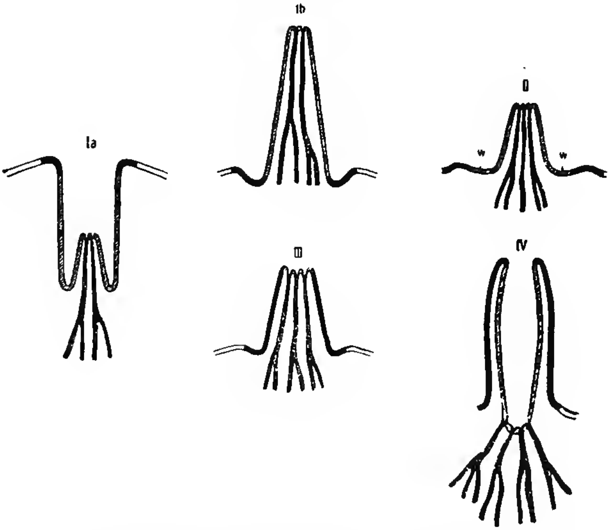


FIG. 39.—NIPPLE DEVELOPMENT OF PLACENTALS. (GEGENBAUR AND KLAATSCH.)

I*a*. } In the Rodents (Muridæ).
1*b*. }
II. In the Prosiniæ and Primates.
III. In the Carnivora.
IV. In the Ruminants.

w, Areola mammæ.

distinct from the true nipples of the rest of the Mammals.

But this part also of the Gegenbaur-Klaatsch theory is based on premises entirely false. For, quite apart from the fact of the non-existence of the mammary pouches, there are no such fundamental differences between the nipples of the different groups of Placentals as Gegenbaur and his followers assumed on the strength of insufficient embryological investigations. The various types of nipples of the Placentals are rather to be regarded, in spite of differences in detail, as further developments of a single type of nipple, which was peculiar to the common ancestors of the Marsupials and Placentals.

I propose now to substantiate this view with the help of the accompanying semi-diagrammatic figures (Fig. 40).

We have already traced the development of the nipples of the Placentalia to the stage of the knob-shaped primordia, which stage is equally characteristic of the nipple primordia of Marsupials. But whereas in the Marsupials, with the exception of the Didelphyidæ, the knob-shaped primordia go on growing, this is

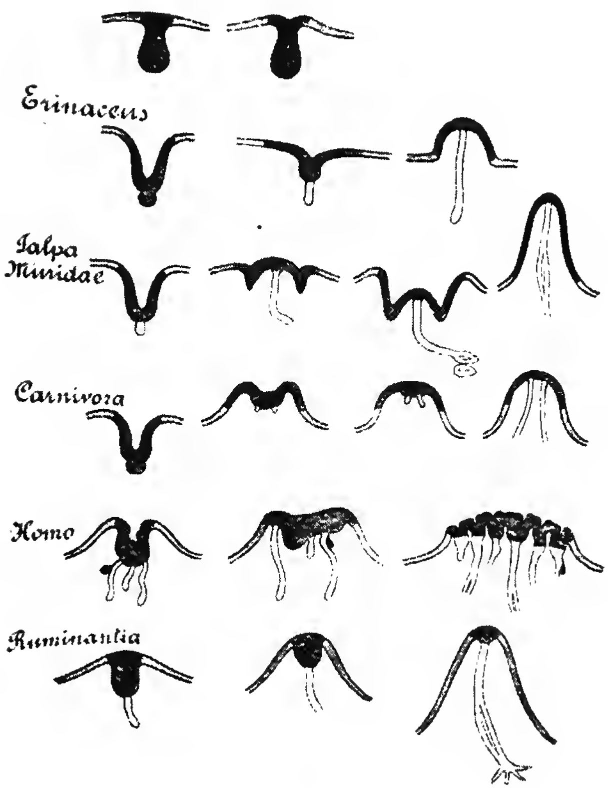


FIG. 40.—NIPPLE DEVELOPMENT OF PLACENTALS.

×, Knob-shaped primordia common to Marsupials and Placentals.

never the case in the Placentalia. Here an involution of the knob-shaped primordium begins, which is marked by the appearance of a shallow depression upon its surface. This is of constant occurrence, and indicates the transformation of the primordia into nipple pouches, even where these pouches do not develop further, as is the case in Ruminants.

