The natural history of the nine-banded armadillo of Texas / by H.H. Newman.

Newman, H. H.
Royal College of Surgeons of England

Lancaster, PA : The Journal, 1913.

c 9

VOL. XLVII, NO. 561 SEPTEMBER, 1913

Three in one.
"
25-27

THE
AMERICAN
NATURALIST

A MONTHLY JOURNAL
Devoted to the Advancement of the Biological Sciences with
Special Reference to the Factors of Evolution

CONTENTS

THE SCIENCE PRESS

LANCASTER, PA. GARRISON, N. Y.

NEW YORK: SUB-STATION 84

The American Journal of Science

Established by Benjamin Silliman in 1818

The Leading Scientific Journal in the United States

Devoted to the Physical and Natural Sciences, with special reference to Physics, and Chemistry on the one hand, and to Geology and Mineralogy on the other.

Editor: EDWARD S. DANA.

Associate Editors: Professor GEORGE L. GOODALE, JOHN TROWBRIDGE, W. G. FARLOW and WM. M. DAVIS of Cambridge; Professors A. E. VERRILL, HENRY S. WILLIAMS and L. V. PIRSSON, of New Haven; Professor JOSEPH S. AIMES, of Baltimore; MR. J. S. DILLER, of Washington.

Two volumes annually, in monthly numbers of about 80 pages each.

This Journal ended its first series of 50 volumes as a quarterly in 1845; its second series of 50 volumes as a two-monthly in 1870; its third series as a monthly ended December, 1895. A Fourth Series commenced in 1896.

Subscription price, $6 per year or 50 cents a number, postage prepaid in the United States $6.25 to Canada; $6,40 to Countries in the Postal Union. Back numbers at reduced prices.

☞Ten-Volume Indexes, Vols. I-X XI-XX, fourth series, price one dollar. Address

The American Journal of Science
New Haven, Conn.

University Control

By J. McKeen Cattell, Professor of Psychology in Columbia University

Together with a series of Two Hundred and Ninety-nine Unsigned Letters by Leading Men of Science holding Academic Positions and Articles by Joseph Jastrow, George T. Ladd, John J. Stevenson, J. E. Creighton, J. McKeen Cattell, George M. Stratton, Stewart Paton, John Jay Chapman, James P. Munroe and Jacob Gould Schurman.

A great variety of questions concerning general university administration are dealt with in an original and helpful way.—*Nature.*

These quotations and examples are taken from Professor Cattell's informed and thorough discussion of the subject of university control, a subject upon which he has had much to say of late, finding occasion for caustic criticism of existing American conditions, and standing as the champion of an academic democracy and a teaching profession upon which a man may enter without forfeiting his self-respect.—*The Dial.*

Sentences and paragraphs that betoken the expert, highly-trained mind, the suggestions that come to refresh and tell us that a new day is about to dawn in educational writing.—*The Boston Evening Transcript.*

SCIENCE AND EDUCATION

A series of volumes for the promotion of scientific research and educational progress

VOLUME I. **The Foundations of Science.** By H. Poincaré. Containing the authorized English translation by George Bruce Halsted of "Science and Hypothesis," "The Value of Science," and "Science and Method." *In Press.*

VOLUME II. **Medical Research and Education.** By Richard M. Pearce, William H. Welch, W. H. Howell, Franklin P. Mall, Lewellys F. Barker, Charles S. Minot, W. B. Cannon, W. T. Councilman, Theobald Smith, G. N. Stewart, C. M. Jackson, E. P. Lyon, James B. Herrick, John M. Dodson, C. R. Bardeen, W. Ophüls, S. J. Meltzer, James Ewing, W. W. Keen, Henry H. Donaldson, Christian A. Herter, and Henry P. Bowditch. *In Press.*

VOLUME III. **University Control.** *Now Ready. Pages x+484. Price, $3.00 net.*

GARRISON, N. Y. THE SCIENCE PRESS **LANCASTER, PA.**
SUB-STATION 84, NEW YORK CITY

THE
AMERICAN NATURALIST

Vol. XLVII September, 1913 No. 561

(25)

THE NATURAL HISTORY OF THE NINE-BANDED ARMADILLO OF TEXAS

PROFESSOR H. H. NEWMAN
The University of Chicago

For some years past the writer has been engaged in a study of various phases of the biology of the Texas armadillo and has published a number of papers, some of them in collaboration with J. T. Patterson and some of them alone, dealing with matters of development, cytology, sex and heredity. There now appears to be a demand for a brief, non-technical summary, giving the gist of the findings discussed in detail in these papers. The present account will furnish such a summary and will in addition deal with certain matters not yet published.

Nomenclature and Affinities

In the publications thus far issued the armadillo of Texas has been referred to under various generic titles (*Dasypus, Tatusia* and *Tatu*) and it would be well to come to a final decision as to nomenclature. The systematists seem to have finally settled upon the name *Dasypus novemcinctus texanus.* They recognize two other subspecies of this form in North America, viz., *D. novemcinctus fenestratus,* the common Mexican armadillo, and *D. novemcinctus hoplites,* a type described by Allen from the hills of Grenada. These three subspecies are probably no more than local varieties of which many others could no doubt be discovered were one inclined to make a careful survey of the range of the species. There is scarcely a doubt that the North American armadillos are all derivatives of the Peba armadillo (*Dasypus novemcinctus*) of South America, a species of wide range, occurring from Panama to Paraguay. The mulita of the Argentine and Kappler's armadillo of Surinam were formerly classified as species of *Dasypus,* but the former is now *Cryptophractus hybridus* and the latter *Tatusia kappleri.* Nothing is known about the development of the latter, but the preliminary paper of Fernandez shows that the mulita is strikingly like our species in the details of polyembryonic development. Such a fundamental resemblance would seem to indicate that the two species are very closely related and should be classed in the same genus. About a dozen other species of armadillo, assigned to several other genera, are native to South America. About their natural history little is known.

RANGE, DISTRIBUTION AND FUTURE OF THE ARMADILLO IN TEXAS

In his "Biological Survey of Texas" Bailey (1905) states that

> The armadillos are strictly Lower Sonoran, but in the rough country between Rock Springs and Kerrville they range fairly into the edge of the Upper Sonoran Zone. As a rule they do not extend east of the semiarid or mesquite region, nor to any extent into the extremely arid region west of the Pecos, but occupy approximately the semiarid Lower Sonoran region of Texas north to near latitude 33°.

