Pleistocene *Macrauchenia;* the other an astonishing imitation of the horses, an imitation so detailed and so close that it has misled Ameghino into believing that this is the actual phylum of equine descent. The resemblance is striking in all parts of the structure; in the teeth, the skull, the backbone, the limbs and especially the feet. The less advanced forms have tridactyl feet, but with the lateral digits already greatly reduced, while the more differentiated species surpass the true horses in strict monodactylism, the splint-bones being almost suppressed and represented only by minute nodules of bone. Yet these wonderfully horse-like creatures prove, on examination, to be not even perissodactyls! A more remarkable and instructive case of convergent evolution it would be difficult to imagine.

The Astrapotheria were the largest of Santa Cruz mammals. In them the great, vaulted skull had such shortened nasal bones as to suggest the presence of a proboscis, and slender, edentulous premaxillaries. The canine teeth in both jaws are enlarged to form powerful and formidable tusks, the premolars are reduced in size and number, while the molars are enlarged. The grinding teeth display a remarkable likeness in size and pattern to those of the northern rhinoceros, *Metamynodon*, from the White River beds—another example of convergent development. The Astrapotheria would appear to have become extinct before the Pleistocene, and it must be the object of subsequent studies to determine whether the group is really entitled to ordinal rank, or whether it should be referred to the Litopterna.

I am not prepared to express an opinion as to the taxonomic position of *Homalodontotherium*, one of the most curious of the many curious Santa Cruz hoofed-animals.

The Primates are not very well known as yet, for the fossils are seldom so complete as those which so often rejoice the heart of the student who works with the other groups. So far as they are understood, the Santa Cruz monkeys would appear to be as characteristically South American, and as different from those of the northern hemisphere, as we have seen to be the case among the Rodentia.

This exceedingly brief outline sketch will have served its purpose if it makes clear the wonderful character of the Santa Cruz fauna and its radical differences from the contemporary life of the northern hemisphere. Much remains to be done before the full account of these splendid collections can be published. I have attempted merely to describe their general nature and the impression which they make upon an observer whose studies have hitherto dealt with northern types.

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IS THERE ANY DISTINCTION BETWEEN SEXUAL REPRODUCTION AND ASEXUAL REPRODUCTION?

The following pages contain rather a full outline of the views advanced by Professor Richard Hertwig in a recent lecture* in which he discusses the relation between fertilization and reproduction. I have endeavored to make this more in the nature of an abridged and revised translation than a review, for it seemed best to follow as closely as possible Professor Hertwig's own way of presenting the subject, which is as follows:

Everyone will admit that most of our general conceptions in biology are greatly influenced by our knowledge of the higher animals and plants. This fact is made very evident to all who study the reproduction

* 'Mit welchen Recht unterscheidet man geschlechtliche und ungeschlechtliche Fortpflanzung?' Vortrag, gehalten am 7, November, 1899. Aus den Sitzungsberichten der Gesellschaft für Morphologie und Physiologie in München. 1899. Heft. II.

of Protozoa, and the inevitable conclusion from such study is that our schema of the kinds of reproduction needs reforming.

In common usage we distinguish the sexual multiplication of animals, in which the formation of the new individual is preceded by an act of fertilization, from the asexual multiplication which takes place without fertilization. The existence of parthenogenesis makes such a distinction difficult to maintain. We can no longer consider this phenomenon as the 'monogonous' method of reproduction, since the typical cases, which are found in the Arthropods, have apparently been derived from sexual reproduction by the loss of fertilization. The same is probably true of what occurs in the Sporocysts and Rediæ of the Trematodes. In order to overcome this difficulty and place parthenogenesis where it naturally belongs, I would propose for sexual reproduction the term *reproduction by means of germ cells*. But I would not stop with this alone, for my study of Protozoa has developed in my mind a strong conviction that our whole view of reproduction needs a radical reformation.

Reproduction by the asexual method alone was formerly considered an important characteristic of the Protozoa, but this breaks down entirely in the face of the increasing number of observed cases in which true fertilization occurs. From the observations recorded for Ciliates, many Flagellates, Rhizopods of the most widely different orders and numerous Sporozoa, I believe that *fertilization occurs in all Protozoa*, and that its rarity and the difficulty of demonstration are the only reasons its general occurrence has not hitherto been observed.

