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PRESENT PROBLEMS IN

EVOLUTION AND HEREDITY.

BY

HENRY FAIRFIELD OSBORN.

presented by the author

FROM THE SMITHSONIAN REPORT FOR 1892.

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In the past decade of practical research and speculation in biology, two subjects have oustripped in interest and importance the rapid progress all along the line. These are, first, the life history of the reproductive cell from its infancy in the ovum onward, and second, the associated problem of heredity, which passes insensibly from the field of direct observation into the region of pure speculation.

As regards the cell it was generally believed that the nucleus was an arcanum into the mysteries of which we could not far penetrate; but this belief has long been dispelled by the eager specialist, and it is no exaggeration to say that we now know more about the meaning of the nucleus than we did about the entire cell a few years ago. At that time the current solution of the heredity problem was a purely formal one; it came to the main barrier, namely, the relation of heredity and evolution to the reproductive cells, and leapt over it by the postulate of Pangenesis. The germ-cell studies of Balfour, Van Beneden, the Hertwig brothers, Weismann, Boveri, and others, have gradually led us to hope that we shall some day trace the connection between the intricate metamorphoses in these cells and the external phenomena of heredity, and more than this, to realize that the heredity theory of the future must rest upon a far more exact knowledge than we enjoy at present of the history of the reproductive cell both in itself and in the influence which the surrounding body cells have upon it.

These advances affect the problem of life and protoplasm, whether studied by the physician, the anthropologist, or the zoölogist, thus concentrating into one focus opinions which have been formed by the observation of widely different classes of facts. As each class of facts bears to the observer a different aspect and gives him a personal bias, the discusson is by no means irenical, and it is our privilege to live through one of those heated periods which mark the course of every revolution in the world of ideas. Such a crisis was brought about by

*The Cartwright Lectures for 1892; delivered before Alumni of the College of Physicians and Surgeons, February 12, 19, and 26, 1892. (From the *Medical Record* for February 20, March 5, April 23, and May 14, 1892.)

the publication of the theory of Darwin, in 1858, and, after subsiding, has again been aroused by Weismann's theory of heredity, published in 1883.

This is the situation I have ventured to present to you as Cartwright lecturer, not, of course, without introducing some conclusions of my own, which have been derived from vertebrate palæontology, but which I shall direct mainly upon human evolution.

So far as theories need come before us now, remember that Lamarck (1792) attributed evolution to the hereditary transmission to offspring of changes (acquired variations) caused by environment and habit in the parent. Darwin's latest view was that evolution is due to the natural selection of such congenital variations as favored survival, supplemented by the transmission of acquired variations. Weismann denies the transmission of acquired variations, or characters, entirely, and attributes evolution solely to the natural selection of the individuals which bear the most favorable variations of the germ or reproductive cells. We must therefore clearly distinguish between "congenital variations" which are part of our inheritance and "acquired variations" which are due to our life habits; the question is, are the latter transmitted?

At the outset I would emphasize the extreme complexity of evolution by a few words upon variation, or in terms of medical science, upon anomalies.

When we speak of a part as "anomalous" we mean that it varies at birth from the ordinary or typical form; it may be minute, as the small slip of a tendon, or large, as the addition of a complete vertebra to the spinal column. Wood has found that in the muscular system alone there are nine anomalies in the average individual. It is clear that the evolution of a new type, so far as the muscular system is concerned, must consist in the accumulation of anomalies in a certain definite direction by heredity. Thus the anomalous condition of one generation may become the typical condition of a very much later generation, and we observe the paradox of a typical structure becoming an anomaly and an anomalous structure becoming typical; for example, the supracondylar foramen of the humerus was once typical, it is now anomalous; the retardation in development of the wisdom tooth was once anomalous, it is now typical.

The same principle applies to races which are in different stages of evolution; an anomaly in the white, such as the early closure of the cranial sutures, is normal in the black. Now the deductions of the Weismann school of evolutionists seem to be founded upon the principle "*de minimis non curat lex;*" that we need only regard such major variations as can, *ex hypothesi*, weigh in the scale of survival. Against this I urge that we must regard the evolution of particular structures, the components of larger organs, the separate muscles and bones for example, for the very reason that while in some cases they play a most

humble rôle in our economy we can prove beyond a doubt that they are in course of evolution. Minor variations in foot structure, which are possibly of vital importance to a quadruped whose very existence may depend upon speed, sink into obscurity as factors in the survival of the modern American.

The evolution of man in the most unimportant details of his structure promises, therefore, to afford a far more crucial test of the Lamarckian *vs.* the pure natural selection theory, than in the domain of his higher faculties, for the reason that selection may operate upon variations in mind, while it taxes our credulity to believe it can operate upon variations in muscle and bone. This is my ground for selecting the skeleton and muscles for the subject of the introductory lecture. Nevertheless, let us review variation in all its forms in human anatomy before forming an opinion. Let us remember, too, that congenital and acquired variations are universal as necessities of birth and life; they are exhibited in the body as a whole—in its proportions, in the components of each limb, finally in the separate parts of each component, as in the divisions of a complex muscle. Thus the possibilities of transformism are everywhere. What is the nature and origin of congenital variations? Their causes? Do they follow certain directions? Do they spring from acquired variations by heredity? These are some of the questions which are still unsettled.

But striking as are the anomalies from type, the repetitions of type as exhibited in atavism and normal inheritance are still more so, and equally difficult to explain. Therefore our theory must provide both for the observed laws of repetition of ancestral form and the laws of variation from ancestral form, as the pasture-land of evolution. Add to these, that for a period in each generation this entire legislation of nature is compressed into the tiny nucleus of the fertilized ovum, and the whole problem rises before us in its apparent impregnability which only intensifies our ardor of research.

LECTURE I.—THE CONTEMPORARY EVOLUTION OF MAN.

The anthropologists and anatomists have enjoyed a certain monopoly of *Homo sapiens*, while the biologists have directed their energies mainly upon the lower creation. But under the inspiring influences of the Darwinian theory these originally distinct branches have converged, and as man takes his place in the zoölogical system, comparative anatomy is recognized as the infallible key to human anatomy.

For our present purpose we must suppress our sentiment at the outset and state plainly that the only interpretation of our bodily structure lies in the theory of our descent from some early member of the primates, such as may have given rise also to the living Anthropoidea. This is also the only tenable teleological view, for many of our inherited organs are at present non-purposive, in some cases even harmful,—as the appendix vermiformis.

From the typical mammalian standpoint man is a degenerate animal; his senses are inferior in acuteness; his upright position, while giving him a superior aspect, entails many disadvantages, as recently enumerated by Clevenger,* for the body is not fully adapted to it; his feet are not superior to those of many lower Eocene plantigrades; his teeth are mechanically far inferior to those of the domestic cat. In fact, if an unbiassed comparative anatomist should reach this planet from Mars he could only pass favorable comment upon the perfection of the hand and the massive brain. Holding these trumps, man has been and now is discarding many useful structures. I refer especially to civilized man, who is more prodigal with his inheritance than the savage. By virtue of the hand and the brain he is nevertheless the best adapted and most cosmopolitan vertebrate. The man of Néanderthal or Spy, with retreating forehead and brain of small cubic capacity† was limited both in his ideas and his powers of travel; yet he was our superior in some points of osteological structure. But the period of Néanderthal was recent compared with that in which some of our rudimentary organs were serviceable, such as the vermiform appendix or the panniculus carnosus‡ muscle. These rudiments in turn are neogenetic when we consider the age of the two antique sense organs in the optic thalamus, the remnants of the median or pineal eye and the pituitary body, both of which were undoubtedly present, and probably useful, in the recently discovered Silurian fishes.

I mention these vestiges of some of the first steps in creation to illustrate the extraordinary conservative power of heredity (which is even more forcibly seen in our embryological development), partly also to show how widely our organs differ in age. Galton has compared the human frame to a new building built up of fragments of old ones; extend this back into the ages and the comparison is complete.

Development, balance, degeneration.—It is probable that none of our organs are absolutely static and that the apparent halt in the development of some is merely relative, as where a fast train passes a slow one. The numerous cases of arrested evolution in nature are always connected with fixity of environment, an exceptional condition with man, and we have ample evidence that some organs are changing more rapidly than others.

Adaptation to our changing circumstances is mainly effected by the simultaneous development and degeneration of organs which lie side by side, as in the muscles of the foot or hand; in terms of physiology,

*Disadvantages of the Upright Position, article in *American Naturalist*, January, 1884, vol. XVIII. p. 1.

†The remarkable skulls and skeletons which have recently been discovered at Spy remove all doubts as to the normal, *i.e.*, racial character of the famous Néanderthal skull, which were entertained by Quatrefages and others. See Fraipont and Lohest, *Archives de Biologie*, 1887, p. 697.

‡This is an epidermal or twitching muscle in the quadrupeds.

we observe the hypertrophy of adaptive organs and atrophy of inadaptive or useless organs. This compensating re-adjustment, whereby the sum of nutrition to any region remains the same during re-distribution to its parts, may be called metatrophism. It is the "gerrymander" principle in nature.

In practical investigation it is very difficult in many cases to determine whether an organ is actually developing or degenerating at the present time, although its variability or tendency to present individual anomalies indicates that some change is in progress. I may instance the highly variable peroneus tertius muscle (Wood). The rise or fall of organs is so constantly associated with their degree of utility that in each case the doubt can be removed by a careful analysis of the greater or less actual service rendered by the part in question. Apart from the question of causation, it is a fixed principle that a part degenerating by disuse in each individual will also be found degenerating in the race.

Degeneration is an extremely slow process; both in the muscular and skeletal systems we find organs so far on the down grade that they are mere pensioners of the body, drawing pay (*i. e.*, nutrition) for past honorable services without performing any corresponding work—the plantaris and palmaris muscles for example. Of course an organ without a function is a disadvantage, so that the final duty of degeneration is to restore the balance between structure and function, by placing it *hors de combat* entirely. One symptom of decline is variability, in which the organ seems to be demonstrating its own uselessness by occasional absence. As Humphrey remarks: "The muscles which are most frequently absent by anomalies are in fact those which can disappear with least inconvenience, either because they can be replaced by others or because they play an altogether secondary rôle in the organism." The stages downward are gradual; the rudiment becomes variable as an adult structure, then as a fœtal structure; the percentage of absence slowly increases until it re-appears only as a reversion; finally the part ceases even to revert and all record of it is lost. This long struggle of the destructive power of degeneration, which you see is essentially an adaptive factor, against the protective power of heredity is the most striking feature of the law of repetition. (See Galton's similar principle of regression in anthropology.)

A careful study of our developing, degenerating, rudimental, and reversional organs amply demonstrates that man is now in a state of evolution hardly less rapid, I believe, than that which has produced the modern horse from his small five-toed ancestor. As far as I can see, the only reason why our evolution should be slower than that of the ancient horse is the frequent intermingling of races, which always tends to resolve types which have specialized into more generalized types. Wherever the human species has been isolated for a long period of time, divergence of character is very marked, as will be seen in some of the races I refer to below.

To lighten the long catalogue of facts, gathered from many authors, I shall frequently allude to habit, but will ask you to consider it for the time as associational rather than causal. Pouchet says: "Man is a creature of the writing table, and could only have been invented in a country in which covering of the feet is universal;" he should have added the "eating table." From the average man our fashions and occupations demand the play of the forearm and hand, the independent and complex movements of the thumb and finger; the outward turning of the foot in walking. These are some of the most conspicuous features of modern habit.

*The skeletal variations.**—In a most valuable essay by Arthur Thomson upon "The Influence of Posture on the Form of the Articular Surfaces of the Tibia and Astragalus in the Different Races of Man and the Higher Apes,"† we find clearly brought out the distinction between congenital variations and those which may be acquired by prolonged habits of life. It is perfectly clear from this investigation that certain racial characters, such as "platycnemism" or flattened tibia, which have been considered of great importance in anthropology, may prove to be merely individual modifications due to certain local and temporary customs. Thomson's conclusions are that the tibia is the most variable in length and form of any long bone in the body. Platycnemia is most frequent in tribes living by hunting and climbing in hilly countries, and is associated with the strong development of the tibialis posticus. The great convexity of the external condyloid surface of the tibia in savage races appears to be developed during life by the frequent or habitual knee flexure in squatting; it is less developed where the tibia has a backward curve, and is independent of platycnemia. Another product of the squatting habit is a facet formed upon the neck of the astragalus by the tibia. This is very rare in Europeans; it is found in the gorilla and orang, but rarely in the chimpanzee. We must therefore be on our guard to distinguish between congenital or hereditary skeletal characters which are fundamental, and "acquired" skeletal variations which may not be hereditary. The latter are of questionable value in tracing lines of descent, if not actually misleading; on the other hand, the teeth, as shown by Cope in his essay on "Lemurine reversion in human dentition," have distinct racial patterns and are reliable indices of consanguinity, because their form can not be modified during life.

The main features of present evolution in the backbone are the elaboration of the spines of the cervical vertebræ, the increase of the spinal curvatures, the shortening of the centra of the lumbar vertebræ and

* For recent general articles, see Blanchard, "L'Atavisme chez l'Homme," *Rev. de Anthrop.*, 1885, p. 425; and Baker, "The Ascent of Man," *Proceedings of the American Association for the Advancement of Science*, 1890. Also, *Smithsonian Report* for 1890, p. 447.

† *Journal of Anatomy and Physiology*, 1889, p. 617.

shifting of the pelvis upward, whereby a lumbar vertebra is added to the sacrum and subtracted from the dorso-lumbar series.

Cunningham has found that the division of the neural spines in the upper cervical vertebræ distinguishes the higher races from the lower.* The spine of the axis is always bifid, but the spines of the cervicals three, four, and five, are also, as a rule, bifid in the European, while they are single in the lower races. The same author shows that the bodies of the lumbar vertebræ are altering, by widening and shortening, to form a firmer pillar of support, with a compensating increase in the length of the intervertebral cartilages.† In the child, the vertebræ present more nearly their primitive elongate compressed form. With this is associated an increase of the forward lumbar curvature (Turner);‡ the primitive (*i. e.*, Simian) curve was backward; even in the negroes the collective measurement of the posterior faces of the five lumbars is greater than the anterior, in the proportion of 106 to 100; whereas in the white the collective anterior faces exceed the posterior in nearly the same proportion—100 to 96.

The lower region of the back is also the seat of one of the most interesting and important of the changes in the body, namely, the correlated evolution of the inferior ribs, the lumbar vertebræ, and the pelvis,—to which embryology, adult and comparative anatomy, and reversion all contribute their quota of proof. In most of the anthropoid apes, and therefore presumably in the pro-anthropos, there were thirteen complete ribs and four lumbar vertebræ, while man has twelve ribs and five lumbars. Thus we may consider the superior lumbar of adult man as a ribless dorsal; not so in the human embryo, however, for Rosenberg§ has found a cartilaginous rudiment of the missing thirteenth rib upon the so-called first lumbar. Atavism contributes an earlier chapter in the history of this region, for Birmingham‖ reports, out of fifty cases examined in one year, two in which there were six lumbars, and in each the thirteenth rib was well developed; this is an interesting example of "correlated reversion," for as the pelvis shifted downward to its ancestral position upon the twenty-sixth vertebra, the thirteenth rib was also restored. The other ribs are in what the ancients styled a "state of flux;" our eighth rib has been so recently floated from the sternum that, and according to Cunningham,¶ it reverts as a true rib in twenty cases out of a hundred, showing a decided preference for the right side. Regarding also the occasional fusion of the fifth lumbar with the sacrum and the unstable condition of the twelfth rib, which is by variation rudimentary or absent, Rosenberg makes bold to predict that in the man of the future the pelvis will shift another step upward to the twenty-fourth vertebræ, and we shall then

* *Journal of Anatomy and Physiology*, 1886, p. 636.

† *Ibid.*, 1890, p. 117.

‡ *Ibid*, 1887, p. 473.

§ *Morph. Jahrb.*, 1876.

‖ *Journal of Anatomy and Physiology*, 1891, p. 526.

¶ *Ibid.*, 1890, p. 127.

lose our twelfth rib. The upright position, and consequent transfer of the weight of the abdominal viscera to the pelvis, may be considered the habit associated with this reduction of the chest; at all events, in the evolution of quadrupeds there is a constant relation of increase between the size of the posterior ribs and the weight of the viscera, until the rib-bearing vertebræ rise to twenty and the lumbars are reduced to three.* It would be interesting to note the condition of the ribs in some of the large-bellied tribes of Africans in reference to this point.

The coccyx has naturally been the center of active search for the missing flexible caudals. As is well known, the adult coccyx contains but from three to five centers, while the embryo contains from five to six. Dr. Max Bartels has made "Die geschwänzten Menschen" the subject of an exhaustive memoir upon cases of the reversion of the tail, while Testut records all the primitive tail muscles in various stages of reversion. Watson reports that the curvatores coccygia (depressores caudæ) occur only in 1 in 1,000 cases.

This suggests a moment's digression to consider the different phases of reversion. The thirteenth rib recurs by what Gegenbaur calls "neogenetic reversion,"† for it is simply the anomalous adult development of an embryonic rudiment. Under neogenetic reversions many authors also include cases of the "arrested development," or persistence of an embryonic condition to adult life, such as the disunited odontoid process of the axis vertebra, which happens to repeat a very remote ancestral condition. I think such cases may illustrate a reversional tendency, although many cases of arrested development, such as anencephaly, have no atavistic significance whatever.‡ More rare and far more difficult to explain are the "palæogenetic reversions," in which the anomaly, such as the supracondylar foramen, reverts to an atavus so remote that the rudiment is not even represented in the embryo.

The features of skull development are primarily the increase of the cranium and the late closure of the cranial sutures, in contrast with the more complete and earlier closure of the facial sutures.

So far as I can gather, this seems to be another region where the white and colored races present reversed conditions; the early closure and arrest of brain development in the negroes is well known; the later closure among the whites is undoubtedly an adaptation to brain growth. In his valuable statistics upon the Cambridge students, Galton says: "Although it is pretty well ascertained that in the masses of the population the brain ceases to grow after the age of nineteen, or even earlier, it is by no means the case with university students. In high honor men head growth is precocious, their heads predominate over the average more at nineteen than at twenty-five."

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*In the elephant and rhinoceros.

†*Morph. Jahrb.*, Bd. VI, p. 585.

‡Anencephaly, it should be said, is frequently associated with numerous reversions.

