THE PHYLOGENETIC TREE: AN ANALYSIS OF ITS DEVELOPMENT IN STUDIES OF HUMAN EVOLUTION

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Preface

This paper is an examination of the Phylogenetic Tree as this concept has been applied to the study of human evolution.

Considerations about which the analysis is oriented are the following:

1. The development of ideas concerning human phylogeny and the history of their diagrammatic representations.

2. The problems peculiar to the study of human phylogeny.

3. The influence of non-scientific data: nationalism, religion, academic systems.

4. The effect of traditional phylogenetic concepts upon interpretation of the fossil record.

5. The worth of the Phylogenetic Tree as a tool in paleoanthropology today.

Preceding the discussion of these problems in the conclusion of the paper are an examination of phylogenetic theories based on the fossil hominid record from the time of Darwin to the present (Part I), and a series of sixteen reproductions of Phylogenetic Trees representative of major schools of thought in Great Britain, the United States, France, and Germany (Part II). An Appendix contains background information for an historical insight into this analysis, i.e. the development of taxonomic concepts from antiquity to the Darwinian era. These data are set apart from the main body of the paper because of that absence of phylogenetic theory in pre-Darwinian biology, i.e. Phylogenetic Trees were not conceivable as long as species were regarded as immutable and life was confined to a Biblical time concept. Yet the progress made in comparative anatomy and taxonomic systems before the mid-nineteenth century provided the framework upon which the later ideas of mutability and temporality found support. Hence, the inclusion of this resumé in the Appendix is pertinent to the thesis of this paper.

Part I: Development of the Idea of the Phylogenetic Tree

"All that the Chain of Being actually needed to become a full-fledged evolutionary theory was the introduction into it of the conception of time in vast quantities added to mutability of form," (Eiseley, 1958, p. 9). The change from a static conception of nature to a dynamic view gave scholars a new

field of research--the history of life. The earlier classificatory systems which grew out of and supported the Scala Naturae were maintained, but with the acceptance of evolutionary theory, scholars perceived these in a wholly different light. This ironic situation has been summarized by Simpson:

> From their classifications alone, it is practically impossible to tell whether zoologists of the middle decade of the Nineteenth Century were evolutionists or not, and classifications intended to be phylogenetic differed as much among themselves as they did from frankly archetypical classifications. This was partly because the superficial aspects of classification do not necessarily change when the underlying meaning changes--we still use the Linnaean hierarchy and nomenclature, although we have rearranged and multiplied his categories and give them a totally different significance (Simpson, 1945, p. 4).

As a biological principle, the Chain of Being was forgotten in the nineteenth century, but it found its way into evolution. Darwin was influenced by it when he speaks of the whole organic world's "progress toward perfection." Until fossils were recognized as the remains of animals that had become extinct, the other doctrine implicit in the Chain of Being, the continuity of all species through time, remained unresolved. This section of the paper is concerned with the process by which the study of human evolution became free from its traditional context in the Chain of Being and Linnaean Taxonomy. The catalysts for this reactionary move were (a) the discovery of fossil hominid material and (b) the work of nineteenth century biologists who sought phylogenetic affinities in the data. This history will be discussed within the limits of three periods of time based upon important fossil discoveries: 1856-1890, 1891-1924, 1925-1958.

1856-1890

Although the Engis and Neander Valley specimens were known to Darwin, he postulated his theory of evolution through natural selection without benefit of fossil material. However, the idea of gradations between biotic phenomena, i.e. "missing links," was immanent in the Chain of Being and had conditioned Darwin and his colleagues to expect their appearance in yet undiscovered living forms. This led to an interest in the simians which most nearly approached modern man and in primitive peoples who were arranged in racial gradations that led downward to the ape. The candidates for this lowly position were legion: Hottentots (Eiseley, 1958, p. 260), Australians (Pouchet, 1864, p. 15), American Indians (Dunn, 1862), African Negroes (Vogt, 1864, p. 128). The "noble savage" of the French Enlightenment held no place in nineteenth century England where he was useful in filling a gap later left open by fossil evidence.

The involvement of evolutionists with contemporary apes and living races of man led to the misconception epitomized in the phrase "missing link" which has plagued the study of hominid phylogeny. Huxley did more than anyone to foster belief in uniserial evolution of primates from lemuroids to man. In Man's Place in Nature (Huxley, 1863), he stressed the idea that the apes differed morphologically to a greater degree among themselves than they did from modern man, and the monkeys were further removed from both groups (Huxley, 1863, p. 123).