Bailey lists many localities from which armadillos have been taken or authentically reported. To this list I should like to add the following localities, which I have visited and from which I have obtained considerable numbers of specimens: Boerne (over 100), Comfort (nearly 200), Fredericksberg (about 40), Kerrville (about 25), Ingram (90), Helotes (3). Many of those reported from Boerne, Comfort and Ingram were brought from distances of twenty miles or more. At the towns of Boerne and Comfort we find a flourishing industry in which the armadillo furnishes the raw material. Many thousands of the adult animals are slaughtered annually for their armor, which is shaped into baskets and sold all over the world as curios. Armadillo hunting has come to be a recreation and a source of additional income for large numbers of young American and Mexican farmers. When they come to town to sell produce and purchase supplies they bring also many armadillo baskets which they have learned to make in an expert fashion and for which there is a ready market. One dealer with whom I am well acquainted claims to have shipped no less than 40,000 baskets during the last six years. At least two other firms have been almost equally active. In spite of this extensive slaughter the animals seem to be increasing in numbers, for I had no difficulty in obtaining in about two weeks nearly two hundred pregnant females. Those used in my work would have been slaughtered for their armor alone, so I felt no compunction about destroying so many unborn young. Hunters and dealers generally have the idea that the range of the armadillo is extending rapidly

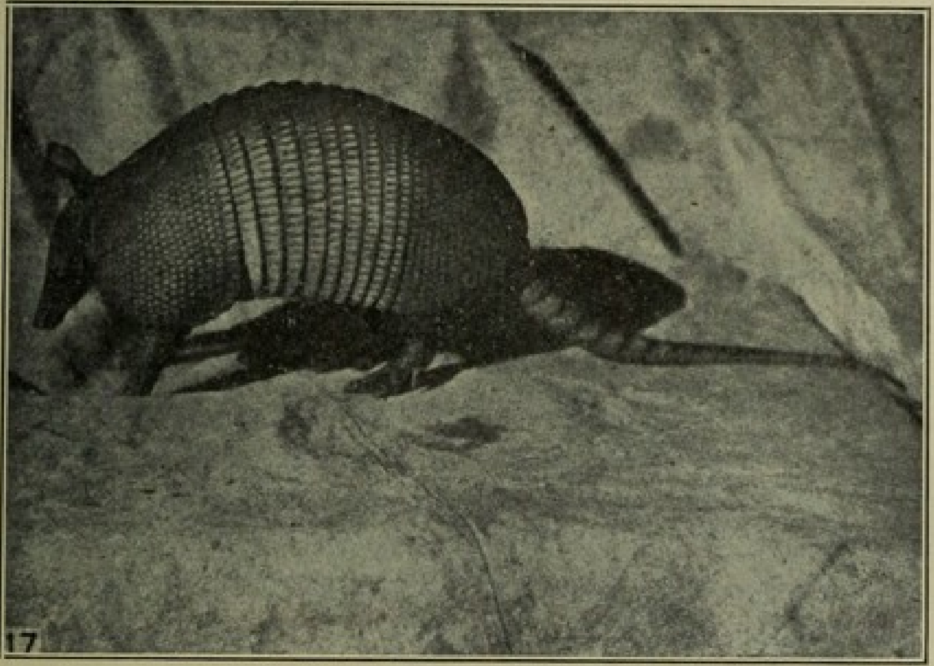


FIG. 1. Photograph of a living armadillo showing the complete armor and the usual resting attitude. The head is usually withdrawn between the two flaps of the shoulder shields when the animal is feeding in the thickets.

northward and eastward. There seems to be no reason to doubt that the species is multiplying and spreading, for I have it on good authority that in the regions where it is now most plentiful it was almost unknown 20 years ago. Its range is, however, strictly circumscribed by definite ecological conditions as I shall proceed to show.

Ecology and Habits

The armadillo spends its life on the defensive and its defensive equipment consists of structural and functional adjustments to a very special environment. Of the structural adaptations the armor (Fig. 1) is the most obvious, but its use is not what it is commonly supposed to be. While the carapace doubtless serves partially to protect the animal when it is attacked by large carnivors, the fact that dogs often bite through the bony plates and seriously damage the shell shows that for this type of enemy the protection is very inadequate. In fact it is the experience of hunters that, when closely pressed by dogs, the harassed animal turns on the back and strikes most effectively with the powerful claws. The armor has a much more important significance in that it enables the animal to invade the dense, thorny thickets of cactus and chapperal, etc., that characterize its normal habitat. When pursued it is possible for the armadillo to plunge headlong into a mass of thorny vegetation that would be totally inaccessible for an unarmed enemy. Then too they can penetrate all sorts of underbrush in search of insect food without danger from thorns or spines. In some regions of the country the animals take advantage of the rough and rocky character of the hillsides and river banks, seeking shelter from enemies by retreating into holes and crevices among the rocks that are just large enough to admit them but too small for their enemies. Armadillos living in these regions have the armor much worn from rubbing and scraping against the angles and sharp edges encountered in the rocky passages of their retreats. If one is able to reach the tail of an armadillo concealed in a rock pile the animal braces the armored back against the roof or sides of the hole and holds so hard that the tail will come off before the body can be moved. Thus in divers ways the armor serves a protective function other than the primary one connoted by the name. Still further, there can be no doubt but that the carapace serves as a reducer of surface evaporation, an important factor in making life possible in the semiarid regions, for there are many periods of extreme drought during which it must be of vital importance to conserve moisture. It is possible, indeed probable, that the armor is phylogenetically older than the particular conditions comprising the present environment of the armadillo, hence we can scarcely claim that the armor is in any strict sense an adaptation. It seems far more likely that in the exercise of its prerogative of choice of habitat the species has selected an environment affording an unpreempted food area and an adequate shelter from enemies.

The armadillo is preeminently insectivorous, although in captivity it appears practically omnivorous. Stomach examinations of freshly caught wild animals show the remains of insects, chiefly ants, together with much earth and more or less vegetation. In captivity they eat meat of all kinds, even exhibiting canibalistic propensities under certain conditions, for when shipped in crates or boxes the stronger ones kill and disembowel the weaker, and mothers devour their own new-born offspring. Hunters and basket dealers justify the extensive slaughter of the armadillo by giving to the animal a bad name. It is said, on how good authority I am unable to state, that the "'dillo" is a robber of newly made graves and a destroyer of vast numbers of the eggs of such ground birds as wild turkeys and quails. They are also said seriously to damage the grazing value of certain territories by rooting up quantities of grass. I am of the opinion that much of the destruction of bird eggs and of grass might more justly be blamed upon the Texas peccary, which has a range quite similar to that of *Dasypus*.