Many of the cases of arrested closure of facial sutures are reversional, as they correspond with the adult condition of other races, such as the divided malar, or as Japonicum. The human premaxillary, a discovery with which Goethe's name will always be associated, is sometimes partially, more rarely wholly, isolated; it is late to unite with the maxillary in the Australians, and has been reported entirely separate in a new Caledonian child (Deslongchamps) and in two Greenlanders (Carus). The orbito-maxillary frontal suture, cited by Turner as a reversion to the pithecoid condition, is believed by Thomson, after the examination of 1,037 skulls, to be merely an accidental variation, without any deeper significance.* The development of the temporal bone from two centers, observed by Meckel, Gruber, and many others, is considered by Albrecht a reversion to the separate quadrate of the sauro-mammalia. This I think is in the highest degree improbable (see "Limits of Reversion"). The open cranial and closed facial sutures are apparently associated with our increasing brain action and decreasing jaw action; in one case the growth is prolonged and the sutures are left open, in the other, the growth is arrested and the sutures are closed.

Is the lower jaw developing or degenerating? This question has recently been the subject of a spirited controversy between Mr. W. Platt Ball,† representing the Weisman school, and Mr. F. Howard Collins,‡ supporting Herbert Spencer's view that a diminishing jaw is one of the features of our evolution which can only be explained by disuse. Mr. Collins find that, relatively to the skull, the mass of the recent English jaw is one-ninth less than that of the ancient British and, roughly speaking, half that of the Australian. He appears to establish the view that the jaw is diminishing.

Closely connected with this is the evolution of the teeth; how are they tending?

Flower§ has shown, as regards the length of our molar series, that we, together with the ancient British and Egyptians, belong to a small-toothed or "microdont" race; the Chinese, Indians (North American), Malayans, and negroes in part, are intermediate or "mesodont," while the Andamanese, Melanasians, Australians, and Tasmanians are "macrodont." While undersize marks the molars as a whole, the wisdom tooth is certainly in process of elimination; it has the symptoms of decline; it is very variable in size, form, and in the date of its appearance, is often misplaced, and is not uncommonly quite rudimentary (Tomes).‖ Here is another instance where the knife-and-forkless races reverse our degeneracy, for in them not only is the last normal molar

Journal of Anatomy and Physiology, 1890, p. 348.

† Are the Effects of Use and Disuse Inherited? *Nature Series*, 1890.

‡ The Lower Jaw in Civilized Races, 1891.

§ *Journal of the Anthropological Institute*, 1880.

‖ *Dental Anatomy*, p. 416.

(m. 3) large and cut long before the traditional years of discretion, but in the first two lower molars are found two intermediate cusps (Tomes)* which are variable or absent in us (Abbott); moreover, in the macrodont races a surplus molar† (m. 4) is sometimes developed. Mummery reports nine such cases among 328 West Africans (Ashantis). As an instance of associated habit I may here mention that Dr. Lumholtz, the Australian explorer, informs me that in adult natives the teeth are worn to the gum; in the absence of tools they are used in every occupation, from eviscerating a snake to cutting a root. A tour of inspection through any large collection of skulls brings out the contrast between the sound and hard-worn molars of the savage, and the decayed and little-worn molars of the white.

Upon the descent theory, the reduction of teeth in the progenitor of man began as far back as the Eocene period, for not later than that remote age do we find the full complement of three incisors and four premolars in each jaw; now there are but two remaining of each. Baume, a high authority, believes he has discovered eleven cases of a rudimental reversion of one of these lost premolars‡ not cutting the jaw. Not infrequently both these missing teeth occur by reversion. It is difficult to conceive of reversion to such a remote period, yet it is supported by other evidence. An embryonic third incisor has, I believe, been discovered. As long ago as 1863 Sedgwick§ recorded a case of six upper and lower incisors in both jaws, and appearing in both the milk and permanent dentitions; this anomaly was inherited from a grandparent, a striking instance of hereditary reversional tendency. We might consider that these cases of supernumerary teeth belong in the same category as polydactylism, or additional fingers, which are not atavistic, but for the fact that they do not exceed the typical ancestral number, whereas the fingers do.

We owe to Windle‖ a careful review of the incisor reversions, in which he shows that the lost incisors re-appear more frequently in the upper than the lower jaw (coinciding with the fact that the lower teeth were the first to disappear in the race); he considers that the lost tooth was the one originally next the canine, and concludes by adding our present upper outer incisor to the long list of degenerating organs.¶ He supports this statement by measurements and by citing cases in which it has been found absent. Yet the reduction of the jaws is apparently outstripping that of the teeth, if we can judge from the

* *Dental Anatomy*, p. 416.

† This tooth has been found in several other macrodont tribes (Australians, Tasmanians, Neo-Caledonians), Fontan.

‡ *Odontologische Forschungen*, p. 268. This rudiment is found between the first and second normal premolars.

§ *British and Foreign Medico Chirurgical Review*, 1863.

‖ *Journal of Anatomy and Physiology*, 1887, p. 85.

¶ Baume believes that the missing incisor is the primitive median one, while Turner believes it is the second. The fossil record supports Windle.

frequent practice among American dentists of relieving the crowded jaw by extraction.

We now turn to the arches and limbs. Flower has pointed out that the base of the scapula is widening in the higher races, so that the "index," or ratio of length to breadth, is quite distinctive. Gegenbaur associates this with the development of the scapulo-humeral muscles and the greater play of the humerus as a prehensile organ.

In general, the arm increases in interest as we descend toward the hand, both in the skeleton and musculature, because here we meet with the first glimpses of facts which enable us to form some estimate of the rate of human evolution. The well-known humeral torsion (connected with increased rotation) ascends from 152° in the polished stone age to 164° in the modern European. The intercondylar foramen, or perforation of the olecranon fossa, is exceptionally well recorded;* it is found in 30 per cent of skeletons of the reindeer period; in the dolmen period it fell to 24 per cent; in Parisian cemeteries between the fourth and tenth centuries it is found in 5.5 per cent; it has now fallen to 3.5 per cent. The condylar foramen, occasionally forming a complete bridge of bone above the inner condyle and transmitting the median nerve and brachial artery, is known as the "entepicondylar" foramen in comparative anatomy, and is one of the most ancient characters of the mammalia; it reverts palæogenetically in 1 per cent of recent skeletons, but much more frequently in inferior races (Lamb). In the wrist bone is sometimes developed another extremely old structure—the oscentrale. Gruber† reported its recurrence at 0.25 per cent approximately. This is a case of neogenetic reversion, for Leboucq‡ shows that there is a distinct centrale in every human carpus in the first part of the second month, which normally fuses with the scaphoid by the middle of the third month.

The divergence of the female from the male pelvis is an important feature of our progressive development; it is proved by the fact that, as we descend among the lower races it becomes increasingly difficult to distinguish the female skeleton from the male, for the pelves of the two sexes are nearly uniform. Here it seems to me is a most interesting problem for investigation. Arbuthnot Lane's§ views of the mechanical causes of this divergence, which are strongly Lamarckian, may be weighed with the theory of survival of the fittest, for the large female pelvis is perhaps the best example that can be adduced of a skeletal variation which would be preserved by natural selection, for reasons which are self-evident. The third trochanter of the femur is believed by Prof. Dwight,‖ of the Harvard Medical School, to be a true re-

* See Blanchard, op. cit., p. 450.

† Virchow's *Archiv*, 1885, p. 353.

‡ *Ann. de la Soc. de Méd. de Gand, 1884.*

§ *Journal of Anatomy and Physiology*, 1888, p. 214.

‖ *Ibid.*, 1890, p. 61.

version (1 per cent) in our race and not an acquired variation, as it is very frequently found among the Sioux, 50 per cent, Laplanders, 64 per cent, and Swedes, 37 per cent; like the condylar foramen it is an ancient mammalian character.

The foot is full of interest in its association of degeneration and development with our present habits of walking; the great toe is increasing and the little toe diminishing, causing the oblique slope from within outward which is in wide contrast with the square toes in the infant or in the lower races. In many races the second toe is as long as the first, and the feet are carried parallel instead of the large toe turning out. If anyone will analyze his sensations in walking, even in his shoes, he will be conscious that the great toe is taking active part in progression while the little toe is passive and insensitive. We are not surprised, therefore, to learn from Pfitzner* that we are losing a phalanx, that in many human skeletons (41.5 per cent in women and 31 per cent in men) the two end joints of the little toe are fused. The fusion occurs not only in adults, but between birth and the seventh year, and in embryos of between the fifth and seventh month. The author does not attribute this to the mechanical pressure of tight shoes because it is found in the poorer classes. He considers it the first act of a total degeneration of the fifth toe.

Variations in the muscles.—The evolution of the muscles of the foot looks in the same direction. As you know, the large toe in many of the apes is set at an angle to the foot and is used in climbing. It is still employed in a variety of occupations by different races. According to Tremlett,† the celebrated great toe of the Annamese, which normally projects at a wide angle from the foot, is contemptuously mentioned in Chinese annals of 2285 B. C., the race being then described as the "cross-toes." The long flexor of the hallux is apparently degenerating, showing a tendency to fuse with the flexor communis; the abductors and adductors of this toe are also degenerating, the latter being proportionately large in children (Ruge). The little toe exhibits only by reversion its primitive share of the flexor brevis (Gegenbaur); more frequently it varies in the direction of its future decline by losing its flexor brevis tendon entirely. Two atavistic muscles, the abductor metatarsi quinti‡ (always present in the apes), and the peroneus parvus (Bischoff), also point to the former mobility of the outer side of the foot. In general the bones of the foot are developing on the inner and degenerating on the outer side, with loss of the lateral movements of the hallux and of all independent movements in the little toe. The associated habit is that the main axis of pressure and strain now connects the heel and great toe, leaving the outer side of the foot comparatively functionless.

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* See Humboldt, 1890; also *Nature*, 1890, p. 301.

† *Journal of the Anthropological Institute*, 1880, p. 461.

‡ Darwin: *Descent of Man*, p. 42.

The variations in the muscular system mark off more clearly the regions of contemporary evolution, and therefore are even more instructive than those in the skeleton. Muscular anomalies have however never been adequately analyzed. Even the remarkable memoir of M. Testut, "Sur les Anomalies musculaires," is defective in not clearly distinguishing between variations which look to the future, those which revert to the past, and those which are fortuitous, for the author is strongly inclined to refer all anomalies to reversion.

The law of muscular evolution is specialization by the successive separation of new independent contractile bands from the large fundamental muscles, while the law of skeletal evolution is reduction of primitive parts and the specialization of articular surfaces. The number of muscles in the primates as a whole has therefore been steadily increasing, while the number of bones has been dimimishing. In man the number of muscles is probably increasing in the regions of the lower arm, and diminishing in every other region. The analysis is rendered very difficult by the fact that some muscles (*e. g.*, those connecting the shoulder with the neck and back) revert to a former condition of greater specialization when they were employed in swinging the body by the arms, and in quadrupedal locomotion; while other muscles (*e. g.*, those connecting the forearm and fingers) revert to a former simpler arrangement when the hand was mainly a grasping organ, and the thumb was not opposable.

As in the skeleton, we find that muscular anomalies include (1) palæogenetic reversions, or complete restorations of lost muscles; (2) neogenetic reversions, or revivals of former types in the relations of existing muscles; (3) progressive variations, which either by degeneration or specialization point to future types; (4) fortuitous variations, which cannot be referred to either of the above.

Duval observes that the flexor longus policis repeats in reversion all the stages of its evolution between man and the apes, in which it is a division of the flexor profundus. Gruber and others have even observed the absence of the thumb tendon. This is true of all the new muscles. Of this Testut writes:

"Ne dirait-on pas, en le voyant s'éloigner si souvent de son état normal, que la nature voudrait le remener à sa disposition primitive, luttant ainsi sans cesse contre l'adaptation, et ne lui abandonnant qu' à regret l'une de ses plus belles conquêtes."

Speaking of the hand, Baker says:

"On comparing the human hand with that of the anthropoids, it may be seen that this efficiency is produced in two ways—first increasing the mobility and variety of action of the thumb and fingers; second, reducing the muscles used mainly to assist prolonged grasp, they being no longer necessary to an organ for delicate work requiring constant re-adjustment."*

*"The Ascent of Man," *Proceedings Am. Assoc. Adv. Sci.* 1890, vol. xxxix, p. 353. Also, *Smithsonian Report*, 1890, p. 449.

You have noticed the recent discovery that the grasping power of infants is so great that the reflex contraction of the fingers upon a slender crossbar sustains their weight; this power and the decided inward rotation of the sole of the foot and mobility of the toes are persistent adaptations. Our grasping muscle, the palmaris longus, is highly variable and often absent; like the plantaris of the calf, it has been replaced by other muscles, and its insertion has been withdrawn from the metapodium to the palmar fascia. In negroes we frequently find the palmaris reverting to its former function of flexing the fingers by insertion in the metacarpals.

The rise of muscular specialization by degeneration is beautifully shown in the extensor indicis, which, while normally supplying the index only, reverts by sending its former slips to the thumb, middle, and even to the ring finger. Testut* believes that the extension power of the middle and ring fingers has declined, as the cases of reversion point to greater mobility; the extensor minimi digiti is distinct and highly variable (Wood), often sending a slip to the ring finger.

The entire flexor group of the hand, excepting the palmaris, is apparently specializing. The demonstration by Windle† and Bland Sutton, that the origin of the flexors and extensors is shifting downward from their original position, is evidence of an adaptation to the short special contractions required of them.

The abductor pollicis‡ is also progressive and variable (Wood); the reduplication of its inferior tendon, which is sometimes provided with a distinct muscle, apparently points to the birth of a second abductor. The opponens of the thumb is well established and constant. Variability seems to characterize both the developing and degenerating muscles; the latter are apt to be absent; it is rare that an important muscle, such as the extensor indicis, is absent, but such cases are reported.

It is interesting to note that the lost muscles of the body are almost exclusively in the trunk or shoulder, and pelvic arches, and not in the limbs. It will be remembered that the human shoulder joint is exceptionally rigid, whereas in the quadrupedal state it was a factor in progression. Some of the muscular reversions in this quadrupedal region are the levator clavieulæ (1 to 60, Macalister), trachelo-clavicularis, scalenus intermedius, acromio-basilaris (Champneys), transversus nuchæ (Gegenbaur). Apparently associated with the former swinging of the body by the fore limb in the arboreal life are the atavistic coraco-brachialis-brevis (Testut), the epitrochleo-dorsalis (Testut), and pectoralis tertius (Testut).§

Centers of variability.—As the literature is so readily accessible I will not multiply illustrations of the innumerable congenital variations

* *Sur les Anomalies Musculaires*, p. 564.

† *Journal of Anatomy and Physiology*, 1890, p. 72.

‡ Or extensor ossis metacarpi pollicis. See Testut, p. 553.

§ Quain describes seventy anomalous muscles (*Ant.*, vol. I.). Testut describes a still larger number.

related to human evolution. I call attention to several important inductions. First, there are several centers in which both the skeletal and muscular systems are highly variable. Second, that the most conspicuous variations, and therefore the most frequently recorded, are reversions. Third, that structure lags far behind function in evolution.

The conclusions of Wood, and of Testut,* are that variability is independent of age or sex, of general muscularity, and of abnormal mental development. Wood found 981 anomalies in 102 subjects; of these, 623 were developed upon both sides of the body, while 358 were unilateral. Of still greater interest are the statistics collected by Wood between 1867–'68 in the dissecting room of King's College, upon 36 subjects (18 of each sex). These show that there are more anomalies in the limbs than in the trunk; that anomalies are rare in the pelvis; that there were 292 anomalies in the anterior limbs to 119 in the posterior; that in both limbs the anomalies increase toward the distal segments, culminating in the muscles of the thumb, where they rise to 90 per cent. (mainly flexor longus pollicis, and abductor longus pollicis). These facts seem to prove conclusively that while variation is universal it rises to a maximum in the centers where human evolution is most rapid; here are Herbert Spencer's conditions of unstable equilibrium. This has a direct bearing, as I shall show, upon our theory of heredity.

Fortuitous congenital variations.—I have thus far considered only those variations which apparently have a definite relation to the course of human evolution. There is an entirely different class of congenital variations which may be described as fortuitous or indefinite because they do not occur in any fixed percentage of cases; they are liable to take any direction; they can not be considered reversional because they are not found in the hypothetical atavus, and there is not sufficient evidence to cause us to consider them as incipient features of our future structure.

Some may not be truly congenital (*i. e.* springing direct from the germ cells) but may be merely deviations from the normal course of development. I may instance the variations in the carpus recorded by Turner† in which the trapezium and scaphoid unite, or the trapezoid and semilunar divide, or the astragalus and navicular unite (Anderson).

The best example of fortuitous congenital variations are seen in supernumerary fingers and vertebræ. The eighth cervical vetebra, bearing a rudimentary rib,‡ is not a reversion because the most remote ancestors of man have but seven cervicals. In cases where a rib is developed upon the seventh cervical, however, the reversion theory is perhaps applicable because rib-bearing cervicals are relatively less re-

* *Sur les Anomalies Musculaires*, p. 760.

† *Journal of Anatomy and Physiology*, 1884, p. 245.

‡ Arb. Lane: *Journal of Anatomy and Physiology*, 1885, p. 266.

mote. The same distinction applies to polydactylism. How absurd it is to consider a sixth finger atavistic, when we remember that even our Permian ancestors had but five fingers.

We can not however class, as purely fortuitous a variation which occurs in a definite percentage of cases presenting twenty four different varieties, but occurring in the same region. Such is the much-discussed* musculus sternalis, a muscle extending vertically over the origin of the pectoralis from the region of the sterno-mastoid to that of the obliquus externus. Testut lightly applies his universal reversion theory, and as this muscle is not found in any mammal considers it a regression to the reptilian presternal (Ophidia)! Turner also considered it as reversional in connection with the panniculus carnosus, the old twitching muscle of the skin, which plays so many freaks of reversion in the scalp and neck; this view is negatived by the fact that this muscle is innervated by the anterior thoracic (Cunningham, Shepherd) which would connect it with the pectorial system, or by the intercostal nerves (Bardeleben). Although the high percentage of recurrence in the sternalis in anencephalous monsters (90 per cent according to Shepherd) supports the reversion view, it is offset by the high percentage (4 per cent.) in normal subjects, for this is far too high for a structure of such age as the reptilian presternal. Cunningham has advanced another hypothesis, first suggested by the frequency of this anomaly in women, that this is a new inspiratory muscle, having its origin in reversion, but serving a useful purpose when it recurs, and therefore likely to be perpetuated.

These fortuitous variations, as well as variations in the proportions of organs, play an important part in the present discussion upon heredity, for it is believed by the Weismann school that such variations, if they chance to be useful, will be accumulated by selection and thus become race characters.

The limits of reversion.—There is such a wide difference of opinion upon the subject of reversions that it is important to determine what are some of the tests of genuine reversions. How shall we distinguish them from indefinite variations or from anomalies like the sternalis muscle, which strain the reversion theory to the breaking point?