This idea was not new, for Buffon a century earlier had remarked, ". . . as regards his [orang-utan] body, he differs less from man than he does from other animals which are still called apes" (Buffon, 1766, Tome XIV, p. 30). But in the biological context of the late-nineteenth century, "Huxley's Law" became misunderstood. Haeckel used the idea dogmatically in the reconstruction of his "Pithecanthropus alalus"--a medley of contemporary gibbonoid and human physical traits. And Mivart, on the basis of the complexity of cross comparisons between primate genera, rejects this misunderstanding of the "missing link" as follows:

> It has been put forward by Mr. Darwin and widely accepted, that the resemblances between man and apes are such that man may be conceived to have descended from some ancient members of the broad-breastboned group of apes, and the gorilla is still properly credited with the closest relationship to him which is to be found in all existing apes (Mivart, 1873, pp. 172-173).

Owen also misunderstood and rejected "Huxley's Law" (Owen, 1868, fn. p. 323).

Darwin in 1871 warned against tracing man's descent by means of living anthropoids, but due to the lack of fossil material, he could not avoid focussing attention upon them. He favored a comparatively weak fossil ancestor for man, since a gorilla-like creature would be less likely to become socialized. These less powerful ancestors lived cloistered lives in an isolated continent, possibly Australia. Darwin agreed with Huxley in explaining away the lack of fossil evidence by the fact that older deposits, miocene or pliocene, have not yet been thoroughly examined for hominid remains (Huxley, 1863, pp. 181-182).

Contrary to early evolutionary speculations was the notion that man is outside the pale of nature, a throwback to pre-Linnaean taxonomy. This was another device for dismissing the problem of fossils which were not yet found. A letter from Huxley to Lyell in 1859 implies a belief in a macromutation which took place anciently (Eiseley, 1958, p. 267). Lyell used the idea himself in 1863 when he speculated whether man had not "cleared at one bound" the distance between animal nature and beings with advanced intelligence (Ibid., p. 266). Darwin rejected this idea. That man had not arisen from savagery but had sunk into it, particularly in areas peripheral to Europe, was the cant of the Degenerationists who could accept neither an evolutionary nor a saltatory theory. Whately and Miller believed early man attained civilization through divine intervention shortly following his special creation, but certain groups had degenerated both culturally and morphologically. "The farther we remove in any direction from the Adamic center [Palestine], the more animalized and sunk do we find the various tribes or races" (Miller, 1869, p. 229). Progressionism was another popular theological-scientific view in England, as preached by Sedgwick (1845) and Owen (1894), and in the United States by Agassiz (1850). However, this concept was evolution minus transformation of species. All steps in the process of evolution were divinely created and show direction to an end in man himself. The threat that Darwin posed for this complacent view in demonstrating that struggle rather than design was the process of nature was unrealized until alternative interpretations had been postulated which were supported by fossil evidence.

The fossil hominid material available for study before 1856 was limited to Schmerling's find in the Engis Cave in Belgium (1833), Buckland's "Red Lady" from the Paviland Cave in Wales (1823) and remains of dubious antiquity from Cannstadt in Würtemberg (1700) and from Denise in Haute-Loire (1844). The Neanderthal specimen from Gibraltar (1848) remained unrecognized. The search for additional fossil forms did not begin in earnest until Boucher de Perthes had proved to Falconer, Evans and Prestwick the existence of antediluvial man from tools found in the gravels of the Somme (1859) and until Fuhlrott had described the calvaria from the Neander Valley (1856). Interpretations of these and subsequent finds, before Dubois' excavations in Java, were the foundation for the Phylogenetic Tree, as this concept has been applicable for understanding human evolution.

Neither Darwin nor Huxley designed a family tree illustrative of the evolution of man, but the latter scholar set up a possible evolutionary sequence in which were first used several of the fossil discoveries. The gradation ran from a hypothetical ape-man to Neanderthal to the Borreby crania of Denmark to the Engis specimen and thence to the source of such modern primitive races as Australians, Bushmen, Vedda, Papuans and pygmies from which sprang the three present races of man. Huxley thought of Neanderthal as a Homo sapiens and regarded the special features of the calvaria of this fossil Homonid, as noted by his colleagues, as exaggerated (Huxley, 1863, pp. 181-182). As Darwin and Haeckel, Huxley regarded the ape and human groups as constituting an autonomous branch which had been early separated from the mother branch of the Catarrhini (Vallois and Boule, 1957, p. 513; Gregory, 1934b, p. 488). The common human ancestor at this point of divergence Huxley named "Eohomo" whom he reconstructed, in a moment of felicity, as mounted upon an Eohippus (von Koenigswald, 1956, p. 15).