A still further objection to the term *sexual reproduction* arises from the fact that *we often, if not generally, fail to discover any causal relation between fertilization and reproduction.* The actual reproduction of the Protozoa is accomplished either by their division into two or more individuals of equal size or by the pinching off of smaller daughter animals from a larger mother. Now, before we have a right to speak of reproduction as 'sexual,' we must show that fertilization exercises a determinative influence upon its course. This might be proved by showing that fertilization hastened reproduction or by showing that certain kinds of reproduction occurred only in connection with fertilization. Any such determinative influence is now positively excluded in a large majority of cases.

In the ciliated Infusoria, where fertilization in the Protozoa was first recognized as such and has been most carefully described, conjugation is not the forerunner but the after result of active reproduction. Conjugation is even a hindrance to the multiplication of Infusoria, because the necessary reconstruction of the nucleus often occupies many days, that are lost for the purpose of reproduction. The power of division of an Infusorian which has just finished conjugation is, if anything, less than before, and is never increased. In like manner, the power of division in an Infusorian is not decreased as it approaches the time of conjugation, for when two individuals are separated before the actual nuclear exchange has begun, they will divide even more actively than animals after the conjugation has been normally ended. In fine, one comes to the conclusion that the advent of conjugation in Infusorian cultures is not a favorable sign for their further increase.

Beyond any doubt, fertilization causes a pause in the multiplication of many Flagellates and Rhizopods. Volvox when fertilized yields resting spores, which will only develop after a long period, during which they have been frozen or dried.

The same thing is observed after the conjugation of Algæ, with which *Volvox* is quite rightly placed by most investigators.

The cyst of *Actinophrys sol*, which arises

during fertilization, has exactly the same significance. In *Actinosphœrium eichorni* the encystment is connected with multiplication, but the multiplication (making of the primary and secondary cysts) precedes fertilization, and the fertilization itself (fusion of the secondary cysts) leads to a resting period of considerable duration (making of the germ spheres).

In the Protozoa then *a lessened power of division follows upon fertilization.* In many Gregarines encystment is certainly accompanied by fertilization, for the division into pseudo-navicellæ, which in turn separate into the sickle-shaped germs, begins within the cyst. In the Gregarines proper, multiplication seems to be restricted entirely to this encysted condition. In some Sporozoa, on the other hand, there are two kinds of division. Coccidiæ and Hæmosporidiæ multiply in the tissues of their hosts by division and without fertilization (auto-infection). At length, however, peculiar divisions begin which are characterized by two things, (1) that they are prepared for by fertilization and (2) that the transportation from one host to another is necessary for their proper course. The fertilization may be completed in the old host, but the multiplication is connected with the transportation into a new one or with some change of place. Since a regular cycle between division with and division without fertilization is here established and each kind of division has its peculiarities, we may speak of an alternation of generations as Schaudinn has done. Another illustration of alternation of generations would be the reproduction of *Noctiluca.* This form multiplies for a long time by ordinary fission. Cross-fertilization then takes place between two individuals, each of which produces a generation of zoospores, which in turn grow up to *Noctilucæ.* According to Schaudinn's description, *Trichosphœrium sieboldi* is still another example.

The above *résumé* shows that in all the cases cited multiplication by division, and after a time the advent of fertilization, is constant. There is, however, the greatest diversity in the relation between fertilization and division. There are three possible cases, (1) the fertilization is the cause which stops the division (*Volvox, Actinosphœrium, Actinophrys*), (2) the fertilization is the cause which brings about division of another sort which is often very rapid (*Noctiluca*), (3) the fertilization has no marked influence upon the power of division, because the same kind of division prevails after fertilization as before.

In view of these facts is it possible to speak of 'sexual' reproduction in the Protozoa? I think we cannot use such a designation without causing false conceptions of the relation between reproduction and fertilization. There exists in the Protozoa only one kind of reproduction, *i. e.*, division in its manifold varieties. Besides this the Protozoa need to reorganize the structure of their unicellular bodies by fertilization. What the nature of this reorganization is, or its physiological significance, I will not attempt to discuss.