Testut,† Duval, and Blanchard take the extreme position that almost all anomalies reproduce earlier normal structures, and that the exceptions may be attributed to the incompleteness of our knowledge of comparative anatomy. I may here observe that popular as the descent theory has recently become in France, neither these anthropologists nor the palæontologists show a very clear conception of the phyletic or branching element in evolution. If they do not find a muscle in the primates they look for it in other orders of mammals. Now, since these other branches diverged from that which gave rise to man at a

* See Turner, Shepherd, and Cunningham: *Journal of Anatomy and Physiology.*
† *Sur les Anomalies Musculaires*, p. 4.

most remote period, the discovery of a similar muscle may be merely a coincidence; it is by no means a proof of reversion.

The first test of reversion is therefore the anatomy of the atavus and this is derived partly from the palæontological record of the primates, partly from the law of divergence, viz., that features which are common to all the living primates were probably also found in the stem form which gave rise to man; finally, from the comparative anatomy of the living anthropoidea.

The second test is whether a structure passes the limits of reversion as determined by cases of atavism in which there can be no reasonable doubt. Two of these phenomena have recently been discussed, which seem to extend the possibilities of reversion back to structures which were lost at a very remote period. I refer to papers by Williams and Howes. Williams* has analyzed 166 recorded cases of polymastism; he finds that supernumerary nipples of some form occur in two per cent, and that in all except four of the cases examined the anomalies, tested by position, etc., support the reversion hypothesis. In the living lemurs, which form a persistent primitive group of monkeys, we find that the transition from polymastism to bimastism is now in progress by the degeneration of the abdominal and inguinal nipples; it is fair to assume that the higher monkeys also lost their abdominal nipples at a primitive stage of development, and therefore that cases of multiple nipples indicate reversion to a Lower Eocene condition! Howes† has recently completed a most interesting study of the "intranarial epiglottis," or cases in which the epiglottis is carried up into the posterior nares, as in young marsupials and some cetacea, to subserve direct narial respiration. This has now been observed to occur by reversion in all orders of mammals, including the monkeys and lemurs. One case has also been reported by Sutton of its occurrence in a human fetus. This is apparently a human reversion to a structure much older than the age of the lemurs.

The third test is the inverse ratio to time. It would seem, *a priori*, that the percentage of recurrence of atavistic structures should decrease as the extent of time elapsing since the structure disappeared increases. This law is apparently established in the case of the condylar and intercondylar foramina, and if we examine all the percentages which have been established we see at once that they bear a ratio to time; compare the relative frequency of the ischio-pubic (50 per cent), dorso-epitrochlearis (5 per cent), and levator-claviculæ (1.66 per cent) muscles with the periods which have elapsed since their past service. This is why it is so important to establish percentages for all our atavistic organs; fuller statistics will not only bear upon heredity, but I can conceive of their application to the extremely difficult problem of estimating geological time. We must, of course, establish as a stand-

* *Journal of Anatomy and Physiology*, 1891, p. 224.
† *Ibid*, 1889, p. 587.

ard cases of congenital variation in which the frequency of recurrence has been steadily declining in the same race between two known periods of time—an available structure is the intercondylar foramen or supratrochlear foramen, as recorded by Blanchard, Shepherd, and others.

The reversional tendency is hereditary. There are many cases, both of reversions (as in the teeth) and indefinite variations being hereditary, that is, re-appearing in several generations, or skipping a generation and recurring in the second.

Summary.—There are clearly marked out several regions in the human body in which evolution is relatively most rapid, such as the lower portion of the chest, the upper cervicals, the shoulder girdle in its relation to the trunk, the lower portion of the arm and hand, the outer portion of the foot. We notice that these regions especially are centers of adaptation to new habits of life in which new organs and new relations of parts are being acquired and old organs abandoned.

We observe also that all parts of the body are not equally variable, but these centers of evolution are also the chief centers of variability. The variations here are not exclusively, but mainly, of one kind; they rise from the constant struggle between adaptation and the force of heredity. Here is a muscle like the extensor indicis attempting to give up an old function and establish a new one; it maintains its new function for several generations, and then goes back without any warning to a function which it had thousands of years ago. Thus the force of reversion strikes us as a universal factor.

Now the singular fact about reversion is the frequent proof it affords of what Galton has called "particulate inheritance." When the extensor indicis reverts, all the muscles around it may be normal; therefore we are obliged to consider each of these muscles as a structure by itself, with its own particular history and its own tendencies to develop or degenerate. Thus it is misleading to base our theory of evolution and heredity solely upon entire organs; in the hand and foot we have numerous cases of muscles in close contiguity, one steadily developing, the other steadily degenerating. Reversion very rarely acts upon many structures at once; when it does, we have a case of diffused anomaly, some repetition in the epidermis, or in the entire organism of a lower type.

Yet in spite of reversion and the strong force of repetition in inheritance, the human race is steadily evolving into a new type. We must, it seems to me, admit that an active principle is constantly operating upon these particular structures, guiding them into new lines of adaptation, acting upon widely separate minor parts, or causing two parts, side by side, to evolve in opposite directions, one toward degeneration, the other toward development.

I may now recall the two opposed theories as to what this active principle is:

The first, and oldest, is that individual adaptation, or the tendencies

Partial table of characters in evolution.

General regions of evolution.	Developing organs.	Degenerating organs.				
		Reduction.	Variable.	Rudiments (occasionally absent).	Reversions (from embryo).	Reversions (from germ cells).
Skull and jaw.	Cranium.	Facial sutures.			Premaxillary.	
Spinal curvatures.		Infer. maxilla.				
		Hyoids.	Lumbars and pelvis.	Coracoid.		
Cervicals lumbars, and coccyx.	Female pelvis.			4th and 5th caudals.	5th and 6th caudals.	Caudals+.
Lower ribs.		8th rib.	12th rib.		13th rib.	7th cerv. ribs.
Scapula and lower humerus.	Scapula.					Condylar for.
	Clavicle.					S. trochlear. for.
Outer side of pes.	Hallux.	4th and 5th digits of pes.	Terminal phalanx of 5th dig. of pes.			3d trochanter.
	Tibia.				Centrale-manus.	
					Intermedium. pes.	
Teeth		Canines			? Lateral incisor.	×
		Incisors, lateral sup.			? Third premolar.	4th premolar.
		3d molar.	3d molar.			
Flexors and extensors of arms	Flex. prof. and perf.			Panniculus carnosus	×	Trans. nuchæ.*
	Extensor indicis.					Epitrochl. dors.
	Flex. long. pollicis.					Acromio-basilar.
	Abd. long. pollicis.					Levator claviculæ.
						Pect. tertius.
						Cor. brach. brev.
		Pyramidalis.				Ischio-pubic.
Shoulder to trunk.	Triceps extensor suræ.	Psoas parvus.				Depressores caudæ.
						Scansorius.
Trunk to femur.	Glutæal group.	Abd. and add. hallucis.	Muscles, 5th toe.	Plantaris.		Abd. metars. 5th.
	Facial group.			Palmaris.		Peroneus parvus.

* It is probable that some of these muscles are represented in the fœtus.

established by use and disuse upon particular structures in the parent are in some degree transmitted to the offspring and thus guide the main course of variation and adaptation.

The second is that all parts of the body are variable, and that wherever variations take a direction favorable (that is, adaptive) to the survival of the parent they tend to be preserved; where they take the opposite direction they tend to be eliminated. Thus, in the long run, adaptive variations are accumulated and a new type is evolved.

It is evident at once, from a glance over the facts brought forward in this lecture, that the first theory is the simplest explanation of these facts; that use and disuse characterizes all the centers of evolution; that changes of structure are slowly following our changes of function or habit.

But while the first explanation is the simplest it by no means follows that it is the true one. In fact, it lands us in many difficulties, so that I shall reserve the pros and cons for my second lecture upon heredity. The Lamarckian theory is a suspiciously simple explanation of such complex processes.

LECTURE II.—THE DIFFICULTIES IN THE HEREDITARY THEORY.

Nur muss ich nochmals betonen, dass nach meiner Auffassung der Anfang einer neuen Reihe erblicher Abweichungen, also auch der Eintritt einer neuen Art ohne eine vorausgegangene erworbene Abweichung undenkbar ist.—VIRCHOW.

State of opinion.—The above quotation from one of the most eminent authorities of our times represents the unshaken conviction of a very large class upon one side of the question of transmission of acquired characters, which is met by equally firm conviction upon the other side.

Herbert Spencer, whose entire system of biology, psychology, and ethics is based upon such transmission, says: "I will only add that, considering the width and depth of the effects which acceptance of one or other of these hypotheses must have on our views of life, mind, morals, and politics, the question which of them is true demands, beyond all other questions whatever, the attention of scientific men."* This shows that Spencer considers the matter still *sub judice*, and lest you may think I am bringing before you an issue in which learning and experience are ranged against ignorance and prejudice, I have taken some pains by correspondence with a number of friends abroad to learn the present state of opinion. The two leading English and French authorities upon this subject express themselves doubtfully.

Galton's mind is still wavering, as in his work of 1889 he says:

"I am unprepared to say more than a few words on the obscure, unsettled, and much-discussed subject of the possibility of transmitting acquired faculties. - - - There is very little direct evidence of its influence in the course of a single generation, if the phrase of 'acquired faculties' is used in perfect strictness and all inheritance is excluded that could be referred to some form of natural selection, or of infection before birth, or of peculiarities of nurture and rearing."†

Nineteenth Century, 1889.

† *Natural Inheritance*, 1889, p. 14.

Ribot, although in the center of the French Lamarckians, says: "Notwithstanding these facts the transmission of acquired modifications appears to be very limited, even when occuring in both of the parents."

Excepting from Kölliker; His, the Leipsic anatomist; Pflüger, the physiologist; Ziegler, in pathology; and De Vries, in botany, Weismann has not found much sympathy from his own countrymen in his opinion "that acquired characters can not be transmitted; - - - that there are no proofs of such transmission, that its occurrence is theoretically improbable, and that we must attempt to explain the transformation of species without its aid."* Besides Virchow † and Eimer,‡ Haeckel has expressed himself strongly against Weismann. My colleague, Prof. Wilson, writes me (Munich, December 31, 1891) that, while Weismann's modified theories as to the phenomena in the reproductive cells are pretty generally accepted, Hertwig, Hofer, Paully, Boveri, and others are pronounced advocates of the acquired-character-transmission theory.

In Paris Brown-Séquard, who was among the first to test this problem experimentally by observing the inheritance of the effects of nerve lesions, his assistant, Dupuy, Giard, Duval, Blanchard, and others are on the affirmative, or Lamarckian side.

Physiologists generally have fought shy of the question, although I think in the end they will be forced to take it up with the morphologists, and give us the physio-morphological theory of heredity of the future. Prof. Michael Foster, of Cambridge, and Prof. Burdon-Sanderson, of Oxford, both write me that the question has hardly come into the physiological stage of inquiry at all. Yet in England Weismann has found his strongest supporters among some of the naturalists: Wallace, Lankester, Thiselton Dyer, Meldola, Poulton, Howes, and others; while, excepting Windle, the anatomists, including Mivart and Lawson Tait, with Sir William Turner as the most prominent, are all Lamarckians. Huxley, Romanes, and Flower are said to be doubtful. In this country the opinion of naturalists is directly the outgrowth of the class of studies in which each happens to be engaged. So far as I know every vertebrate and invertebrate palæontologist is a Lamarckian,§ for in this field all evolution seems to follow the lines of inherited use and disuse; most of those engaged upon invertebrate zoölogy incline to follow Weismann. I have conversed upon this subject with many physicians, and find that without exception the transmission of acquired characters is an accepted fact among the profession.

Exact statement of the problem.—It is important at the outset to

Biologisches Centralblatt, 1888, pp. 65 and 97.

† Ueber den Transformismus, *Archiv f. Anthropologie*, 1889, p. 1.

‡ Organic Evolution, upon the Law of Inheritance of Acquired Characters. Tübingen, 1888. Trans.

§ See the writings of Hyatt, Cope, Ryder, Dall, Scott, and others.

state most clearly what is and what is not involved in this discussion. Weismann* does not claim that the reproduction or germ cells are uninfluenced by habit; on the other hand, he admits that most important modifications in these cells may and do result from changes of food, climate, from healthy or unhealthy conditions of the body; also from infectious disease, where it is quite as possible that the microbes may enter the reproductive cells as any other cells of the body; from alcoholism, where the normal molecular action of the protoplasm of the germ cells may be disturbed, resulting in abnormal development, and there are some very interesting experiments which I shall cite on this point; from some nervous disorders which profoundly modify cell-function in all the tissues; in other words, *ovum sanum in corpore sano.* But to accept all this, and even to include all our rapidly increasing knowledge of the direct relation between such phenomena as production of deformities and determination of sex, and the influences of environment upon the ovum; or the influences of the mother upon the fœtus—this is all aside from the real question at issue.

It may be stated thus: Given *G*, the ova and spermatozoa, the germ cells or material vehicles of hereditary characters; *S*, the body or somatic cells of all the other tissues conveying the hereditary characters of nerve, muscle, and bone; *V*, the variations in these body cells "acquired" during lifetime; given these factors, the real question is: Do influences at work producing variations in certain body cells of the parent so affect the germ cells of the parent that they re-appear in corresponding body cells of the offspring? To take a concrete case, will the increased use of the cells of the extensor indicis muscle in the parent so stimulate that portion of the germ cells which represents this muscle that the increment of growth will in any degree re-appear in the offspring?

This is what is required of heredity upon the Lamarckian hypothesis, and I think you will see at once that while this hypothesis simplifies the problem of evolution it in a corresponding degree renders more difficult the problem of heredity—for we have not the first ray of knowledge of what such a process involves. There is no quality more essential to scientific progress than common honesty; if we take a position let us face all its consequences; the more we reflect upon it the more serious the Lamarckian position becomes.

In the present lecture let us first briefly review the progress of the science of heredity which has led up to the present discussion. Second, let us examine the evidence for and against the Lamarckian theory, and inquire how far natural selection can explain all the facts of evolution. Third, let us examine the evidence for such a continuous relation between the body cells and germ cells as must exist if the Lamarckian theory is the true one.

History of the heredity theory.—In a valuable summary of the past

* See Essays upon Heredity and Kindred Biological Problems, 1889. Trans.

theories of heredity* J. A. Thompson distinguishes three general problems, which are often confused: 1st. What characters distinguish the germ cells from other cells of the body? 2d. How do the germ cells derive these distinguishing characters? 3d. How shall we interpret "particulate" inheritance, or the re-appearance of single peculiarities in the offspring?

The various theories may be grouped under two heads, "Pangenesis of Germ cells" and "Continuity of Germ cells" according to the dominating idea in each.

1. Pangenesis.—The idea pervading pangenesis was first expressed by Democritus that the "seed" of animals was derived by contributions of material particles from all parts of the bodies of both sexes, and that like parts produced like. Two thousand years later, Buffon revived this conception of heredity in his "Molecules organiques." In 1864 Herbert Spencer suggested the existence of "physiological units," derived from the body cells of the parent, forming the germ cells and then developing into the body cells of the offspring.

It is interesting to note the course of Darwin's thought upon this matter in his published works and in his "Life and Letters." He was at first strongly opposed to the views upon evolution advanced by Buffon, by Erasmus Darwin, his grandfather, expanded by Lamarck, and now known as Lamarckian. But gradually becoming convinced that his own theory of natural selection could not account for all the facts of evolution, he unconsciously became a strong advocate of Lamarck's theory, and contributed to it a feature which Lamarck had entirely omitted, namely, a theory of heredity expressly designed to explain the transmission of acquired characters. Darwin's "provisional hypothesis of pangenesis"† postulated a material connection between the body cells and germ cells by the circulation of minute buds from each cell; each body cell throws off a "gemmule" containing its characteristics, these gemmules multiply and become especially concentrated in the germ cells; in the latter they unite with others like themselves; in course of development they grow into cells like those from which they were originally given off. (See Fig 1, Diagram II.)

Galton, who has always been doubtful in regard to use inheritance, while advancing a theory of "continuity," partly approved Darwin's pangenesis idea in the cautious statement: "Each cell may throw off a few germs that find their way into the circulation and thereby have a chance of entering the germ cells."‡ At the same time Galton contributed very important experimental disproof of the existence of "gemmules," and in fact—of the popular idea of the circulation of hereditary characters in the blood, by a series of careful experiments upon the

*See *Proc, Roy. Soc. Edin.*, 1888, p. 93.

† See *Animals and Plants under Domestication*, 1875, vol. II, p. 349.

‡ *Contemporary Review*, vol. XXVII, p. 80-95.

transfusion of blood in rabbits; he found that the blood did not convey with it even the slightest tendency to transfer normal characteristics from one variety to another.

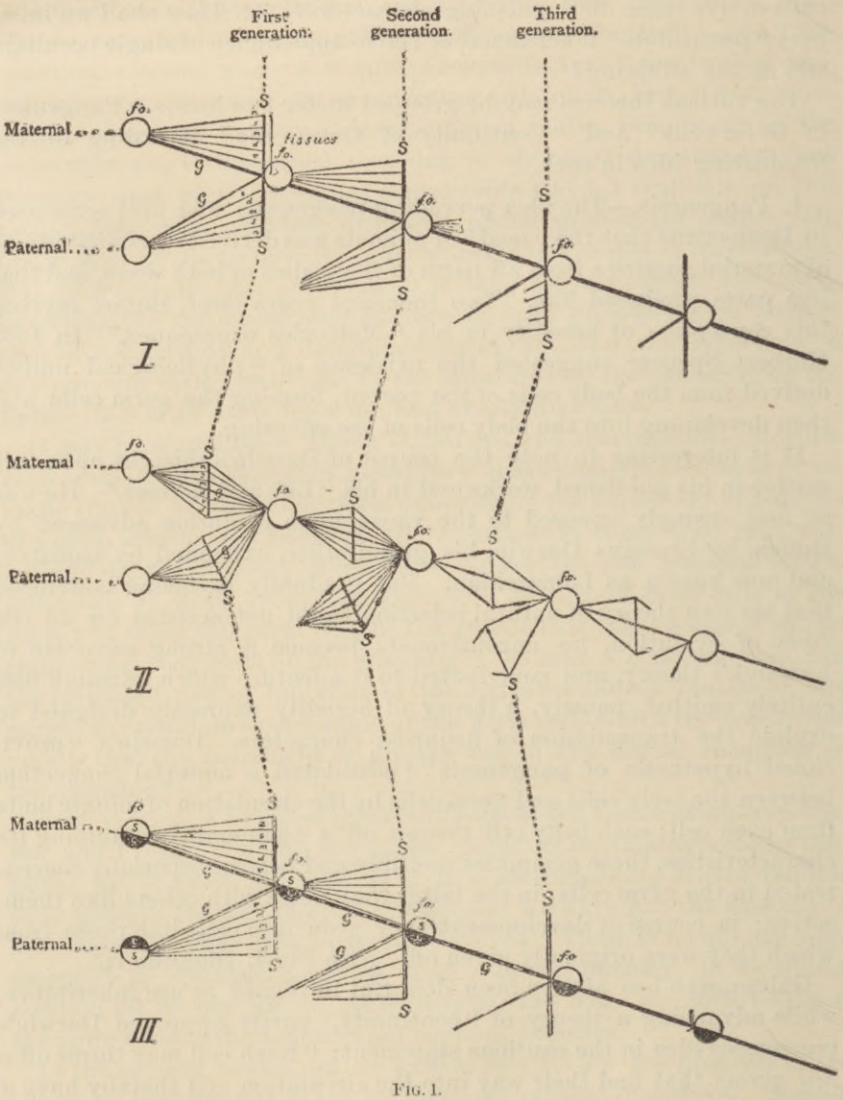

FIG. 1.

f. o., fertilized ovum or *embryo*, containing maternal and paternal characteristics; *S*, soma, or adult body, containing *s, m, d, v, somatic cells* of the various tissues; and *G, germ cells* of the reproductive glands.

