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THE NEW ANTHROPOGENY: TWENTY-FIVE STAGES OF VERTEBRATE EVOLUTION, FROM SILURIAN CHORDATE TO MAN[1]

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THE subject of anthropogeny, as it was developed at the hands of Ernst Haeckel, involved an attempt to read the earlier stages of prehuman evolution largely from the data supplied by human and comparative embryology. Thus its main postulate was the so-called "law of recapitulation." But the attacks of modern zoologists on this "law" seem to have led, in this country at least, to a loss of confidence in Haeckel's chief conclusions. In certain quarters there has sprung up a regular epidemic, which may be named *Haeckelophobia*.

Meanwhile the new anthropogeny has been gradually taking shape. But before speaking of its origins and tentative results to date, it might be well to note that a humble exponent of the new doctrine is liable to experience a slightly guilty feeling if he finds himself obliged to speak in any official gathering of his scientific brethren. For example, the brethren of the orthodox anthropologist sect are always piously busy, wielding their magic measuring wands and ringing the bells on their magic calculators, or thinking machines, while the poor anthropogenist stands idly by and must confess that he is not primarily bent on measuring or counting anything, but only in piecing together the broken story of the "big parade" that nature has staged across the ages.

Another contrast between the anthropogenist and

[1] Address of the vice-president and retiring chairman of Section H—Anthropology, American Association for the Advancement of Science, Atlantic City, December 29, 1932.

the orthodox anthropologist is that the regulars stand happily among the topmost branches of the family tree of man and count all its twigs, while the anthropogenist, like a silly ant, runs up and down the main branches and trunk and gropes blindly around the roots.

Moreover, up to the present time the new anthropogeny is operating to a considerable extent on a borrowed, or perhaps appropriated, capital of facts. And up to date it has found no way to repay the lenders.

For example, from historical geology the new anthropogeny appropriates the standard divisions of geologic time in which the drama of evolution has been played. But until relatively recent times geology could determine only the sequence of terrestrial events, without measuring their duration in years.

To physics, mineralogy and stratigraphy, the new anthropogeny now owes the "radium clock" of geologic time. If the readings of this clock give even a preliminary approach to the truth, as they seem indeed to do, then the events which the new anthropogeny attempts to discover and describe took place during a period of the general order of magnitude of five hundred million years.

From zoology and comparative anatomy the new anthropogeny has received the precious doctrine of the *"Échelle des Êtres,"* or scale of beings, which was elaborated by the French naturalists of the eighteenth century, but which has since been almost abandoned and forgotten. Instead of throwing this doctrine on the junk-heap along with Euclidean geometry, the new anthropogeny finds that after being slightly revamped and fitted with a few new parts, the old apparatus still functions well; for it has led to a fuller recognition of the significance and importance of "living fossils," which have preserved in greater or less degree the successive grades of organization that were characteristic of many past ages. The study of the scale of beings has led also to the realization that if there were no "living fossils," that is, if every phyletic line had evolved at the same equal and constant rate, all the descendants of a common ancestral stock would now be indistinguishable throughout their anatomy. In other words, the very existence of comparative anatomy depends upon the fact that there is a more or less closely graded scale of beings, or rather, many scales of beings, leading not only toward man but toward every other highly specialized animal.

To paleontology, however, we owe the discovery of actual fossil skeletons that correspond more or less closely to the grades of organization inferred from the study of the scale of beings. Thus there is no longer any need of inventing hypothetical stages, as Haeckel did from doubtfully valid extensions of embryological processes, when the paleontological evidence is so unexpectedly adequate if viewed in the light of evidence from several different fields.

If the obligations of the new anthropogeny to all the previously named sciences are great, still greater is its dependence upon the science of vertebrate taxonomy; this branch of science endeavors to identify and follow the large and small branches of the vast tree of the vertebrates. We may be inclined to smile at first at the simplicity of Haeckel's picture of the tree of life, which might now be condemned as "monophyletic" and rejected in favor of a "polyphyletic" diagram with innumerable lines all running back to infinity. However, the cumulative experience of modern paleontologists and zoologists leads to the concept that while the tree of vertebrate life has a fairly large number of minor twigs which run back for long distances in geologic time, the number of major branches is quite limited and can be fairly well grasped during the lifetime of an ordinarily industrious student of fossil and recent vertebrates. But the supreme mistake would be to suppose that the branches have grown at equal rates, that is, that the "chronometer of evolution" runs at the same rate in all lines; it would be another mistake to infer that the branches never did run together because we have not yet located all the junctions. For the progress of vertebrate paleontology constantly leads to the discovery of new forms, yet in most cases the new forms represent branches that lie in between two or more branches already recorded.

Perhaps the most essential of all services rendered to the new anthropogeny by the science of phylogenetic taxonomy is the identification of branches that can be definitely excluded from what we choose to call the main line of ascent to man. Another service is the determination of the probable distance of a given branch from that main line.

Anthropogeny likewise borrows from chemistry, physics and physiology the very basic principle that man, like other organisms, is a sort of solar engine that runs by means of the energy stored up in plant and animal food. It follows that this potential energy forms a hidden prize of great worth, to obtain which all animal life struggles unceasingly. Hence the drama of terrestrial evolution is motivated by the complexly ramifying competition and strife for food and for reproductive mates; this principle operates as strongly in the latest stages of life as it did in the earliest.

We may start then with one of the most firmly grounded landmarks in the new anthropogeny, namely, that man belongs on the vertebrate tree of life, and that, while his present habitus is that of the human biped, his general heritage is that of a quadrupedal vertebrate of the class of mammals and of the order of Primates. These general facts were well known to Huxley, Haeckel, Darwin, Lamarck, and even to a large extent to Linnaeus, but they are always being buried and forgotten under the details about which scientific men love to dispute. What was not known to the older naturalists, however, is the modern wealth of material that supplies us with a paleontological series representing the main successive structural stages in the long ascent from the jawless chordates of the Silurian age up to man.

At present we may distinguish about twenty-five structural stages from and including the oldest known pre-fishes up to modern man. It is not claimed that these stages lie exactly in the direct line of ascent but only that they are more or less near to it after the elimination of more specialized side branches.

Let us attempt to run over these stages very briefly with the lantern slides.