Following Larlet's discovery of a modern-type fossil skull at Cro-Magnon (1868), similar finds were described by Rivière from Menton in Monaco (1892), by Fraipont and Lohest from Spy in Namur (1887), and a reëvaluation was made of the La Naulette mandible found by Dupont near Dinant (1866).

The finding of geologically ancient big-brained hominids tended to substract from evolutionists their enthusiasm for the necessity of finding primitive and small-headed human ancestors which would more closely comply with their evolutionary scheme (Gill, 1874, p. 644). This problem was explained away by some researchers through the argument that these were primitive giant hominids whose skulls were absolutely larger only as a correlate of their bodily proportions (Buchner, 1872, p. 261; Keith, 1894, pp. 188-189). Sollas stated this paradoxical situation as follows: "As we proceed backwards in time, man departs further from the ape in the size of his brain, but approaches nearer to the ape in the character of his bodily framework" (Sollas, 1911, p. 121). While the significance of these early discoveries could not be properly understood until the data were fuller, the fossils of Upper Pleistocene Homo sapiens led scholars to see that Neanderthaloids were not diseased idiots nor feral creatures of medieval romance, rather they were set apart as a specific variant of Homo.

Pithecanthropus was the first specimen of low cranial capacity to be suspended from a Phylogenetic Tree. While the calvaria elicited a fraternal welcome from Haeckel: "He is, indeed, the long-searched-for 'missing link' for which in 1866 I myself had proposed the hypothetical genus Pithecanthropus, species alalus" (Haeckel, 1898, p. 26), its reception was considerably less warm from the majority of scholars who called the skull microcephalic or refused to accept it as fossil evidence. Only Marsh and Manouvrier also accepted Dubois' find and, curiously enough, Dubois regarded the Neanderthal and Cro-Magnon specimens as pathological, but not his own find of Pithecanthropus. Dubois believed his fossil was that of an arboreal hominid standing midway in morphology between living anthropoids and man (Dubois, 1898, p. 429).

Fortified with a convincing "missing link," through a technique borrowed from Huxley of proving closeness of relationships by frequency of compared morphological traits ("Huxley's Law"), and with the recapitulation theory formulated on the basis of von Baer's ontogenetic studies, Haeckel felt himself equipped to define the phylogenetic problem (Jones, 1929, p. 57). Several useful ideas issued from his work. One such idea was that:

> . . . not one of the still living apes and consequently not one of the so-called man-like apes, can be the progenitors of the Human Race. . . The ape-like progenitors of the Human Race are long since extinct. We may possibly still find their fossil bones in the Tertiary rocks of southern Asia or Africa. In any case they will, in the zoological system, have to be classified in the group of tailless, narrow-nosed apes (Catarrhine, Lepocerci or Anthropoides) (Haeckel, 1876, p. 277).

Another significant contribution regarded the position of modern races in human phylogeny; namely that primitive traits are not concentrated within one or more racial group but are rather scattered in different parts of the globe, Europeans themselves being not entirely free of heirlooms from the past (Ibid., p. 276). He noted that racial differences attributed to man are greater than the criteria upon which species distinctions are based by zoologists for non-human organisms (Ibid., p. 305). His thinking was less objective, however, when maintaining that cerebral development had advanced the farthest among Indo-Germanic peoples, the proof of this blessing being their ready acceptance of his evolutionary doctrines! (Ibid., p. 332). As noted above, Haeckel had defined the fossil ancestor of these races years before embracing Dubois' Pithecanthropus as his savior:

> . . . considering the extraordinary resemblance between the lowest wholly-haired men, and the highest man-like apes, which still exist at the present day, it requires but a slight stretch of the imagination to conceive an intermediate form connecting the two, and to see in it an approximate likeness to the supposed primaeval men or ape-like men (Ibid., p. 326).