I. HISTOGENESIS.—Showing the successive rise *G*, and union *f. o.* of the maternal and paternal germ cells by direct histogenesis.

II. PANGENESIS.—Showing the tissues of the body *S*, contributing to the germ cells *G*, so that each *f. o.* is composed of elements from both the somatic and germ cells.

III. CONTINUITY.—Showing the division of the embryo *f. o.*, into somatoplasm, *s* (from which arise the body cells), and germ plasm, *G* (which passes direct to the germ cells), establishing a direct continuity.

Prof. Brooks, of the Johns Hopkins University, then contribute and original modification of pangenesis in which the functions of the ova and

spermatozoa were sharply differentiated.* (1) He regarded the ovum as a cell especially designed as a storehouse of hereditary characteristics, each characteristic being represented by material particles of some kind; thus hereditary characters were handed down by simple cell division, each fertilized ovum giving rise to the body cells in which its hereditary characters were manifested and to new ova in which these characters were conserved for the next generation (this portion of Brooks's theory is very similar to Galton's and Weismann's). (2) The body cells have the power of throwing off "gemmules," but this is exercised mainly or exclusively when its normal functions are disturbed, as in metatrophic exercise or under change of environment. (3) These gemmules may enter the ovum, but the spermatozoan is their main center. According to this view the female cell is rather conservative and the male cell progressive; the union of these cells produces variability in the offspring, exhibited especially in the regions of the offspring corresponding to the regions of functional disturbance in the parent. This hypothesis was well considered, and while that feature of it which distinguishes the male and female germ cells as different in kind has been disproved, and the whole conception of gemmules is now abandoned, the fact still remains that we shall nevertheless be obliged to offer some hypothesis to explain the facts disregarded by Weismann for which Brooks provides in his theory of the causes of variation.

2. Continuity of germ cells.—The central idea here is an outgrowth of our more modern knowledge of embryogenesis and histogenesis, and is therefore comparatively recent; it is that of a fundamental distinction between the "germ cells," as continuous and belonging to the race, and the "body cells," as belonging to the individual. Weismann has refined and elaborated this idea, but it was not original with him.

Richard Owen,† in 1849, Haeckel,‡ in 1866, Rauber,§ in 1879, in turn dwelt upon the distinction which Dr. Jaeger, now of manufacturing fame, first clearly stated:

"Through a great series of generations the germinal protoplasm retains its specific properties, dividing in every reproduction into an ontogenetic portion, out of which the individual is built up, and a phylogenetic portion, which is reserved to form the reproductive material of the mature offspring. This reservation of the phylogenetic material I described as the continuity of the germ protoplasm. - - - Encapsuled in the ontogenetic material the phylogenetic protoplasm is sheltered from external influences, and retains its specific and embryonic characters." The latter idea has, under Weismann, been expanded into the theory of isolation of the germ cells.

Galton introduced the term "stirp" to express the sum total of

* *The Law of Heredity*, 1883.

† See Parthenogenesis, in his *Anatomy of Vertebrates*.

‡ *Generelle Morphologie*, vol. II, p. 170.

§ *Zool. Anz.*, vol. IX, p. 166.

hereditary organic units contained in the fertilized ovum. His conception of heredity was derived from the study of man, and he supported the idea of continuity in the germ cells in order to account for the law of transmission of "latent" characters; it is evident from this law that only a part of the organic units of the "stirp" become "patent" in the individual body; some are retained latent in the germ cells, and become patent only in the next or some succeeding generation. For example, the genius for natural science was "patent" in Erasmus Darwin, grandfather of the great naturalist, it was "latent" in his son, and re-appeared intensified in his grandson, Charles Darwin. I have elsewhere* summed up as follows Galton's general results, which so remarkably strengthen the "continuity" idea: We are made up, bit by bit, of inherited structures, like a new building, composed of fragments of an old one, one element from this progenitor, another from that, although such elements are usually transmitted in groups. The hereditary congenital constitution thus made up is far stronger than the influences of environment and habit upon it. A large portion of our heritage is unused, for we transmit peculiarities we ourselves do not exhibit. The contributions from each ancestor can be estimated in numerical proportions, which have been exactly determined from statistics of stature in the English race; thus the contributions from the "patent" stature of the two parents together constitute one-half while the contributions by "latent" heritage from the grandparents constitute one-sixteenth, etc. One of the most important demonstrations by Galton is the law of regression; this is the factor of stability in race type which acts as gravitation does upon the pendulum; if an individual or a family swing far from the average characteristics of their race, and display exceptional physical or mental qualities, the principle or regression in heredity tends to draw their offspring back to the average.

Now how shall we distinguish regression from reversion? Very clearly, I think; regression is the short pull which tends to draw every variation and the individual as a whole back to the contemporary typical form, while reversion is the long pull which draws the typical form of one generation back to the typical form of a very much earlier generation. These forces are evidently akin, and in the shades of transition from one type to another we would undoubtedly find a constant diminution numerically in the recurrence of characters of the older type, and thus "regression" would pass insensibly into "reversion."

Weismann has carried the idea of continuity to its extreme in his simple and beautiful theory of heredity, which is founded upon the postulate that there is a distinct form of protoplasm, with definite chemical and molecular properties, set apart as the vehicle of inheritance; this is the germ plasm, *G*, quite separate from the protoplasm of the body cells or somatoplasm, *S*. Congenital characters arising in

* *Atlantic Monthly*, March, 1891, p. 359.

the germ-cells are called blastogenetic, while acquired characters arising in the body cells are somatogenetic.

To clearly understand this view, let us follow the history of the fertilized ovum in the formation of the embryo. It first divides into somato-plasm and germ-plasm (see Fig. 1, Diagram III), the former supplies all the tissues of the body—*n*, *s*, *m*, *d*, *v*, nervous, muscular, vascular, digestive, etc.—with their quota of hereditary structure; the residual germ-plasm is kept distinct throughout the early process of embryonic cell division until it enters into the formation of the nuclei of the reproductive cells, the ova or spermatozoa. Here it is isolated from changes of function in the somato-plasm, and in common with all other protoplasm is capable of unlimited growth by cell division without loss or deterioration of its past store of hereditary properties; these properties are lodged in the nucleus of each ovum and spermatozoan, and these two cells, although widely different in external accessory structure (because they have to play an active and passive part in the act of conjugation), are exactly the same in their essential molecular structure, and the ancestral characters they convey differ only because they come along two different lines of descent. When these cells unite they carry the germ-plasm into the body of another individual. Thus the somato-plasm of each individual dies, while the germ-plasm is immortal; it simply shifts its abode from one generation to another; it constitutes the chain from which the individuals are mere offshoots. Thus the germ-plasm of man is continuous with that of all ancestors in his line of descent, and we have an explanation of the early stages observed in development in which the human embryo passes through a succession of metamorphoses resembling the adult forms of lower types.

In order to emphasize, as it were, the passage of the germ-plasm from one generation to another without deterioration in its marvellous hereditary powers, Weismann added the idea of its isolation. Not only does he repudiate the pangenesis notion of increment of germ-plasm by addition of gemmules, but he believes that it is unaffected by any of the normal changes in the somatic or body cells. As this continuity and isolation would render impossible the transmission of characters acquired by the somato-plasm, Weismann began to examine the evidence for such transmission, and coming to the conclusion that it was insufficient, in his notable essay on "Heredity," in 1883, he boldly attecked the whole Lamarckian theory and has continued to do so in all his subsequent essays.

Being forced to explain evolution without this factor, he claimed that variation in the germ plasm was constanly arising by the union of plasmata from different lines of descent in fertilization, and that these variations are constantly being acted upon by natural selection to produce new types. He thus revived Darwin's earlier views of evolution, and this in part explains his strong support by English naturalists.

It will be seen at once that there are a number of distinct questions involved.

The matter of first importance in life is the repetition and preservation of type, the principle which insures the unerring accuracy and precision with which complex organs are built up from the germ cells; the force of regression and the more remote forces of reversion all work in this conservative direction; the theory of the preservation of these forces in a specific and continuous form of protoplasm is by far the most plausible we can offer at present.

The matter of second importance, but equally vital to the preservation of races, in the long run, is the formation of new types adapted to new circumstances of life. I shall now attempt to show that the facts of evolution, while not inconsistent with the idea of continuity of the germ plasm, are wholly at variance with the idea of its independence, separation, or isolation from the functions of the body. This can be done by proving, first, that the theory of evolution solely by natural selection of chance favorable variations in the germ plasm is inadequate; second, that the inheritance of definite changes in the somatic cells is also necessary to explain evolution, and therefore there must exist some form of force or matter which connects the activities of the somatoplasm with those of the germ plasm.

In the following table are placed some of the facts of human evolution which we have observed in the first lecture, and as they are part of inheritance, they also constitute the main external phenomena of heredity:

Phenomena of heredity.

Conservative (toward past type).	Natural.	Progressive (toward future type).
a. Repetition of parental type.	Fortuitous and indefinite.	*a*. Definite variation in single characters, by accumulation =.
b. Regression (in many characters) to contemporary race type.		*b*. Definite variation in many characters (from contemporary race type).
c. Reversion (mainly in single characters) to past race type.	Variability.	

What are causes of these various phenomena?

Factors of evolution.—The term "kinetogenesis" has been applied to the modern form of the Lamarckian theory, for it is an application of kinetic or mechanical principles to the origin of all structures such as teeth, bone, and muscle. It would be fatal to this theory if it could be shown that the changes taking place in course of a normal individual life, under the laws of use and disuse, are inadaptive, or do not correspond to those observed in the evolution of the race.

The relative growth of Organs.—Ball,* in his long argument against Lamarckianism, claims that such is the case, and that use

* *Op. cit.*, p. 129.

inheritance would be an actual evil: "Bones would often be modified disastrously. Thus the condyle of the human jaw would become larger than the body of the jaw, because as the fulcrum of the lever it receives more pressure. Some organs (like the heart, which is always at work) would become inconveniently or unnecessarily large. Other absolutely indispensable organs which are comparatively passive or are very seldom used would dwindle until their weakness caused the ruin of the individual or the extinction of the species." He later cites from Darwin* the "Report of the United States Commission upon the Soldiers and Sailors of the Late War," that the longer legs and shorter arms of the sailors are the reverse of what should result from the decreased use of the legs in walking and increased use of the arms in pulling. A little reflection on Mr. Ball's part would have spared us this crude objection, for whatever difficulties may arise from theoretical speculation as to the laws of growth, or from statistics, the fact remains that activity must increase adaptation in every part of the organism; otherwise the runner and the trotting horse should be kept off the track to increase their speed, the pianist should employ as little finger exercise as possible. If the growth tendencies in single organs are transmitted, it is evident that the adaptive adjustments between these tendencies will also be transmitted.

The Feet.—In point of mechanical adaptation, man, with the single exception of his thumb and forearm, has not progressed beyond the most primitive eocene quadruped. The laws of evolution of the foot in the ungulate or hoofed animals, which have been especially studied by Kowalevsky, Ryder, Cope, and myself, affords a conclusive demonstration that the skeletal changes in the individual coincide with those which will mark the evolution of the race. In the earliest ungulates the carpals and tarsals are disposed, as in man, directly above each other, with serial joints, as in diagram *A*, Fig. 2; in the course of evolution all these joints became interlocking, as in diagram *B*, Fig. 3; thus producing an alternation of joints and surfaces similar to those which give strength to masonry. In studying these facts Cope† reached a certain theory as to the motion of the foot and leg in locomotion. In trying to apply this, I found it could not be harmonized with all the facts, and I worked out an entirely different theory.‡ This I found subsequently coincided exactly with the results previously obtained by Muybridge, by the aid of instantaneous photographs, and summarized by Prof. Harrison Allen, of the University of Pennsylvania.§

The monodactylism of the horse was attained by the atrophy of the

* *Descent of Man*, p. 32.

† *American Naturalist*, 1887, p. 986.

‡ See *Trans. of American Philosophical Society*, 1889, p. 561. Philadelphia.

§ The Muybridge Work at the University of Pennsylvania. Philadelphia, 1888.

lateral toes, and concentration of the major axis of body weight and strain upon the middle finger and toe. Man is also tending toward monodactylism in the foot by the establishment of the major axis through the large toe and atrophy of the outer toes. The present atrophy of our small toe is as good a parallel as we can find of the changes which were occurring in the eocene period among the ancestors of the horse.

The Teeth.—But how about the teeth, in which there is an absolute loss of tissue in consequence of use? This is another objection raised by Ball, Poulton, and others, which disappears upon examination.

The dental tissues, while the hardest in the body, and, unlike bone, incapable of self-repair, are not only both living and sensitive, but, to

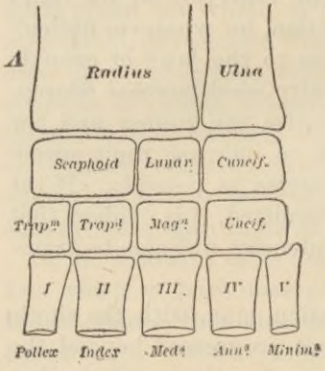

FIG. 2.

PRIMITIVE UNGULATE FOOT.—Lines of vertical cleavage on either side of the middle toe, III. Spreading of toes would cause separation of the carpals.

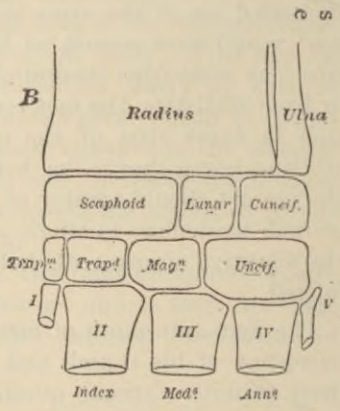

FIG. 3.

RECENT UNGULATE FOOT.—No lines of vertical cleavage. All joints broken by enlargement of scaphoid, unciform, and radius, the bones receiving greatest impact in walking. Lateral toes, I, V, degenerate.

a very limited degree, plastic and capable of change of form. *Ex hypothesi*, it is not the growth, but the reaction tendency which produces the growth, which is transmitted. The evolution of the teeth, therefore, falls into the same category as bone.* In the accompanying figures I have epitomized the slow transformation of the single-fanged conical reptilian tooth, such as we see in the serpents, into the low-crowned human grinder. We now know all the transition forms, so that we can homologize each of the cusps of the human molar with its varied ancestral forms in the line of descent. For example, the anterior lingual or inner cusp of the upper true molars traces its pedigree back to the reptilian cone. The anterior triangle of cusps, or trigon, seen in the mesozoic mammalia and persisting in the first inferior true molar of the modern dog, is still seen as the main portion of the crown of the human upper molars (*pr*, *pa*, *me*). To this was added, ages ago, the

* See especially the papers of Ryder, Cope, and the writer, "Evolution of Mammalian Molars to and from the Tritubercular Type," *American Naturalist*, 1889.

posterior lingual cusp, or hypocone, which, as Cope has shown, is exhibited in various degrees of development in different races and is an

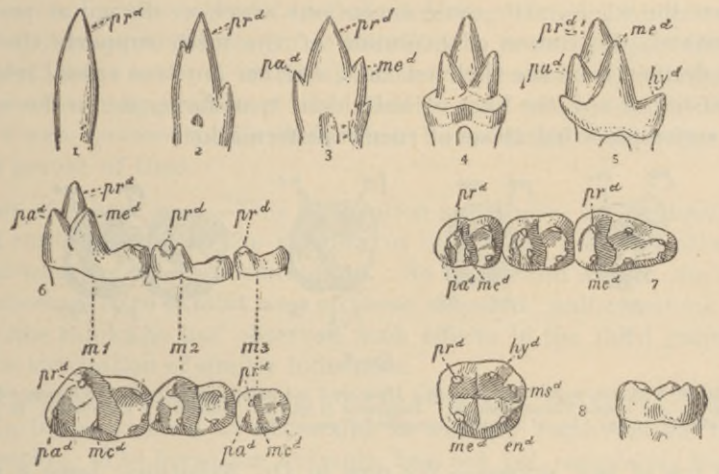

FIG. 4.

EVOLUTION OF THE CUSPS OF THE HUMAN LOWER MOLAR.—pr^d, protoconid (anterior buccal cusp); pa^d, paraconid; me^d, metaconid (anterior lingual cusp); hy^d, hypoconid (posterior buccal); en^d, entoconid (posterior lingual cusp); ms^d, mesoconulid (intermediate cusp). Diagram 1.—Reptilian stage. Diagrams 2–5.—Mesozoic mammals, first lower molars showing rise of ancestral cusps. Diagram 6.—Eocene carnivore (*miacis*), showing how the low tubercular crown *m3* is derived from the high crown *m1*. Diagram 7.—Eocene monkey (*Anaptomorphus*), showing how the primitive anterior lingual cusp pa^d disappears. Diagram 8.—Human first molar with its ancestral cusps.

important race index.* A glance through the diagrams shows that the development of the crown has been by the successive addition of new cusps. Without entering upon the details of evidence, which

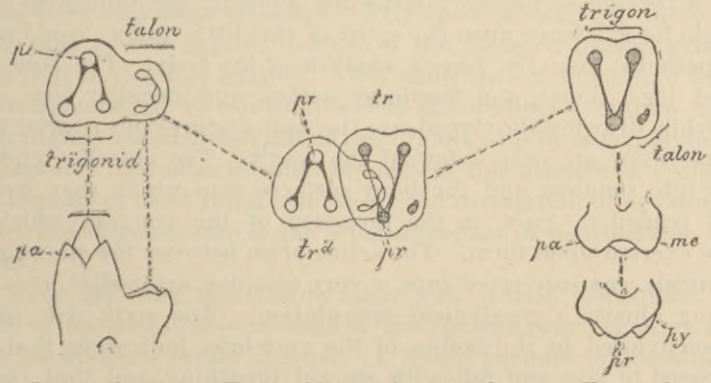

FIG. 5.