We may consider for a moment the general history of the locomotor apparatus, especially the skeleton. We start with the fact that the larger units of the vertebrate locomotor system are the W-shaped muscle flakes, or myomeres, on the side of the fish; the smaller units are the striped muscle fibers with their far smaller fibrillae, which run into the billions in a human body. The beginnings of all the complex motions of the human body are to be sought in the rhythmic contraction and relaxation of the W-shaped muscle flakes of the fish, and there are already on record many structurally intermediate stages between the simple muscles of the fish and the complex muscles of man. And it is sufficient to mention in passing that the human embryo agrees with that of the fish in that not only its axial muscles but also the segments of the backbone arise from segmentally arranged buds of mesoderm on either side of the embryonic notochord.

Stage 1. Pre-fishes (Ostracoderms) of Paleozoic times (Ordovician to Devonian).

For the purpose of this address we must leave out of account the disputed problem of the origin of the vertebrates and begin with a grade of organization that was already far nearer to that of man than to the one-celled starting-point. Thanks to the Danish scientific expeditions to Greenland, Norway and Spitzbergen, we now possess a surprisingly detailed fund of information regarding the general characters of the brain and cranial nerves and blood-vessels of these oldest known Chordates; these have recently been described in the beautiful monographs by Stensiö and Kiaer. Thus we now have a firm foundation of facts to replace conjecture. These pre-fishes, or ostracoderms, were bilaterally symmetrical, with a median axis, or notochord, moving by lateral undulations of the body, by contractions of W-shaped muscle segments. The head was of the complex vertebrate type, including a braincase that contained three pairs of main sense organs, corresponding to the olfactory, optic and otic capsules of higher vertebrates and arranged in a fore-and-aft series.

A continuous endoskeletal tissue, containing bone-cells in one order of ostracoderms, enclosed the three main pairs of sense organs and formed a trough for the brain and tunnels for the cranial nerves and blood-vessels. When these tunnels and this braincase became filled with mud, which subsequently became mineralized, there was left a record of the general anatomy of the nervous system which has endured for perhaps four hundred millions of years, down to our own time.

Beneath the braincase was a greatly expanded chamber containing the mouth cavity, the gill-pouches, the skeletal partitions between the gill-pouches and the ducts leading to and from the gill-openings and the exterior. This arrangement is closely paralleled in the larval stage of the existing lampreys. The same is true of the brain and cranial nerves. The neurologists and students of the classical problem of the vertebrate head-segments had long ago fixed upon the larval stage of the lamprey as standing nearest among existing forms to the archetypal vertebrates. Thanks to the labors of many investigators, we can now affirm that the ostracoderms as a class were the archetypal vertebrates from which were derived, on the one hand, the so-called jawless cyclostomes, or lampreys and hags, and on the other hand, the gnathostomes, or jaw-bearing vertebrates, comprising true fishes, amphibians, reptiles, birds and mammals (including man).

Stage 2. "Antiarchs" of Devonian age.

These strange-looking forms had the head and body enclosed in an armor of bony plates and propelled themselves by a pair of jointed appendages that remind us of the walking legs of crabs. They were probably quite far off the direct line leading to higher vertebrates, but the beautiful fossils from Scaumenac Bay, Quebec, described by the late Professor Patten and now by Stensiö, leave little doubt that these antiarchs had recently crossed the line separating the so-called jawless from the true jaw-bearing forms. For they had obviously acquired external jaw plates, homologous with those plates in the true fishes which were destined to give rise ultimately to our own upper and lower jaws; while, according to Stensiö, their external jaw plates could only have been supported internally by cartilaginous bars homologous with the true or inner jaws of adult sharks and of embryonic higher vertebrates.

Stage 3. "Pre-sharks" of Devonian age.

The earlier acanthodians may well be called "pre-sharks" because, although shark-like in general characters, they represent an older and more primitive type nearer to the line of ascent to higher vertebrates.

Externally the acanthodians give us a glimpse of an early stage in the evolution of paired limbs. They support the conclusions of Balfour, Dean and others that the paired fins are essentially the same as the median fins and that both arose as folds of skin and projections of the muscular body-wall that served originally as stabilizers and keels. Such fin-folds in the early stages had wide bases and limited mobility.

The pre-sharks had attained an early stage in the evolution of the gnathostomes, or jaw-bearing vertebrates, since they had inner or true jaws, in series with the gill-arches. In another early shark, *Cladoselache,* we see in this view of the under side of the head how closely the upper and lower jaw bars are in series with the gill-arches, from one pair of which the jaws were doubtless derived.

Stage 4. "Basal ganoid fish" (Palaeoniscoid), Old Red Sandstone (Devonian).

These earliest known forerunners of the modern bony fishes used to be called "osseous sharks" by the late Professor Bashford Dean, because they combine a generally shark-like body-form with the bony armor over the head and shoulder-girdle of the earlier typical fishes. This bony armor is composed of plates, each one of which has a definite name. Many of these plates, such as the frontals, the parietals and the surface bones of the upper and lower jaws, can be traced forward, as we shall presently see, from these very early fishes up through the amphibians, the earlier reptiles, the mammal-like reptiles, to the earlier mammals and thence through the lower primates to man. Other elements of the fish skull, such as the bones of the opercular series that covered the gill-chamber, disappeared when fish turned into amphibians.

These earlier true fishes also exhibit the fins in successive stages of development. The anal fin is still just like the dorsal fin, with an extended base supported by a regular series of little bony rods. The pelvic fins show an early stage in the crowding of the basal pieces, especially at the front end. The pectoral fin has already attained the stage of a broad paddle with a crowded base.

This sequence is still clearly seen in the fins of the spoon-bill sturgeons, or paddle-fishes, which are the otherwise specialized descendants of the earlier ganoids. Here we see three stages in the evolution of the mobile pectoral paddles, as figured by Dr. Tate Regan, of the British Museum of Natural History.

Stage 5. "Lobe-finned" fishes, of Upper Devonian and Lower Carboniferous ages.

The tendency toward the evolution of freely turning paddles, presumably out of fin-folds, reaches a climax among the lobe-finned fishes of late Paleozoic times. In the tassel-finned branch of these forms the paddles grow at the distal end and give rise to a string of joints with slender rods on each side. But in the "fan-finned" branch the paddles spread out like the sticks of a fan, and the bony rods that support them seem destined to give rise to the skeleton of the arm and hand of higher vertebrates. This fan-shaped stage is well illustrated in an Upper Devonian form to which the geologist James Hall in 1843 gave the appropriate name *Sauripterus*—"lizard-fin." We shall see a little later how such a paddle might give rise to the cheiropterygium, or five-rayed hand, of a higher vertebrate.

