The descent of the primates : lectures delivered on the occasion of the sesquicentennial celebration of Princeton University

THE

DESCENT OF THE PRIMATES

LECTURES DELIVERED ON THE OCCASION OF
THE SESQUICENTENNIAL CELEBRATION
OF PRINCETON UNIVERSITY

BY

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THE DESCENT OF THE PRIMATES

NEW FACTS AND OLD PROBLEMS

For a student of natural history, be he a zoölogist or a botanist, the examination of the external characters of animals or plants is generally the first step by which he acquaints himself with the objects of his study. Next comes the investigation of their internal fabric, of their organs and of their tissues; finally, the yet more laborious unravelling of their development. The slow and numerous steps by which these organs and tissues have come into being are always identical; they lead on from a simple fecundated egg-cell to the complexity of the adult animal or plant. In this way embryology throws a welcome light upon questions which anatomy alone would not enable him to solve. When once he has thus become thoroughly familiar with a considerable number of facts concerning the particular object of his researches, he extends these to other objects, the final goal of his life being to obtain a glimpse of

the plan on which living things are built, and of the way in which they work.

In order to classify the collected facts methodically, he looks out for some system or other according to which a satisfactory arrangement of the varied forms of life may be made. More than a hundred years ago Linnæus produced the first really all-embracing arrangement, in his "Systema Naturæ."

Up to 1859, however, all this seemed more or less artificial; and although a difference was undoubtedly made between what was called an artificial and what was looked upon as a natural system, still the latter did not commend itself to naturalists as the expression of some great law which is even now at work throughout nature, but more as a cupboard in which the facts happen to fit in together nicely; whereas in what is called an artificial system they are, so to say, heaped together according to size, color, or number.

Since 1859 a fundamental change has come over natural history. Thanks to the labors of Charles Darwin, evolution is now as universally acknowledged as is gravitation, and we have come to look upon all systems of classification as preliminary attempts definitely to establish that

most venerable tree of descent, that most real and palpable pedigree, by which all things living at this present moment are directly connected with their ancestral forms, that existed in preceding geological epochs, as far as the earth's past history reveals the presence upon it of living beings.

Henceforth there can thus be no two competing or rival systems, between which biologists may choose according to their convenience. There is only one, and every conscientious naturalist should strive to disentangle, with all the tenacity and accuracy he is capable of, the complexity of as many of its twigs or branches as may happen to be within his reach.

If there is one fact which in the last twenty-five years has become self-evident, it is the comparatively insignificant place which the whole number of living species, as we know them, occupies in this immense tree of descent. Life reaches down into the early stages of the earth's youth, and there already we find it divided into minor stems and branches, the majority of which do not send up off-shoots into the present period. Fortunately, palæontology here steps in, and for the animals or plants of bygone geological epochs of which we shall forever miss the possi-

bility of studying the complete anatomy, or the development, we yet dispose of skeletons, teeth, shells, leaves, portions of bark, etc., by which we are guided in determining their relation either to living beings or to other fossil remains.

In no country has the discovery of important fossils advanced at such a rapid rate as in America, both north and south of the equator. And it is to the undaunted zeal of your explorers, and to the keen discrimination of your palæontologists, such as Leidy, Cope, Marsh, Scott, Osborn, and others, that we owe most valuable material, which is at the same time the firmest foundation upon which Evolution can be established.

It is just twenty years ago that Huxley, in the three famous lectures which he delivered at New York, called this "the demonstrative evidence of Evolution." And in those twenty years the accumulation of new evidence, all tending in the same direction, has never ceased. It has been especially voluminous with respect to reptiles and mammals. In this latter class new orders have sprung up, new genera have had to be created by the dozen, and certain skeletons have come to light which must have belonged to what have

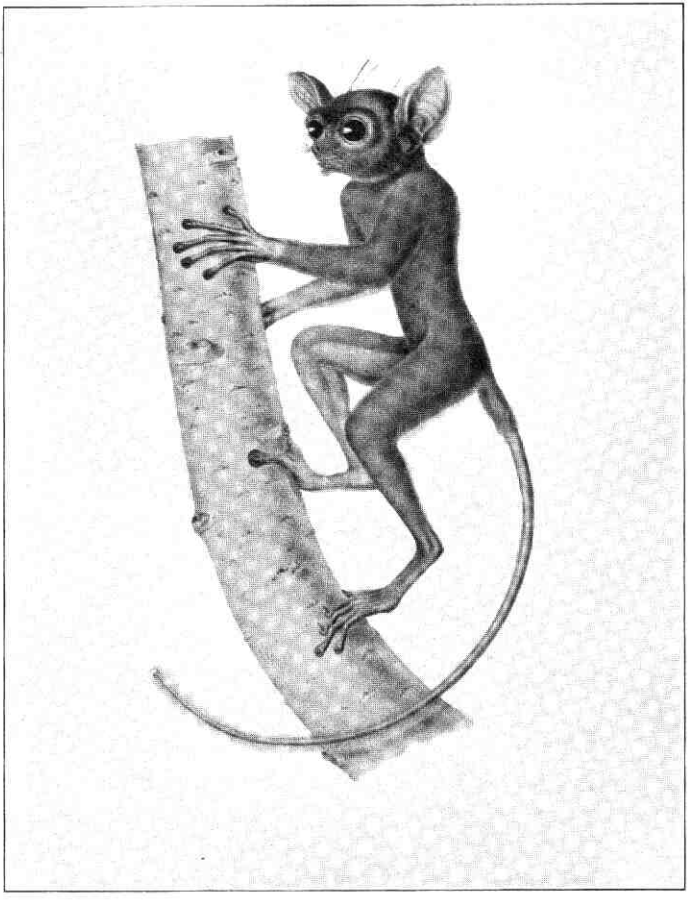
been very suggestively called collective, or synthetic, types.

Collective types are such as will allow us to pass by comparatively small and gradual changes from them to two or more different types, which in them may have found their starting-point. Such collective types are not limited to the fossil fauna. Among living mammals of the higher type (that is, after exclusion of Duckbills and Marsupials) a very marked collective type is presented by such animals as the hedgehog and its hairy relative, the Indian Gymnura. This has been firmly established by no less an authority than Huxley, who in 1880, in a celebrated paper, "On the Application of the Laws of Evolution to the Arrangement of the Mammalia," vindicated that position for these two genera, and declared that in them, even more than in other Insectivora, we "possess the key to every peculiarity which is met with in the Primates, the Carnivora, and the Ungulata."