If, now, we turn to consider the details of nipple development in certain of the Placentalia, we find in the hedgehog that the knob-shaped primordia become hollowed out into real nipple pouches. These are then everted before the end of embryonic development in such a way that they flatten out on the surface. At the same time there arises in the centre of each a little papilla, which here, as in many other forms, gives origin only to one gland bud. This papilla grows further, and so produces the nipple, the epithelial investment of which is essentially derived from the original nipple pouch, even though the cutis wall may participate in the formation of its basal part.

Very similar conditions are found in the Muridæ and in the mole, where at first a nipple pouch likewise originates. But with eversion, the further development takes a different course. After the elevation of the papilla there arises around it and within the limits of the area of the original nipple pouch a solid circular fold, which becomes hollowed out shortly after birth, and so forms the secondary nipple sheath. Into this the papilla, until now situated on the surface, withdraws, and does not emerge until the approach of the lactation period, when it forms the definitive nipple. Thus these nipple sheaths are by no means identical with the nipple pouches of the Marsupials, which originate by the direct hollowing out of the knob-shaped primordia.

The homologues of the marsupial nipple pouches are here only observable in the first stages of development, and disappear very quickly, just as in the case of the hedgehog. If, then, after birth, the nipple sheaths arise, it is clear that they are secondary formations. Indeed, consideration of the mode of life of the mole and the Muridæ suggests a very simple explanation of the acquisition of such organs. In these small burrowing animals freely projecting nipples would be liable to injury, and the nipple sheaths therefore may be regarded as of the nature of an adaptive device.

The conditions in the Carnivora, too, are easily connected with the type of nipple development observable in the hedgehog. The knob-shaped primordium is here likewise hollowed out into a nipple pouch, and then everted to a little nipple, only the eversion proceeds somewhat differently. First of all, the part of the nipple pouch adjoining the cutis wall evaginates, whilst the bottom remains unaltered. At the same time the cutis wall begins to grow up, and in consequence there arises a nipple elevation, on the tip of which the remnant of the nipple pouch forms a small groove, from which the milk-gland buds spring. This groove later disappears through the completion of the eversion process. In this way already during embryonic life the nipple attains its final form, with the separate milk ducts opening on its apex. It is formed chiefly from the nipple pouch; its basal section is, however, produced by the cutis wall.

If we now proceed to consider the nipple development in the human subject, on which we have obtained reliable information in recent times, especially through Brouha (1907), we find here an important divergence from the previously discussed types, inasmuch as the knob-shaped primordia are no longer transformed into regular nipple pouches, but are only more or less imperfectly hollowed out. Then, after the milk-gland buds have appeared at their bases, they gradually become shallower, in order to form the surface of the nipple, whilst the elevation of the nipple is entirely due to the cutis wall. As regards other forms of nipple development in Placentals, it need only be said that we can recognize a series of types in which the knob-shaped primordia contribute less and less to the formation of the nipple surface, and the cutis wall more and more. These types culminate with the nipples of the Ruminants. Here the knob-shaped primordia, except for the primary depression, do not hollow out, and the entire nipple is produced exclusively by the cutis wall. The knob-shaped primordium gives origin to a single milk-gland bud, and then gradually becomes reduced during the elevation of the nipple. It persists only on the tip of the nipple as the minute area on which the milk duct opens. These facts are quite easily observable, as I myself, as well as a number of recent observers, have ascertained. It is thus inconceivable how the old erroneous views can be repeated again and again in all textbooks.

It is therefore evident that three out of the four types of nipples recognized by Gegenbaur and Klaatsch are to be interpreted in an entirely different manner. In the Carnivora alone did they correctly maintain that the original nipple pouch is completely absorbed in the development of the later nipple. In all other forms they made the mistake of deriving from the nipple pouches not only the nipples but also accessory formations, such as the secondary nipple sheath in the Muridæ, the areola mammæ in man, and the so-called "Strichkanal" in Ruminants. There can be no question of all this as we have seen. The secondary nipple sheaths of mice and of the mole are not the permanent nipple pouches, but are undoubtedly *new* formations. The areola mammæ of man, and certainly also of the rest of Primates, has nothing to do with the nipple pouch, but merely represents a specially differentiated part of the cutis wall around the mammilla, such as is similarly found in numerous other Mammals, particularly in Rodentia and Carnivora. The "Strichkanal" of the Ruminants is really nothing but a milk duct, whose strong development is entirely due to compensatory growth.