Before going on to the next higher stage we must pause for a moment in order to rule out the dipnoans, or lung-fishes, from the line of ascent to the higher vertebrates and to expose their true place on a side branch further away from the main line than that which they occupy in the genealogical trees figured by Haeckel and by his modern follower, Professor Naef. The dipnoan lung-fishes are excluded from the main line by three sets of characters: first, they belong in a division with feather-shaped, or leaf-shaped, paddles, in which the many-jointed central axis is predominant; secondly, their dentition is specialized in a very peculiar way, which leads to nothing but that of their modern descendants and is widely different from the dentition of the earliest amphibians. Thirdly, the lung-fishes are excluded from ancestry to the higher forms by the highly peculiar specialization of the extremely massive inner skull, and by the bizarre pattern of the many small plates covering the braincase.

On the other hand, the ancient lobe-finned fishes present nearly ideal conditions, not only of the paddles, but also of the dentition and skull patterns, to favor their claim to be on or near the main line of ascent to the four-footed, air-breathing vertebrates.

The living *Polypterus* of Africa is a justly famous survivor of the most ancient ganoids. From whichever of the two oldest orders of ganoids he may have been derived, he does show us how readily a lobe-finned paddle may be directed downward on either side of the body in a position to assist in wriggling on the mud.

Stage 6. Basal Amphibian. Upper Devonian and Lower Carboniferous.

Even the modern amphibians, including the frogs, newts and salamanders, retain so many essentially fish-like characters, especially in their larval stages, and in the general pattern of the cranial and spinal nerves, that zoologists have never had any reason to doubt that amphibians have been derived from ancient air-breathing fishes of some sort.

Thanks to the recent labors of Bryant, Watson, Stensiö and others, on the fossil lobe-finned fishes, and to those of Watson on the Lower Carboniferous amphibians of Great Britain, the gap in our records between fishes and amphibians is being measurably lessened.

Indeed, it may now be said to be highly probable that although no known genus of lobe-finned fish was the immediate ancestor of the amphibians, yet the group as a whole has the characters to be expected in the descendants of an earlier common stock that gave rise, on the left, to the lung-fishes, near the center, to the known lobe-fins, and on the right, to the earliest tetrapods or amphibians.

Since the last sentence was written I have received the latest report of the Danish Geological Survey of Greenland, containing a monograph by G. Säve-Söderbergh entitled "Preliminary Note on Devonian Stegocephalians from East Greenland." These oldest known amphibians, which were discovered in 1931, aroused a great deal of interest in the American press a short time ago under the name of "four-legged fish." The present report fully justifies the expectation that when amphibians of Devonian age became known they would be decidedly nearer to the lobe-finned fishes than were the already known amphibians of the Lower Carboniferous. This now proves to be the case in the patterns of the skull top and palate as figured from beautifully preserved material.

The breathing of atmospheric air had already been acquired by several groups of fishes of the ancient coal swamps, as it has by several unrelated modern fishes. If we may judge from modern conditions, an oxygen-secreting pouch long served to tide the fish over periods of drought, and possibly the stout fan-shaped paddles of the lobe-fins may have assisted them in wriggling from one pool to another.

The greatest advance made by the earliest known amphibians over their fish ancestors is to be seen in their paired limbs. For each limb is now sharply angulated at the elbow and at the wrist, the basal supports of the bony rays have been crowded together so that they converge toward the postaxial arm-bone, while five of the paddle-rays have become modified to serve as fingers and the outer fin-rays have disappeared, leaving only the nails as a trace of their former existence.

As a result of studies in several fields, Gregory, Miner and Noble have attempted to visualize a possible intermediate stage between a fan-shaped lobe-fin of the *Sauripterus* type and the known pattern of the fore limb in a primitive amphibian.

When, however, we compare the skulls and jaws of the lobe-fins with those of the earliest amphibians, we have no difficulty in identifying homologous elements, or in accounting for those which are lacking in the amphibians.

When breathing by the air-sac finally superseded breathing by the gills, in the adult stage, it is not surprising that the opercular bones, which play an important part in branchial respiration, should have failed to ossify, leaving only a dermal flap. The region of the otic notch in Amphibia corresponds closely to that of the opercular flap in fishes.

As in many other stages of vertebrate ascent, we learn much from the highly specialized descendants of to-day, which in this case are the frogs, toads, salamanders, etc. Their skulls represent fenestrated and depauperized derivatives of the ancient amphibian type.

Stage 7. The Stem Reptiles (Cotylosaurs), Upper Carboniferous and Permian.

It used to be supposed that there was a great gap between the Amphibia and the reptiles, the former being classified with the fishes as Ichthyopsida, the latter with the birds and mammals as Amniota. But thanks to the labors of the late Professor Samuel W. Williston and others, we now know certain fossil forms that break down the old distinctions between amphibians and reptiles. It was said by the elder Huxley, for example, that the amphibians had paired condyles at the back of the occiput, while the reptiles had but one median condyle. It is now known that the primitive amphibians had tripartite condyles, from which were evolved, on the one hand, the double condyles of the typical amphibians and, on the other hand, the ball-like median condyle of modern reptiles and birds.

One of these early reptiles, *Seymouria,* is so nearly on the borderline between amphibians and reptiles that one set of his skull characters has been used to classify him as an amphibian, while other skull characters, together with the detailed construction of his vertebral column, justify his claim to be one of the stem reptiles.

In short, the most conspicuous advance among the reptiles was the elimination of the fish-like or aquatic stage of individual development. By enclosing an artificial watery environment within a water-tight egg the reptiles hit upon a "basic patent" which enabled them to invade the uplands and eventually to conquer almost the whole earth.

The earliest reptiles retained generalized 5-rayed hands and feet, and this constitutes one of their many claims to be on or near the "main line" of ascent to man. The opposite course of digital reduction has been followed by most of the descendants of the ancient reptiles. It has invariably carried them away from the "main line" of ascent.

Stage 8. The Captorhinids, progressive cotylosaurs. Permian.