Armadillos are essentially nocturnal in habit, although one may encounter them at dusk. On warm nights they spend their time rooting about in the dry leaves and ground vegetation after the manner of hogs. Their grunting, snuffing noises are heard at some distances on quiet evenings. The strong burrowing claws are used to a considerable extent in digging for food, but their primary function is that of burrowing. Burrows may be for temporary or permanent shelter. A permanent burrow may be dug six or seven feet deep with a chamber at the bottom about two feet in diameter, which is filled loosely with dried leaves and grass. This is the winter retreat of the armadillo, where he undergoes partial hibernation during the periodic cold spells. Buried in the grass and leaves, the animal defies its worst enemy, cold. In this connection it may be said that there is probably no mammal so sensitive to cold as the armadillo. In captivity they shiver at temperatures when other mammals are warm, and often die during the night if insufficiently bedded down with straw. Their further spread northward will no doubt be blocked by temperature barriers. Temporary burrows are made as a retreat from enemies when other shelter is unavailable. Hunters claim that an armadillo will dig a hole in ordinary soil in a minute or two, disappearing even after having been sighted.

They seem to have their regular haunts and do not ordinarily go far from their burrows or caves. From the smoothly worn mouths of these retreats beaten paths lead to thickets, pools and streams. Bailey has seen evidences that they, after the manner of pigs, enjoy a mud bath. The trail of the tail along the paths is a ready means of distinguishing the haunts of the "'dillo," for it leaves a mark like that of a dragging rope.

In captivity the animals display the utmost gentleness and tractability so long as one does not attempt to lay hands upon them. If one attempts to hold one of them by the shell he will realize how strong and active is its resistance, for it bucks vigorously like a broncho and throws off all holds. The tail is the weak point in its defence, as it offers a perfect handhold, but, even when grasped by the tail, it furnishes an interesting struggle by violently rotating the body and often succeeds in twisting free from the enemy's grasp. Then one is surprised at the speed of which the animal is capable, its galloping gait being apparently unhindered by its armored cuirass.

Of the senses, that of smell is the only one upon which the animals seem to rely. When feeding they frequently raise the snout on high and sniff the air in all directions. The eyes are rudimentary and practically useless. If disturbed an armadillo will charge off in a straight line and is as apt to run into a tree trunk as to avoid it. That the hearing is not at all keen is evidenced by the fact that one may approach them on the leeward side even if the approach is somewhat noisy.

Breeding Habits

Information as to mating and care of young has come indirectly through hunters, among whom there is a considerable degree of consensus of statement. It is claimed that armadillos pair for life or at least for the season. It is very common to capture a male and a female together or to dig a pair out of a burrow. The period of œstus comes early in the autumn, extending over a variable period of time. A large proportion of the females taken in October show the early stages of pregnancy, but early stages have been found as late as December. It seems probable that the young ''does'' of the previous season's crop reach maturity late in the autumn, for the largest females are almost invariably pregnant in October while many of the smaller females are non-pregnant at that time. The young are for the most part born in March, although births during April are not rare.

From these observationts it may be estimated that the period of gestation averages from the middle of October to the middle of March, a period of five months or 150 days, an extended gestation period for so small a mammal. The young are fully formed at birth, with eyes open and with a complete though not very hard armor. They are able to walk in a more or less uncertain fashion within a few hours after birth.

Copulation occurs with the female turned on the back, this position being necessary on account of the armor and the ventral location of the genitalia.

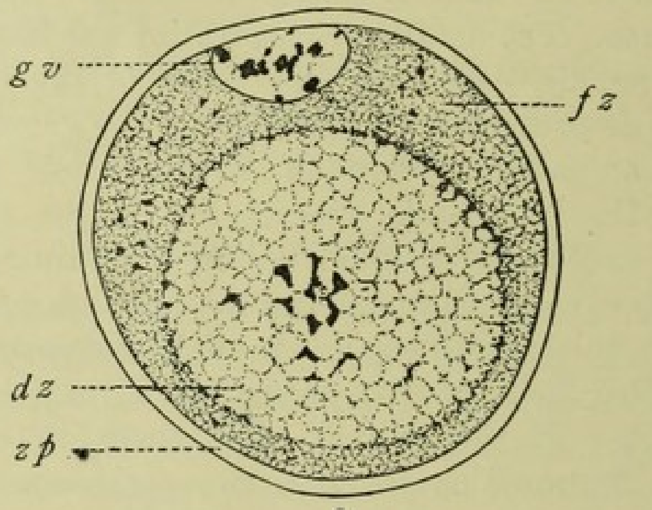
Polyembryonic Development

Our earliest observations dealing with the development of the Texas armadillo revealed the facts that the four embryos are enclosed in a common chorion and that these monochorial quadruplets are always unisexual. These early observations stimulated an investigation of the embryological and cytological conditions that underlie polyembryony and sex-determination. The published accounts carry the history of development through the period of ovogenesis up to the time of fertilization and from the primitive streak stage to birth. The hiatus between fertilization and the formation of the primitive streak is almost completely filled by two sets of observations, one by Patterson, who has secured late cleavage stages and all of the history up to the primitive streak, and the other by the writer, who has described the early cleavage of parthenogenetically developing ova. The observations of Patterson were reported at a meeting of the central branch of the American Society of Zoologists at Urbana in 1912; the paper on parthenogenetic cleavage is now in press and will no doubt appear before the present contribution. By piecing together the subject matter of these separate investigations the writer is able to offer the following account of the development.