KEY TO PLAN OF UPPER AND LOWER MOLARS IN ALL MAMMALS.—Each tooth consists of a triangle, *trigon*, with the protocone, *pr*, at the apex. The apex is on the inner side of the upper molars and on the outer side of the lower molars.

would be out of place here, I may say, briefly, that the new main cusps have developed at the points of maximum wear (*i. e.*, use), and con-

* The upper molars in many Esquimaux are triangular (as in Fig. 6, diagram 11); in most negroes they are square (diagram 12). In our race they are intermediate.

versely in the degeneration of the crown, disuse foreshadows atrophy and disappearance.

Upon the whole, with some exceptions which we do not at present understand, the course of evolution of the teeth supports the evidence derived from the skeleton that, whether any true causal relation has existed or not, the lines of individual transformation in the whole fossil series preceded those of race transformation.

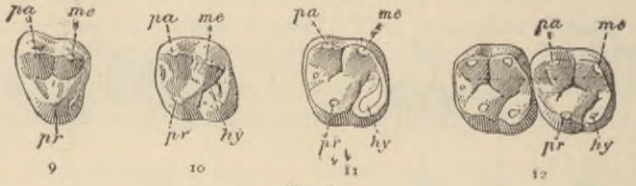

FIG. 6.

EVOLUTION OF THE HUMAN UPPER MOLARS.—Diagram 9.—*Anaptomorphus*, a Lower Eocene monkey. Diagram 10.—An Upper Eocene monkey. Diagrams 11 and 12.—Human: 11, Esquimaux; 12, negro. See addition of "talon," *hy.* to "trigon" composed of *pa, pr, me.*

The rise of new organs.—We owe to Dr. Arbuthnot Lane a most interesting series of studies upon the influences of various occupations upon the human body. He proves conclusively that individual adaptation not only produces profound modifications in the proportions of the various parts, but gives rise to entirely new structures.

His anatomy and physiology of a shoemaker* shows that the life-long habits of this laborious trade produce a distinct type, which if examined by any zoölogical standard would be unhesitatingly pronounced a new species—*homo sartorius*. The psychological analysis which a Dickens or Balzac would draw, showing the influences of the struggle for existence upon the spirit of this little tailor, could not be more pathetic than Dr. Lane's analysis of his body. The bent form, crossed legs, thumb and forefinger action, and peculiar jerk of the head while drawing the thread, are the main features of sartorial habit. The following are only a few of the results: The muscles tended to recede into tendons, and the bony surfaces into which they were inserted tended to grow in the direction of the traction which the muscle exerted upon them. The articulation between the sternum and the clavicle was converted into a very complex arthrodial joint, constituting almost a ginglymoid articulation. The sixth pair of ribs were anchylosed to the bodies of the vertebræ, indicating that they had ceased to rise and fall with sternal breathing, and that respiration was almost exclusively diaphragmatic. The region of the head and first two vertebræ of the neck was still more striking: the transverse process of the right side of the atlas, toward which the head was bent, formed a new articulation with the under surface of the jugular process of the occipital bone, "a small synovial cavity surrounded this acquired articulation, but there was no appearance of a

Journal of Anatomy and Physiology, 1888, p. 595.

capsular ligament;" the left half of the axis was united by bone to the corresponding portion of the third cervical; there was found a new upward prolongation of the odontoid peg of the axis, and a new accessory transverse ligament to keep it from pressing upon the cord. In short, "the anatomy of the shoemaker represents the fixation and subsequent exaggeration of the position and tendencies to change which were present in his body when he assumed the position for a short period of time.

Rate of inheritance.—This illustration serves also to emphasize the great contrast between the rapidity of individual transformation and the slowness of race transformation. No one would expect the son of this shoemaker to exhibit any of these acquired malformations. Yet Dr. Lane thinks he has observed such effects in the third generation by the summation of similar influences.

All palæontological evidence goes to show that the effects of normal habits, if transmitted at all, would be entirely imperceptible in one generation. The horse, for example, has not yet completely lost the lateral toes which became useless at the end of the Upper Eocene period. This objection as to rate of evolution may be urged with equal force against the natural selection theory. It is obvious that the active progressive principle in evolution (whatever it is), must contend with the enormous conservative power of inheritance, and this, to my mind, is one of the strongest arguments against the possibilities of the rise of adaptive organs by the selection of chance favorable variations in the germ plasm.

Application to human evolution.—Principles underlying these illustrations may now be applied to some of the facts in human evolution brought out in the first lecture. They show that if functional tendencies are transmitted we can comprehend the distinct evolution history of each organ; the rise and fall of two organs side by side; the definite and purposive character of some anomalies; the increase of variability in the regions of most rapid evolution; the correlation of development balance, and degeneration in the separate organs of the shoulder, hand, and foot.

Yet even granting this theory there still remain difficulties. The relation of use and disuse to some of the contemporary changes in the human backbone is rather obscure. I would hesitate to pronounce an opinion as to whether our present habits of life are tending to shorten the lumbars, increase the spinal curvatures, and shift the pelvis without making an exhaustive study of human motion. Among the influences which Dr. Lane has suggested* as operative here are the wearing of heeled shoes and the increase of the cranium. He considers the additional or sixth lumbar vertebra as a new element rather than as a reversion, and works out in some detail the mechanical effects of the

Journal of Anatomy and Physiology, 1888, p. 219.

presence of the fetus upon female respiration (*i. e.*, in the sternal region) and upon the pelvis. Now, if it be true that the pelvis is larger in the higher races than in the lower, I do not think that Dr. Lane can sustain his point, because in the lower races the fetus is carried for an equally long period, during a much more active life, and in a more continuously erect position. Therefore, if these mechanical principles were operating, the pelvis in the modern lower races should be larger than in the higher. On the other hand, the form of the female pelvis in the higher races is one of the best established selecting or eliminating factors, a large pelvis favoring frequent births and the preservation of those family stirps in which it occurs. I mention this to show how cautious we must be in jumping to conclusions as to kinetogenesis.

The transformism in all the external features of the skull, jaws, and teeth may be attributed to inherited tendencies toward hypertrophy or atrophy; but how about the convolutions of the turbinal bones or the complex development of the semicircular canals and cochlea of the internal ear and the many centers of evolution which are beyond the influences of use and disuse? These are examples of structures which fortify Weismann's contention, for if complex organs of this character can only be accounted for by natural selection, why consider selection inadequate to account for all the changes in the body?

Difficulties in the natural-selection theory.—The answer, I think, is readily given: We do not know whether use and disuse are operating upon the mechanical construction of the ear; we do know that the organ can be rendered far more acute by exercise; but even if it were true that habit can exert no formative influence, the ear is one of those structures which since its first origin has been an important factor in survival and may therefore have been evolved by natural selection. Now, the very fact that selection may have to care for variations in such prime factors in survival as the ear, renders it the more difficult to conceive that it also is nursing the minutiæ of variation in remote, obscure, and uncorrelated organs.

Even in the brief review of human evolution in the first lecture I have pointed out eight independent regions of evolution, upward of twenty developing organs, upward of thirty degenerating organs. A more exhaustive analysis would increase this list tenfold. Now, where chance variation should produce an increase in size in all the developing organs, and a decrease in size of all the degenerating organs, and an average size in all the static organs, we would have all the conditions favoring survival. But the chances are infinity to one against such a combination occurring unless the tendencies of variation are regulated and determined, as Lamarckians suppose, by the inheritance of individual tendencies. But may not the favorable variations in the body be grouped to either out-weigh or under-weigh the unfavorable variations? This would be possible if combinations occurred; but we can readily see that combinations, such as we observe

in the separate elements of the foot alone, completely neutralize each other so far as "survival" is concerned; how the foot would neutralize the hand, or the foot and hand would neutralize the lumbar region.*

It is this consideration of single organs, the observation of their independent history, the rise of new compound organs by steady growth from infinitesimal beginnings of their separate elements, the combined testimony of anatomy and palæontology which force us to regard the theory of evolution by the natural selection of chance variations as wholly untenable. With the utmost desire to regard the discussion in as fair a spirit as possible, the explanations offered by the adherents of Weismann's doctrine strike me as strained, evasive, and illogical.†

We can however by no means undervalue or dispense with natural selection, which must be in continuous operation upon every character of sufficient importance to weigh in the scale of survival. I need hardly remind you that this selecting principle was first discovered in 1813 by Dr. W. C. Wells, of Charleston, in connection with the immunity from certain tropical diseases enjoyed by negroes and mulattoes.‡

The eliminating factor in selection is illustrated almost daily in cases of *appendicitis*. I regret I have not had time to ascertain whether or not this disease is considered due purely to accident or to congenital variation in the aperture of the appendix, which favors the admission of hard objects. If so, modern surgery is only benefiting the individual to the detriment of the race by its efficient preventive operations; and every individual who succumbs to this disease can reflect with melancholy satisfaction that he does so *pro bono publico*.

Conclusions as to the factors of evolution.—The conclusions we reach from the study of the muscular and skeletal systems are therefore as follows: 1. That individual transformism in the body is the main determinant of variations in the germ cells, and is therefore the main cause of definite progressive or retrogressive variations in single organs. 2. That evolution in these organs is hastened where all members of the race are subject to the same individual transformism. The contrast between the rate of individual transformism and race transformism is due to the strong conservative forces of the germ plasma. 3. That evolution is most rapid where variations are of sufficient rank to become factors in survival. Then selection and use inheritance unite forces as active progressive principles opposing the conservative principle in the germ plasma. 4. That fortuitous and chance variations also arise from disturbances in the body or germ cells; they may be perpetuated, or disappear in succeeding generations.

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*I have expanded this idea fully in recent papers upon the theory of evolution of the horse. See "Are Acquired Variations Inherited?" *American Naturalist*, February, 1891.

†See Weismann's last essay, "Retrogressive Development," in *Nature*, Biol. Mem., trans., in press.

‡See Introduction of Darwin's *Origin of Species*.

Applying these views to variation there should theoretically appear to be just those two distinct classes of anomalies in the human body which we have seen actually occurring: First, those in the path of evolution, arising from perfectly normal changes in the somato-plasm and germ-plasm: second, those wholly unconnected with the course of evolution, arising fortuitously or from abnormal changes in the somato-plasm or germ-plasm; to this head may be attributed the whole scale of deformities. Thus tranformism and deformism should be kept distinct in our minds. Nevertheless the facts of deformism contribute the strongest body of evidence which we can muster at present to prove that there does exist a relation between the somato-plasm and germ-plasm which renders transformism possible.

The relations between the somato-plasm and germ-plasm.—We have seen reasons to take a middle ground as to the distinct specific nature of the body cells and germ cells, and this position is, I think, strengthened the more broadly we extend our inquiry into all the fields of protoplasmic activity.

There are three questions before us.

1. What is the evidence that the germ-plasm and somato-plasm are distinct?

2. What is the specific nature of the germ-plasm?

3. What is the nature of the relations which exist between the two?

1. The separation of the germ-plasm is in the regular order of evolution upon the principles of physiological division of labor. The unicellular organisms combine all the functions of life in a single mass of protoplasm, that is, in one cell. In the rise of the multi-cellular organisms the various functions are distributed into groups of cells, which specialize in the perfecting of a single function. Thus the reproductive cells fall into the natural order of histogenesis, and the theory of their entire separation is more consistent with the laws governing the other tissues than the theory which we find ourselves obliged to adopt, that while separate they are still united by some unknown threads with the other cells.

The morphological separation of what we may call the race protoplasm becomes more and more sharply defined in the ascending scale of organisms. Weismann's contention as to the absolutely distinct specific nature of the germ-plasm and somato-plasm has however to meet the apparently insuperable difficulty that in many multi-cellular organisms, even of a high order, the potential capacity of repeating complex hereditary characters, and even of producing perfect germ cells, is widely distributed through the tissues.

For example, cuttings from the leaves of the well-known hot-house plant, the begonia, or portions of the stems of the common willow tree, are capable of reproducing complete new individuals. This would indicate either that portions of the germ plasm are distributed through the tissus of these organisms, or that each body cell has retained its potential quota of hereditary characters.

Among the lower animals we find the same power; if we cut a hydra or bell animalcule into a dozen pieces, each may reproduce a perfect new individual. As we ascend in the animal scale the power is confined to the reproduction of a lost part in the process known as recrescence. As you well know, in the group to which the frog and salamander belong, a limb or tail, or even a lower jaw, may be reproduced. The only logical interpretation of these phenomena is that the hereditary powers are distributed in the entire protoplasm of the organism, and the capacity of reproduction is not exhausted in the original formation of the limb, but is capable of being repeated. There has been considerable discussion of late as to the seat of this power of recrescence. It seems to me not impossible that in the vertebrates it may be stored in the germ cells, and it would be very interesting to ascertain experimentally whether removal of these cells would in any way limit or affect this power; we know that such removal in castration or ovariotomy sometimes profoundly modifies the entire nature of the organism, causing male characters to appear in the female, and female characters to develop in the male.

So far as man is concerned it has been claimed by surgeons that genuine recrescence sometimes occurs; for example, that a new head is formed upon the femur after exsection; but my friend Dr. V. P. Gibney informs me that this is an exaggeration, that there is no tendency to reproduce a true head, but that a pseudo-head is formed, which may be explained upon the principle of regeneration and individual transformism by use of the limb.

Pflüger's opinion is that recrescence does not indicate a storage of hereditary power, that there is no pre-existing germ of the member, but that the re-growth is due to the organizing and distributing power of the cells at the exposed surface, so that, as new formative matter arrives, it is built up gradually into the limb. This view would reduce re-crescence to the level of the regeneration process which unites two cut sections of the elements of a limb in their former order. It is partly opposed to the facts above referred to, which seem to prove the distribution of the hereditary power. Yet it seems to me quite consistent to consider these three processes—*a*, reproduction of a new individual from every part; *b*, recrescence of a new member from any part; *c*, regeneration of lost tissues—as three steps indicating the gradual, but not entire withdrawal of the reproductive power into the germ cells.

I have not space to consider all the grounds which support the view of the separation of the germ cells in man. Some of the more prominent are: the very early differentiation of these cells in the embryo, observed with a few exceptions in all the lower orders of animals, and advancing so rapidly in the human female that several months before birth the number of primordial ova is estimated at seventy thousand, and is not believed to be increased after the age of two and a half years. The most patent practical proof is that we may remove every

portion of the body which is not essential to life and yet the power of complete reproduction of a new individual from the germ cells are unimpaired. Among the many reasons advanced for pensioning the crippled soldiers of our late war you never hear it urged that their children are incapacitated by inheritance of injuries. The strongest proof however rests in the evidence I have already cited from heredity of the extraordinary stability of the germ cells, which is the safeguard of the race.

2. The specific nature of the germ-plasm must be considered before we consider its relations. Wherein lies the conservative power of the germ-plasm, and in what direction shall we look for its transforming forces? You see at once that marvellous as is the growth of cells in other tissues, the growth of the germ cell is still more so.

We find it utterly impossible to form any conception of the contents of the microcosmic nucleus of the human fertilized ovum, which is less than one twenty-five-hundredths of an inch in diameter, but which is nevertheless capable of producing hundreds of thousands of cells like itself, as well as all the unlike cells of the adult organism. We can only translate our ideas as to the possible contents of this nucleus in the terms of chemistry and physics.*

Spencer† assumed an order of molecules or units of protoplasm lower in degree than the visible cell units, to the internal or polar forces of which, and their modification by external agencies and inter-action, he ascribes the ultimate responsibility in reproduction, heredity, and adaptation. This idea of biological units seems to me an essential part of any theory; it is embodied in Darwin's "gemmules," in Haeckel's "plastidules;" yet, as Lankester says the rapid accumulation of bulk is a theoretical difficulty in the material conception of units. In the direction of establishing some analogy between the repetition power of heredity and known function of protoplasm, Haeckel‡ and Hering§ have likened heredity to memory, and advanced the hypothesis of persistence of certain undulatory movements; the undulations being susceptible of change, and therefore of producing variability, while their tendency to persist in their established harmony is the basis of heredity. Berthold, Gautier, and Geddes‖ have speculated in the elaboration of the idea of metabolism; the former holding the view that "inheritance is possible only upon the basis of the fundamental fact that in the chemical processes of the organism the same substances and mixtures of substances are reproduced in quantity and quality with regular periodicity."¶

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*See Ray Lankester, *Nature*, July 15, 1876.

†*Principles of Biology*, vol. i., p. 256.

‡*Perigenesis der Plastidule oder die Wellenzeugung der Lebenstheilchen*. Jena, 1875.

§*Ueber d. Gedächtniss als ein eallgemeine Function d. organischen Materie*. Vienna, 1870.

‖See also Thomson, *op. cit.*, p. 102.

¶Berthold: *Studien über Protoplasma-Mechanik*. Leipsic, 1886.

I have merely touched upon these speculations to show that the unknown factors in heredity are also the unknown factors in operation in living matter. All we can study is the external form, and conjecture that this form represents matter arranged in a certain way by forces peculiar to the organism. These forces are exhibited or patent in the somatic cells; they are potential or latent in the germ cells.

The last stage of our inquiry is as to the mode in which the action of habit or environment upon the somatic cells can be brought to bear upon the germ cells.

The nature of the relation between the body cells and germ cells.—I have already shown that we are forced to infer that such a relation exists by the facts of evolution, although these facts show that the transmission of normal tendencies from the body to the germ cells is ordinarily an extremely slow process.

Virchow* says every variation in race character is to be traced back to the pathological condition of the originator. All that is pathological is not diseased, and inheritance of a variation is not from the influence upon one individual necessarily, but upon a row of individuals. This is in the normal condition of things. In the abnormal condition the rate of transmission may be accelerated.

Does this transmission depend upon an interchange of material particles, or upon an interchange of forces, or both?

There are three phenomena about which there is much skepticism, to say the least, which bear upon the question of a possible interchange of forces between the body and the germ-cells. These are the inheritance of mutilations, the influence of previous fertilization, and the influence of maternal impressions. They are all in the quasi-scientific realm, which embraces such mental phenomena as telepathy. That is, we incline to deny them simply because we can not explain them.

Mutilations.—Since the publication of Weismann's essays the subject of inherited mutilations has attracted renewed interest. I would first call attention to the fact that this matter has only an indirect bearing, for a mutilation is something impressed upon the organism from without; it is not truly "acquired;" the loss of a part by accident produces a sudden but a less profound internal modification of the organism than the loss of a part by degeneration. Most of the results are negative; many of the so-called "certain" cases prove upon investigation to be mere coincidences. Weismann† himself experimented upon white mice, and showed that 901 young were produced by five generations of artificially mutilated parents, and yet there was not a single example of a rudimentary tail or of any other abnormality in this organ. The cases of cleft ear lobule have recently been summed up.‡ Israel reports two cases of clefts in which the parent's ears were normal. Schmidt and

* "Ueber den Transformismus," *Archiv f. Anthropologie*, 1888, p. 1.