We shall in due time have to remind ourselves of this momentous utterance of Huxley, and for the moment will turn our attention to an animal which could in no sense be looked upon as a collective type, although some of its details suggest its significance as an intermediate link between

genera otherwise widely separated. It is a small mammal and has been excavated in the lower Eocene of the United States, at least its skull, jaws, and teeth. These remains offer certain points of peculiar interest. Cope, to whom we owe the first description of this fossil, gave it the suggestive name of *Anaptomorphus homunculus*. He thereby intended to convey the expression of the curious fact that, with respect to certain peculiarities of its dentition, this small creature reminded him strongly of man and the higher monkeys.

Anaptomorphus must have been about the size of a squirrel, but whether it had a tail or not we cannot at present say. It had big eyes and was most probably a nocturnal animal of omnivorous habits, whereas its brain capacity exceeded that of any of the lower mammals of corresponding size. There is, however, one genus of living mammals with which its discoverer immediately saw it to be closely related, namely, the rare and quaint spectral Tarsius, of which the natives of Sumatra, Banka, and Borneo stand in suspicious dread because of its weird appearance. Raffles tells us that when the natives perceive a specimen on a tree near their rice fields, they abandon these and plant their rice elsewhere, being



Tarsius spectrum, after Burmeister. 2-5 natural size.

firmly convinced that misfortune would be in store for them or their families if they did not do so. Cuming, who has observed live Tarsius in the Philippines, praises its particular cleanliness, and remarks that when it is disturbed in its cage, it clenches its teeth together and simultaneously contracts its facial muscles in the same way as a monkey would do. Certain peculiarities in the structure of its legs enable it to accomplish long jumps. In taking its food it sits down on its hind-quarters, holding the morsel in its forepaws.

We have reason to believe that this description of the habits and aspect of Tarsius would, to a great extent, apply to the fossil genus Anaptomorphus. And we will now further inquire in what respect these two isolated genera might prove useful to us in the determination of certain points of mammalian affinities. I hope to be able to make it clear to you that under certain circumstances the value of such outlying and apparently aberrant forms, imperfect and few in number as their remains may be, can become quite as decisive to us for the determination of certain points of mammalian descent, as can, on another occasion, a great number of fossil remains, such as those of the slow gradation by which in the successive Tertiary deposits the gulf between,

say, the five-toed Eocene Condylarthra and the modern horse may be bridged over.

In the case under consideration, the importance of Anaptomorphus and Tarsius will be thoroughly understood as soon as we call upon comparative anatomy and embryology to furnish us with certain crucial facts, by which their exact position in the mammalian system may be more definitely determined.

In order to obtain material for studying the embryology of Tarsius and other mammals, I undertook some years ago a voyage to the Indian Archipelago. I did not succeed, however, in procuring *one* live specimen of Tarsius during my seven months' stay in Java, Sumatra, and Borneo. Nevertheless, I left behind me drawings and descriptions of the animal, fluids for the preservation of its uterus, and full instructions. I have since been fortunate enough, thanks to the active co-operation of friends and correspondents, to obtain an unbroken developmental series of this rare mammal. More than four hundred and fifty stages, which range between the moment of fecundation and that of birth, are already in my possession; it is upon these that the conclusions which I will place before you are based.

Hitherto both Tarsius and Anaptomorphus

have ranked with the Lemuroids or Prosimiæ, an order of mammals which has been looked upon (as the German name of "Halbaffen" and the Latin term "Prosimiæ" implies), as a sort of half-way house between the lower mammals and the monkeys and man. These Lemuroids are in the present time restricted to the tropical forests of the old world.

The island of Madagascar may be said to be a regular Lemurian "reserve," — numerous species, quite unknown elsewhere, being there very curiously distributed, some being even restricted to small districts of the central mountain chain or of the coast forest.

The abundance of Lemuroids in Madagascar has induced Haeckel to give to a supposed submerged continent between Madagascar and continental India the name of Lemuria, and to fix upon this hypothetical dry land as the original starting-place whence the higher primates, — monkeys and man, — *slowly evolving out of Lemuroids*, have spread over the globe. We will by and by see in how far this hypothesis is confirmed or invalidated by what we know at present.

In the past history of the earth the distribution of Lemurs was far less restricted than it is at

present. Both in Europe and in America the Tertiary deposits contain very numerous remains of species undoubtedly more or less closely allied to the present Lemuroids, and we may look upon this order as one which, like the Ungulates, has ever so many more fossil than living representatives, and which has in those former epochs taken a much more prominent part in the constitution of the mammalian fauna than it does now. At the same time comparative anatomy shows us that the Lemurian type of structure can have been derived from one which need not have been very distant from that of a collective type, such as, for example, the Condylarthra, in which not only Ungulate and Creodont, but also Mesodont (Lemurian) characteristics are represented.

At any rate the Lemurs are in no respect a very specialized order of Mammals.

Now it is in this order, as I have just told you, that both Tarsius and Anaptomorphus have been placed by the systematists. With what right? we are bound to inquire. I, for one, would reply to this question: With none at all; and I am going to argue the case with you.

The only real resemblance is the opposable thumb, which we find on the fore and hind limbs both in the Lemurs and in Tarsius, as also the

flat nails to the fingers. These are however replaced on two fingers of the hindfoot by hooked claws, the Lemurs having only one finger thus exceptionally provided.

On the contrary, a whole family (Arctopitheci) of monkeys have a more considerable number of claws instead of nails, and an opposable thumb to only the hinder of the four extremities, so that we see that even this most prominent point of resemblance can claim only a restricted taxonomical value. Systematists have undoubtedly been led by the peculiar external aspect, perhaps even by the nocturnal habits, to approach Tarsius so closely to the Lemuroids. At the same time they have never failed to recognize it either as "une espèce anormale" [1] or as "a very aberrant form." [2]

Indeed, in very many respects Tarsius does not fit in with the Lemurs at all. Its dentition is much more archaic. Its upper and lower incisors, especially the latter, as well as its canine teeth, resemble more closely those of the Insectivora than they do the modified and specialized incisors of the Lemurs. And its molar

[1] H. Schlegel, Museum d'Histoire naturelle des Pays-Bas, Tome VII., Leyde, 1876, p. 331.