Taking into consideration the relative size of the adult animals, we find exactly the same condition in the Insectivora and Muridæ, where there is also only a single milk duct.

Thus the fundamental differences, postulated by Gegenbaur and Klaatsch between their four types of placental nipple, do not exist. In all the Placentalia the nipple develops just as in the Marsupials, through the co-operation of nipple pouch and cutis wall ; only these two factors participate in a more or less varying degree in the different types. According as the nipple pouch or the cutis wall takes the greater share in nipple formation nipples result belonging to either the eversion or the proliferation type. But these types cannot be sharply contrasted, since there is a whole series of connecting stages between them.

If, on the strength of these facts, an inquiry is made as to the mutual relations of the marsupial and placental nipples, the answer is plain—namely, that the proliferation or the eversion nipples of the latter are not to be derived directly from the corresponding nipple forms of the former. On the contrary, all the evidence points to the fact that the different nipple forms have developed independently in the series of the Placentalia, and from such a condition as is seen in the hedgehog or the Carnivora. Here, indeed, we have essentially the same type of nipple as is observable in *Marmosa murina* amongst the Marsupials. This simple type of eversion nipple represents, then, the original nipple form as it arose in the Metatheria, and constitutes, therefore, the common point of departure for the phylogenetic development of the marsupial as well as of the placental nipples.

If then the nipples of the marsupials and Placentals have had a common origin, it is not astonishing that the milk glands in both orders should also completely harmonize with each other. Ontogenetically we have obtained in recent years especially clear evidence of this homology through the proof that in some Placentals (horse, ass, cat, man) the milk-gland buds arise in connection with rudimentary primordia of mammary hairs and sebaceous glands. The milk glands of the Placentalia thus belong, like those of the Marsupials, to the sweat-gland type. As regards the mammary hairs, it may be mentioned that whilst these in the Marsupials attain complete development, in the Placentals they never advance beyond the first stages of development. The process of retrograde development indicated in the Marsupials by the premature shedding of the mammary hairs has in this case proceeded much farther.

Curiously enough, there is an exception to this statement, which is interesting also for other reasons. This is the case of the squirrel, whose nipple development we may now consider (Figs. 41-45).

In the literature of the last twenty years the statement has recurred that the squirrel possesses double nipple rows on each side, and it has been supposed that these arose from double milk lines. That seemed to me improbable, and so I have recently looked into this question. As I had expected, the older supposition proved to be incorrect. Only a single milk line is developed on either side of the body, which extends from the axilla to the inguinal region (Fig. 41). In its pectoral region a nipple primordium (*p*) has already been differentiated, and a little behind, the first abdominal primordium is appearing. In somewhat older embryos, where the nipple primordia are completely developed but still connected together (Fig. 42), the pectoral primordium (*p*) is seen to be prolonged medioventrally. Shortly afterwards it divides into two primordia—a smaller medial and a larger lateral one (Fig. 43, *p*). But before this division is completed, the first abdominal primordium begins to follow suit (Fig. 43, *a*). Further, supernumerary primordia

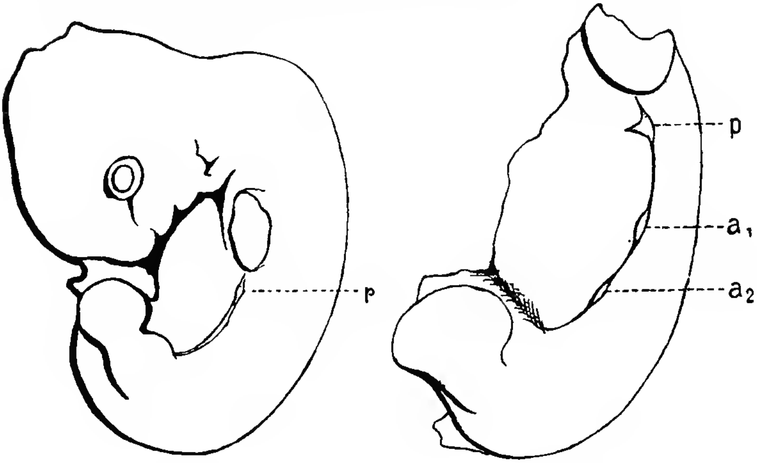


Fig. 41. Fig. 42.