Fertilization is thus interposed from time to time in the life history of a Protozoan. The life epoch at which this interposition occurs is often connected with the times of more subordinate importance. It depends upon suitable conditions which always vary according to the conditions of life in the different classes and orders and perhaps even in the families of the same order. In many Protozoa division takes place within the cyst in a manner somewhat similar to what occurs without the cyst in others. Since we attribute no great significance to these differences in encystment, so it would be a mistake to emphasize the question whether the division of a Protozoan was or was not brought into close connection with fertilization. In the Protozoa fertilization

exercises no influence upon the power of multiplication which in any wise differs from the influence exerted by any other vital process of the cell. Fertilization and reproduction are phenomena which may be found together, but which in their essence have no connection with one another.

Leaving the Protozoa, I will now consider the kinds of reproduction in the Metazoa. We formerly supposed that the asexual reproduction of Metazoa had been inherited from the Protozoa and that their sexual reproduction was a new acquisition. This theory prevailed as long as we thought the Protozoa could only reproduce in an asexual manner. The wide distribution of fission and budding in the lower Metazoa and its entire absence in the Molluscs, Arthropods and Vertebrates, seemed to harmonize with such a view. Although I once held this same opinion, I now consider it incorrect. It seems to me much nearer the truth to make just the opposite statement, viz., that the sexual reproduction of Metazoa is a continuation of the method of reproduction in the Protozoa, while the budding and fission of Metazoa are adjustments having only an outward resemblance to the budding and fission of the Protozoa.

If we consider the multicellular animal as a cell community, its life history may be resolved into a series of innumerable cell divisions which were preceded by an act of fertilization. This is the same kind of developmental cycle as we find in many Protozoa. For example, in the Gregarines the formation of the pseudo-navicellæ and later the sickle-shaped germs follow fertilization. The sickle-shaped germ is comparable with the egg cell, for the Gregarine arising from it suspends multiplication until it has been fertilized. A different character would result in the Metazoa, from the fact that most of the products of division remain united and only certain ones, the sex cells, become self-sustaining. While every cell-division in the Protozoa is a similar act of reproduction, we now distinguish between cell-divisions which bring about the growth of existing individuals and those which permit the creation of new individuals. There is a further difference. The cells which effect the growth and life functions of the multicellular organism, the somatic cells of Weismann, have an enormous power of multiplication. The sex cells which are differentiated sooner or later differ from these proliferating cells in that they lose their power of division relatively early. Their characteristic maturation processes are the last expression of this power. The need of fertilization does not necessarily result from multiplication because the sex cells stop multiplying much sooner than the somatic cells which they closely resemble in all other respects. The cell community needs the combination of different kinds of idioplasm and therefore has seized the opportunity which is presented when the organism is in a unicellular state.

Our conclusion here is similar to that reached in the Protozoa. The occasional mingling of two idioplasms is necessary for the integrity of the cell's life and this is fertilization in the narrower sense. A second phenomenon may be associated with it, viz., the stimulus to development or reproduction. While in the Protozoa fertilization is now connected with reproduction and now separated from it, in the Metazoa it is always combined with reproduction. The two occur together as a necessary consequence of the multicellular condition, for a mingling of two idioplasms is possible only when the whole organism is contained in a single cell. We have thus fallen into the error of considering fertilization and reproduction inseparable. The recent investigations upon the details of fertilization have caused some of us to break away from this idea, but our opinion has not extended sufficiently to produce a general conviction

that reproduction and the combination of idioplasms are separate phenomena.

To emphasize the difference between the two processes suppose we consider fertilization as a complicated morphological process, and reproduction as something which can be accomplished in another way. The first serves to unite substances which possess a stable organization. The second, like all cell-divisions, merely changes a physiological condition of equilibrium. Parthenogenesis is an example of how the power of development may be present in the absence of fertilization. My own view of this phenomenon is that the necessary reciprocal relations of nucleus and protoplasm are in some way established and division ensues. The so-called fertilization of non-nucleated egg-fragments seems to me an analogous case which no one who considers the nuclei the bearers of the idioplasm can call true fertilization. It is much more likely that the necessary reciprocal relation is established by a fusion of the egg-plasm with the plasma of the spermatozoan, in which event we should be dealing with a counterpart of parthenogenesis.