[2] Flower and Lydekker, Mammalia, Living and Extinct, London, 1891, p. 683.

teeth are most decidedly of a more primitive type, both in the upper and in the lower jaw, than they are in the Lemurs. The crowns of the molars of Tarsius, as also those of Anaptomorphus, which resemble each other most closely, conform to that type and to the initial variation of it which Cope has first designated as the tritubercular type. They are tri-cuspid, but the middle cusp is not in one line with the two outer cusps. It lies at a certain distance inward, the three cusps thus enclosing a triangle which is the first indication of what in a more elaborate type of molar teeth will be the grinding surface. Now, in the Lemurs this primitive arrangement is less purely preserved, the true molars being mostly quadri-tubercular. We find it, on the contrary, most distinctly in those fossil precursors of the Tertiary mammals that lived in the Mesozoic period and to which Osborn has given the name of *Insectivora primitiva*. Numerous other points of difference by which Tarsius is distinguished from the Lemurs, could be enumerated, many of them having undoubtedly a deeper significance than might appear at first sight. We will, however, allude to them no further, but rather direct our attention to a very remarkable divergence between Tarsius and the Lemurs with which we

have only become acquainted in the past few years.[1] This divergence concerns the mode of attachment of the unborn animal to its mother during the period of fœtal life.

Lemurs from Madagascar and Lemurs from India are found to be enveloped while inside their mother's womb in a closed sac that carries all over its outer surface an immense number of small knobs and excrescences. If we would make a comparison with a texture perhaps more familiar to you we might say that the outer surface of this sac, which entirely hides the young animal from our view, resembles Astrakhan fur. In technical language it is called "villiferous." The numerous separate little knobs, or villi, carry extremely fine blood-vessels that directly communicate with the embryo's vascular system. In this way the whole of the outer surface of the sac may be considered as being eminently fit for respiratory function or for nutritive absorption. The latter functions are actually incumbent upon this villiferous surface, which fits beautifully into corresponding little cavities by which the internal surface of the maternal womb is honey-combed. These two surfaces, the ma-

[1] A. A. W. Hubrecht, Spolia Nemoris; Quarterly Journal of Microscopical Science, vol. xxxvi., p. 77.

ternal and the embryonic, have, during pregnancy, developed parallel to each other, this interlocking having simultaneously advanced step by step. Fine maternal blood-vessels are distributed everywhere close under the surface of these maternal cavities, and so the mother's blood which is laden with fresh oxygen, thanks to the mother's breathing, and with nutritive matter, thanks to the mother's digestion, contains a full store of all the necessaries which the embryo draws from it by means of the peculiar arrangements on the surface of the sac within which it is enclosed.

The attachment between the sac and the mother is nevertheless quite superficial; they remain permanently distinct and stand in the same relation to each other as the hand does to the glove which covers it, or as the rootlet does to the damp soil into which it has penetrated. This latter comparison, taken from the vegetable kingdom, is, however, in so far inaccurate as it is often most difficult to uproot a plant without tearing some of its rootlets, whereas we may enucleate a Lemur-fœtus out of its mother's womb without as much as tearing or displacing even a single cell.

How entirely different these arrangements are if we now come to consider the young Tarsius!

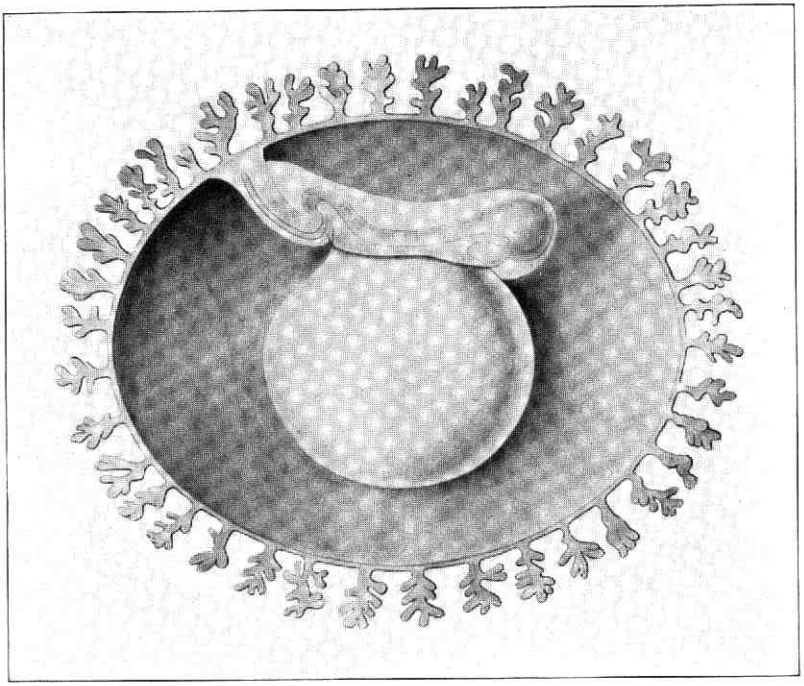


Diagram of an early human blastocyst (combined after Coste and His), before the discoid placenta has yet evolved out of the chorion frondosum.

There is no interlocking of maternal and fœtal surfaces. There is no loose attachment between two extensive vascular expansions. But there is a very perfect, sharply defined, and complicated organ by means of which the fœtus anchors itself, so to say, into the maternal tissue. This organ is called the placenta. At the time of its very early origin, when the young Tarsius has only just started on its development, this placenta is seen in its true nature as an embryonic proliferation. The small embryonic vesicle may be said to scoop out a circular spot of the mother's tissue and then and there to attach itself most firmly, more firmly than a leech or a bloodhound, to the inner surface of its mother's womb. The blood which under other circumstances would flow from a wound thus made, is carefully stored and conducted by the proliferated embryonic tissues which after some time succeed in establishing a very complex spongelike, cavernous structure of purely embryonic derivation, in the cavities of which maternal blood freely circulates. The solid meshwork, on the other hand, eventually carries very fine and very numerous embryonic blood-vessels, which then find themselves bathed in maternal blood. The way in which this result has been attained

is, as you will have understood, diametrically different from what we have just discussed for the Lemurs.

It should here be remarked that the Lemurine arrangement is analogous to what we find in the pig, the horse, and other Ungulates, whereas the Tarsius arrangement corresponds in varying degree to what obtains in Insectivora, Rodents, Bats, Monkeys, and Man. We must thus come to the conclusion that, with respect to its placentation, Tarsius more closely resembles an Insectivore than it does a Lemur, a conclusion similar to that which was derived from its dentition. Now, with respect to another peculiarity in its early development, I am going to demonstrate to you that Tarsius is more akin to a monkey than a Lemur. And thus I may hope to justify the conclusion which I have put forward that Tarsius is not a Lemur at all, that it should never have been placed alongside of the Lemurs, but that its position is somewhere between an unknown type of Insectivores and our modern monkeys and man.