Figs. 41 and 42.—Nipple Development of "Sciurus vulgaris," showing Milk-Line. (Bresslau.)

p, Primary-primordium of pectoral nipple; a_1, primary-primordium of first abdominal nipple; a_2, primary-primordium of second abdominal nipple.

are often developed, which always originate between the pectoral and the first abdominal primordia (Fig. 43, *). Finally, when fission is ended, the smaller shift more and more in a medioventral direction away from the larger ones (Fig. 44).

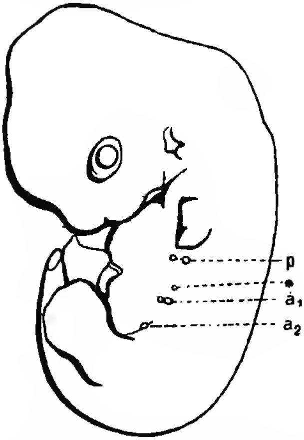


FIG. 43.—NIPPLE DEVELOPMENT OF "SCIURUS VULGARIS."

p, Primary-primordium of pectoral nipple ; *, primary-primordium of supernumerary ; a_1, primary-primordium of first abdominal nipple ; a_2, primary-primordium of second abdominal nipple.

One understands from this how the view arose that in the squirrel double nipple rows exist. It must be noted, however, that the two caudal pairs of nipples are not doubled.

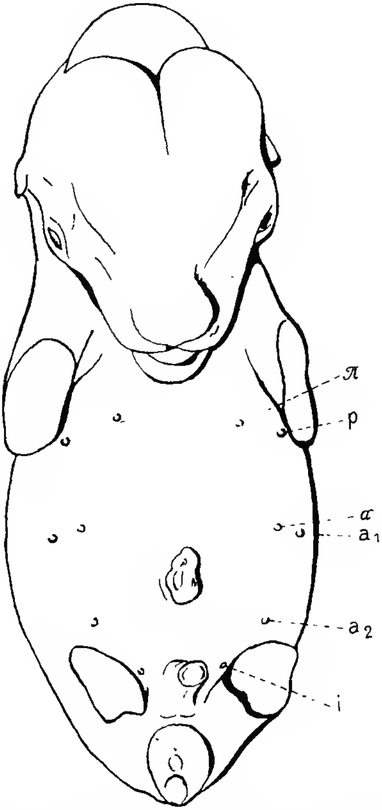


Fig. 44.—Nipple Development of "Sciurus vulgaris." Embryo, No. 7. (Bresslau.)

p, a_1, a_2, and i, The four primary-primordia; π and a, smaller pectoral and abdominal primary-primordia separated from larger primordia and shifted medio-ventrally.

Moreover, the doubling of the two anterior pairs is only apparent. If we examine sections

Fig. 45a.

Fig. 45b.

Fig. 45c.

Figs. 45a, 45b, and 45c.—"Sciurus vulgaris." Transverse Sections (Diagrammatic) showing Successive Stages of Nipple Development. (Bresslau.)

π, Smaller pectoral nipple primordia shifting medio-ventrally from *p*, primary-primordia pectoral.

Fig. 45b shows separation of pectorsl nipple primordia at a later stage.
Fig. 45c shows a still later stage with *p*, the larger pectoral nipple primordium, and π, the smaller, as elongated epithelial cylinder growing into cutis.

of successive stages (Figs. 45a, 45b, and 45c), we see that at first the smaller primordia π and *a* separate from the larger ones *p* and *a*, and gradually shift ventrally. But whereas *p* and *a* at once develop into typical knob-shaped primordia, *π* and *α* behave quite differently. These, in fact, become elongated epithelial cylinders growing into the cutis, and gradually assume the form of well-marked hair primordia, connected with special nerves and bloodvessels.