In the ancient "lobe-finned" ganoids the entire surface of the head was enclosed in a shiny armor of surface plates with openings only for the paired nostrils, the median pineal eye, the paired eyes. The outer jaws were merely the bony plates covering the inner, or gill-arch, jaws. The upper jaw plates were in series with the bony mask covering the head, the lower jaw plates covered the primary, or gill-arch, jaws. The jaw muscles were hidden under the shining facial mask. All this was equally true of the oldest amphibians and reptiles, except that the shiny surface of the bony skull plates was lost just before the amphibian stage.

In the captorhinids, which were rather progressive stem reptiles, the same conditions obtained, but these enterprising little forms had, so to speak, patented what we may call a "four-way palate brace" and were also using the oldest recorded orthodontic appliance, the "descending pterygoid flange," which kept the lower jaw in vertical alignment. Lack of time forbids further references to these devices except for the statement that they seem to be prerequisites for the development of the peculiar type of palate that appeared in the mammal-like reptiles.

Stage 9. The Texas Theromorphs, of Permian times.

As noted above, the jaw muscles of primitive vertebrates were covered externally by a shell or bone, forming the so-called "unperforated temporal roof." While this arrangement may have been advantageous by reason of the protection it afforded to the jaw muscles, it may also have had its inherent disadvantages, such as cramping the free expansion of the jaw muscles. But the Texas theromorphs hit upon the device of "fenestrating" by absorbing the central area of the temporal shell while strengthening its periphery. After this, nothing could or did stop the advance of the jaw muscles until the completely mammalian type of cheek arch had been reached. This was one of the reasons why Professor Cope classified these Texas Permian forms as Theromorpha, or mammal-like reptiles, and regarded them as ancestral to the mammals. The big ones are obviously too specialized in having a chevaux-de-frise of spines on top of the backbone, but the smaller ones, such as Williston's *Mycterosaurus,* avoided these specializations.

Stage 10. The Earlier Mammal-like Reptiles, of the Permian of South Africa and Russia.

South Africa is justly famous for its diamond mines, but from the view-point of anthropogeny its extinct mammal-like reptiles are of far greater significance. Even the earlier reptiles of the Karroo series had already progressed far on the long evolutionary road toward the mammalian grade of organization. For, while their own forerunners had been clumsy beasts, crawling with sharply bent elbows and knees, the South African theromorphs had begun to lift the body off the ground by bringing the fore and hind feet under the body. The skeleton, in fact, abounds in indications of progressively heightened activity associated with predatory habits. The skull was beginning to approach the mammalian grade, in the differentiation of the dentition into incisors, canines and cheek teeth, in the presence of a temporal opening and cheek arch of mammalian type, and in other features.

Stage 11. The Cynodonts or Pro-mammals (Triassic of South Africa and Russia).

The South African cynodonts advanced so far toward the mammals that they ought to have been called pro-mammals, and they are only technically still within the upper limits of the reptilian class. For instance, the skeleton is now well fitted for running, while the skull abounds in new advanced features directly foreshadowing the mammalian grade. The skull of the smaller cynodonts is strikingly like that of a primitive mammal in general appearance, arrangement of bones of upper jaw and nasal region of cheek bar, fossa for jaw muscles, etc., etc. That these cynodonts stand in between primitive reptiles and typical mammals is shown in almost every feature of their skeletons.

The lower jaw also was very progressive, but their official status as reptiles was validated by the retention of the old "reptilian joint" beneath the new or "mammalian joint."

The secondary palate was approaching that in mammals and stands between the primitive reptilian and the typical mammalian conditions.

The living relatives of the cynodonts are the mammals, including ourselves.

Stage 12. Ictidosaurians, Upper Triassic of South Africa.

These highly progressive derivatives of the pro-mammals (recently described by Robert Broom from two skulls) were on the borderline between reptiles and mammals. They practically break down the distinction between reptiles and mammals and show the absurdity of the statement that there are "no links between classes." They possessed the new joint between the mandible and the temporal bone that is characteristic of the mammals, but they also retain the old reptilian joint between the quadrate bone and the articular bone of the mandible.

Possible survivors or relatives of Upper Triassic mammal-like reptiles may be seen in

Stage 13. The Duckbill Platypus and the Spiny Anteater of Australia.

Both these forms lay large reptilian eggs, have reptile-like oviducts and many reptilian features in skull and skeleton, also a relatively primitive brain. They represent an early stage in the evolution of mammalian characters, especially those that tend to maintain a higher, more stable body temperature and more sustained activity. These qualities have helped mammals to conquer the world and drive out the reptiles.

Stage 14. Pretrituberculate, Jurassic mammals.

There was once a dogma that "no mammals are found in Jurassic rocks," and when one was found there, some denied that it was a mammal, others that the rocks were Jurassic. But Cuvier pronounced it "the jaw of a little opossum," a nearly correct allocation. Three orders, numerous genera and species of Mesozoic mammals have been described from the Jurassic of England and Wyoming, but mostly from broken jaws and teeth.

The teeth represent several stages of evolution toward primitive mammalian types. The skull in general had advanced beyond mammal-like reptiles in the direction of the most primitive marsupials. In the more advanced members the teeth were of primitive tritubercular type, ancestral to those of later mammals, including man.

Stage 15. Cretaceous Opossum-like Marsupials.

Huxley, Dollo and later students have emphasized the extremely primitive character of existing American opossums, our oldest and most precious "living fossil."

Unfortunately, most Americans appreciate the opossum more for those qualities which have earned for him the title of "African turkey." It rather pains me to hear of great statesmen taking a holiday down South to hunt these poor animals to eat, when they ought to be securing them for the museums of the future or laboring to establish opossum sanctuaries. The opossum has an American ancestry which would make even the longest known human genealogy look like a last year's birth record from Ellis Island. For Barnum Brown, our curator of Fossil Reptiles, found in rocks of Upper Cretaceous Age in Alberta a fossilized skull of an early member of the opossum family embedded underneath a dinosaur skull. Its estimated age is about eighty to one hundred millions of years.

The opossum skeleton is highly instructive in many ways; *e.g.,* it shows incipient adaptations to tree-living habits, the use of the pectoral limbs as hands and of the hind feet for grasping. While not in the direct line to higher mammals, it preserves many characters which we may confidently look for in the direct ancestors of the Primates.

Stage 16. Cretaceous Insectivorous Placentals of Mongolia.