The peculiarity to which I here allude is of a somewhat abstruse nature, and I will not attempt to initiate you into the details of it. Suffice it to say, that human embryologists have noticed in

the very early human embryo a peculiar structure which the Germans have called the "Bauchstiel," or "Haftstiel" of the embryo. Its homologue is found in no other order of Mammals. Only lately it has been definitely settled that the monkeys also have it,[1] but up to the present time it was a distinguishing feature of which the first origin was as yet quite obscure. This "Haftstiel" or ventral stalk, as it has been called in English, is a string of tissue connecting the very young embryo with its envelope, and differing in many respects from the so-called umbilical cord which at a later period does the same. In those Mammals that have a ventral stalk, the embryo is suspended by it from the very first, whereas in the others this suspension is only secondarily brought about by means of a special outgrowth which travels from the embryo towards the envelope.

Tarsius throws full light on the obscure origin of the ventral stalk, and at the same time reveals itself to be possessed not only of this very Haftstiel, which is characteristic of man and monkeys, but also to share with those two another very striking peculiarity by which they

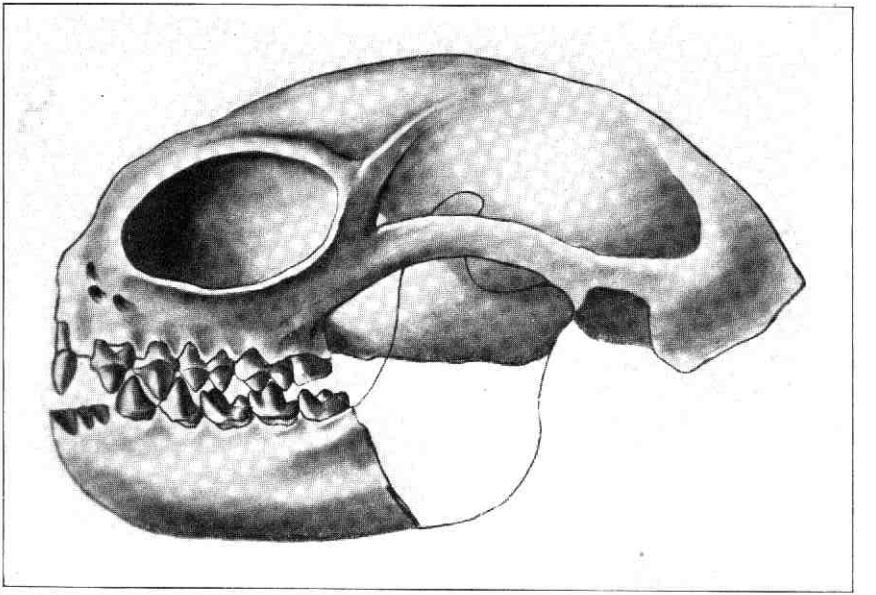
1 E. Selenka, Studien über Entwickelungsgeschichte der Tiere, Heft V, Wiesbaden, 1892.

differ from all other Mammals, namely, the possession of a diminutive yolk-sac which never entirely fills the cavity of the embryonic vesicle.[1] This latter point, which I am not going to elucidate any further either, is of all the more importance as it must keep pace with special differences of primary importance in the development of the germlayers.

And so henceforth we are obliged to range Tarsius with man and monkeys in one order which may retain Linnæus' adequate name of Primates. We must at the same time recognize that the facts here alluded to render it highly improbable that many of the most important characteristics of the Primates could ever have been derived from arrangements such as we find them in the Lemurs; so that the designation of the latter order by the well-known name of Prosimiæ is worse than misleading, because distinctly false.

A delicate question has yet to be solved with respect to the fossil genus Anaptomorphus, — delicate in so far as I can understand your smiling at the idea that I could give you any details of the fœtal development of a small

[1] A. A. W. Hubrecht, Die Keimblase von Tarsius. Festschrift für Gegenbaur, Leipzig, 1896.



Skull of Anaptomorphus; enlarged reproduction, about three times natural size, of a composite figure, in the American Museum of Natural History.
Loaned by Prof. Henry F. Osborn.

monkey of the Eocene period, of which up to now we possess only one imperfect skull, and of which no human eye will ever see an embryo! And still, if you consider the whole of the reasoning as it has here been given, you will agree that it would be difficult to admit that these intricate peculiarities which Tarsius shares with the monkeys, to the exclusion of all other known mammals, should not also have been possessed by a fossil genus which resembles Tarsius so very closely, and which by its dentition approaches closer yet to man and the anthropoid apes.

The moment you admit, as I expect you will be willing to do, that Anaptomorphus has not considerably differed from Tarsius with respect to its embryology, then the order of the Primates, between which and that of the Lemurs we have been accumulating anatomical and embryological divergence, also becomes severed from it in geological time. If as early as the lower Eocene period, animals have existed that were possessed of those peculiarities by which the Primates are eminently distinguished (and it should be well understood that of late *true* monkeys have also been discovered in the older Tertiary of South America), then it would be

obviously impossible to place the Lemurs of the Tertiary period anywhere on the line of ascent of the Primates. The moment we have traced the Primates as far as the earliest Tertiary they can only be connected genetically to ancestors of the Secondary period. And we are prevented from assuming that these Mesozoic ancestors were in any way Lemur-like, because both anatomy and embryology point most distinctly in another direction, namely, in that of the Insectivora. I would here remind you of Huxley's verdict pronounced sixteen years ago, to which I have already alluded, that among the Insectivora, the spiny and the hairy hedge-hog (Erinaceus and Gymnura) represent the most central type. Curiously enough, these two offer in their embryonic development certain particulars with which we can connect the divergences of the Primates much more easily than with the Lemurine development.

The formation of the human placenta, of the human amnion, of the human decidua reflexa, is foreshadowed in the hedgehog's development[1] in such a way as to strongly support the views concerning the pedigree of the Primates here

[1] A. A. W. Hubrecht. The Placentation of Erinaceus europæus; Quarterly Journal of Microsc. Science, vol. xxx. 1889.

advocated. And so the outcome of all these considerations may be said to be a definite simplification of the line of descent of man and the higher monkeys. We need no longer be puzzled at that rapid increase in complication of the all-important placentary arrangement which we were bound to admit as long as we accorded to the Lemurs any place among our direct ancestry.