† *Biological Memoirs*, p. 432.

‡ *Journal of Anatomy and Physiology*, 1891, p. 433.

Ornstein report affirmative cases. His shows that an affirmative case, cited by V. Zwieciki, is merely an inherited peculiarity. The entire evidence is unsatisfactory, and upon the whole, is decidedly negative.

Not so however in cases where the mutilation results in a general disturbance of the normal functions of different organs, as in the experiments conducted by Brown-Séquard* upon guinea-pigs, in which we see "acquired variation" intensified. In these, abnormal degeneration of the toes, muscular atrophy of the thigh, epilepsy, exophthalmia, etc., appeared in the descendants of animals in which the spinal cord or sciatic nerve had been severed, or portions of the brain removed. It was also shown that the female is more apt to transmit morbid states than the male; that the inheritance of these injuries may pass over one generation and re-appear in the second; that the transmission by heredity of these pathological results may continue for five or six generations, when the normal structure of the organs re-appears. These cases, which are incontestable, at first sight appear to establish firmly the transmission of acquired characters; they were so regarded by Brown-Séquard. These lesions act directly upon the organs, and the abnormal growth of these organs appears to be transmitted. But can they not be interpreted in another way, namely, that the pathological condition of the nerve centers has induced a direct disturbance in those portions of the germ cells which represent and will develop into the corresponding organs of the future offspring?

Previous fertilization.—Consider next the influence exerted upon the female germ cell by the mere proximity of the male germ cell, as exhibited in the transmission of the characteristics of one sire to the offspring of a succeeding sire, observed in animals, including the human species, also in plants. The best example is the oft-quoted case of Lord Morton's mare, which reproduced in the foal of a pure Arab sire the zebra markings of a previous quagga sire.

Some physiologists† have attempted to account for these remarkable indirect results from the previous fertilization or impregnation, by the imagination of the mother having been strongly affected, or from interchange between the freely inter-communicating circulation of the embryo and mother, but the analogy from the action in plants (in which there is no gestation but early detachment and development of the fertilized cells) strongly supports the belief that the proximity of male germ cells acts directly upon the female cells in the ovary. All that we can deduce from these facts is that in some manner the normal characteristics and tendencies of the ova are modified by the foreign male germ cells without either contact or fertilization.

Maternal impression.—The influence of maternal impressions in the

* *Comptes-Rendus*, March 13, 1882. These experiments have been confirmed by Obersteiner.

† See the cases cited by Ribot, and Darwin: *Animals and Plants Under Domestication*, vol. 1, p. 437.

causation of definite anomalies in the fœtus is largely a matter of individual opinion.

It is denied by some high authorities, led by Bergman and Leuckhart.* Most practitioners, however, believe in it, and I need hardly add that it is a universal, popular belief,† supported by numerous cases. I myself am a firm believer in it. The bearing which the subject has upon this discussion is this: If a deviation in the development of a child is produced by maternal impression, we have a proof that a deviation from normal hereditary tendencies can be produced without either direct vascular or nervous continuity.

We see an analogy between the experiments of Brown-Séquard, the influence of the previous sire, and the maternal influence. Neither, in my opinion, directly supports the theory of transmission of acquired characters, for they do not prove that normal changes in the body cells directly react upon the germ cells; they all show that the typical hereditary development of single organs may be diverted by living forces which have no direct connection with them according to our present knowledge.

What the nature of these forces is I will not undertake to say, but I believe we must admit the existence of some unknown force, or rather of some unknown relations between the body cells and germ cells.

A year ago, recognizing fully the difficulty of advancing any theory of heredity which would explain the transmission of acquired characters, I came to the following result: "It follows as an unprejudiced conclusion from our present evidence that upon Weismann's principle we can explain inheritance but not evolution, while with Lamarck's principle and Darwin's selection principle we can explain evolution, but not, at present, inheritance. Disprove Lamarck's principle and we must assume that there is some third factor in evolution of which we are now ignorant."

In this connection it is interesting to quote again from my colleague, Prof. E. B. Wilson. He writes that the tendency in Germany at present is to turn from speculation to empiricism, and this is due partly "to the feeling that the recent wonderful advances in our knowledge of cell phenomena have enormously increased the difficulties of a purely mechanico-physical explanation of vital phenomena. In fact, it seems that the tendency is to turn back in the direction of the vital-force conception. - - - As Boveri said to me recently, "Es gibt zu viel vorstand in der Natur um eine rein mechanische Erklärung der Sache zu ermöglichen."

In the final lecture we turn to the forces exhibited in the germ cells.

*Handerwörterbuch der Physiologie, Wagner, Artikel "Zeugung," Leuckhart.

†See *Medical Record*, October 31, 1891, an article by Joseph Drzewiecki, M. D.

LECTURE III.—HEREDITY AND THE GERM CELLS.

According to the general law* the germ cell was considered as matter potentially alive and having within itself the tendency to assume a definite living form in course of individual development. The nucleus must be extraordinarily complex, for it contains within itself not only the tendencies of the present type, but of past types far distant. The supposition of a vast number of germs of structure is required by the phenomena of heredity; Nägeli has demonstrated that even in so minute a space as one one-thousandth cubic millimeter, 400,000,000 micellæ must be present.

The study of heredity will ultimately center around the structure and functions of the germ cells. The precise researches of Galton show that the external facts of heredity, questions of average and of probabilities, of paternal and maternal contributions to the offsprings, are capable of being reduced to an exact science in which mathematical calculations will enable us to forecast the characteristics of the coming generation.

There will still remain however a large residuum of facts which will present themselves to a mathematician like Galton, as fortuitous, or inexact, such as the physiological conditions of reversion; the course of pre-potency, by which the maternal or the paternal characteristics prevail in parts or in the entire structure of the offspring; the material basis of latent heritage upon which reversion depends, and which compels us to hypothecate either an unused hereditary substance or a return to an older disposition of the forces in this substance; the nature and determination of sex. These apparently chance phenomena must also be due to certain fixed laws, and by far the most promising routes to discovery have already been taken by Van Beneden, the Hertwig brothers, Boveri, Maupas, and others.

They have attacked the problem of the relation of the germ cells to the heredity on every side, and by the most ingenious and novel methods, which are familiar enough in various branches of gross anatomical and physiological research, but seem almost out of the limits of application to minute microscopic objects. For example, the Hertwig brothers have ascertained the influence of various solutions of morphine and other drugs of the alcohols, and of the various degrees of temperature upon the ovum and spermatozoon during the conjugation period, with results which are highly suggestive of the causes of congenital malformations, anomalies, and double births. The Hertwigs and Boveri have succeeded in robbing ova of their nuclei and watching the results of the subsequent entrance of spermatozoa. In order to further test the relations of the nucleus to the remainder of the cell, Verworn has experimented along the same line with extirpations of every kind from the single cells of Infusoria. Of equal novelty are the recent studies of

*See Huxley, Article "Evolution," *Enc. Britannica*, vol. VIII, p. 746.

Maupas upon the multiplication and conjugation of the Infusoria, giving us a host of new ideas as to the cycle of life, the meaning of sex, and the origin of the sexual relation.

In all this research and in the future outlook there are two main questions:

1. What is the hereditary substance? What is the material basis of heredity, which spreads from the fertilized ovums to every cell in the body, conveying its ancestral characteristics? Is there any substance corresponding to the hypothetical idioplasm of Nägeli?

2. What are its regulating and distributing forces? How is the hereditary substance divided and distributed? How far is it active or passive?

I may say at the outset that the idioplasm of Nägeli, a purely ideal element of protoplasm which he conceived of as permeating all the tissues of the body as the vehicle of heredity, has been apparently materialized in the chromatin or highly coloring materials in the center of the nucleus. This rests upon the demonstration by Van Beneden and others that chromatin is found not only in all active cells, but is a conspicuous element in both the ovum and spermatozoon during all the phenomena attending conjugation.

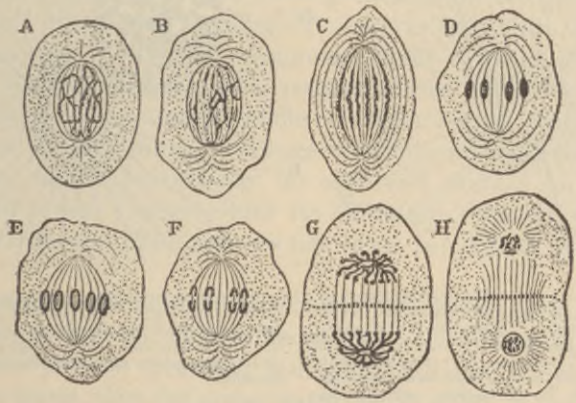

FIG. 7.—TYPICAL CELL DIVISION, SHOWING THE DISTRIBUTION OF CHROMATIN.—(From Parker after Carnoy.) A–C, arrangement of the chromatin in threads; D–E, formation of the chromatin rods and loops; F, splitting of the loops; G–H, retraction of the chromatin into the two daughter cells.

Secondly, that while the chromatin is apparently passive, it is played upon by forces resident in the clear surrounding protoplasm of the nucleus, but chiefly by the extra nuclear archoplasm, which seems to constitute the dynamic and mechanical factor in each cell. This, unlike the chromatin, only comes into view when there is unusual activity, as during cell-division, and is not evident (with our present histological technique, at least), when the cell is arrested by reagents in any of the ordinary stages of metabolism.

The distribution of hereditary substance.—I may first review some of the well-known phenomena attending the distribution of the chromatin substance to the tissues.

I have borrowed from Parker, figures by Carnoy, to illustrate the resting and active stages of the cell, and from Watase, a Japanese student of Clark University, figures representing the high differentiation of the cell contents during division (Figs. 8, 9). They bring out the active and passive elements of the typical cell.

The phenomena of karyokinesis which attend the division and distribution of the hereditary substance throughout the whole course of embryonic and adult development are well illustrated in Carnoy's figures (Fig. 7). First we have the quiescent period, in which the chro-

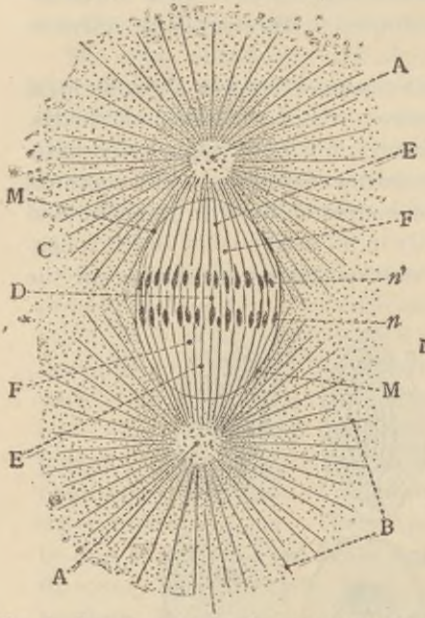

FIG. 8.—BEFORE DIVISION. DIFFERENTIATION OF THE CYTOPLASM AND NUCLEUS DURING CELL DIVISION OF A SQUID EMBRYO, LOLIGO. (After Watase). M, The nuclear membrane; F, Achromatin or nucleoplasm; C, Cytoplasm, or protoplasm outside of the nucleus; A-A, The two centrosomes of archoplasm; B, Extra nuclear archoplasmic filaments; E, Intra-nuclear archoplasmic filaments attached to *n*, *n'*, the chromatin rods.

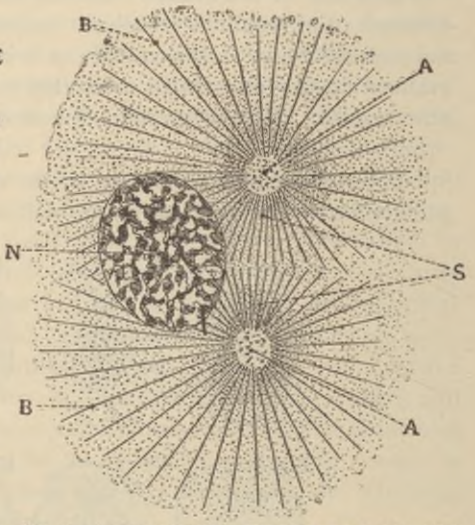

FIG. 9.—AFTER DIVISION. INTERIOR OF A DAUGHTER-CELL IN THE SQUID. (After Watase.) Division has just taken place and the daughter nucleus, N, shows the chromatin coil. The daughter centrosome is just forming two new centrosomes, A-A, by direct division.

matin presents the appearance of a coiled, tangled thread; surrounding this is the clear nucleo-plasm (or achromatin) bounded by the nuclear membrane; the extra-nuclear substance, or cyto-plasm, is apparently undifferentiated. As soon as cell division sets in, however, radiating lines are seen in the cyto-plasm above and below the nucleus; these are called the archo-plasmic filaments by Boveri, since they proceed from what is now believed to be the dynamic element, the archoplasm (Fig. 8). As the activity becomes more intense the filaments are seen to diverge from a center—the archo-plasmic *centrosome*—which lies just without the nucleus at either pole; this radial display of cell forces suggested the term "asters" to Fol, and "spheres attractive" to Van Beneden. The behavior of the chromatin, or hereditary substance,

under these archo-plasmic forces, is beautifully shown in Carnoy's diagrams (Fig. 7). First, the nuclear wall breaks up, then the chromatin coil unfolds into lines of vertical striation which become thread-like, hence the term mitosis, and then more compact, until finally a number of distinct vertical rods, chromatin rods, or *chromasomes* are found.

A remarkable and significant fact may be noted here, that the number of chromasomes varies in the cells of different species, and even in the cells of different varieties (as in the thread-worm of the horse—*Ascaris megalocephala*), but is constant in all the cells of the same variety through all stages; thus the same number of chromasomes appear in the first segmentation of the fertilized ovum as in the subsequent cell division in the tissues.

Carnoy next indicates the vertical splitting of each rod into a loop or link preceding the horizontal splitting; thus we may conceive of a thorough re-distribution of the chromatin before it passes into the daughter-cells. The split loops are each retracted toward a centrosome, suggesting to some authors a contractile power in the archo-plasmic filaments, each chromasome being apparently withdrawn by a single filament. But as the chromasomes separate, the filaments also appear between them, and are variously termed "interzonal," "verbindungs fäden," "filaments réunissant;" there is therefore some difference of opinion as to what the mechanics of the chromasome divisions really are. The chromatin is now retracted into two coiled threads, each the center of the daughter nucleus with a single centrosome beside it. But as the line of cleavage is drawn between the two cells (Fig. 9), the single centrosome in each cell divides so that each daughter-cell is now complete with its chromatin coil and two archo-plasmic centrosomes. This process has been beautifully described by Watase.*

It thus appears that both the chromatin and archo-plasm are permanent elements of the cell, such as we formerly considered the nucleus; the apparently passive chromatin is divided with great precision by the active archo-plasm, then the archo-plasm simply splits in two to resume the cleavage function.

Fertilization—the union of hereditary substances.—Before looking at the host of questions which fertilization suggests, let us review a few of the well-known phenomena preparatory to the union of the germ cells in order to give greater emphasis to the importance of recent discoveries.

First, the ovum is a single cell, the typical structure of which, with its nucleus and cytoplasm, is generally obscured by a quantity of food-material, surrounded by a rather dense cell wall. The ovum is said to be ripened or "matured" for the reception of the spermatozoön, by the extrusion of two small "polar bodies," containing both chromatin and

*See Marine Biological Laboratory Lectures, 1889. Boston: Ginn & Co.

hyaline protoplasm, and separating off by karyokinetic division. After maturation is complete, a single spermatozoön normally penetrates; then a reaction immediately sets in in the cell wall of the ovum which prevents other spermatozoa from entering. The head of the spermatozoön and the nucleus of the ovum now fuse together to form a single nucleus, which it is obvious contains the hereditary substance of two individuals. This is the starting point of the segmentation or distribution process above described, and it follows that the fertilized ovum at this stage must contain its typical complement of chromatin, archoplasm, etc., for the whole course of growth to the adult.

How shall we connect these phenomena of fertilization with the facts of heredity? The most suggestive enigma in connection with the fertilization process has been *the meaning of the two polar bodies*, especially since Van Beneden demonstrated that they contained chromatin? For twenty-five years, speculation has been rife as to why the ovum should extrude a portion of its substance in two small cells; why not in one cell? why not in a larger number? Thanks to the intense curiosity which these polar bodies have aroused, and to the great variety of explanations which have been offered for them, we have arrived to-day at a solution which links the higher animals with the lower, breaks down the supposed barrier between the sexes, and accords with the main external facts of heredity.

It seems to me best to disregard the order of discovery, and to state the facts in the most direct way. First, a few words as to the speculations upon the meaning of the polar bodies.

The early views of fertilization* were naturally based upon the apparent significance of this process in the human species, in which the sexes are sharply distinguished from each other in their entire structure, and the reproductive cells are also widely differentiated in form, the ovum large and passive, the spermatozoon small and active. The readiest induction was to regard these elements as representing distinct physiological principles, corresponding to the essential sexual characteristics—in short, as male and female cells, the former vitalizing and rejuvenating the latter. Thus one of the earliest definite "polar-body" theories was that the ovum was hermaphrodite, containing both male and female principles, and that it was necessary to get rid of the male substance before the spermatozoon could enter.

As Von Siebold and Leuckart had demonstrated that some ova reproduce parthenogenetically, that is without fertilization by spermatozoa, Weismann turned to such forms for the solution of this problem, and was surprised to find that parthenogetic ova only extrude one polar body. This led him to attach one meaning to the first polar body, and another meaning to the second, which he viewed as designed to reduce the heredity substance in the ovum without regard to sex. Thus both this and the older theory conveyed alike the idea of *reduc-*

*See also the introduction of Weismann's last essay, "Amphimixis."

sion, but with an entirely different supposition as to the nature of the material reduced or eliminated.

Maupas on Conjugation among the Infusoria.*—Among the newer researches which throw light upon this old problem, those of Maupas are certainly the most brilliant. After a most exact and arduous research, extending over several years, he collected his results in two memoirs, published in 1889 and 1890.

His experiments were first directed upon the laws of direct multiplication by fission, which revealed a complete cycle of life in the single-celled Infusoria and showed that after a long period this mode of reproduction becomes less vigorous, then declines, and finally ceases altogether unless the stock is rejuvenated by conjugation of individuals from different broods. In other words, these broods of minute organisms grow old and die unless they are enabled to fertilize each other by an exchange of hereditary substance altogether analagous to that observed in the higher multicellular organisms.