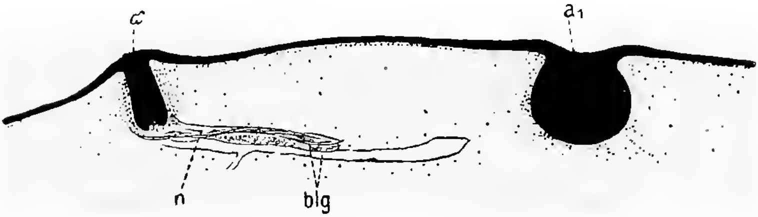


FIG. 45D.—NIPPLE DEVELOPMENT OF "SCIURUS VULGARIS." EMBRYO NO. 6. TRANSVERSE SECTION (DIAGRAMMATIC) THROUGH THE PRIMORDIA.

a_1 and *α*, First abdominal and smaller abdominal primary nipple primordia; *blg*, bloodvessel; *n*, nerve.

Thus each of these primordia produces a strong vibrissa (Fig. 46). Such vibrissæ are of course well known on the head and the extremities, but here in the squirrel we find them also on the abdomen to the number of at least four in correspondence with their origin from the two anterior pairs of nipple primordia. Further it is extremely interesting that the accessory primordia, which sometimes occur on the right or left or both sides, also give origin to vibrissæ and not to nipples. The number of

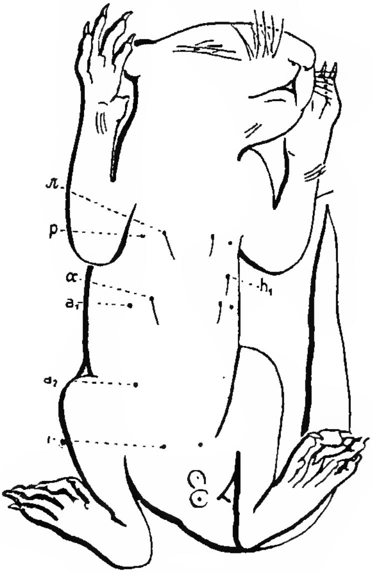


FIG. 46.—NIPPLE DEVELOPMENT OF SQUIRREL. (BRESSLAU.)

p, a_1, a_2, and *i*, Primary-primordia of pectoral, first and second abdominal and inguinal nipples; *h*, accessory nipple primary-primordium with vibrissæ; π, α, corresponding hair primordia with vibrissæ.

ventral vibrissæ varies, therefore, from four to six (Fig. 46). The number of these vibrissæ is still larger in some of the exotic squirrels, so, for instance, in the Ceylon Giant Squirrel (*Ratufa macrura*), where sixteen vibrissæ in two rows extend from the navel region forwards over the whole chest (Fig. 47). The striking feature here is that in connection with the prolific production of vibrissæ the pectoral pair of nipples has been lost, and that thus a part of the milk-line system has failed in its original purpose of producing nipples and milk glands. As regards the function of these hairs they are without doubt of use to the squirrel in connection with its arboreal habits, since from their position they come directly into contact with the surfaces of the branch, along which it moves in such characteristically rapid fashion.

It would be quite unintelligible that such vibrissæ could spring from the nipple primordia if we did not know, from the phylogenesis of the mammary apparatus, of the close relations between hair and milk glands, traces of which we have already recognized as occurring in the Placentalia. Normally here the nipple primordia produce only vestiges of mammary hairs, but in the accessory primordia of the squirrel, the otherwise latent capacity of producing mammary hairs comes into action, whilst in compensation there is a cessation of the development of the milk glands. As the result of the disappearance of the latter and the consequent freeing of their vascular supply, the mammary hairs would

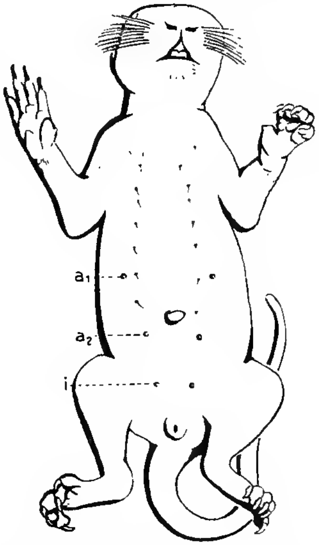


FIG. 47.—"RATUFA MACRURA," SHOWING SIXTEEN VIBRISSÆ. (BRESSLAU.)

a_1, First abdominal nipple primary-primordium; a_2, second abdominal nipple primary-primordium; *i*, inguinal nipple primary-primordium.

appear to be enabled to develop further into vibrissæ.