One of the greatest prizes of Dr. Andrews' expedition to Mongolia, discovered by Dr. Granger. Huxley, Osborn and others had predicted that ancestors of the higher or placental mammals would be found to be Mesozoic insectivores. These little forms are judged to be placentals, through the close resemblances of their skulls and teeth to those of existing insectivores. Uniting characters of the earliest insectivores and carnivores, they show an ideally primitive stage in tritubercular upper molars and give long-looked-for paleontological proof that the primitive cusp was not on the inner side, as believed by Cope and Osborn, but was located on the main cusp, homologous with the main tip of the premolars.

The surviving relatives of the Cretaceous insectivores are the Centetid insectivores of Madagascar.

Stage 17. Primitive Tree-shrews (? Upper Cretaceous to Lower Eocene).

Somewhere in late Cretaceous times a group of small placental insectivores took to climbing up trees, with momentous consequences. For here they gradually acquired those primary arboreal characters which, as there is much evidence to conclude, were deeply stamped into the anatomy and ways of life of our own remote ancestors.

The tree-shrews, however, took only the initial steps; their skeleton retained much of the generalized mammalian type; but while the hands and feet retained claws, initial stages in the evolution of the nails are seen in late members of the group (from the Tertiary of Mongolia).

The existing tree-shrews suggest ordinary insectivores in their large muzzle, but their skulls and teeth approach those of lemurs in certain important characters. In fact, some authorities want to classify them with the lemurs, but as they were a separate family far back in Eocene times, they may be treated as pre-Primates.

Stage 18. The earliest true Primates (Eocene).

There is one fraternal order to which all Americans belong by right of birth, though few are willing to admit it, that is, the Order of Primates. This ancient and honorable order has an antiquity vastly exceeding even the claims of any that hold conventions in the big hotels; the bones of its founders have been discovered in the Bridger formation of Wyoming—their estimated age, about fifty millions of years. This most important skeleton I had the pleasure of naming in honor of the president of the American Museum of Natural History, Henry Fairfield Osborn.

The conspicuous characters are: While retaining five digits, it has grasping hands and feet fitted for climbing; the skull is progressive in its fairly large orbits; the brain is essentially lemur-like but lower and smaller; the dentition is very generalized for a primate; the dental formula is $I\frac{2}{2}C\frac{1}{1}P\frac{4}{4}M\frac{3}{3}$. Thus there were forty teeth in the adult, while in anthropoid apes and man the number has sunk to thirty-two.

Some paleontologists, including Drs. Wortman and Gidley, saw in *Notharctus* an ancestor of the South American monkeys, but to me it is too generalized to be classified with the South American monkeys. It is rather closely related to the Adapidae of Europe, which in turn are probably near the stem of the Madagascar lemuroids. Thus *Notharctus* may not be in direct line of ascent to man, but it is most instructive in showing how deeply arboreal characters had been impressed on the Primates by the Lower Eocene, fifty million years ago. Many lines of evidence support the view that the Primates as an order were fundamentally arboreal and that later semi-terrestrial types, like the baboon, or fully terrestrial types, like man, were all secondary.

Stage 19. The Tarsioids (Eocene).

The active arboreal life of the Primates requires a high development of sight. Hence the Primates were primarily big-eyed forms. This tendency early ran to extremes in the tarsioids, which Dr. Wood Jones regards as nearer than any other known forms to remote ancestors of man. But while it is not necessary to accept the tarsioids as *direct* ancestors, they show certain advances in the optical organs which the ancestors of man must have passed through. Excessive specialization, however, even in the Eocene *Anaptomorphus,* has led to extreme squeezing of the interorbital region and extreme diminution of the nasal chamber. The tarsioids were also early overspecialized in the hopping adaptations of their feet; this again rules them out of the direct line. Nevertheless, even in the modern *Tarsius* their brain and soft anatomy are pretty primitive and in many respects they bridge the gap between lemurs and monkeys; not impossibly they stand rather near to the unknown direct line leading to apes and man, though their relationship to man, in the judgment of most students of the subject, is not nearly as close as is the relationship of the apes to man.

Stage 20. The separation into New World and Old World series.

The question of the precise degree of relationship between the New World and the Old World monkeys has been considered from many angles, but there is no unanimity of opinion. In spite of certain common characters of the brain, placenta, etc., it seems possible that the New World monkeys were derived from some as yet unknown family other than that which gave rise to the Old World series, as maintained by Stehlin. They are widely separated in space and time and widely differentiated in many anatomical characters; *e.g.,* in details of skull and dentition.

The Old World monkeys are distinguished from the New World series not only by the narrow nostrils ("Catarrhinae") but also by the dental formula, already reduced to the same figures as in man and apes, namely, $I\frac{2}{2}C\frac{1}{1}P\frac{2}{2}M\frac{3}{3}$.

Dr. Wood Jones has referred to certain skull characters in which Old World monkeys appear to be too specialized to give rise to man. The same is true of their molar teeth. Nevertheless, the skeleton as a whole is far nearer the ancient Primate type in that the Old World monkeys are still mostly pronograde, *i.e.,* they do not practice brachiation, or arm-swinging, as much as do the anthropoids. Their hands and feet also are much more primitive, and the same is true of their brains.

Stage 21. The founding of the Anthropoid dynasty.

From the Lower Oligocene formation of upper Egypt, Professor Max Schlosser, of Munich, described two priceless little fossil jaws, illustrating two stages of evolution of the Primates. The smaller one, *Parapithecus,* already a living fossil in its own time forty million years ago, was apparently a hold-over from the tarsioids of the Eocene. At least it agreed with them in having a very short jaw, very wide at the back as seen from above, implying a much expanded braincase, and pointed in front. The teeth combine some characters of tarsioids with others of the anthropoid-human series.

The second stage was definitely a small anthropoid ape but of immense antiquity and primitiveness. It was named by its discoverer *Propliopithecus,* as a forerunner of *Pliopithecus,* the ancestor of the gibbon, but much more primitive than the gibbons in jaw and teeth. It has advanced beyond the tarsioid stage in widening of the front end, implying widening of tongue (embryonic jaw moulded by tongue). Dental formula: $I_2C_1P_2M_3$, as in anthropoid apes and man.

Molar teeth of primitive anthropoid type with five main cusps. It has been regarded by an eminent anthropologist (Sergi) as an ideal ancestor of man, but it might be a near ancestor of the entire ape-man series in characters of the lower jaw and dentition.