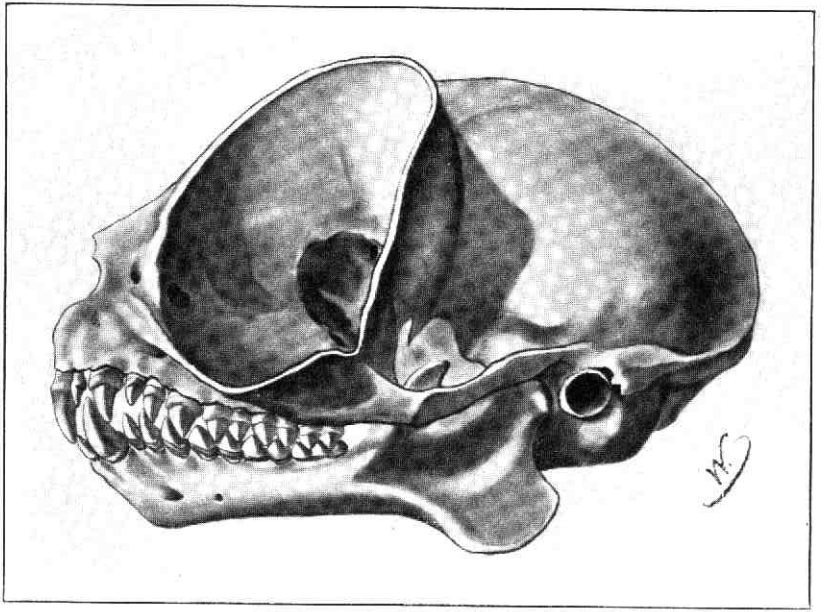
We may now safely say that these complications are of an ever so much more remote antiquity, and that the insectivorous predecessor of the Eocene Primates may in many respects have been a further differentiated mammal than its contemporary, the ancestor of the Tertiary Lemurs.

The tiny little Tarsius has thus shown us that by judiciously converging anatomical, embryological, and palæontological sidelights into one focus, we may sometimes succeed in clearing up genetic relationships that would otherwise remain hopelessly intricate or vaguely confusing.

We must now try to turn to more general account what we have here established, remembering that in so doing we are starting on a hypothetical track that leads us somewhat fur-

ther away from the landmarks of observable facts to which we have up to now held fast most conscientiously. Firstly, then, I would call your attention to the probability that man and the anthropoid apes may be only more distantly allied to the non-anthropoid old-world monkeys, at all events less closely than is at present generally admitted. In respect to details of dentition Anaptomorphus points rather to the Anthropoidea than to the Catarhine monkeys. So does Homunculus patagonicus, one of Ameghino's fossil Cebidæ, whose dentition, to quote Osborn's words, is "as advanced in reduction as that of man." Secondly, certain Insectivora seem to realize the archetype of the placentation of man and the anthropoids, whereas the placentation of the old-world monkeys, as far as it is known, would more easily compare to what we find in Tarsius, there being no decidua reflexa, which is so essential for the formation of that very peculiar type of discoid placenta that is common to Erinaceus, the Anthropomorphæ, and Man.

On these grounds I would not feel justified in contradicting a hypothetical view, if one of you might be found willing to propound it, according to which a direct ancestor of the



Skull of Tarsius, side view. x 2½.

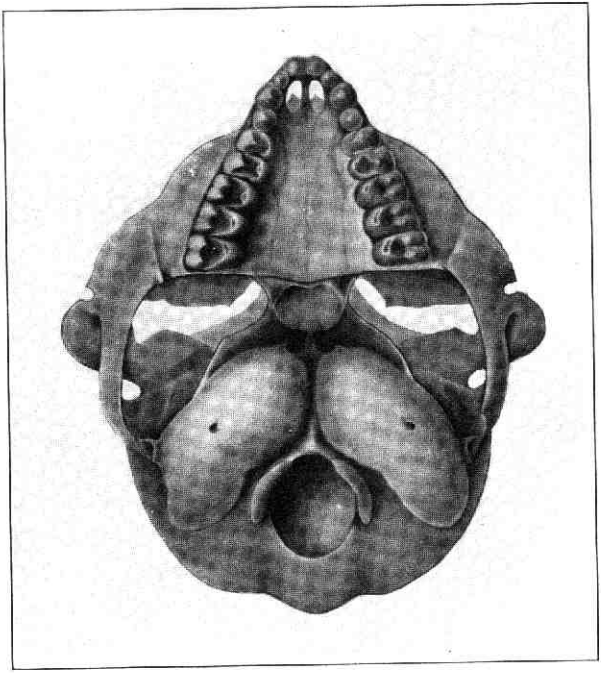
anthropoids and man, differing from Simiæ Catarhinæ, Platyrhinæ, and Tarsidæ, must have existed throughout the Tertiaries, and must have directly sprung from a Mesozoic insectivorous ancestor, small in size, but already more or less erect in posture, provided with a spacious brain cavity, with a decidua reflexa, and with a discoid placenta of the Erinacean type of development. Now, in suggesting the existence of this unknown intermediate form, you would not be overdrawing the amount which is booked to the credit of scientific speculation in the bank of probability. As to the smallness in size of Mesozoic Trituberculata, palæontology not only gives ample evidence, but it distinctly does not encourage any other assumption. With regard to a spacious brain cavity, it should be remembered that among the South American monkeys certain living genera, by the relative size of their brain, outstrip the Anthropoidea and man himself. Already in 1844 Geoffroy places Chrysothrix "au premier rang entre tous et à côté de l'homme même, si ce n'est au-dessus, par la masse proportionnelle de leur cerveau," at the same time drawing attention to the fact that the brain convolutions are very much less developed, these convolutions being to a great

extent correlated, as Flower reminds us,[1] with the absolute bulk of the body.

And as to the erect posture, which is generally looked upon as being the monopoly of man, the anthropoid apes having it in only a very imperfect degree, we are in no way obliged to follow the general belief that this has been a comparatively late acquirement of our ancestors! Nor that they must needs first have passed through a stage similar to the actual stage of one of our living anthropoid apes.[2] The earliest origin of the erect posture may most reasonably be moved backwards in geological time if we are mindful of the following two facts: First, that the occipital foramen of certain American monkeys (Cebidæ and Hapalidæ) is placed ever so much more below the skull than is the case in many of the anthropoid apes. We noticed the same in Tarsius and Anaptomorphus. Now, Tarsius is generally found in the erect posture, with which this position of the foramen magnum is undoubtedly corre-

[1] Flower and Lydekker, Mammals, Living and Extinct, London, 1892, p. 705.

[2] Cf. Dubois, "Pithecanthropus erectus, eine menschenähnliche Uebergangsform." His conclusions were discussed and dissented from by me in the Dutch Review, "De Gids," for April, 1896.