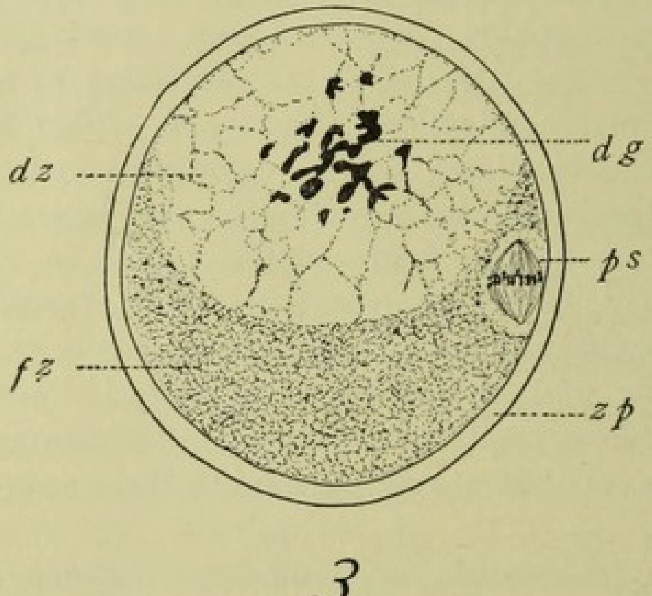
OVOGENESIS AND FERTILIZATION

The early phases of ovogenesis are in no way peculiar and in themselves offer no clue as to the physiology of polyembryonic development. A detailed study of the growth period of the ovocytes and of folliculogenesis shows that in normal ovaries there is only one ovocyte to the follicle and that in ovulation only one egg is given off at a time. The details of maturation are like those of other mammals, especially like those of the marsupial *Dasyurus* as presented by Hill ('10). The growth period involves an accumulation of deutoplasmic material, which in the full-grown ovocyte lies in the form of a coarsely vacuolated central sphere containing deeply staining granules. Surrounding the deutoplasmic sphere is a fairly thick peripheral zone of homogeneous protoplasm, called the formative zone (Fig. 2), which is somewhat thicker at the animal pole where the germinal vesicle is flattened against the zona pellucida. During the maturation process a remarkable reorganization of the cytoplasmic regions of the ovocyte occurs. The fluid deutoplasmic sphere forces its way to the surface and comes to lie in contact with the periphery of nearly the whole animal hemisphere of the cell. This forces the formative protoplasm to the vegetative pole where it assumes the form of a cap thick at the pole and thin at the equator, having a crescentic outline in meridional section (Fig. 3). The maturation spindle, forced from its normal position at the animal pole, lies as near the latter as possible without leaving the formative protoplasm, and assumes a position tangential to the nearest periphery of the cell, but nearly parallel to the primary axis of the latter.

The two maturation divisions occur without disturbing this new arrangement and no other radical change seems to take place until after fertilization, at least so one must conclude from the fact that a tube egg in a late phase of fertilization still shows the formative and deutoplasmic zones arranged as in Fig. 2. This one fertilization stage (Fig. 4) shows two polar bodies and the male and female pronuclei lying close together in the thickest part of the formative zone. There is nothing in maturation nor in fertilization to suggest or account for polyembryony. Their chief evidential value lies in the fact that they demonstrate the fact of polyembryony and show that the latter is not due to any



2



3

Fig. 2. A section through a full-grown ovocyte before the changes incident to maturation have taken place. Note the peripheral formative zone (*fz*), in which lies the flattened germinal vesicle (*gv*). The deutoplasmic zone or sphere (*dz*) lies in the center. The zona pelucida (*zp*) is a dense shell-like membrane.

Fig. 3. An ovocyte during the first maturation division, showing the reorganized cytoplasmic zones. The polar spindle (*ps*) is situated far from the animal pole. The deutoplasmic granules (*dg*) are conspicuous at this period. Other lettering as in Fig. 2.

morphological peculiarity of the germ cells. In brief the egg is a simple egg with one nucleus and is fertilized by a single spermatozoon. Hence the embryo starts out as a single and not as a multiple individual.

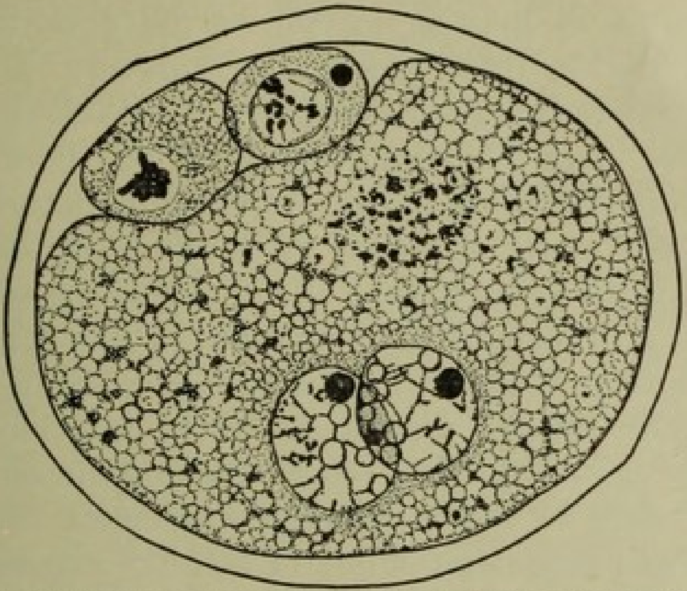


FIG. 4. A fertilized egg found in the fallopian tube, showing the male and female pronuclei in contact and occupying the thickest part of the formative protoplasm. There are two polar bodies. The deutoplasmic zone does not appear in this section.

The claim of Rosner ('01), based on an examination of one pair of ovaries inadequately preserved, that the four embryos are the result of the fusion of several follicles and the subsequent fusion of the several eggs or vesicles given off by the rupture of a compound follicle, is completely refuted by the present studies. It may be of interest to show how Rosner came to fall into so serious an error. The writer after the examination of a large number of normal ovaries chanced upon one pair showing substantially the conditions described by Rosner. These ovaries were from a very large, old female and when examined cytologically showed many multiple follicles, containing from two to eight or more ovocytes in various stages of development. Everything about these ovaries, however, is atypical and there can be no doubt as to their pathological character. That Rosner should by chance have stumbled upon such an ovary and that he drew a general conclusion as to the normal condition from so slender an evidential basis constitutes a biological comedy of errors scarcely equaled in our literature.

Cleavage

Nothing is at present known of the early cleavage stages of the fertilized egg and I shall offer here as a tentative substitute facts dealing with the parthenogenetic cleavage of eggs in atretic follicles. The first step in the development of such eggs is the elimination of the deutoplasmic material, which probably is thrown out of the protoplasm by a rupture of the plasma membrane of the egg. The formative protoplasm of the egg in this way unburdens itself of a considerable volume of inert and probably deleterious material, which, although outside of the egg-cell proper, remains within the zona pellucida and more or less completely surrounds the egg in the form of pseudo-epithelium of cell-like masses, which I have called cytoids. The egg now consists of a homogeneous, clarified protoplasm and there is every reason to suppose that the elimination of byproducts of metabolism has served to rejuvenate the cell so that its normal processes of growth and reproduction may be resumed. The nucleus, which, previous to and during maturation, had ceased to carry on metabolic exchanges with the cytoplasm, now evinces renewed activity in that astral rays, entirely absent during maturation divisions, now penetrate the entire cytoplasm and a typical cleavage spindle appears. Two-, four- and eight-cell stages occur in fairly regular fashion, but even at the eight-cell stage unmistakable signs of degenerative changes manifest themselves, which bring about a rapid dissolution of embryonic integrity and inhibit further progressive changes. There is no evidence in this material that parthenogenetic development proceeds to the formation of teratoma or tissue formation; in fact, the total lack of cleavage stages later than about the eight-cell stage argues strongly against the possibility of the development of any such structures. This study serves two purposes, that of affording a critical demonstration of parthenogenetic development of mammalian ova, and that of furnishing a clue as to what we may expect to find when we come to know the facts about the early cleavage of normally developing eggs. In the latter connection it is of interest to note that in *Dasyurus,* whose developmental peculiarities up to the time of cleavage parallel those of the armadillo, there is, as a preliminary to cleavage, an elimination of the deutoplasmic material almost precisely like that shown in our parthenogenetic material. This fact lends support to the conjecture that, in essential features, parthenogenetic cleavage parallels that of normal development and may be used as a substitute for the latter, at least up to the eight-cell stage.