The modern gibbon, as a descendant of *Propliopithecus,* is a somewhat overspecialized side branch with excessively long arms and legs and saber-like upper canine tusks. Nevertheless, in many ways it represents a transitional stage between monkeys and apes. It retains the last traces of ischial callosities. Several characters of the skull and skeleton, but especially the molar teeth, definitely and surely classify the gibbon as an ape, not a monkey. The Johns Hopkins University school of anatomists concludes that the human line came off far down the anthropoid stem, a little above the level of the origin of the gibbon. I feel that there are too many strong bonds between man and the higher anthropoids to make the pro-gibbon ancestry of man probable, but all are agreed that man has come off from the anthropoid stock either earlier or later.

The gibbon skeleton is thoroughly adapted for brachiating. This is generally defined as "arm-swinging," but if we watch living gibbons we see that the legs play a very important part in leaping. The habit of brachiation has brought the backbone into a vertical position at right angles to its primitive horizontal position, and some authorities believe that brachiation is a prerequisite to human evolution. We may readily concede, however, that the gibbon is now in an advanced overspecialized phase of brachiation which need not be imputed to the early Tertiary anthropoids.

Stage 22. The Miocene Anthropoids.

During the Miocene epoch the anthropoid group was represented by many species found as fossil jaws and teeth in France, Germany, the Vienna basin, Spain, northern Egypt and India; hence there was a broad zone extending across Europe and India with later offshoots in tropical Africa, South Africa, China, and southeastern Asia. This wide-ranging group was highly variable in size and in details of the dentition. They are known to date only from scattered jaws, one humerus and one femur. An eminent mammalogist demands fossil ape skeletons that include well-preserved hands, feet, pelves, etc., before admitting the evidence of fossil apes to his private court of judgment; but fossil apes do not come to us in that form. Nevertheless, these jaws and teeth of fossil apes are of extraordinary value, for they reveal both the wide plasticity and wide geographic distribution of the anthropoid stock. Barnum Brown discovered in India several important jaws shown in composite form in the figure. The jaw is deep and massive; there are thirty-two teeth; the canines are prominent, the opposite tooth rows are parallel as in apes.

The cheek teeth are of great interest because the pattern appears to be archetypal to that of man. The lower molars have three cusps on the outer side, two on the inner side, with elaborate "*Dryopithecus* pattern" of grooves, also a "fovea anterior" and "fovea posterior." Exactly this combination is found in primitive human jaws along with new and distinctly human characters. The characters of the premolars and molars support the view that man is an offshoot from some member of the *Dryopithecus* stock and with closer relationships to the African anthropoids than to the gibbon and the orang. The reduction of the canine in man is quite secondary, as supported by the extensive researches of Remane.

Dr. Gerrit S. Miller, Jr. (as quoted in a recent note in SCIENCE) objects that men and anthropoids are different kinds of giants, as compared with Primates of average size, and that there is no fossil-proved precedent for one kind of giant's turning into a different kind of giant. He therefore classes the derivation of man from a Tertiary anthropoid stock as "an alluring speculation," choosing to ignore the hundreds of anatomical characters that tie man with the anthropoids in a single systematic group. But there are giants and giants. The crown of the third lower molar of *Dryopithecus fontani* measures about 11 by 9.2 millimeters in anteroposterior and transverse diameters, respectively, while that of *Dryopithecus giganteus* measures 19 by 15.3 millimeters.[2] This wide range of variability in size in the older group does not seem to favor Dr. Miller's assumption of unalterable, fixed divergences between the two.

The conclusion that man is closer to the *Dryopithecus* stock than to the gibbons seems also to be opposed by my colleagues in Johns Hopkins University, and although I am prepared to defend it in detail, I do not regard it as essential for the present purpose, which is merely to reaffirm the conclusion that man in much the greater part of his characters is nearer to the anthropoid apes than to the more primitive Primates.

Stage 23. The extinct South African Anthropoid (Australopithecus)

This amazingly well-preserved fossil was described by Professor Raymond Dart, of the University of the Witwatersrand, South Africa, in 1925. It was found in a fissure deposit near Taungs, on the eastern edge of the Kalahari desert. Its geological age is

[2] William K. Gregory and Milo Hellman, Anthropological Papers of the American Museum of Natural History, Vol. xxviii, Part I, 1926, p. 74.

not precisely established but, according to Dr. Robert Broom, two species of fossil baboons and an extinct species of *Hyrax* have been found in the same level. He therefore considers the age of *Australopithecus* to be Pliocene. But whether the age be Pliocene, Pleistocene or Recent, this skull is of exceptional interest. Extremes of judgment about the skull are first, that of Professor Dart, who regards it as the representative of a new family "Homosimiidae" widely removed from the African anthropoids; at the opposite extreme is the conclusion of Dr. Wolfgang Abel, of Vienna, who regards it as closely related to the gorilla and having nothing whatever to do with human ascent. Dr. Milo Hellman and I, who have studied the excellent casts of the upper and lower teeth, conclude that while it is a young anthropoid, related to the existing African genera, yet its deciduous canines and molars and its first permanent molars are, on the whole, unequivocally more man-like than those of the existing young gorilla and chimpanzee; while its permanent molars are definitely not those of *Gorilla* but present beautiful examples of a modified *Dryopithecus* pattern akin to those of the Ehringsdorf and Mousterian fossil human stage. In short, while we do not yet know the form of the adult skull of *Australopithecus,* it is safe to affirm that this child skull is strikingly "prehuman" in the general appearance of its cranium and facial skeleton and that it tends to lessen the phylogenetic gap between man and the existing African anthropoids.

Stage 24. Man appears.

With regard to the fossil human remains known as *Pithecanthropus,* found in Java, and *Eoanthropus,* found in England, scientific controversies have raged to such an extent that the eminent mammalogist already cited has urged that these names be, so to speak, wiped off the scientific slate until they are documented by better material. Fortunately, we need not for the moment at least contest this quite arbitrary ruling, for new and unimpeachable material of early man has been discovered near Peking and admirably described by Dr. Davidson Black. One of the Peking skulls was only little more advanced than that of *Pithecanthropus,* while the second was slightly further advanced toward the Neanderthal type. But according to the masterly field investigations of Teilhard de Chardin, the Peking human remains are contemporaneous with an extensive mammalian fauna that retains many elements characteristic of the Pliocene age, along with others indicating Lower Pleistocene age. Moreover, the Peking horizons belong in the Red Earth series, which are older than the thick loess deposits of Pleistocene age. Hence the Peking man, according to Chardin, is far older than the typical Neanderthals of the late Pleistocene of Europe, while its skull-contours, as figured by Black, are all lower and more primitive.