Skull of Tarsius, seen from below. Enlarged x 2.

lated, the balancing of the skull and brain on the spinal column being thereby facilitated. Many of the lower Primates thus realize conditions highly favorable for the adoption of the erect posture. Secondly, we should remember that this erect posture is not even restricted to the Primates, as we find among the Lemurs the genus Propithecus which, when it has come down from a tree, walks about on its hind legs, even without resting its arms on the ground as do the Gibbons. This important peculiarity of Propithecus, figured by Milne-Edwards and Grandidier in 1875, was already known to Flaccourt not less than two hundred years ago. To ascribe the same to the remotest Cænozoic, or even to the Mesozoic, ancestors of man is then not in itself irreconcilable with observation. As to the placental characteristics of this hypothetical intermediate stage, I should think that the considerable degree to which already now the extremes (Erinaceus and Homo) resemble each other in certain respects, justify us in accepting them as here indicated. It would, nevertheless, be worth while to inquire if in any of the living genera of American monkeys, a decidua reflexa and a discoid placenta of Erinacean type of development might also be shown to exist.

That certain newly discovered facts, here repeatedly alluded to, tend to justify us in somewhat loosening the human pedigree from that of the existing monkeys, may perhaps induce more timid minds (the number of which has not been decreasing of late) no longer to shrink from extending the doctrine of evolution to the prehistoric development of man himself. Authentic data proving the existence of refined civilization and of highly developed art recede backwards into an ever-increasing number of prehistoric centuries as the archæologists extend their researches in different parts of the globe. And it should at the same time not be forgotten that Huxley, more than thirty years ago, expressed himself in an almost prophetic way in a sentence which might serve as a motto for this lecture, when he said: "If any form of the doctrine of progressive development is correct, we must extend by long epochs the most liberal estimate that has yet been made of the antiquity of man."

We may furthermore ask in how far the reasoning which we have applied to the order of Primates, to their affinities and to their development in geological time, will in any way con-

tribute to the solution of certain questions of primary importance concerning the relationship of the three great subdivisions of the Mammalia to each other and to the lower classes of Vertebrate animals. It seems to me that the usual way of looking upon these three subdivisions, the Duckbills, the Marsupials, and the Placental Mammals, as a real and historical sequence, in which the first, having so many reptilian affinities and standing lowest, gave rise in their turn to Marsupials, which later on again became modified into Placentalia, is not in accordance with their true relationship.

I am in no way starting a new idea in lodging a protest against the theory of the linear descent of the Mammalian subgroups. Huxley was perhaps the first to ventilate the same question. Three years ago Osborn shook this traditional arrangement to its foundations, by very cogent reasoning based on palæontological research, in his address, "On the Rise of the Mammalia in North America." There was, as he expresses it, "not a succession, but a unity of ancestry of the Monotremes, Marsupials, and Placentals." Still, the number of those who do not concur in this conclusion is very considerable, and not likely to be diminished for the next few years. Semon has

gone to Australia purposely to study the development of the Ornithodelphia, an inquiry which many years ago had been commenced, but never been terminated, by an English embryologist. And the principal reason why so much interest is felt in the development of these very animals is, that they and not any others are expected to give us the clue to many points at present insufficiently understood in the embryonic history of the placental mammals.

In this respect I would wish to choose a position more or less diametrically opposed to that of Semon.[1] The Monotremes cannot reasonably be expected to teach us anything concerning the earliest phases through which the Placentals have passed. And too long has the conclusion remained unchallenged that, because the Monotremes have been shown to lay eggs of the Sauropsidan type, the ancestors of the Placentals must have passed through a stage in which they necessarily reproduced themselves in the same manner, certain details of the embryonic sac of the Mammalia undoubtedly favoring this view. A reptilian ancestor to the Mammalia has thus found more favor than an amphibian one; and

[1] See Semon's Lecture in the Report of the Leyden International Zoölogical Congress of 1895, p. 295, footnote.

even Osborn accepts the term Sauromammalia in exchange for Huxley's Hypotheria, thereby implying that certain distinctive characters of those Proto-mammalia, which can hardly have been other than such as belong to their reproductive and developmental arrangements, were distinctly Saurian.

With respect to this important question I feel inclined to side rather with Huxley — whose brilliant vindication of the amphibian character of his Hypotheria[1] is a perfect model of morphological argument — than with the views last-mentioned, and I will attempt to explain my reasons for so doing. The differences between Reptilia and Amphibia, as exhibited by living representatives of the two classes, are nowhere so obvious as in the fact that the former possess an important transitory embryonic structure known as the amnion, whereas the latter do not. In going back into the Mesozoic and Palæozoic periods we are led to presume that such extinct orders as the Pterosauria, Dinosauria, etc., shared these developmental features with the modern reptiles. In fact the large eggs which some of the latter are supposed to have laid are preserved in certain Museums. But when we come to yet

[1] Proc. Zoöl. Society, 1880, p. 649.

older orders, that flourished in the earliest Mesozoic, and in the Palæozoic period, such as the Theromorpha, we ought to pause before affirming that they too were already Amniota.

On the other hand, the Palæozoic Stegocephala, which are classed with the Amphibians, might for that reason be said to be as yet deprived of an amnion. Nothing however prevents us from assuming that in the period of the earth's history in which this class flourished, the earliest traces of this embryonic structure first originated. In fact, its appearance is understood to have been largely influenced by the formidable changes of habit and of structure which must have come about at the time the aquatic Vertebrates gradually adopted, first, a semiterrestrial (amphibian) existence, and then became specialized in different classes of terrestrial animals. The majority of the aquatic Vertebrates may then, as now, have been oviparous. With the change towards a terrestrial existence, the eggs may yet for a long time have continued to be deposited in the water by many of them. Others may have adopted the most various devices for the hatching and the protection of their eggs, as is still faintly echoed in those not numerous genera of frogs and toads which carry and hatch their eggs, now on their

backs, now on their bellies, sometimes in special pouches, sometimes in carefully constructed nests.

Others again may have developed much larger eggs, with an albumen layer and a shell. There can be no doubt on the other hand that a number of them have retained their eggs in the maternal oviducts and have hatched them there, forming a viviparous section.

In fact, there is really not one cogent reason which would prevent us from deriving arrangements as we find them in placental mammals directly from viviparous amphibian ancestors. The spherical embryonic vesicle with the enclosed umbilical sac and with the embryonic area spread out flat on the top, is not necessarily a derivate of a preceding one in which this umbilical vesicle enclosed an enormous quantity of fluid yolk substance. This spherical extension of the vesicle may also have been reached more directly. At all events, this possibility has certainly no less a claim to our careful consideration. Be it well understood, however, that I do not commit myself to professing that I feel sure that it really has in placental mammals developed thus differently. What I wanted to point out is, that the generative adaptations being so varied even amongst living amphibians, they must have been so on

an extensive scale among their much more numerous Palæozoic ancestors. For the present I hold it to be at the least premature to pin our faith to the one eventuality which those who argue the necessity of an intermediate saurian stage between an amphibian anamniotic ancestor and a mammalian amniotic descendant would wish us to adopt.