This prophetic vision would have a long skull, slanting teeth, woolly hair, a dark skin, long arms, and a half-erect stature. Such an intermediate form

was speechless, but upon the acquisition of language, due to higher differentiation of brain and larynx, various species of men arose (Ibid., pp. 326-327). Further remarks on the differentiation of human races are reserved for a following part of the paper, but their inclusion here is for the purpose of describing what Dubois, an admirer of Haeckel, expected to find in Java. Haeckel had suggested southeast Asia as the home of mankind, but was not adverse to casting a glance at sunken continents in the Indian Ocean ("Lemuria" of Sclater)

With the general acceptance of evolution by scientific scholars at the turn of the century, the subsequent discoveries of fossil hominids were more confirmatory than initiative of ideas about human development. The Piltdown Forgery (1912) may well have been due to a misdirected desire to supply a more favorable "missing link" for confirmation of evolutionary doctrine than the Pithecanthropine evidence could provide (Oakley, 1957, p. 3). The Heidelberg mandible (1907) was favored in filling the gap between Middle Pleistocene hominids and the Neanderthals. The Rhodesian find (1921) did not upset the uniserial view, but simply broadened the "Neanderthal" stage to include another member. The Phylogenetic Trees that now flourished had their roots in the establishment of genealogical affinities between the human branch and the other branches and trunk of the primate tree. Klaatsch conceived of a polygenetic origin for man, each race having as its ancestor one of the four living anthropoid apes which inhabit territory closest to its own. This theory was supposedly based upon similarities of limb structure. The outcome: Mongoloids arose from orang-utans, Negroids from gorillas, and Caucasoids from chimpanzees. Fossil finds with limb bones can thus be classified racially: Aurignacians from orang-utans, Neanderthals from gorillas (Klaatsch, 1910). Klaatsch later recanted, but his ideas were rekindled by Crookshank who added new information to support the data, viz., the comparison of sitting attitudes of different races to the habitual sitting positions of their simian forebears (Crookshank, 1924). More sophisticated views regarding pre-human ancestry within the anthropoid line were those of Keith, Pilgrim, Dubois, Haeckel, and Boule, all but the first contemplating a common progenitor in the gibbonoid branch. Haeckel later changed his views and agreed with Darwin and Huxley that the human group was detached from the Catarrhine limb. Vogt, Sera, and Ameghino found a common ancestor among the Platyrrhini, Cope among the Lemuroids, and Wood-Jones with the Tarsioids (Vallois, 1957, pp. 512-513). All scholars were generally agreed about Asia being the ancestral home of man.

The first quarter of the present century saw, furthermore, a concern for evidence of adaptive radiation, parallelism, convergence and survival factors in the hominid phylogenetic process. Studies were made of particular organs, bones, and teeth by which affinities between fossil and living races might be perceived. The anthropometric approach led to a vogue of measurement and sampling of large skeletal populations. Descent and modification of morphology through time was explained as the basis for resemblances and differences of living forms. And the acceptance of evolution along with the filling in of the fossil record led to the rise of paleontology as a science separate from comparative anatomy.

With the filling out of the paleontological record in the past quarter century, the gardens of Phylogenetic Trees planted earlier by Haeckel, Keith, Wilder, Gregory, and Lull grew into exuberant jungles through which the stoutest of intellectual explorers have lost their way: the more authors, the more theories. Just as the concept of evolution could not be explained until an adequate time-perspective was conceivable, so the ramification of the fossil record gave the necessary refinement to the mechanism of evolutionary process--natural selection. Each new fossil discovery rang the death knell for those scholars who continued to work on the supposition that structural similarities could be sought between man and ape, and so on, down to lower primate forms (Jones, 1929, pp. 58-59). Their resistance to nesting Australopithecus in the hominid branch of the Phylogenetic Tree was because, in their philosophy, "missing links" were assumed to be half-way between anthropoid and hominid forms and half-way with respect to each morphological trait--an argument fashionable in the support of Piltdown (Mayr, 1950, p. 114). That the painting of Pithecanthropus done by Gabriel Max for Haeckel's Natürliche Schopfungsgeschichte (1876) appeared in popular text books on anthropology until as late as the nineteen-thirties, testifies to the fact that many students of the time were disregarding the independent evolutionary history of the anthropoids from that of their own ancestors.

The status of Dubois' Pithecanthropus was confirmed with the discovery of the Sinanthropus material in China (1927-1939) and with the continuation of work in Java (1936-1941). The levitation of Dubois' Wadjak and Trinil osseous material from beneath a house floor in Haarlem during the nineteen-twenties became associated with studies of the Talgai (1914), Cohuna (1925-26) and Keilor (1940) complex. The bulk of fossil data for Upper Pleistocene Homo sapiens from the Dordogne (1868-1923), Grimaldi Caves (1872-1901), and eastern Europe (1891-1927), and the Neanderthal finds from La Chapelle (1908), Le Moustier (1909), La Ferrasie (1909-1912), La Quina (1911), and Krapina (1899) abdicated their orderly place in the uniserial Phylogenetic Tree after the interpretation of the discoveries from Mount Carmel (1931-1933) and from Ehringsdorf (1914) and Steinheim (1933). The Preneanderthal School, supported by Le Gros Clark, Clark Howell, Breitinger, and Sergi, considers a Third Interglacial stem, basically Neanderthal in nature, as a common stem for Neanderthals and Cro-Magnons (Howells, 1959, p. 237). The finds made subsequently at Swanscombe (1935-1936) and Fontechevade (1948) lent evidence to the view that primitive Homo sapiens came into existence during Middle Pleistocene times and evolved parallel with but independently of Neanderthals, the doctrine of the Presapiens School of Vallois and Gieseler. The third "school" that has resulted from interpretation of this imposing bulk of evidence is the Polyphyletic School of Weidenreich's which holds that human evolution occurred independently in the various centers of the globe where fossil ancestors have been uncovered, the living races of man being the end result of these independent lines.