Without entering into controversial questions as to the geological age of the Piltdown and *Pithecanthropus* remains, it seems highly probable that the ancestors of *Sinanthropus* in late Tertiary times would have been properly classifiable as men rather than as apes. Time after time the Pliocene representatives of modern mammalian families have been shown to be almost modern in the appearance of their teeth, skulls and feet.

But here, as always, we must avoid the serious logical error of assuming for man the low average rate of evolution that obtained in non-Primate mammals. Moreover, the Lower Pleistocene *Sinanthropus* stands so far below *Homo sapiens* in cranial capacity that a backward prolongation of the curve at the same rate would presumably bring down the figures to the horizon of the anthropoids at no very distant geological date. Finally, according to the eminent geologist, Professor Schuchert, of Yale University, who has given prolonged consideration to this problem, the duration of the Pliocene epoch is many times greater than that of the Pleistocene. At present I know of no single item of objective evidence for the view that the human family began to diverge from that of the anthropoid apes as far back as Lower Oligocene or Upper Eocene times, forty or fifty million years ago; although in all fairness it should be noted that many other families of mammals did part company with each other at even earlier dates. But upon another occasion I was at some pains to demonstrate that, considering only the molar teeth and the feet, the structural differences between two families, the tapirs and the horses, that are known to have diverged in Lower Eocene times, are now far greater than the differences in the patterns of the molar teeth and of the feet respectively between modern men and modern apes.

But at whatever period, early or late, the human family may have begun to diverge from that of the anthropoid apes, it appears to be virtually proved by hundreds of separate items of evidence that men and apes are the divergent offshoots of a common stock, the existence of which, though not the period, is sufficiently documented by the huge mass of evidence already at hand. But it is not to be expected that this still growing mass of evidence for man's evolution from the lower animals will quiet the loud demands of anti-evolutionists for "objective evidence."

Stage 25. Homo sapiens, the big-brained devastator.

The existing anthropoids have a veritable passion for tearing things apart; but in point of destructiveness they are bungling amateurs, compared with their big-brained relative *Homo sapiens.* In him, by a series of conditioned responses, destructiveness within the family and tribal limits was restrained, but when enemies were to be ravaged and pillaged it was given full rein. For untold millions of years the line of vertebrates that led toward man were unblushing thieves and robbers; even now, the human face beneath its smiling mask carries the old mammalian trap set with sharp teeth. Such being the case, it is no wonder that we suffer from grafters, racketeers and gunmen. The wonder is not that so many of us find ourselves in prison but that any of us ever learned to keep out.

However, as soon as apes began to go in families and hordes, the counter principles of more or less unselfish interest in others began to operate; even in the lowest of existing social organizations there seems to be more or less clear proof of the unselfishness of mothers, the devotion of fathers, the generosity and disinterestedness of friends. Such a patchwork of good and evil is *Homo sapiens!*

But it does not seem that the pessimists are necessarily right. As Dr. Clark Wissler has pointed out, particular cultures may disappear, but culture itself goes on. And in view of the nearly world-wide distribution of *Homo sapiens* it would be hard to imagine any purely terrestrial epidemic or insect scourge that could wipe him out over his entire range.

Finally, man, in respect to the high development of his brain and other characters, may well represent an early stage in the differentiation of a virtually new class of vertebrates. The paleontological record shows repeatedly that, in the long past, once a new class gets started it runs for hundreds of millions of years. So that, taking the available evidence into consideration, it seems safe to predict that *Homo sapiens* will eventually muddle through this depression and survive to endure others in the future.

SUMMARY

The "Anthropogenie" of Ernest Haeckel, a pioneer work of great difficulty, depended to a considerable extent upon the so-called biogenetic law. Since the validity of this law has been attacked by several modern zoologists, public confidence in Haeckel's conclusions seems to have been undermined, at least in certain parts of the country. The "new anthropogeny" has grown chiefly out of the progress of paleontology, comparative anatomy, phylogenetic taxonomy and the comparison of the *échelle des êtres* among recent and fossil series. It seems that we are now in a position to substitute for the more or less hypothetical stages postulated by Haeckel a new and independently discovered series representing groups that depart the least from a continuous ascent. This, of course, involves the exclusion of all other groups which show more than the least observed differences from the more nearly continuous series.

For example, Haeckel relied upon the lung-fishes (Dipnoi) to bridge the gap between earlier fishes and the Amphibia. The Paleozoic Dipnoi are now seen to have been further from the "line of least change" than were their contemporaries, the lobe-finned ganoids (Crossopterygii), which possess in an earlier form a great many of the skeletal characters that were inherited by the Amphibia. It is concluded by Watson and others that the "lobe-fins" were descendants of an earlier group, which also gave rise in one direction to the Dipnoi, in the other to the Amphibia.

The new anthropogeny, as far as developed to date, submits the following series, subject, of course, to correction by further discovery:

(1) *Pre-fish (ostracoderm)* of Ordovician, Silurian and Devonian age. Paired sense organs, brain and cranial nerves, all fundamentally identical with those of the larval lamprey. "Gill-arch" jaws not developed.

(2) *Antiarch.* "Gill-arch" jaws incipient, outer jaw bones present. Known forms: *Pterichthys, Bothriolepis,* etc.; probably well off the main line except in characters noted.

(3) *Pre-shark (acanthodian).* Devonian. "Gill-arch" jaws (in series with gill-arches) fully developed. Paired fins arising from stabilizing fin-folds.

(4) *Basal ganoid fish.* Devonian. Enamel-covered bony mask over face and gill-chamber. Inner (primary) and outer jaw-parts complete. Anal, pelvic and pectoral fins showing progressive evolution from fin-fold to paddle type. Pectoral girdle complex (surface and deep elements). Near line of ascent to typical true fishes.

(5) *Lobe-finned ganoid.* Devonian and Lower Carboniferous. Paired fins with shortened bases and crowded, fan-like skeleton. Teeth labyrinthodont, primary jaws covered with bony plates. Many bones of skull-roof homologous with those in later vertebrates. Cleithrum predominant in pectoral girdle.