Moreover, as the first steps in the phylogenetic development of amnion and allantois are once for all out of the reach of direct observation, we must be guided solely by speculative argument. And in that case we have a right to exact of those who feel convinced that a megalecithal saurian ancestor comes in somewhere in the pedigree of the placental mammals, that they give us a plausible hypothesis by which we can explain the origin of the amnion. As yet they have utterly failed in this respect, and that most conscientious and painstaking embryologist, Professor Minot, of Boston, frankly concluded in 1893, that hardly anything "definite is known as to the evolution or phylogenetic origin of the amnion."

About a year ago a new hypothesis on the origin of the amnion was propounded,[1] in which

[1] A. A. W. Hubrecht, Die Phylogenie des Amnions und die Bedeutung des Trophoblast, Verhandel. Kon. Akademie v. Wetenschappen. Amsterdam, 1895.

no place is left for an intermediate saurian link, but according to which the placental mammals are connected directly with unknown amphibian ancestors, leaving the Monotremes, the Marsupials, and the Sauropsida to come in for lateral connections — as yet wholly unknown — with that more archaic and direct line of descent. This hypothesis is essentially based upon observations that have of late been accumulating concerning the actual mode of development of the amnion in different orders of placental mammals. The development of the amnion in mammals is often said to conform with that which we observe in the chick. This may hold good for the sheep, for the rabbit, and for many other placental mammals, but it certainly does not for man, for the flying fox (Pteropus), for the hedgehog, or for the guinea-pig. In all these representatives of four different orders of mammals, the origin of the amnion totally differs from the traditional process just alluded to, although the latter mode is nevertheless met with in other members of those same four orders. Up to the present time embryologists have been in the habit of looking upon the traditional process present in the chick as the typical one from which it ought to be possible to derive

the other modes of development in some way or other, as special adaptations that have indeed to be explained, but that are of no primary importance.

The reason why this point has been so little in dispute may partly be ascribed to the force of habit, partly to the consideration that a mode of amnion formation which is prevalent among *all* birds and reptiles, must in the nature of things be a more ancient and a more primitive mode. All the more this appeared to be the correct view, as the majority of the mammals do conform with Sauropsida in the way in which they form their amnion.

And so it requires a certain amount of determination to single out the exceptional cases which we encounter amongst a small minority of mammals, and to pretend that in them a more primitive arrangement is preserved.

I will try to explain to you in a few words which are the chief points at issue in these conflicting views. Let me first, then, remind you that the amnion is a membrane, continuous with the body wall and stretching hindwards so as to form a closed sac over the embryo's back. In it the young animal is enveloped as in a protective watercushion. Indeed, the amnion is un-

deniably a protective apparatus, which is comparatively more spacious in the younger and more delicate stages than in the older embryos.

Such a protective water-sac is evidently of more paramount significance to an embryo that resides inside its mother's generative organs — where it is exposed to various pressures, peristaltic and otherwise — than to one which is already protected either by a thick layer of albumen or by a hard shell, or by both. And so it seems more reasonable to look for its very earliest origin rather among viviparous than among oviparous animals. Take, for example, the shark's and ray's eggs, with their black, horny egg-case, the fluid albuminous contents, and the yolk, on the top of which the young undergoes its successive developmental changes. We observe a close resemblance with a sauropsidan egg, the shell of which is not always hard and calcareous, but in many cases of leathery consistency (snakes, crocodiles). Mechanically speaking, the eggs of both these classes of vertebrates are similarly conditioned, and still the sharks and rays never possess any amnion, whereas the crocodiles, turtles, snakes, and birds do. We may evidently not seek the starting-point for the amnion formation in any peculiar

relation of the embryo either to a big yolk or to a hard shell.

Most of the hypothetical explanations hitherto proposed have, however, moved upon that basis, with what success we have heard Minot affirm. They do not tell us how the amnion can possibly have developed phylogenetically. In the traditional cases we see it arise as a fold, which slowly and gradually encloses the embryo. And *only when the closure has become final is the amnion effective.* What, then, were here the incipient stages?

All this appears in another light when we trust to the exceptional cases above mentioned to guide us in determining the phylogeny of the amnion. We can then start from the much more reasonable basis that the amnion at its earliest appearance *must have been a closed sac.* Only on this supposition can it be understood that it was of high selective significance from the very first. It was modified only gradually,— one of the modifications being this, that it did not any longer arise so very early in individual development, but only later by means of the folds alluded to. Now let me emphasize that at the present day we do find this very same development of the amnion as a closed sac in the

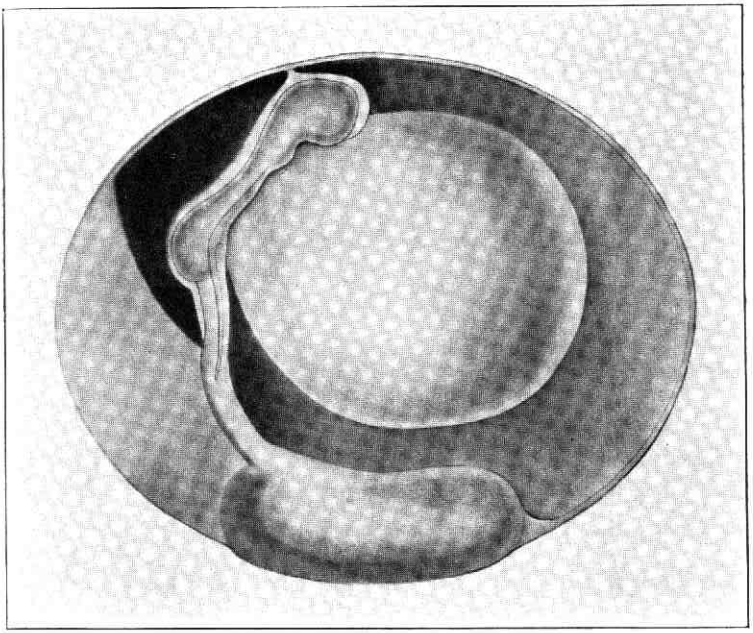


Diagram of an early blastocyst of Tarsius, with discoid placenta, ventral stalk, closure of the amnion above the head and reduced umbilical vesicle.

above-named representatives of four different orders of mammals: *Cavia* (guinea-pig), *Erinaceus* (hedgehog), *Pteropus* (bat, flying-fox), *Homo* (man). This will suffice to convince you that as far as placental mammals go, the statement that the amnion arises as an upward-growing fold, which finally encapsules the embryo, does not find universal application. There is indeed an equal chance of the other mode of formation having been the original one. My own choice is fixed upon the latter hypothesis because in the Amphibia, from which I suppose the earliest placental mammals to have been derived, we find arrangements that appear to explain the earliest origin of the amnion in the way here advocated. There is, moreover, no difficulty in tracing both umbilical and allantoidean placentation to a disposition of parts such as we encounter in the Amphibia. It would, however, lead me too far if I should attempt to take you over the whole ground covered by this hypothesis, and it is more than time to turn back to the realm of facts.