For the sake of rendering the present account as nearly complete as possible I shall make a statement regarding the late cleavage and early embryology, based partly on Patterson's observations. The earliest stage shown by the latter at the Urbana meeting was an inner-cell-mass stage, like that of any ordinary mammal. Such a vesicle becomes attached by its animal pole to the very apex of the fundus of the uterus, where it lies in a position predetermined for it at a point where two grooves in the uterine mucosa cross each other, the one running laterally between the openings of the fallopian tubes and the other at right angles from mid-dorsal to mid-ventral aspects of the uterus. This position at the crossing of these grooves enables the investigator to locate with certainty even the excessively minute earliest stages of the developing vesicle. As it expands the vesicle becomes depressed in the groove and elongates laterally into an ovoid form with the long axis running from the right to the left sides of the uterus. As soon as it gains attachment to the uterine mucosa the vesicle undergoes germ-layer inversion like that seen in the rodents, the result being that two secondary vesicles are produced, an inner complete ectodermal vesicle and an outer endodermic vesicle, incomplete at the area of attachment where the primitive placenta or Träger arises. Up to this time there is no sign of polyembryony. The first step in the direction of a division of the single embryonic vesicle into four embryonic rudiments is seen in connection with mesoderm formation. The mesoderm arises at two points, to wit the extreme right and left sides of the laterally elongated vesicle, and soon assumes the form of two hollow pouches that subsequently expand and fuse together in the median lines into a common extraembryonic body cavity. This mode of origin of the mesoderm shows that the embryo is no longer developing as a unit, but that there has arisen a bilateral duality of function, due probably to the partial physiological isolation of the right and left sides of the mesoderm. The possible cause of this isolation will be discussed presently. The first recognizable rudiments of the embryos appear as two blunt processes or

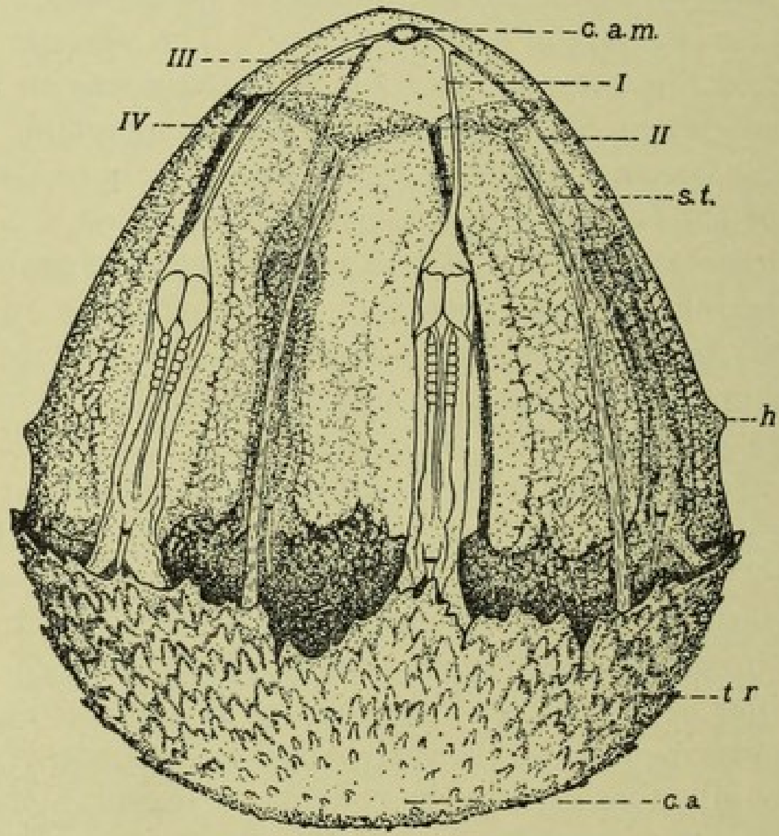


Fig. 5. An early embryonic vesicle showing four embryos enclosed within a common chorionic membrane. The small common amnion (*c. am.*) still retains its connection with the separate amnia of the embryos by means of the slender amniotic connecting canals (I–IV). The four embryos are attached to a common discoid primitive placenta, the Trager (*tr*), by belly-stalk bands.

thickenings of the ectodermal vesicle. These two primary embryonic buds arise in connection with the dual centers of origin of the mesoderm, each appearing directly beneath a primary mesodermal pouch. These two primary buds elongate and soon divide at the tip into paired outgrowths, which constitute the primordia of the two pairs of embryos. The embryos develop on the inside of the inner vesicle and are consequently in a common ectoderm-lined, fluid-filled cavity, which is a sort of common amnion. Subsequently the separate embryos sink into the floor of the common amnion and retain their connection with the latter only by slender amniotic connecting canals, which gradually shrivel up and disappear. An early somite stage with the common amnion and the connecting canals still intact is shown in Fig. 5, which also illustrates the attachment of the four fœtuses to the Träger by means of the allantois and the belly-stalk bands which constitute the primitive umbilicus. The saucer-shaped Träger or primitive placenta develops from the part of the trophoblast which originally formed the point of attachment for the vesicle. This area has not been invaded by the entodermal vesicle, but is reinforced directly by mesoderm, which invades the maternal mucosa and produces primitive villi, that are at first in the form of blunt ridges, but later take on the form of flat scales (see Fig. 5), and subsequently assume the typical arborescent form of definitive placental villi. The subsequent development of the embryos is of little interest except to the specialist and need not be referred to here. The history of the placenta, however, is of unusual interest in that it illustrates the futility of attempting to use the special types of placentation as criteria of animal affinities. The early placenta as shown in Fig. 5 is a single discoid structure. Subsequently the points of attachment of the four umbilical cords become areas of rapid placental development and the parts of the Träger in between them almost lose their villi. At this stage the placenta consists of a set of four separate discs. As these villous regions expand they come into contact at their margins and apparently fuse into a lobate zone, which had been called a compound zonary placenta. Finally the zone separates along the dorsal and ventral lines to form two lateral notched discoid placentæ, to which we need scarcely apply a name. It is obvious that there is nothing to be gained by attempting to classify such a placental complex or by comparing it with those of other groups of mammals, for the peculiar conditions seen here are obviously merely very special adjustment to the peculiar conditions arising from polyembryonic development within a single chorion. The fœtuses after they have once been separately outlined are distinct, complete units and are associated scarcely more closely than are the embryos of other forms of mammals where several individuals develop simultaneously in a single uterus, for they have their own separate amnia and separate placentation, and there is absolutely no admixture of fœtal blood.