In another respect, too, these conditions in the squirrel are of some theoretical interest—namely, in so far as they throw a new light on certain cases of hyperthely. I have already pointed out that since the discovery of the milk-line, the usual explanation of accessory nipples or milk glands as dismembered parts of the mammæ has been abandoned, and instead, all these formations have been regarded as atavistic formations.

Now we see that we are not justified in generalizing so widely. For if in the squirrel parts of the nipple primordia may separate and shift to parts of the body comparatively distant from their origin, it is not impossible for a similar process to happen occasionally in other species. And so in some cases of accessory mammæ in the human being, distinguished by their abnormal position, it is certainly simpler to accept this explanation than the makeshift suppositions of the atavistic interpretation.

Returning to our special subject, on the strength of the proof of the homology of primary-primordia and milk-streaks and the close affinity subsisting between the nipples and milk glands of the Marsupials and the Placentals, we can now clearly picture to ourselves the phylogenetic processes which led to the origin of the mammary apparatus in the Placentalia. We have to start with forms which, like the primitive Didelphyidæ, possessed simple eversion nipples and milk glands developed on the basis of the former brooding organs. These nipples and milk glands could be directly taken over by the first Placentals, whilst owing to the prolongation of the intra-uterine period of development, formations like the incubatorium or marsupium were not needed. Only trifling changes took place, such as the entirely retrograde development of the mammary hairs, and variations in the details of nipple formation, and finally the establishment of a nipple-row arrangement.

The entire course of the phylogeny seems perfectly plain and straightforward, and might, in consequence of its simplicity, have been recognized long ago ! But here again the unfortunate supposition that the marsupium or the non-existent mammary pouches were the oldest organs of the mammary apparatus stood in the way. For it had to be assumed that the Placentalia were derived from pouch-bearing forms, naturally with loss of the marsupium.

And so we have an explanation of the fact that investigators have always been on the lookout for pouch rudiments in the Placentalia, and have accordingly easily believed in the discovery of a whole series of such. It is not necessary, however, to waste time over these assumed pouch rudiments, for we know that such cannot exist, since a pouch stage was not included in the phylogenesis of the Placentalia.

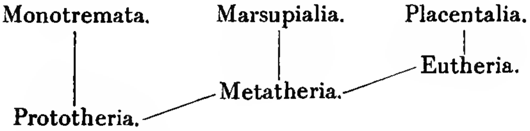
In conclusion, it remains for us to discuss the affinities of the three sub-classes of the Mammals, on the basis of our knowledge of the development of the mammary apparatus. But in so doing we shall not neglect the phylogenetic facts resulting from the study of the entire organization of the Mammals. This is the more necessary, since disregard of such an obvious principle has often led to the construction of erroneous phylogenetic theories. We have indeed an excellent example in the case of the mammary-pouch theory. For, assuming that the mammary organs of the Marsupials were directly derived from those of the Monotremes (especially Echidna), and, again, that the mammary organs of the Placentals came immediately from those of the Marsupials, it followed that these orders must have succeeded each other in a linear fashion :

Placentalia.
↑
Marsupialia.
↑
Monotremata.

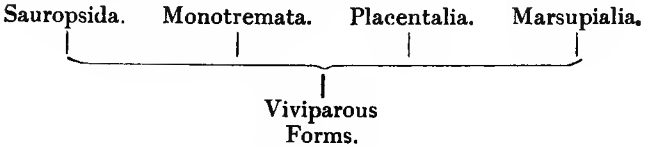
But the possibility of such a genealogical tree has for more than thirty years been raised beyond all discussion, as Huxley showed in his famous essay, "On the Application of the Laws of Evolution to the Arrangement of the Vertebrata and more particularly of the Mammalia" (1880).