To the collection of fossil monkeys and apes already known by the turn of the century, i.e., Pliopithecus (1837), Propliopithecus (1911), Semnopithecus (1837-1838), Dryopithecus (1856), Oreopithecus (1876), were added since 1924 three groups of fossil finds: the rediscovery of Dryopithecine fossils from the

Siwalik Hills (1915, 1927), the finding of Proconsul in East Africa (1951), and the Australopithecine material of South Africa (1924-1958). Three hypotheses have been made regarding the relationship of the Australopithecines to man: (1) They are true Anthropoids sharing certain parallelisms in morphology with man (Abel, Schwartz); (2) They are true Hominids of some genealogical relationship to early man (Dart, Broom, Le Gros Clark), (3) They are a group of Anthropoids in the process of evolving towards humanity but vanished without attaining this status (Gregory) (Vallois, 1957, pp. 91-92). Other schools of thought are centered upon the position of the pre-Pleistocene fossil anthropoids. Yet while the Phylogenetic Tree has ramified since the discovery of these finds, the phylogeny of the Hominidae can now be established in broad outline. The Phylogenetic Tree has arborized from a palm tree with its majority of branches at the top to a veritable bush with limbs radiating at all points along the central trunk.

An examination of how scholars from four different countries handled this increasing amount of evidence in each of the three time periods of fossil discovery is the task that follows.

Part II. Representative Phylogenetic Trees: 1876-1957

The Phylogenetic Trees which have been included in this report are representative of the several major theories respecting human evolution. Selection has been limited to scholars who have drawn actual diagrams and have accompanied these with explanatory texts. Thus those phylogenists who have held influential opinions, but not expressed them diagrammatically are not represented in this paper. Included in this category are Broca (1870), Topinard (1891), Darwin (1871), Huxley (1863), Jones (1929), von Koenigswald (1956), Vallois (1957) and Le Gros Clark (1957). That the ideas of these scholars have influenced the Phylogenetic Trees of their colleagues is obvious from the foregoing.

Ernst Haeckel (1834-1919), German, The History of Creation (Natürliche Schopfungsgeschichte), 1876, pp. 271, 309.

Haeckel classified organic phenomena into twenty-five evolutionary stages of which fourteen belonged to the Vertebrata and the remainder to the Invertebrata (Haeckel, 1876, p. 277). The primates appear, beginning with the prosimians at the twenty-first stage and within a category of Discaplacentalia (mammals with disk-shaped placentas as compared to the Zenoplacentalia or mammals with girdle-shaped placentas). Included in the succeeding four stages were respectively the Catarrhini, the Anthropoidea, the hypothetical Pithecanthropus, and man, who appeared in the early Quarternary as an end product of this uniserial tree (Ibid., p. 267; Laloy, 1890, pp. 742-744). Under the belief that some primitive people can fully oppose their great toes, Haeckel rejects Cuvier's idea of placing man in the separate order Bimana; rather, he favors a view of Huxley's that certain apes are as bimanual in habit as man. He accepts Huxley's seven-fold classification of primates, but lumps the groupings so that Huxley's first three genera become Prosimia or semi-apes, and the Catarrhini (monkeys and great apes), Platyrrhini and Man become Simia. "The human race is a small branch of the group of Catarrhini and has developed out

of long-since-extinct apes of this group in the Old World." (Haeckel, 1876, pp. 268-269, 274, 276).