It would therefore be entirely conceivable that the conditions necessary to division could be produced in ripe unfertilized eggs by chemico-physical influences. Loeb's observation that the eggs of sea-urchins (*Arbacia punctulata*) develop to plutei if they have been previously exposed to the action of a certain salt solution, raises no theoretical objections to this view. I have myself succeeded in making unfertilized eggs develop after treatment with chemical reagents (strychnine), although they possessed the power of development to a lesser degree.

It would be of the greatest interest to trace the sexual reproduction of the Metazoa from its origin in the reproduction of unicellular forms. Unfortunately the solution of this problem is made the more difficult by the wide gap which separates the Protozoa and the Metazoa. The Mesozoa are not suitable for our purpose. Their development is not sufficiently known and has probably been modified by the entire class having become adapted to a parasitic life. Nevertheless the investigations upon the best known Dicyemidæ give strong indications that their reproduction still follows the method of the Protozoa. The endoderm of *Dicyema* produces reproductive cells which in many cases yield young animals directly, in others probably after previous fertilization. The first process serves for auto-infection; the last probably occurs when the parasite would be carried to a new host. The first is known in an entirely arbitrary way as parthenogenesis, when the criterion of parthenogenesis (loss of fertilization) is not proved. It evidently corresponds to the so-called asexual reproduction of the Protozoa. When their multicellular condition and the modifications which it entails are considered the development of the Dicyemidæ seems to admit of a very close comparison with the development of the likewise parasitic Coccidiæ and Hæmosporidiæ.

Plants offer a much more favorable field for the solution of this problem than animals because they exhibit many forms midway between the uni- and multicellular organisms. In the multicellular Algæ there are two kinds of reproduction: (1) asexual, by means of spores and (2) sexual by means of gametes. Both have in common the fact that single cells separate from the cell community and grow up into new plants. In the first case it is each time a single cell for itself, in the second a cell which has previously copulated with one of a different stock. The difference between spores and gametes is often quite pronounced both in their structure and their method of development. In other cases the anatomical and developmental differences

are wiped out. It sometimes happens that cells which are in every other way like gametes develop without fertilization, if they are prevented from copulating. This seems to be analogous to the gradation in the need of fertilization which is found in the Protozoa. We are further reminded of the Protozoa by the fact that fertilization often leads to the formation of resting spores.

If we now attempt an accurate statement of the kinds of reproduction in the plant and animal kingdoms, the old conception of sexual and asexual reproduction must be given up entirely and replaced by the following statement.

All organisms effect their reproduction in a common way by means of single cells which have arisen by cell-division. In single-celled organisms every cell-division is an act of reproduction and results in the formation of another physiologically self-sustaining individual. In multicellular animals, most of the cell divisions lead to the growth of the multicellular individual and only certain of them serve for reproduction. Fertilization goes on side by side with reproduction, because the organism cannot attain its highest development without the union of two individualities by nuclear copulation. Fertilization in its essence has nothing to do with reproduction. In many single-celled organisms the two occur quite independently and are united for what we call sexual reproduction only under special conditions. Such special conditions are imposed upon all multicellular animals, since a mixture of two idioplasms could be easily accomplished only during the unicellular stage. Hence fertilization takes place when the single-celled reproductive bodies are formed. It in no wise follows that all such reproductive bodies must be fertilized. One would naturally expect that reproductive cells not needing fertilization (spores) and such as are destined for fertilization (gametes, eggs, spermatozoa) should exist side by side. This is the case in plants, though in multicellular animals no genuine case of spore-formation has been demonstrated beyond question.