Without further burdening the reader with an elaboration of embryonic details and relations we may briefly summarize the situation in-so-far as the question of specific polyembryony is involved. The ovogenesis is normal; a single egg is fertilized by a single spermatozoon; the cleavage is apparently normal and gives rise to a blastodermic vesicle similar to that of other mammals, especially the rodents; germ-layer-inversion affords an easy mechanism for producing several embryos in a single chorion, for the quadruplets arise by means of dichotomous budding of the inner ectodermic vesicle without affecting the enveloping membranes of the vesicle, which form the common chorion; the subsequent embryonic development of the several embryos is as independent as it can be under monochorial conditions, since each individual has its own separate amnion, allantois, umbilicus and placenta. This in brief is the polyembryonic situation, a consideration of which offers for solution several problems peculiar to the material. What are the physiological causes of polyembryony? What factors determine the definite bilateral orientation of the embryos in the vesicle, or what factors are responsible for pairing of embryos? What light does the situation throw on the problem of sex determination? Does the condition give us any fulcrum on the problem of predetermination and epigenesis? What are the modes of inheritance peculiar to polyembryony? Does the polyembryonic situation offer any new facts bearing on the general problems of genetics? These problems will be discussed in the order given.

The Causes of Polyembryony

In a previous paper (Newman, '12) were listed a series of seven possible explanations of polyembryony, nearly all of which assumed some abnormality in ovogenesis, maturation or fertilization. The discovery that all of these processes are normal in the armadillo served to eliminate all but the last suggestion, which was to the effect "that the cause of specific polyembryony may lie in factors strictly external to the ovum, among which one of the most probable is in some way associated with the bilaterality of the uterus." At that time no discussion of that possibility was attempted. The discovery of a specific parasite within the armadillo egg, together with a consideration of certain unpublished data presented orally by Patterson, leads me to hazard the following hypothesis.

A careful examination of many ovaries and many thousands of ovocytes has revealed the universal presence of what I consider to be a protozoan parasite in the egg cytoplasm. This parasite is a large body as compared with the size of the host cell and must have a deleterious effect on the egg, probably weakening it or lowering its vitality. Such a depressed egg, in which the parasite has grown and multiplied, develops into a vesicle of some size before the effects of a lowered vitality become apparent. When, however, under the pressure exercised by the transverse groove in the uterine mucosa, the vesicle becomes elongated laterally so that its right and left sides come to be separated a maximum distance from each other. In such a depressed and weakened vesicle unity of functioning ceases to exist and two new centers of growth arise at points where the pressure is less severe, viz., the opposite ends of the elongated vesicle. We have seen that mesoderm forms at two lateral points and that the embryonic buds of the ectodermal vesicle follow suit. The rebudding of the primary buds must be due in like manner to the establishment of two growing points in each primary bud. Such an explanation of polyembryony involves the whole problem of the physiology of budding, about which there is great diversity of opinion. According to Professor Child's theories of development and reproduction, any part of a system which, through a lowering of the rate of metabolism of

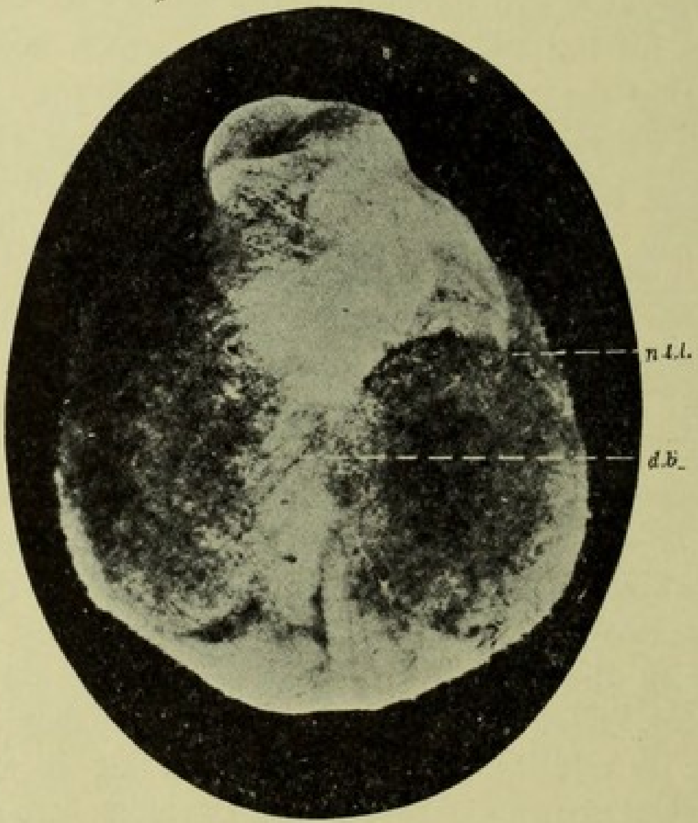


Fig. 6. Photograph, about one half natural size, of an embryonic vesicle just before birth, showing the two lateral placental areas, attached to the right and left sides of the maternal uterus, separated from each other by an area practically free of villi. The outlines of the four fœtuses may be seen through the transparent, non-villous areas of the common chorionic vesicle.

the controlling part of the system, say the animal pole of the blastodermic vesicle, is liable to physiological isolation of parts at certain distances from the dominant region. When such isolation of parts occurs new centers of control arise, which produce buds capable of establishing whole new systems like the original. Thus in the particular case under discussion the rate of metabolism of the whole vesicle is lowered by parasitism to such an extent that the dominant growth center of the system no longer is able to hold the various subsidiary growth regions under control, and new centers of control arise at points determined by secondary pressures exercised by the uterine grooves, as explained above. Further complexities in development are of the nature of adjustments of four separate fetuses compelled to carry on growth and differentiation within a common chorion which had already been established before physiological isolation of the four embryonic rudiments had taken place. According to current theories, reproduction is a result of senescence and, on this basis, it may be assumed that the young blastodermic vesicle, weakened by the ravages of parasites, is precociously old, and therefore tends to reproduce by a process of dichotomous budding. Later, when the parasite completes its active period and goes into encystment, and when the embryos begin to gain new vigor through the absorption of the maternal nutrient fluids, general rejuvenation occurs, the rate of metabolism increases, so that no further isolation of parts occurs. In this connection it is of interest to note that in the mulita armadillo of the Argentine budding goes one or two steps further than in our species and from eight to twelve fetuses result. The writer recognizes the extremely hypothetical character of the explanation of polyembryony here offered and would welcome any suggestion that would lead to a more satisfactory theory. It would be of interest, however, to know whether there is an egg parasite in the mulita, and the writer intends to test this possibility in the near future. If this should prove to be the case the hypothesis here offered would receive a striking support. A detailed description of the life history of the parasite here discussed is in preparation and will no doubt soon appear in print.