The gap between the Man-like Apes (Anthropoidea) and modern man is bridged by the Ape-like Men (Pithecanthropi), who were evolved in the late Tertiary and characterized from their Anthropoid ancestors by having an upright gait and a specialization of hands and feet. Language was the hallmark of true Men and was related to development of the brain and larynx. (Seemingly, Haeckel was unconcerned with palatal features.) On the basis of a philological dogma that all human languages are not derived from a common primitive tongue, Huxley concludes that a polyphyletic origin of language is accompanied by a polyphletic transition from Pithecanthropi to Genuine Men (Ibid., pp. 292-294):

> . . . if the origin of an articulate language is considered as the real and principal act of humanification, and the species of the human race are distinguished according to the roots of their language, it might be said that the different races of men had originated, independently of one another, by different branches of primaeval, speechless men directly springing from apes, and forming their own primaeval language (Ibid., pp. 303-304).

While admitting that various species of men may have arisen from the common speechless ancestor but became extinct through pressures of natural selection before modern man could have learned of their existence, Haeckel conceived of two races--a woolly-haired and a straight-haired--which were most strongly divergent, were capable of overpowering the other species, and so became the primary progenitors of living races. The woolly-haired people (Ulotrichi) spread southward and westward and are represented by Hottentots, Negroes, Papuans; the straight-haired (Lissotrichi) moved to the southeast and are represented by Malays, Mongolians, Caucasians. The Indo-Germanic people who were derived from this latter branch have become, in Haeckel's view, the epitome of racial evolution--the race furthest removed mentally and morphologically from the Pithecanthropi (Ibid., pp. 327-328, 332).

Haeckel omitted a time scale from his Phylogenetic Tree, but annotated the time of evolution for the particular primate forms according to the following scheme: Prosimea (Semi-Apes)--early Tertiary; Menocerea (Tailed-Apes)--late Tertiary; Anthropoidea (Man-like Apes)--Miocene; Pithecanthropi (Ape-like Men)--late Tertiary; Homines (Genuine Men)--early Quarternary (Diluvial), (Haeckel, 1876, pp. 291-294).

Such are the opinions that Haeckel held in 1874-1876. With his acceptance of Dubois' Pithecanthropus, he came to regard man as a late ramification of a proto-gibbonoid branch with the Javanese fossil standing midway along the limb (Haeckel, 1903, p. 676). Formerly he had placed the hypothetical Ape-like Men on the limb parallel to that of contemporary Anthropoid Apes (as in the tree presented here, p. 17), (Haeckel, 1874, p. 491; 1876, pp. 293-294). He also came to believe that speech was a phenomenon incipiently developed among certain non-human primates (Haeckel, 1899, p. 466). But by the turn of the century when his revised opinions were published, considerable changes had developed in phylogenetic theory

and eclipsed the popularity that Haeckel had formerly enjoyed. These earlier more influential views are the ones pertinent to this study.

Arthur Keith (1866-1955), British, The Antiquity of Man, 1915, pp. 501-509.
New Discoveries Relating to the Antiquity of Man, 1931, frontispiece.