The one case which can be pointed to with strong probability is the above mentioned reproduction of the Dicyemidæ. Everywhere else in the Metazoa spore formation seems entirely supplanted by sexual reproduction. All cases of development from single unfertilized eggs are apparently parthenogenesis and to be explained as sexual reproduction in which fertilization has been lost. The significance of heterogenesis in the di-genetic Trematodes is doubtful. In accordance with the prevailing view, I make a sharp distinction between spore-formation and parthenogenesis resp., heterogenesis, between reproduction by single cells which never have been fertilized and reproduction by cells in which the fertilization has been lost. I doubt if such a distinction could be practically carried out in every case. As long as the reproductive cells are developed in special germinal glands, as for example in the Crustacea, there can be no doubt that we are dealing with parthenogenesis. It is quite different, however, where no egg-glands are differentiated, as in the Rediæ and Sporocysts of the Trematodes. In such cases only a more accurate study of the first stages of development will elucidate the matter. In all cases of parthenogenesis which have been carefully investigated the maturation has been preserved. This has hitherto been always regarded as the forerunner of fertilization. Even in the Protozoa it is connected with the sexual process. Its existence in reproductive cells which develop without fertilization therefore favors the view that fertilization formerly did take place. On the other hand, one would suppose that spore-formation, like the ordinary division of the Protozoa, is without polar bodies. Unfortunately we can only speculate upon

this exceedingly interesting question, for so far as I know the literature, not one case of spore-formation has been carefully investigated and most cases of parthenogenesis insufficiently. And yet such investigations, particularly in the lower plants and animals, would be a profitable and important work.

In my summary I have not mentioned the budding and the fission of the multicellular animals and the so-called 'vegetative reproduction' of plants. We commonly unite these processes with the budding of the Protozoa and the spore-formation of the Algæ, under the name of asexual reproduction. I have considered them only briefly as new acquisitions of multicellular organisms. In 'vegetative reproduction' whole multicellular stocks are set free from a mother animal which has rapidly increased in size. The phenomenon presents the greatest diversity. The budding of the Tunicates is quite different from that of the Bryozoa or Hydroids or from the fission of the Annelids. The diversity in the forms of vegetative reproduction is still greater in plants. The investigations in the past twenty years have also proved that the division and budding of the Metazoa do not follow the laws laid down by the germ layer theory. In this respect they resemble regeneration. The whole matter will be a self-evident phenomenon if we accept the view of reproduction which I have set forth above and recognize in the division and budding of the multi-cellular animals adaptive phenomena which have come about in the several groups independent of their development. These processes of asexual reproduction are well named by the botanist 'vegetative reproduction.' If they are more common in the lower than in the higher forms it is because the higher organization sets a limit to the vicarious substitution of one part for another. Similar conditions therefore underlie vegetative reproduction and regeneration and there are many analogies between the two processes. It is worth noticing that in the lower plants, where spore-formation is very common, 'vegetative reproduction,' if we use the term as we have just defined it, is not present. Stocks which have been accidentally broken off from the threads of Algæ can, it is true, develop further, but under natural conditions the Algæ seldom make use of the process for reproduction.

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*Study of the Correlation of the Human Skull.**

The substance of this paper was a thesis for the London D.Sc. degree; it was shown to Professor Pearson, at whose suggestion considerable modifications were made, and a revision undertaken with a view to publication.

In order to deal exactly with the problem of evolution in man it is necessary to obtain in the first place a quantitative appreciation of the size, variation and correlation of the chief characters in man for a number of local races. Several studies of this kind have been already undertaken at University College. These fall into two classes, (i) those that deal with a variety of characters in one local race, and (ii) those which study the comparative value of the constants from a variety of races. Thus Dr. E. Warren has dealt with the long bones of the Naqada race,† Mr. Leslie Bramley-Moore has compared the regression equations for the long bones from a considerable number of races in a memoir not yet published, Professor Pearson has dealt with the regression equations for stature and long bones as applied to a

* 'Data for the Problem of Evolution in Man,' No. VI. By Alice Lee., D.Sc., with some assistance from Karl Pearson, F.R.S. Abstract read before the Royal Society of November 15, 1900.

† *Phil. Trans.*, B, Vol. 189, p. 135.