The Problem of the Orientation of the Compound Vesicle in the Uterus and the Origin of Pairs

One of the most striking facts that came to light in the early stages of the present studies is that the vesicle is distinctly a bilateral object and that this bilaterality is strictly in accord with the bilaterality of the uterus. It was noted that one pair of fetuses was attached to the right and the other to the left placental disc. It was furthermore discovered that this pairing is not merely a mechanical adjustment of the fetuses to the shape of the uterus, but involves resemblances in stage of development, size and the minutiæ of inherited peculiarities. To explain this condition we offered the conjecture that each

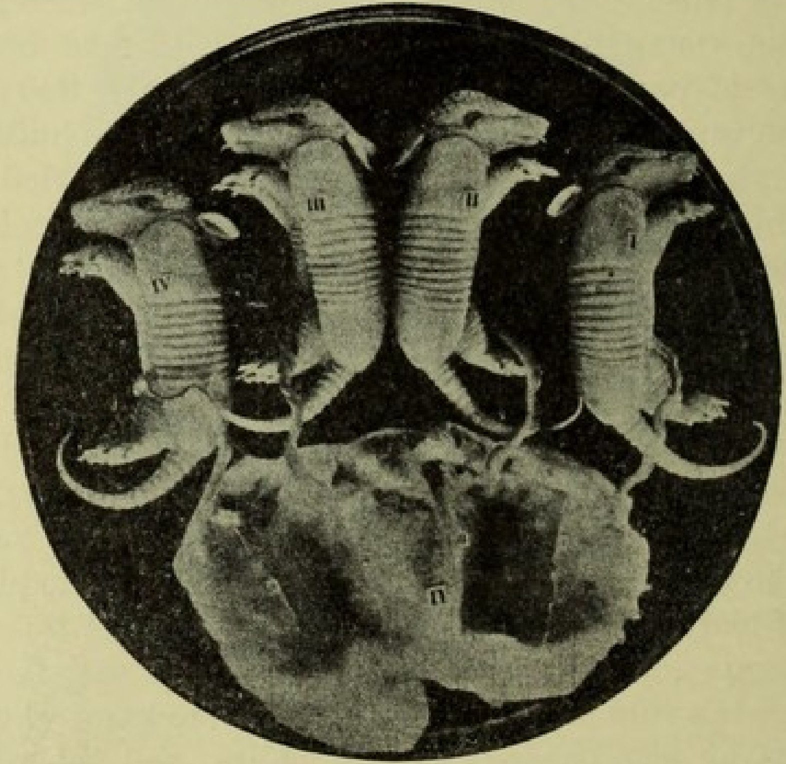


Fig. 7. Photograph of a vesicle a little younger than that shown in Fig. 6, split open along the mid-ventral line, showing the umbilical attachments of the quadruplets.

pair is derived from one of the first two cleavage blastomeres, an idea borrowed from the literature on human duplicate twins. Such a theory, however, involves the difficulty of explaining how the cell descendants of one blastomere would come to occupy a position with reference to one or the other lateral halves of the uterus. The axial orientation of the vesicle is determined by the fact that it always becomes attached by an area of trophoblast at the animal pole, but there is no mechanism for preserving a bilateral orientation. There is on the other hand good evidence, as brought out in the last section of this paper, that the definitive bilaterality of the compound embryonic vesicle is imposed upon it by certain definite bilateral conditions within the uterus, which result in the vesicle being pressed dorso-ventrally and elongated laterally so as to acquire a bilaterality in conformity with that of the uterus. Thus bilaterality and pairing of fetuses are strictly secondary results and bear no relation to any axes of the egg or planes of cleavage. The closer resemblances between the individuals of pairs and their closer placental association are due to their common origin from one primary bud, which means that they are genetically more closely related than are the members of opposite pairs. Mirrored-image effects are also made more intelligible by our knowledge of the mode of origin of a pair from a single primary bud, in that when an inherited peculiarity on the right margin of one individual of a pair is found on the left margin of its partner, it means that some median primordium of the primary bud has been split by the secondary budding, so that the resultant character is found repeated on the adjacent sides of the two fetuses. Dichotomies of primordia of this sort also serve to explain the distribution of many peculiarities inherited by the quadruplets from the parents.

Sex Ratios and Sex Determination

In a collection of 182 sets of fetuses sufficiently advanced to determine with certainty the sex there has appeared no exception to the rule that all fetuses in a set or litter, whether the number of individuals in a set be 2, 3, 4 or 5, are of the same sex. Of these 182 sets 88 were female and 94 male, which would seem to indicate that the two sexes are about equal in numbers. A total of 210 sets have come under the writer's observation, and of these four showed 5 fetuses, four showed 3 normal and 1 degenerate individuals, and in one case twins were born, due probably to the degeneration of a pair of fetuses. There are no authentic cases of less than four embryos being produced, but there are four cases, or less than 3 per cent. of the total number, in which there is exhibited a tendency toward an increase in the normal or typical quadruplet condition. This may be a progressive tendency and might conceivably result in numbers of fetuses resembling those produced by the mulita. The fact that the individuals of a polyembryonic litter are invariably of the same sex supports certain current views regarding the problem of sex determination. In particular it shows clearly that sex must be determined prior to the separation of the embryonic materials from which the four fetuses arise. Since, from the standpoint of cell lineage, this separation must take place at least as early as the cleavage stages, it would appear practically certain that sex is predetermined in the undivided oosperm. It has been claimed that the data with reference to sex in the armadillo might as readily be used as evidence of the control of sex by environment; for it is claimed that the environment of the four fetuses in a common chorion is as nearly identical as it could be made under controlled conditions. I claim, however, that there is no greater environmental uniformity here than exists in cases where several fetuses develop simultaneously in a single uterus. In both cases the individual fetuses have separate amnia, separate placentæ and unmixed fetal blood. The enclosure within a common chorion is a matter of secondary importance since each fetus is isolated completely in the really important ways just mentioned. Moreover it is certain that pronounced differences in nutrition and rate of development frequently occur, as is evidenced by the facts that one pair of fetuses is often strikingly larger than the other. If sex is capable of being altered by nutritive factors one would expect to note some differences of sex within a set in which some fetuses have evidently had a much less favorable developmental environment than others. There are in my collection several sets of quadruplets in which one pair of fetuses is very decidedly larger and more advanced than the other. A condition of this sort is probably to be traced back to a very early period, as early as that shown in Fig. 5, where it is readily seen that one pair is distinctly in advance of the other. Patterson has also stated that it is not uncommon to find one of the primary bud primordia dividing in advance of the other. If sex is capable of being influenced by metabolic inequalities of any sort, there should be opportunity here for the operation of such influence. Yet there is not a single instance in which there is any diversity of sex within a set of fetuses derived from a single germ cell.