The facts to which I wish to call your attention, and which are confirmatory of the views here developed, have been brought to light by different observers, at different times. They all

tend to emphasize the possibility of a more direct comparison between mammals and Amphibia than between mammals and Sauropsida. In this way Klaatsch[1] calls attention to the close relations existing between the intestinal arteries of mammals and the most primitive arrangements of these vessels among amphibians. Elsewhere he declares that the mammals must be connected with very primitive forms that have already diverged from the common stem of the Chordata below the point of divergence of the amphibians now living. Howes[2] makes a direct comparison between the amphibian epiglottis and that of the mammals. Rabl[3] states that the formation of the heart is accomplished in the same way in amphibians and mammals. Maurer[4] comes to the conclusion that with respect to the epidermal sense-organs and the hairs, the mammals diverge considerably from the Sauropsida, whereas the connection with the Amphibia seems to be all the more close.

In the definite settling of this question palæon-

[1] H. Klaatsch, Zur Morphologie der Mesenterialbildungen am Darmcanal der Wirbelthiere. Morphol. Jahrb., Bd. 18, § 643.

[2] G. Howes, Proceed. Zoöl. Society of London, 1887, p. 50.

[3] C. Rabl, Morphologisches Jahrbuch, Bd. 12, p. 273.

[4] F. Maurer, Morphologisches Jahrbuch, Bd. 18.

tology will, of course, have a most influential voice. We must hope for new discoveries to fill up the immense gaps which our knowledge of the Mesozoic and Palæozoic Vertebrata yet contains. And in respect to that we cannot say but that the last decades have surpassed our expectations. Still, it should not be forgotten that even when all the fossils from those remote periods were brought to light and were spread out before us, they would yet remain perfectly mute with respect to the details of the embryonic development of the animals of which they had formed part, so that on this head even posterity will have to be satisfied with speculative considerations.

Leaving these for what they are, we may conclude by recognizing that Tarsius has taught us several things: Firstly, to attach more value than has hitherto been done to the inferences which can be drawn from certain embryonic phenomena for classificatory purposes; secondly, to entertain a certain amount of healthy scepticism with respect to the traditional tables of mammalian descent. The genera known to us very rarely converge towards known predecessors as we go backwards in geological time; their respective genealogies run much more parallel

to each other, the point of meeting being thus continually transported further backwards towards yet older geological strata. Thirdly, the necessity of inquiring into the early embryonic details and placentation of every known genus of Insectivora and of Primates is imposed upon us, — the Insectivora being especially instructive by the suggestive divergences which they offer in their numerous types of placentation; the Primates being more especially important with regard to human development.

Selenka has just made a commencement with the ape-tribe, but nevertheless our acquaintance with their development is as yet only very fragmentary. For a patient explorer there is yet a very extensive field, and the monkeys of the New World, as they are somewhat circumlocutionally called, are certainly the first on our list of embryological desiderata. I earnestly appeal to your "scientists," — or, if as a European I might be allowed to coin an Americanism, I would rather say, to your "forshers," [1] — to institute that investigation without delay, even though it is not in the United States that the material can be obtained. However, the solidarity of the con-

[1] Perhaps the term "researchers," here and there used to supplant the word "scientists," might be preferable.

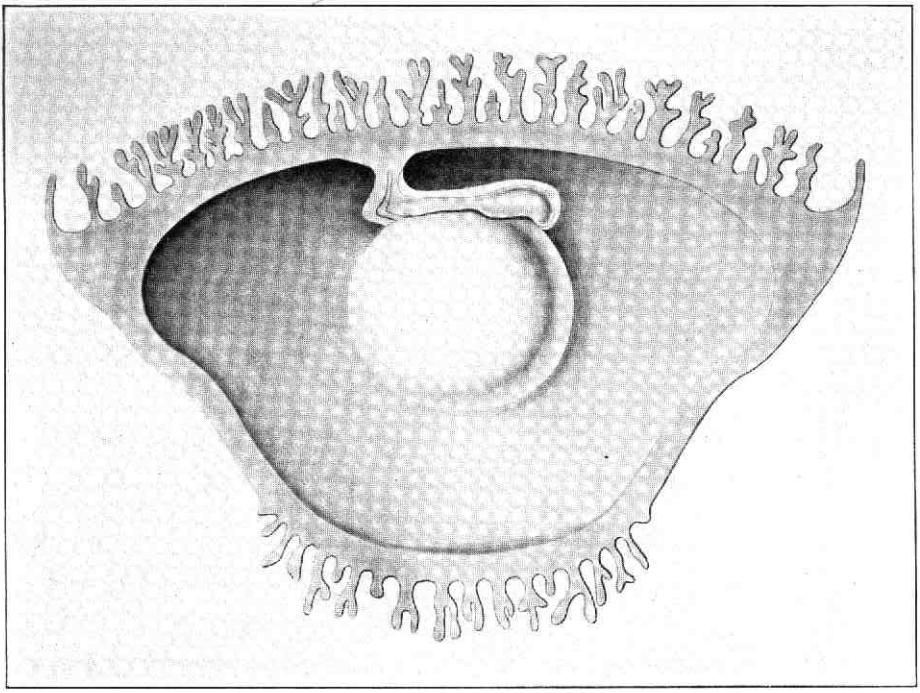


Diagram of an early blastocyst of an old-world monkey, Cercocebus (after Selenka), with dorsal and ventral placenta.

tinent as such, being so distinctly insisted upon, I presume I may express this wish even in a latitude as high as that of Princeton.

I trust that you will kindly account for my readiness in formulating this desire by my confessing that in the last few weeks I have contracted the somewhat awkward habit of believing that the expression of a wish is in this country the surest and shortest way towards the rapid realization of it.