(6) *Basal amphibian.* Lower Carboniferous. Paired limbs with five-rayed digits. Vertebrae cut up, large intercentra. Pectoral girdle at first retained cleithrum from fish stage. Teeth labyrinthodont. Opercular bones absent. Skull patterns archetypal to all later tetrapods. Occipital condyle tripartite. Aquatic (tadpole) mode of development.

(7) *Stem reptile.* Upper Carboniferous. Presumed elimination of tadpole stage. Vertebrae simplified, intercentra small. Occipital condyle tripartite to single and median. Cleithrum reduced. Limbs of crawling type.

(8) *Progressive cotylosaur (captorhinid).* Permian. Retaining primitive shell of bone over temporal muscles. "Four-way palate arch" developed from primary upper jaw. Skeleton lizard-like.

(9) *Texas theromorph.* Permian. Temporal roof fenestrated by jaw muscle, leaving zygomatic arch of pre-mammalian type.

(10) *Earlier mammal-like reptile.* Permian of South Africa and Russia. Limbs adapted for running. Dentition carnivorous, with incisors, canines and cheek teeth. Temporal region of pre-mammalian type. Dentary bone of lower jaw with obliquely ascending ramus. Occipital condyle single.

(11) *Cynodont or pro-mammal.* Triassic of South Africa. Skull sub-mammalian in: zygomatic arch, secondary palate, differentiated dentition, double occipital condyle, etc. Lower jaw with increasing ascending ramus finally approaching squamosal bone. Jaw bones behind dentary reduced. Quadrate small. Skeleton of sub-mammalian running type.

(12) *Ictidosaurian, near-mammal.* Upper Triassic, South Africa. Skull almost mammalian. Lower jaw with large, nearly vertical, ascending ramus of dentary and much reduced jaw bones behind dentary.

(13) *Prototherian mammal.* Known chiefly from recent Duckbill (*Ornithorhynchus*) and *Echidna* of Australia. Retaining semi-reptilian type of eggs and oviducts. Primitive skeletal features, especially in girdles and limbs. Incipient stage of milking habit. Lower jaw with new or mammalian type of joint with skull (*i.e.*, between dentary and squamosal bones). Various aberrant specializations in modern representatives.

(14) *Pre-trituberculate mammal.* Jurassic. Lower jaw of primitive mammalian type, crowns of lower cheek teeth with elevated, three-cusped ''trigonid'' and low, small ''talonid'' or heel.

(15) *Pre-opossum*, conservative Metatherian. Cretaceous. Not near direct line to placentals but retaining many primitive skeletal features, especially in skull and dentition. Young probably born in very incomplete condition. Brain with only beginning of ''neopallium''; corpus callosum not developed.

(16) *Cretaceous insectivorous placental.* Skull of small generalized insectivore type. Small brain with large olfactory lobes. Brain in modern descendants with corpus callosum. Upper cheek teeth with incipiently divided main cusp (paracone) and low inner spur (protocone). A placenta developed in modern relatives.

(17) *Primitive tree-shrew.* Basal Eocene. Incipient adaptations of hands and feet for tree-climbing. Skull essentially as in No. 18, that is, lemur-like but with unreduced olfactory chamber. Skeleton of generalized placental type. Modern tree-shrews retaining many primitive characters.

(18) *Stem Primate.* Lower and Middle Eocene. Adaptations for arboreal habits deeply stamped on hands and feet of grasping type. Dental formula $I^2_2C^1_1P^4_4M^3_3$. Eyes large, orbits with postorbital rim.

(19) *Eocene Pre-tarsioid.* Known forms aberrantly specialized; but more generalized stage should be near to main line. Eyes large, protruding forward, interorbital space reduced. Brain very wide, jaw short, wide posteriorly, pointed in front. Extremities grasping (grasping-hopping in known forms). Premolars typically $\frac{3}{3}$. *Parapithecus* possibly belongs here.

(20) *Stem Old World monkey.* Pronograde or essentially quadrupedal, with grasping hands and feet. Dentition $I^2_2C^1_1P^2_2M^3_3$. Cheek teeth in recent forms aberrantly specialized; *i.e.*, with well developed cross-crests. Nose catarrhine (V-shaped nostrils). Orbits separated from temporal fossae by bony partition.

(21) *Pre-anthropoid* (*Propliopithecus*). Lower Oligocene. Ancestral gibbons with short, deep lower jaw, more primitive lower canines and premolars. Dentition: $I^2_2C^1_1P^2_2M^3_3$. Molars with five cusps. Frugivorous. Recent gibbons overspecialized for upright progression by brachiation, with excessively long arms and legs; nevertheless retain certain monkey characters (*e.g.*, traces of ischial callosities). Brain less advanced than those of the chimpanzee and gorilla.

(22) *Mid-Tertiary anthropoid group.* Ranging from Spain, through France, Germany, Austria, Egypt, East Africa to India and (later) to South Africa. Lower molars with five cusps and ''*Dryopithecus* pattern.'' Limb bones of anthropoid type. Brain capacity of recent great apes ranging from 290 to 610 cc. (Keith).

(23) *Southern Ape* (*Australopithecus*). Pliocene or Pleistocene of South Africa. This ''ape-child'' skull probably belonged to a race of adults with muzzles more ape-like than its own. Nevertheless, its deciduous teeth and first true molars, while primarily of the ''*Dryopithecus*'' type, are not very far below the earlier human levels.

(24) *Early Human Stage.* Lower Pleistocene or earlier. Represented at least by *Pithecanthropus* of Java and *Sinanthropus* of China. Vertically low skulls with strongly projecting brow-ridges. Brain of relatively low type; endocranial capacity 900 $\pm$ cc. (Dubois). Clear traces of ''*Dryopithecus* pattern'' in lower molars of Ehringsdorf young.

(25) *Homo sapiens.* Pleistocene and Recent. Braincase typically high, with little or no brow-ridges. Cranial capacity: racial means ranging between 1200 and 1500 cc. (Hooton). Skeleton adapted for upright bipedal posture, but hands and feet retaining many clear traces of generalized ape ancestry. Lower molars often four-cusped, with traces of ''*Dryopithecus* pattern'' usually on m_1. Brain retaining many unmistakable marks of derivation from an anthropoid stage, but with progressive development of centers and areas associated with speech and verbalized thinking.

As to the possible future of mankind, it is pointed out that, to judge from the history of many other new groups (not species), and in consideration of his cosmopolitan distribution, mankind should be a "good risk" for survival for an indefinite period.