Cytological studies of the germ cells are in strict accord with current chromosomal hypotheses of sex determination. The female diploid number of chromosomes is 32 and the haploid 16; the male diploid 31, producing two kinds of spermatozoa, one with 15 and the other with 16 chromosomes. There occurs in the reduction division an odd chromosome like that described for other vertebrates, notably the birds and man as shown by Guyer. The presumption is that this odd chromosome plays the same rôle in the determination of sex as it is assumed to play in an extensive array of animals. The character of the evidence is the same in all cases. On this basis it may be claimed that in the armadillo an egg fertilized by the 15 chromosome type of spermatozoon produces a male and one fertilized by a 16 chromosome type, a female. Environmental factors are powerless to alter the sex thus determined.

ANALYSIS OF PREDETERMINATIVE VERSUS EPIGENETIC FACTORS IN DEVELOPMENT

According to the proponents of the pure line hypotheses the genotypic constitution of an individual is fixed at the time of fertilization of the ovum. On this assumption the fertilized egg of the armadillo has a fixed and definite hereditary potentiality and, unless inequalities of some sort are introduced during development, *i. e.*, epigenetically, the four fetuses should be identical. The degree of difference then that actually exists among the individuals of a given set of quadruplets should be a measure of the potency of the epigenetic factors of all kinds, while the degree of correlation among the individuals of a set should serve as a criterion of the relative strength of the predetermining factors. It has been customary to employ the data derived from comparisons of human duplicate or identical twins as a measure of the extent of predetermination, but such data are unreliable for two reasons. It is impossible, on the one hand, to be sure whether or not such twins are the product of one egg, and in practically all cases the measurements and comparisons are made comparatively late, so that the two individuals may have had a divergent environmental experience. In both of these respects the armadillo quadruplets offer superior advantages and should in the future take the place of human twins as material illustrating the potency of predeterminative factors in development, for not only do we know for certain that each set of quadruplets is the product of a single egg, but the amount of material is thoroughly adequate for statistical treatment, and the individuals are compared before birth, so that their pairing and placental relations are known. Coefficients of polyembryonic correlation have been determined for a very large number of characters, such as the numbers of plates or scutes in the various regions of the armor, and these have ranged from 0.92 to 0.98. These coefficients are strictly of the order of those determined for antimerically paired structures of the same individual. In other words, these quadruplets resemble one another as closely as do the right and left sides of single individuals. One might readily make the claim that the quadruplets are simply four parts of one individual, since they have been derived by a process of asexual budding from a single embryonic vesicle. The closest of ordinary blood relations have coefficients of correlation of a decidedly lower order, that of brothers being about 0.5; hence the polyembryonic relation is much closer than a mere fraternal one. We may conclude then that the predetermining mechanism works accurately up to from 91 to 98 per cent. and that epigenetic disturbances or inequalities effect alterations in the end result ranging from 2 to 8 per cent. One of the most fundamental postulates of the sciences of taxonomy and phylogeny is to the effect that degrees of resemblance are criteria of blood relationship. This postulate is strongly supported by the facts just given, since the closest resemblances ever found to exist between individuals are here the result of the closest possible blood relationship; for no closer genetic relationship could well be conceived than that involved in the known origin of these armadillo quadruplets.

A subsidiary question arises as to what kind of epigenetic factors operate in inducing dissimilarity among the polyembryonic offspring of a set. Studies of the heredity of certain characters and of the distribution of certain units among the quadruplets lead to the conclusion that the most important differences are due to imperfections in the mechanism for distributing germinal materials, a mechanism which has visible expression in the mitotic complex of cleavage. It seems probable that certain materials which condition the development of certain characters are not distributed with exact equality to the first two blastomeres. This would make one half of the embryonic vesicle different in potentiality from the other. A similar inequality might exist in the second cleavage and in subsequent cleavages. Mere differences in nutriment, position, etc., are impotent to influence any but dimensional characters, such as length, weight and relative position of units. Inherited characters are affected only by changes in the germinal materials, and such changes might readily be due, as indicated, to inequalities in the distribution of material particles during cleavage.

MODES OF INHERITANCE IN POLYEMBRYONIC OFFSPRING

The material for the study of inheritance consists of nearly two hundred sets of quadruplets and the armor of the mothers. Without breeding in confinement, which is not at present practicable, no data concerning paternal inheritance are available. Since, however, there is no sex dimorphism with regard to the characters studied, and since males and females inherit alike from the mothers, one can discover all the essential laws of inheritance governing the polyembryonic relationship from a comparison of individuals in sets and of quadruplets with their mothers. After an exhaustive study of this large mass of material the chief general laws discovered are to the effect that single meristic variates, such as particular scutes, and also aggregates of these elements, as for example the total numbers of these units in a given region of the armor, are inherited in the alternative fashion and show only a minor degree of blending. This is an unexpected result in view of the fact that it has been the general impression that meristic variations usually exhibit blended inheritance and substantive variations obey the laws of Mendelian inheritance. In this material it has been found that single scutes, recognizable through some marked peculiarity, such as a tendency to split or to fuse with a neighboring element, is inherited as a Mendelian dominant character. If the mother has the character unilaterally or in one band of the armor, one or more of the offspring invariably exhibit the character either unilaterally or bilaterally, either in one band or reduplicated in two or more bands. Again a single scute peculiarity in the mother may be inherited by one, two or all of the offspring, as a row of peculiar scutes starting at the place where the one peculiar element occurs in the mother. Such fluctuations in the expression of a type peculiarity may conceivably be due to epigenetic factors, and suggest duplication of factors of the neo-mendelian sort.

One of the problems of this material is to determine why one individual or one pair inherits a dominant peculiarity from the mother, while the others do not. They all have the same germinal constitution at the beginning and that some should inherit the character and others not seems to imply that there must have occurred a segregation of maternal and paternal inheritance factors during cleavage. The distribution of the characters so as to produce mirrored image effects, together with this segregation of parental characters, seems to imply a sort of dichotomous distribution of some material basis that conditions the development of the characters so segregated and distributed. Such determiners need not be conceived of as Weismannian elements, but that they have corporeal existence appears to the writer as an unavoidable conclusion.

The data upon which these conclusions are based are of highly complex character and have not yet been published in extenso. The demonstration of the tenability of the conclusions can be made only by the use of much more illustrative material than can be presented in a paper of this sort. In conclusion it may be said that, although the inheritance phenomena have occupied more time and attention than any other phases of the armadillo work, the conclusions reached are less precise and less satisfactory than those in other fields. Yet it is imperative that we should find out just what new light this unique material and unparalleled genetic situation may be able to throw upon the general problems of inheritance. The detailed data and conclusions regarding these intricate problems are being elaborated for publication in the near future.