Since that time three contrasting views as to the phylogeny of the Mammals have been put forward.

Huxley himself founded the first of these views by postulating the existence of three hypothetical stages in Mammalian evolution, which he termed the Prototheria, Metatheria, and Eutheria. He regarded these as succeeding each other in time and as having given origin to the Monotremata, Marsupialia, and Placentalia as three great collateral branches :



On the other hand, Dollo and others, on the basis of Hill's brilliant discovery of a placenta in Perameles, tried to derive Marsupials from Placental ancestors, so that in the above genealogical tree the Marsupialia and Placentalia would have to change places with each other. A third set of authorities, especially palæontologists like Mivart, Seeley, and others have supposed a diphyletic origin of Mammals ; and this view is held in its most extreme form at the present time by Hubrecht, who on the strength of his Trophoblast theory sees even in the oviparity of the Monotremes a secondarily acquired feature and would derive this group, together with the Sauropsida, independently of the rest of the Mammals from viviparous ancestors.



If now we bring the conclusions derived from the study of the mammary apparatus into relation with these views, it becomes evident that they speak as clearly *against* the last two sets of views as they do *for* that of Huxley. The fact that the development of the mammary apparatus of the Monotremes and Marsupials begins with primary-primordia, identical in the two, and that mammary hairs are present in both, proves along with other structural features which they have in common that there can be no question of their diphyletic origin. And as concerns the Trophoblast theory of Hubrecht, it need only be remarked that it is against all morphological principles to attach such value to a purely embryological and no doubt adaptive feature, and to leave out of account all other structural characteristics.

Just as certainly must we regard that other view as incorrect, which would see in the Marsupials specialized descendants of Placental ancestors. No matter what parts of the mammary apparatus we consider, we find always that the condition in the Placentalia never throws any light on that of the Marsupialia, but that, on the contrary, the reverse is regularly the case. As we have seen, milk-streaks and milk-lines were unintelligible until the discovery of the primary-primordia of the Marsupials. Again, the vestigial nipple pouches which occur in the Placentalia only during embryonic development could not be explained without the knowledge of the nipple pouches of the Marsupials. The same holds true of the mammary hairs. Thus the course of the phylogenesis cannot possibly have led from a Placental stage to the Marsupials.

On the other hand, all our observations bear witness to the truth of Huxley's view. I would emphasize that it is only at the commencement of the development of the mammary apparatus in the Monotremes and Marsupials that we meet with identical formations—namely, the primary-primordia. All the other structures of the mammary apparatus must have developed independently in both groups. I need only recall to you the names of these parts—gland area and nipples, mammary glands and milk glands, incubatorium and marsupium, sphincter incubatorii and sphincter marsupii. A connection, then, between the Monotremes and Marsupials existed merely in so far as they are derived from common ancestors—Huxley's Prototheria.

The relation between the Marsupials and Placentals is of a similar kind. The parallel development of the various nipple types in both groups, and the absence of the pouch in the Placentals as a *primary* feature, point most decisively against a direct derivation of the Placentals from pouch-bearing Marsupials. On the contrary, all the evidence goes to show that these two orders arose independently from their common ancestors—Huxley's Metatheria.

Thus a knowledge of the ontogeny of the mammary apparatus confirms in the fullest way the correctness of the phylogenetic conceptions put forward by Huxley, with this one slight modification perhaps, that the distinction between the Eutheria as hypothetical racial forms of the Placentalia is superfluous. In more recent times, numerous other authorities have come to the same result as Huxley, notably Bensley, who on the strength of extremely careful investigations of the teeth and foot-structure of the Marsupials was led to phylogenetic conclusions that often coincide with mine most surprisingly.

But I have special satisfaction in drawing attention to the fact that very recently Gregory, a pupil of Osborn, on the basis of a critical examination of all the morphological and palæontological data concerning the phylogenesis of Mammals, has come to Huxley's point of view, and that Hill too, in his last contribution on "The Early Development of the Marsupialia," has furnished new and important proofs of the correctness of the same.

Where so many investigations, pursued on the most varied organ-systems, have led to such concordant results, it may safely be assumed that they express the true course of phylogenesis.

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