The cultures were made in a drop of water upon a slide, and feeding was adapted either to the herbivorous or carnivorous habits of the species. Under these conditions it was found that the rate of fission or direct multiplication varied directly with the temperature and food, rising in some species (*Glaucoma scintillans*) to five bipartitions daily. With the optimum of conditions this rate, if sustained for thirty-eight days, would produce from a single individual a mass of protoplasm equivalent to the volume of the sun. This rate is however found to be steady for a time, and then the offspring decline into "senescence," in which they appear at times only one-fourth the original size, with reduced buccal wreaths and degenerate nuclear apparatus. This is reached sooner in some species than in others; *Stylonichia pustulata* survives three hundred and sixteen generations or fissions, while *Leucophrys patula* persists to six hundred and sixty generations. Finally, even under the most favorable conditions of environment, death ensues.

Not so where conjugation is brought about by mingling the offspring of different broods in the same fluid, as in the natural state. Maupas soon discovered that exhaustion of food would induce conjunction between members of mixed broods. He thus could watch every feature of the conjugation process, and determine all the phases in the cycle of life. These differed, as in the longevity of the species. In *Stylonichia*, for example, "immaturity" extended over the first one hundred bipartitions: "puberty," or the earliest phase favorable to conjugation, set in with the one hundred and thirtieth bipartition; "eugamy," or the most favorable conjugation phase, extended to the one hundred and seventieth; then "senescence" set in, characterized by a sexual hyperæsthesia in which conjugation was void of result or rejuvenesence, owing apparently to the destruction of the essential nuclear apparatus.

*Sur la multiplication des Infusoires Ciliés, *Archiv. de Zoölogie experimentata*, Ser. 2, vol. VI., pp. 165-273; *Le Rajeunissement Karyogamique ches les Ciliés*, vol. VII, pp. 149-517. See also Hartog, *Quart. Jour. Microscop. Science*, December, 1891.

Conjugation begins with the approach of two individuals, and adhesion by their oral surfaces. There is no fusion, but an immediate transformation in the cell contents of each individual sets in, concluding

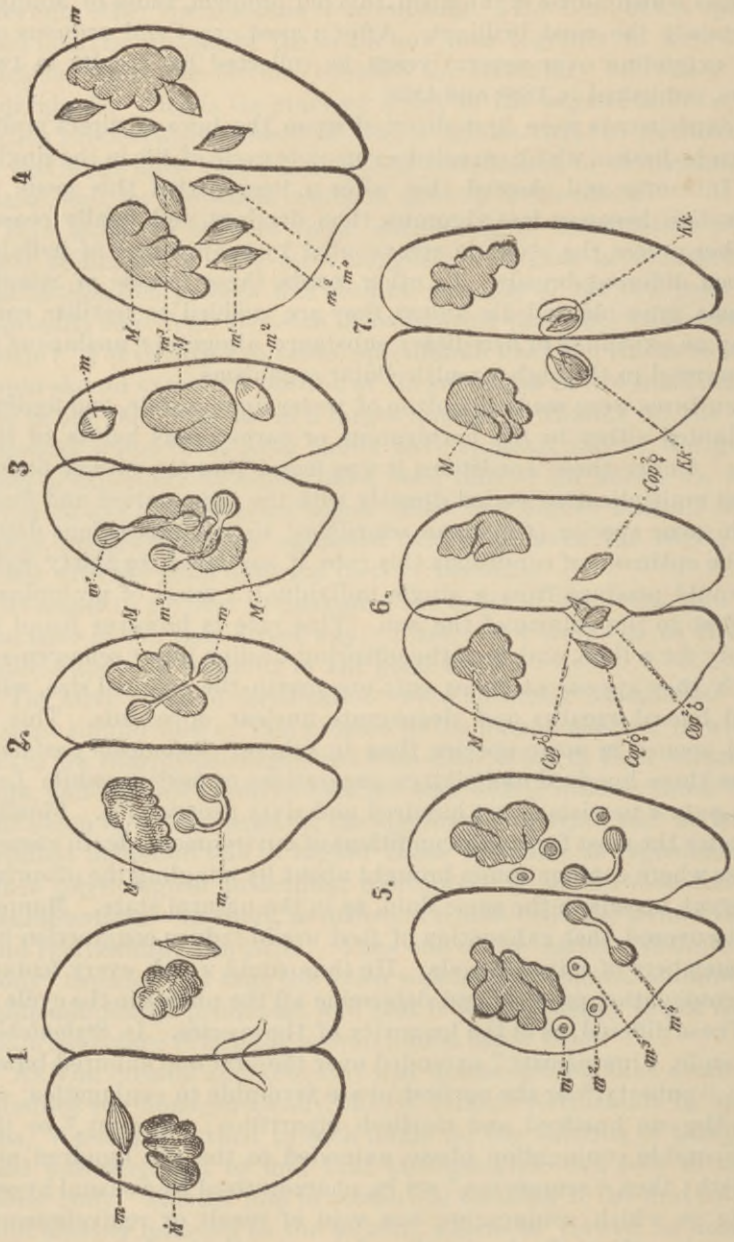

FIG. 10.—THE CONJUGATION OF INFUSORIA. (From Weismann, after Maupas.) 1, Two infusoria copulating; *M*, meganucleus; *m*, micronucleus; 2-5, Successive divisions of micronuclei; 6, The migration of one of the persisting micronuclei from each infusorian into the other; 7, Union of the interchanged micronuclei.

with an interchange of nuclear substance. In each cell Maupas distinguishes between the (*M*) *meganucleus* (Fig. 10, the macronucleus, nucleus, endoplast of authors), which presides over nutrition and

growth and divides by constriction, and the (*m*) *micronucleus* (paranucleus, nucleolus, of authors), which presides over the preservation of the species. The latter contains chromatin; it is the seat of rejuvenescence, the basis of heredity, it divides by mitosis, showing all the typical stages of karyokinesis excepting the loss of the cell membrane.

The transformation in each of these copulating cells first affects the centers of hereditary substance, viz, the micro-nuclei; they divide three times; thus the micronuclear substance is reduced to one-fourth of its original bulk. It is contained in two surviving micronuclei (the others being absorbed or eliminated), one of which migrates into the adjoining cell; the other remains stationary. This migration is followed by a fusion of the migrant and stationary micronuclei; this fusion effects a complete interchange of hereditary substance, after which the two infusoria separate and enter upon a new life cycle. Meanwhile the meganucleus breaks up and is reconstituted in each fertilized cell.

Maupas gathers from these interesting phenomena additional proof that the chromatin of all cells bears the inherited characteristics and that the cyto-plasm and nucleo-plasm, or achromatin, is the dynamic agent, because the micronuclei bearing the chromatin are the only structures which are permanent and persistent, all the other structures—nucleo-plasm, archo-plasm, etc.—being replaced and renewed. The reduction of the chromatin is purely quantitative, the eliminated and fertilizing micronuclei being exactly equivalent; after the chromatin has been quartered the cell becomes incapable of further activity until it is reinforced by chromatin from the copulating cell.

No distinction between the sexes in heredity.—The three laws which underlie these phenomena are: (1) That fertilization consists in the union of the hereditary substance of two individuals. (2) That before the union the hereditary substance in each is greatly reduced. (3) That there is no line between male and female, the conjugating cells are simply in a similar physiological condition wherein a mingling of hereditary characteristics affords a new lease of life. As Maupas says:

"Les différences appelées sexuelles portent sur des faits et des phénomènes purement accessoires de la fécondation. La fécondation consiste uniquement dans la réunion et la copulation de deux noyaux semblables et équivalents, mais provenus de deux cellules distinctes."

In this conclusion as to the secondary and superficial, rather than fundamental, difference between the two sexes, Maupas simply confirms the views of Strassburger, the botanist, Hensen, R. and O. Hertwig, Weismann, and others, namely, that sex has evolved from the necessity of cell conjugation; that even in the higher forms the cells born by the two sexes are absolutely neutral so far as sex is concerned, the wide difference of form of the germ cells is a result of physiological division of labor—the mass and yolk of the ovum having been differentiated to support the early stages of development while the spermatozoon has dispensed with all these accessories and acquired an active

vibratile form for its function of reaching and penetrating the ovum. The evidence of the Infusoria is paralleled among some of the plants, in which conjugation between entirely similar cells is observed.

The causes finally determining sex may come surprisingly late in development, and according to the investigations of Düsing and the experiments of Yung* and of Giron are directly related to nutrition. High feeding favors an increase of the percentage of females, while, conversely, low feeding increases the males. In Yung's experiments with tadpoles the following results were obtained:

	Females.	Males.
Normal percentage	57	43
High nutrition	92	8

Geddes expresses this principle in physiological terms of metabolism, that anabolic (constructive) conditions produce females, while katabolic (destructive) conditions produce males.

I think we may now safely eliminate the factor of sex from our calculations upon the problem of heredity, and thus rid ourselves of one of the oldest and most widespread fallacies. We shall thus, in using the terms "paternal" and "maternal" imply merely the distinction between two lines of family descent.

The theory of reduction.—This leads us back to the significance of the polar bodies. Van Beneden's discovery that these bodies contained chromatin led gradually to the view that they were not fragments of the ova, but represented minute, morphologically complete cells. Bütschli showed that they were given off independently of, and prior to, the contact of the spermatozoon, and, finding in the leeches that the first polar body subdivides to form two bodies, he considered them as formed by true cell division, and containing both nucleoplasm and chromatin. Giard independently reached a similar opinion, assigning an atavistic meaning to the polar cells. Whitman, in 1878, advanced the idea that they represented vestiges of the primitive mode of reproduction by fission, while Mark described them as "abortive ova."

At this point speculation subsided until it was revived by Weismann's attempt to connect these bodies with his theory of heredity,† already referred to. The whole history is clearly given in R. Hertwig's masterly memoir upon Ovo and Spermatogenesis in the Nematodes.‡ Taking advantage of Boveri's discoveries in staining tech-

*See Geddes and Thomson: *The Evolution of Sex*, 1891; also, Düsing: Die Regulierung des Geschlechtsverhältnisses bei d. Vermehrung der Menschen, Tiere und Pflanzen, *Jen. Zeit. f. Natur.*, Bd. 17, 1884.

†On the Number of Polar Bodies and their Significance in Heredity, 1887.

‡Ei und Samenbildung bei Nematoden, *Archiv. f. Mikr. Anat.*, Bd. 26, 1890.

nique, and stimulated by Weismann's prediction that spermatozoa would also be found to extrude polar bodies, this author examined all stages in the peculiarly favorable germ cells of the thread-worm of the horse (*Ascaris megalocephala*).

He made the surprising discovery that ova and spermatozoa are formed in a substantially similar manner by repeated divisions, the single difference being that the last products of division among the sperm cells are effective spermatozoa, capable of development in fertilization, while the last products of division in the ovary are, first

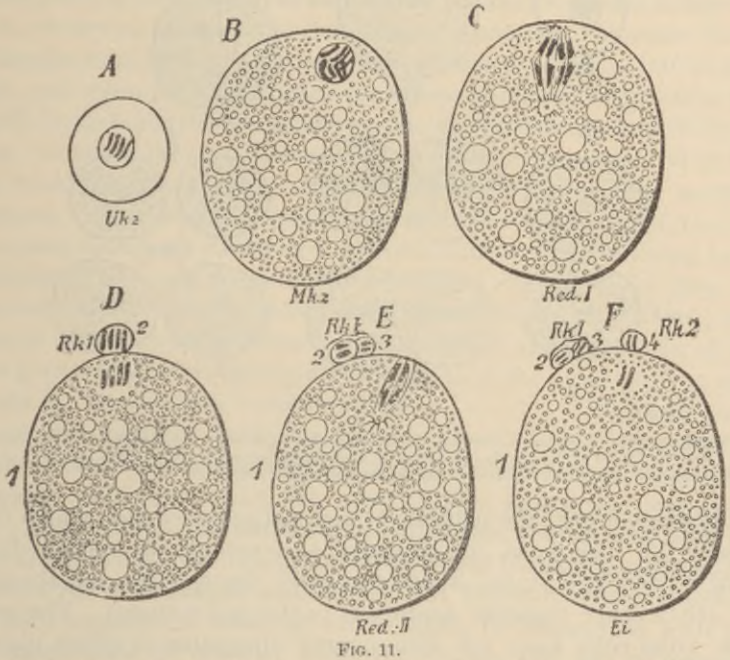

FIG. 11.

THE MATURATION OF OVA, OR FORMATION OF POLAR BODIES IN ASCARIS. (From Weismann afte Hertzwig.) A, original germ-cell in embryonic germ-layer—4 chromatin rods; B, Ovum mother-cell—8 rods; C–D, First polar body extruded; E, Splitting of first polar body. Ovium still contains 4 rods; F, Second polar body extruded; Ovium mature with 2 rods.

the true ova, and, second, the abortive ova (polar cells), incapable of development. In both ova and spermatozoa the nucleus contains but one-half the chromatin which a typical nucleus contains; in the case of *A. megalocephala* each of the germ cells contains but two chromasomes while the normal body cells contain four. The manner in which this maturation of the germ cells for conjugation is brought about is beautifully shown in these diagrams, taken from Weismann's essay, "Amphimixis." You observe that the number of chromasomes in the primary germ cells is four (Figs. 11 and 12, *A*). Then are formed by subdivision the ovum and sperm "mother cells," in which the chromatin substance is doubled, so that we observe eight chromasomes The mother cells then divide and the chromatin is reduced to four rods, a second division rapidly follows whereby the chromatin is reduced

to two rods, or half the original quantity. These last divisions take place by karyokinesis, but, as Hertwig points out, they differ from typical karyokinesis in the fact that the divisions follow so rapidly upon each other that the vesicular resting period of the nucleus is omitted. Thus, he suggests, is prevented an overaccumulation of chromatin substance prior to the fusion of the ovum and sperm.

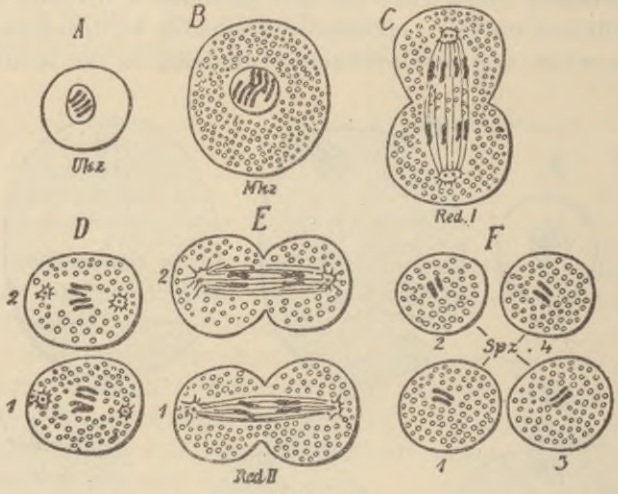

FIG. 12.

SPERMATOGENESIS IN ASCARIS.—(From Weismann after Hertwig.) A, original germ cell—4 chromatin rods; B, sperm mother cell—8 rods; C–D, first daughter cells with 4 rods each; E–F, formation of second daughter cells, or mature spermatozoa, with 2 rods each.

It is evident that the polar cells are rudimentary ova, which do not possess the yolk mass, etc., essential to development, and are divided off at a very late stage, sometimes after the egg has left the ovary, but are in other respects analogous to the spermatozoa. The reason these polar-cells have not disappeared altogether in either plants or animals is that they originally possessed a deep physiological importance. As the first polar cell subdivides and forms two, it follows that from both ovum and sperm mother cells four daughter cells are formed, each containing half the chromatin substance of a normal nucleus. In the ovary three of these daughter cells abort and the fourth forms a true ovum; in the sperm gland, however, all four daughter cells form spermatozoa.

We may thus consider the polar-cell problem as in all probability settled; the whole process is probably an inheritance or survival of a primitive condition in which all four ova, like the four spermatozoa, were fully functional.

The relation between the chromatin and heredity.—We have just seen that the last stages in the preparation of the ova and spermatozoa for conjugation result in halving the number of rods in the original germ cells. Now, as Hertwig and Weismann point out, one point is

still left in doubt. Why is the chromatin substance doubled in the mother-cells so that two successive sub-divisions are necessary to reduce it to half the original quantity? Hertwig has not attempted to answer this question, as he prefers to wait for further research. Weismann, however, who is unfortunately cut off from research by failing eyesight, has offered a speculative solution to this problem which he trusts may guide future investigation.

This leads me to say a few words in regard to his conception of the relation of the chromatin to heredity. (1) His first premise is that in fertilization there is not a fusion of chromatin, but that a certain independence is preserved between the maternal and paternal elements, based upon the observed fact that the two pairs of rods do not fuse but lie side by side, and upon the assumption that these pairs are kept distinct in each cell through all the subsequent stages of embryonic and adult development. If this is the case, the hereditary substance contributed by the father would remain separate from that contributed by the mother, throughout. (2) "Each of these pairs would be made up of the collective predispositions which are indispensable for the building up of an individual, but each possesses an individual character, for they are not entirely alike. I have called such units 'ancestral plasms,' and I conceive that they are contained in numbers in the chromatin of the mature germ cells of living organisms, also that the older nuclear rods are made up of a certain number of these. - - - Obviously these units can not become infinitely minute; however small they may be they must always retain a certain size. This follows from the extremely complicated structure which we must without any doubt ascribe to them." These units are not, however, ultimate, they are in turn extremely complex, and are composed of countless biological units of the kind conceived of by Nägeli and others. (3) The reduction of the chromatin only acquires a meaning when taken in connection with the above supposition of distinct ancestral plasms, and has no meaning if we accept Hertwig's view that there is a complete fusion of maternal and paternal germ plasm. This meaning is that reduction in the maturation of germ cells is *sui generis*, it does not divide the ancestral plasms into two similar groups, but one daughter-cell receives one set of germ plasms or hereditary predispositions, and another daughter cell receives another; reduction is thus differential. According to this view the four sperm and ovum daughter-cells would each contain a different set of ancestral plasms. (4) The fact that the chromatin substance is doubled in the sperm and ovum mother-cells, so that we observe double the number of rods characteristic of the species, is to be explained as an adaptation to the requirements of natural selection, for this doubling and subsequent double division render possible an infinite number of combinations (as many, in fact, as there are individuals) for selection to operate upon.

This explanation of Weismann's is an example of his apotheosis of

the theory of natural selection. Every process is made to suit this theory, which, as we have seen in the first and second lectures, is, in his opinion, the exclusive factor of evolution. But this very high degree of mingling and re-mingling of ancestral pre-dispositions would be fatal to evolution, for after a combination favorable to survival had been established in one generation it would be broken up into a new combination, perhaps unfavorable, to survival, in the next generation. This entire essay upon "Amphimixis," or the theory of mingling of reduced hereditary substance, will, I believe, mark a turning point to decline in Weismann's influence as a biologist. His whole reasoning is now in a circle around the natural selection theory.