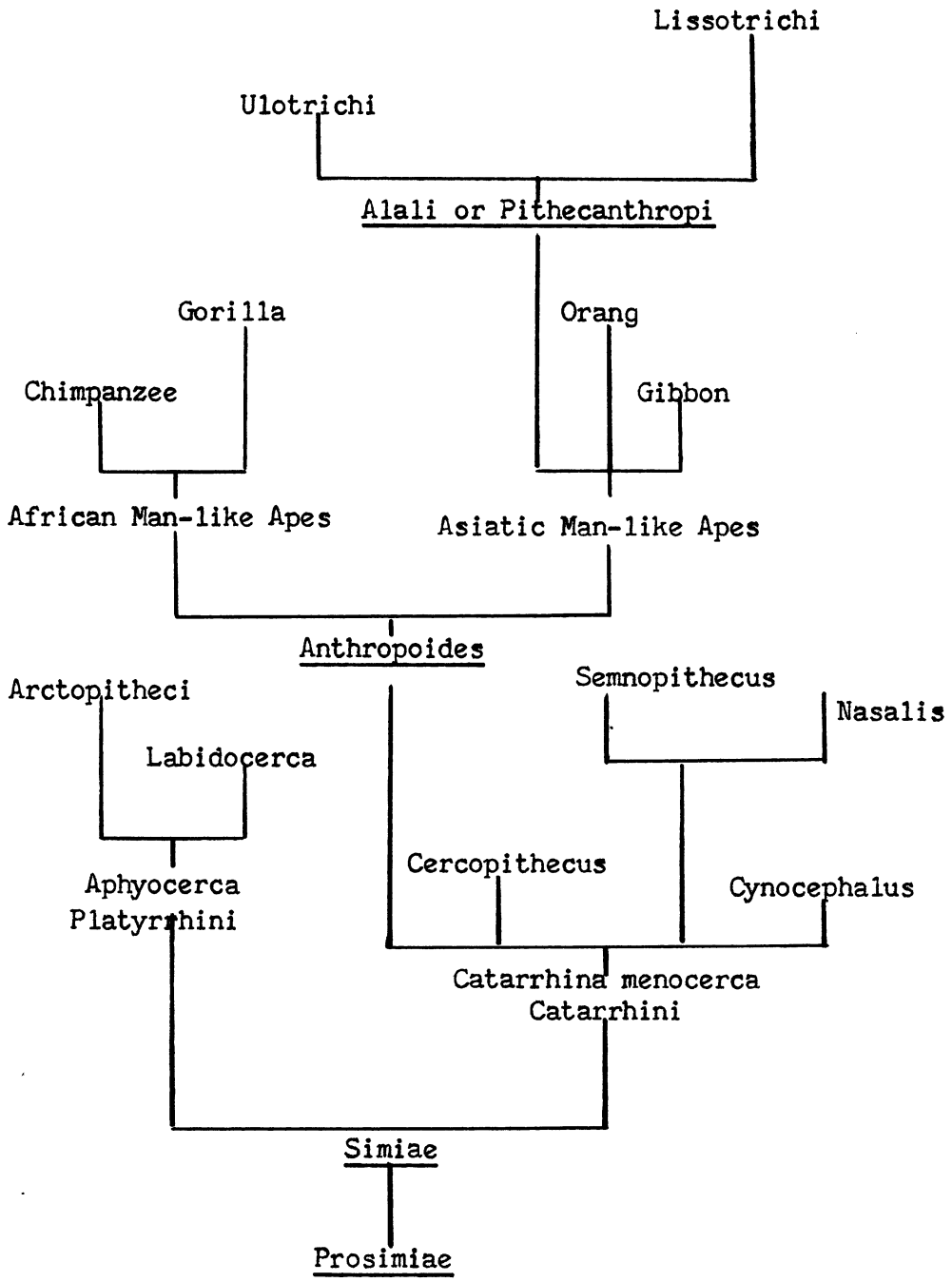
The two Phylogenetic Trees that Keith prepared within a sixteen-year interval well illustrate the influence that the fossil discoveries of the interim had upon studies of human ancestry and both are reproduced here for comparison (pp. 20, 21).

In the earlier diagram he represented the gibbons branching off from a main stem through the specialization of Propliopithecus in the early Oligocene. Later in the Oligocene the great apes separate from the human stem, but he finds the earliest progenitor of the apes in Dryopithecus, which appears well along in the Miocene. Accordingly, ramification of the Anthropoidea occurs in the early Pliocene (Keith, 1915, pp. 506-507).