The meaning of conjugation.—Weismann looks upon sexual reproduction as designed to mingle hereditary tendencies and to create individual differences whereby natural selection may form new species. It is evident that these combinations must be mainly fortuitous and productive of indefinite variation; but we have seen that evolution advances largely by the accumulation of definite variations, or those in which each successive generation exhibits the same tendencies to depart from the typical ancestral form in certain parts of the body, and that these tendencies stand out in relief among the diffused kaleidoscopic or fortuitous anomalies.

The fact moreover that variability and evolution by the accumulation of certain variations in successive generations is also observed in organizisms which reproduce *asexually*, both among plants and animals, shows that we must look in another direction for the underlying cause or purpose of sexual reproduction. Weismann rightly combats the old idea of "vitalization" of the ovum by the spermatozoon, and it is perfectly evident from the researches of Maupas and Hertwig that the ovum may as accurately be said to vitalize the spermatozoon as the reverse. Fecundation is simply the approximation of two hereditary substances of distinct origin and their incorporation into a single nucleus. The action and re-action of these substances may be considered equal and mutual, so far as we now know.

The remarkably ingenious experiments of Hertwig and Boveri, above alluded to, strengthen this idea. Some years ago Weismann wrote: "If it were possible to introduce the female pronucleus of an egg into another egg of the same species, immediately after the transformation of the nucleus of the latter into the female pronucleus, it is very probable that the two nuclei would conjugate just as if a fertilizing sperm nucleus had penetrated. If this were so, the direct proof that egg nucleus and sperm nucleus are identical would be furnished." Boveri succeeded in accomplishing a similar feat by depriving an ovum of its nucleus and subsequently causing it to develop by admitting a spermatozoan which fertilized the denucleated ovum and produced a complete individual.

In opposing the vitalizing properties of the sperm, Weismann how-

ever went further, and advocated the view that there is nothing in the nature of vitalization or "rejuvenescence" in conjugation—that, given proper environment, protoplasm is immortal, and runs upon a course of undiminished activity. This we have seen is not the case in the infusoria, and, as recently remarked by Hartog, there is only one class of organisms which, according to our present knowledge, are completely agamous and immortal—namely, the Monadina. It may in future appear that even in the monads there is a cycle for the development in which conjugation plays its part.

Maupas' experiments seem to establish the primitive, and therefore the true, interpretation of the purpose of conjugation as well as of sex, the latter being a consequence of the former, namely, that after a long period of direct subdivision of hereditary material from a single individual, a limit is reached beyond which the forces of heredity are not reproduced in their original intensity unless combined with another set of similar forces of different origin. This combination restores the original intensity. It is objected to this that two sets of feeble forces can not constitute one vigorous force, but this is met by the observed fact that such union does start a new life cycle, and is therefore rejuvenescent. We may regard this as the fundamental meaning of conjugation, and the production of variations as entirely secondary.

The distribution of the chromatin.—We have now reviewed some of the main phenomena of fertilization; there still remains the relation of the hereditary substance to the future development of the individual. There is, first, the astonishing fact that, as the chromatin goes on dividing, its mass or volume remains apparently undiminished; that is, there is apparently as much chromatin in one of the many million active cells of the body as in the original fertilized ovum, and there is still an enigma as to the nature of this chromatin and its functions. Secondly, there is the problem of the maternal and paternal elements in each cell; do they lie side by side or are they fused?

1. In plants De Vries* and others believed that all or by far the greater number of cells in the plant body contain the total hereditary characters of the species in a latent condition. Kölliker† has fully discussed this question and called attention to Müller's early views that, in spite of the physiological division of labor producing the tissues, the properties of all the tissues can be derived from the nuclear substance of a single tissue, as proved by experiments upon the lower animals. Weismann, on the other hand, has held that the course of development is marked by a constant qualitative distribution of his germ-plasm or hereditary substance, so that, so far as nuclear content is concerned, there are three forms of cells: (1) with nucleo-plasm; (2) with nucleo-plasm and germ-plasm; (3) with germ-plasm only.

* Hugo de Vries: Intracellulare Pangenesis. Jena, 1889.

† Die Bedeutung der Zellkerne für die Vorgänge der Vererbung, Zeit. f. Wiss. Zool., 1885. And, Das Karyoplasma und die Vererbung, op. cit., 1886.

Kölliker opposes this idea and maintains that the "idioplasma" passes into all cells, in which it divides in course of development. Step by step from the embryonic layers to the tissues, the constructive processes are under the direction of the nuclei containing this hereditary substance. It remains in every nucleus for a long period unaltered, in order to finally, here earlier, there later, impress its constructive forces. In certain elements, as in blood corpuscles, epidermal scales, etc., it disappears, as the last product of division.

R. Hertwig takes a similar view. Since embryonic and adult cell division is differential, there must be a form of differentiation in the nucleus; but this does not consist in the total elimination of some qualities and survival of others, nor of a reduction in mass. The mass and the properties remain the same in every cell; the differentiation consists in the activity of certain elements in certain tissues. Thus we may say with De Vries that different "pangene" may leave the nucleus and enter the cell in different tissues; or with Nägeli, that special "micellæ" come into activity at certain points; in other words, the potential of the nucleus is differently exerted. Here again we have the idea of patent and latent hereditary elements, such as appear in the entire individual upon a larger scale.

This is one of the most interesting problems for future investigation, but the direction of research will, I imagine, cover a larger area of cell content than the nucleus, as we are now swinging back to regard the extra-nuclear archoplasm as an important factor in the process.

In the following paragraph Hertwig expressed his view of nuclear control and cyto-plasmic differentiation:

"As I saw in the transformation of the nucleus during fertilization proof that it is the bearer of hereditary substance, I recognized a great advance in the fact that the nucleus leaves in the same form in every cell, and in its vesicular capsule is somewhat removed from the metamorphoses of the cells. As Nägeli spreads his idio-plasm as a net-work throughout the whole body, so, according to my theory, every body-cell contained in its nucleus its quota of hereditary substance, while its specific histological peculiarities were to be regarded as its plasma products."

2d. The next question is the fate of the maternal and paternal contributions to the embryo. Here there is a wide difference of opinion. On the one side Van Beneden is the leader of those who regard each cell of the body as in a sense hermaphrodite; as we have seen, his views of maturation and the significance of the extension of the polar bodies were colored by this theory, for he regarded the germ cells as hermaphrodite until one sex was eliminated. But now that the researches of Hertwig have given the last blow to Van Beneden's theory, and it follows that there can be no male and female chromasomes, there still remains room for the analogous view that the maternal and paternal chromasomes remain distinct throughout the course of development, not as sexual elements, but as substances with the same racial and

specific but different individual tendencies. Rabl, an eminent embryologist, shares this view, and it is supported by Boveri upon the observation that in each division the paternal and maternal elements are kept distinct, and in *Ascaris*, for example, two of the chromasomes of each division figure are paternal and two are maternal.

In favor of this hypothesis we may place the following facts: 1st, that there are an even number of chromasome rods in all cells; 2d, that the number is constant throughout all the subsequent changes in the tissues; 3d, that the number is fixed for each species or variety; 4th, that the number is the same in each sex.

Against this replacement hypothesis we must consider the extreme complexity of the division process, and the long-resting, or thread stage, in which the chromatin lies in a confused coil. Further, Hertwig argues that if the elements are distinct we should find some evidence that the maternal or paternal part is atrophied or replaced, or excluded from the nucleus, for both parts can not share alike in the control of the cell. These are Hertwig's grounds for supporting the "verschmelsungstheorie," or fusion theory, also advocated by Waldeyer, to the effect that by the complete union of the maternal and paternal substance a new product is formed; in this fusion the law of pre-potency may come into play, causing one or other of the parental tendencies to predominate, or there may be an even re-distribution, whereby, as expressed by Hensen, "the hereditary substance of the son is not that of the father plus that of the mother, but is his own, with a new hereditary form resulting from the combination."

While suspending judgment between these two views as to the separation or fusion of the chromatin, we may appeal to the external phenomena of heredity for light upon the probabilities in the question First, I refer to the very decided opinion of Francis Galton in regard to particulate inheritance; he is so impressed with the fact that we are made up bit by bit of separate structures derived from different ancestors that he has even suggested that the skin of the mulatto may represent not a fusion of white and black, but an excessively fine mosaic in which the colors are so distributed as to give the appearance of blending. We do sometimes observe patches of color as evidence of uneven distribution. As Galton distinguishes two types of structures with reference to inheritance, viz, those which blend and those which do not blend, we might correlate these types with pre-potency, replacement, and fusion. Where characteristics do not blend, as in eye-color, it is evident that, while the offspring must receive from both parents the material basis for the formation of the complete color of the eye, either the maternal or paternal material must be prepotent and exclude the development of the other; the logical inference is that the former activity replaces the latter; but it is not necessary that exclusion from the cell chromatin should follow. Now, while some blends seem to support the theory of fusion, the sum total of facts of heredity are

strongly against this as a universal principle, for many maternal and paternal structures are preserved in their absolute integrity for generations without the least indication of mixture.

Cell forces and heredity.—We have thus far been considering only the chromatin as the heredity substance *par excellence*, and have disregarded for the time the archo-plasm or dynamic material of the cell.

If we advance upon the hypothesis that a typical cell contains the more or less passive chromatin, and the archoplasm playing upon this chromatin in course of every phase of re-distribution, it seems *à priori* improbable that elements which are associated with every vital change should be dissociated in the phenomena of heredity. We might suppose that the mechanics of karyokinesis are exactly similar in every cell of one individual, but it is highly improbable that they should be exactly similar in two individuals. We should therefore anticipate the joint transmission of the chromatin and archoplasm, implying by the latter the dynamic centers especially connected with hereditary function as distinguished from the general functions of metabolism.

This leads us to look for evidence from the life of the cell in its totality. We owe to Dr. Max Verworn* a fresh treatment of this subject, based upon experimental researches among the Infusoria, mainly by the extirpation method. As his experiments included only the phenomena of living cells in which the chromatin substance was of course undifferentiated to the eye, he treats of the nucleus as a whole without distinction as to chromatin and achromatin. He concludes that the physiological importance of the nucleus is exhibited in its constant interchange of materials with the remainder of the cell body; only through this interchange does it influence the cell and control its life processes. The interchange is in triple currents, *a*, from outside of cell to cyto-plasm; *b*, from cyto-plasm to nucleus; *c*, from nucleus to cyto-plasm. These movements of interchange are the expression of life phenomena. He compares the *rôle* of the nucleus to that of a cell organoid, like chlorophyll, as not constantly present but as invaribly necessary to activity. Thus he believes even the most lowly organized cells have nuclear centers, and that even bacteria are differentiated into nuclear and extra-nuclear areas. Coupled with this idea of nuclear control is the somewhat paradoxical statement that the nucleus is not a dynamic center, either automatic or regulating, and the conclusion that the nucleus alone can not be the seat of fertilization and heredity, but both the nucleus and extra-nuclear protoplasm must constitute the material basis of heredity. This conclusion is in the direction of the general reaction of opinion which is now taking place against the centralization of cell-government in the nucleus.

Vague as they must necessarily be, our ideas of cell forces are somewhat further defined by the brilliant experiments of the Hertwig

* "Die Physiologische Bedeutung des Zellkerns," *Archiv für Physiologie*, 1891, pp. 113-115.

brothers upon germ cell physiology and pathology, which are full of suggestion as to the causation of abnormalities in inheritance. These were begun in 1884, and were first directed to the influence of gravitation upon the planes of embryonic cell division, following up the experiments of Pflüger and Rauber. In 1885 the conditions of bastard fertilization were studied; in 1887 the causes of polyspermy or multiple fertilization; and in 1890 the effects of extreme heat and cold upon germ-cell functions.* In general the conclusions reached were that in the normal state there exist regulating forces in the ovum which prevent multiple fertilization or bastard fertilizations (*i. e.*, by spermatozoa of other varieties), but these forces are neutralized where the life-energy of the cell is diminished by reagents or by extremes of temperature.

For example, in the normal state the entrance of a single spermatozoon produces a reaction in the ovum wall preventing the entrance of other spermatozoa, but when the ovum is weakened by chloroform solution two or more spermatozoa enter before the reaction appears; in fact that degree of polyspermy is directly proportional to the intensity of the chemical, thermic, or mechanical disturbance of the ovum. Double fertilization or over-fertilization has not in a single case resulted in the production of twins, so that Fol's supposition is negatived, although other forms may behave differently. The cell function may be arrested at any stage by thermic influences; thus two pronuclei, paternal and maternal, about to unite, can be held apart by lowering the temperature. Polyspermy also results from a lowered temperature. It is noteworthy that the conditions of bastard fertilization and polyspermy are different; chloroform produces the latter but not the former. Kupffer has, I believe, succeeded in producing twins, or rather two-headed monsters, by abnormal fertilization in fishes.

These researches, although made with a different object, re-establish the older views as to the inter-dependence of nuclear and extra-nuclear activities, and show that no sharp line of demarcation of function can be drawn between the nucleus as a center of reproduction and heredity and the cyto-plasm, as the seat of tissue building and nutrition. In Boveri's discovery of the archo-plasmic centers, or centrosomes, we find positive ground for this broader view. It is connected with the cell phenomena of heredity in the following manner:

While the union of the nuclei in fertilization is the most obvious feature, this union is dependent upon the archoplasm, which re-arranges the nuclear elements. If the spermatozoon contains no archoplasm, this power can not come from the parental side; but Boveri shows that this is probably not the case and that the spermatozoon brings its centrosome with it, thus entering the ovum with both the parental chromatin substance and dynamic material. It is certain from this and

*Experimentelle Untersuchungen über die Bedingungen der Bastardbefruchtung. Jena, 1885. See series of papers in *Jenaische Zeitschrift*.

from the observations of Roux that the sperm cell is now to be regarded as more than a mere nucleus, that it contains both nuclein and paranuclein.

Intercellular forces.—The forces within the different portions of the cell lead us to consider those which must exist between different cells. This is an obscure question at present; but, as I have observed in the close of the second lecture, it is an extremely important one in connection with the problem of heredity.

As Prof. Wilson writes: "My own conviction steadily grows that the cell is not a self-regulating mechanism in itself, that no cell is isolated, and that Weisman's fundamental proposition is false."

It is a long step between an *à priori* conviction and the demonstration by experiment of a correlation of forces between the cells. This seems to me a most important field of experiment. We have seen in Maupas's work that the contact of two infusoria initiates a rapid series of internal changes; we have only to conceive of analogous changes taking place when two cells are not in actual contact, as in the phenomena of previous fertilization referred to in my second lecture. Hertwig and others have shown how gravitation is related to cell activity. Roux has destroyed half an embryo with a hot needle in the first stages of segmentation and followed the other half through the stages of subsequent development. Another clever experimenter has turned fertilized ova upside down during the early stages of development, and shown how the protoplasmic pole and yolk pole forcibly change places. Driesch has traced the connection and meaning of the first plane of cleavage in the embryos of echinoderms, and has succeeded in raising a small adult from half an embryo artificially separated during the first cleavage stage. Wilson, in the larva of Nereis, has shown how a certain stage of division in one group of cells affects all the other groups. All these experiments are in the line of determining the relations which exist between internal cell forces and other natural forces. What we must now seek to determine is the relation of cell to cell throughout the body, in connection with the phenomena of heredity.

Conclusions.—Perhaps the most impressive result of our review of recent researches in evolution and heredity is the uniformity of life processes throughout the whole scale of life from the infusoria to man. The most striking analogy is that seen in the laws of fertilization and conjugation, which are shown by Maupas's researches to have been established substantially in their present form at a very early period in the evolution of living organisms. Such uniformity furnishes a powerful argument for the advocates of the study of biology as an introduction to the applied science of medicine. Much that is now entirely omitted from medical education, because it is considered too remote, is in reality at the very roots of the science. To understand the disorders of life

we should first thoroughly understand the essential phenomena of normal life. Of course we shall never see life as it really is, because there is always something beyond our highest magnifying powers; but we come nearest to this invisible form of energy when, with such investigators as Hertwig and Maupas, we strip the life processes of all their accessories and view them in their simplest external form.

The problems of evolution are found to be inseparably connected with those of heredity. No theory is at all adequate which does not explain both classes of facts, and we have seen that the explanations offered by the two opposed schools—those who believe in the transmission of acquired characters and those who do not—are directly exclusive of each other. We should suspend judgment entirely rather than cease to gather from every quarter facts which bear upon the most important and central problem of the transmission of acquired characters. I have endeavored to point out the opportunities which medical practitioners enjoy of contributing evidence upon this mooted question. It must not be forgotten that while the inheritance of individual adaptation to environment is the simplest method of explaining race adaptation such as we observe in the evolution of man, we know absolutely nothing of how such inheritance can be effected through the germ cells. We can not at present construct even any form of working hypothesis for such a process. On the other hand, we have found how untenable is the alternative theory offered to us by Weismann, that it is solely natural selection or the survival of the fittest which

> " - - - shapes our ends,
> Rough hew them as we will."

At the same time Weismann's conception of a continuity of germinal protoplasm, which we have found to consist in chromatin plus archoplasm, helps us over many of the phenomena of heredity, especially on the retrogressive side, and if it were not that we must also account for progressive and definite transformation in heredity, we might credit the distinguished Freiburg naturalist with having loosened the Gordian knot.

In summing up, the order of treatment followed in the lectures may be reversed, and we can begin with the germ cells, and condense the more or less ascertained facts.

The germ cells:

(1) The material substance of hereditary transmission is the highly coloring protoplasm, or chromatin, in the nucleus of the germ cells, probably connected with a certain form of archoplasm, or dynamic protoplasm outside of the nucleus.

(2) Before conjugation and fertilization the hereditary substance of both the male and female cells is reduced to one-half that found in a typical cell. This substance is however first doubled and then quartered, the meaning of which process is not understood.

(3) There is a difference of opinion as to whether the paternal and maternal hereditary substances, during fertilization, are fused or lie side by side; also as to how the substance is distributed through the tissues, whether en masse or by qualitative distribution.

Heredity:

(4) No connection between the germ cells and body cells is known, but the facts of heredity seem to render such a connection theoretically necessary. Several classes of facts connected with reproduction seem to support this theory.

(5) The facts of heredity support the theory of a continuous and specific form of protoplasm as the basis of repetition of type.

Evolution:

(6) The facts of evolution, both in present and past time, point to transformism by definite progression toward new types of structure in succeeding generations, opposing the retrogressive forces of heredity.

(7) The theory (natural selection) of definite progression by the accumulation of fortuitous favorable variations is found to be not only theoretically improbable, but not to correspond with the observed laws of variation.

(8) The laws of variation (anomalies) lend support to the theory of hereditary transmission of individual acquired variations, but even this (Lamarckian) theory encounters many difficulties.

I think this is as fair a statement as can be made at the present time, and it rests upon a general survey of the whole field.