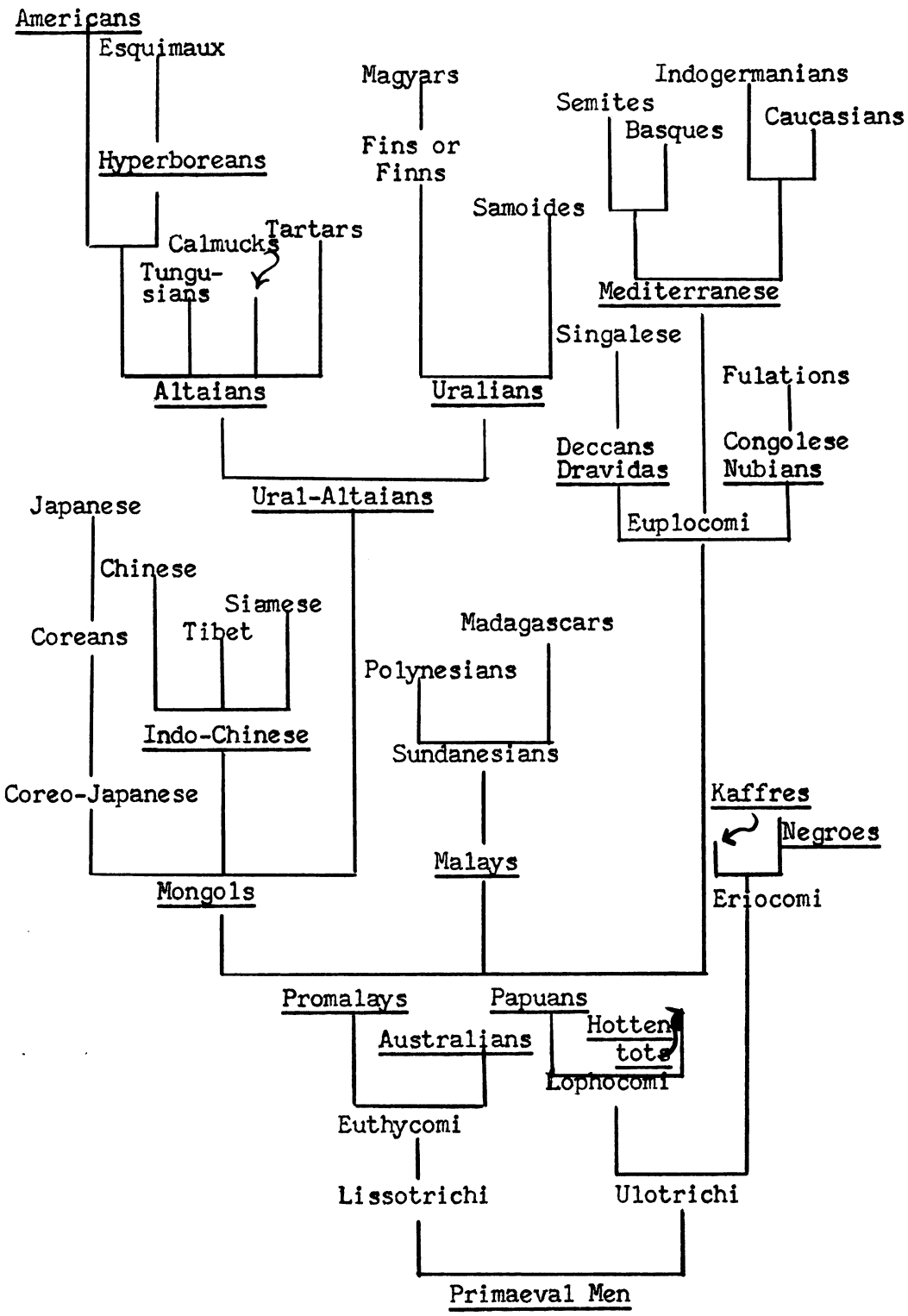
Keith regards all members of the human stem to be of the same genus (Homo) but defines three species: (1) a Neanderthaloid species with a Heidelberg ancestor, which separated from the main human stem in the mid-Pliocene and became extinct in the subsequent period; (2) an Eoanthropus form (which Keith did not give genus rank), which came from the same common ancestor as Neanderthaloids and Homo, but disappeared at terminal Pliocene times; and (3) Homo sapiens, which began a differentiation into four racial branches in the early Pleistocene, by which time it had already inherited its large brain size from the Pliocene ancestor. Of separate genus rank is Pithecanthropus, which left the humanoid stem too early to be ancestral to those three species of Homo on the main human stem (Ibid., pp. 502-505). The reason for Keith's belief that only one species from the main human stem exists today is that Homo sapiens had superior mental faculties which aided him in a competition that was not between races or within the same species (as is the case today), but between different species or even genera (Ibid, p. 506). Yet Keith did not minimize the nature or significance of the morphological affinities between modern man and the contemporary great apes, a fact which was criticized by Jones, who believed his colleague had separated the ancestors of these forms at too low a point on the Phylogenetic Tree for any degree of affinity to be apparent (Jones, 1929, p. 63).

In the 1931 presentation of his views, Keith adds the Taung discovery to the anthropoid stem. He regards all its special features as anthropoid: "It shares so many features with the two surviving African anthropoids--the gorilla and the chimpanzee--that to account for their common heritage, we must suppose that all three come from the same stem" (Keith, 1931, p. 53). However, Dart's placement of Taung at the base of the human stem is indicated by Keith as a dotted line off of this stem.

The earlier Phylogenetic Tree preserves its general shape, but new branches are added. Sinanthropus separated from the main human stem near the points at which Pithecanthropus and Neanderthaloids parted, and its taxonomic affinity to these forms is left unanswered (Ibid., pp. 293-294). Rhodesian man



Haeckel, 1876, p. 271



Haeckel, 1876, p. 309

is regarded as bearing certain points of kinship to Neanderthals, but stands closer to the ancestral line of modern man (Ibid., p. 122).

As the complexity of the Phylogenetic Tree became obvious to Keith he wrote: "Such a tree is merely an anatomist's working hypothesis; a discovery may be made any day which will compel us to take this tree to pieces and reconstruct it--stem and branch" (Ibid., p. 51). That Keith had a preconceived idea of a human stem which was foreshadowed as far back as the Eocene, is observable from the very orientation of the branches: "Divergence of the human stem toward the right is intended to indicate a steady manward movement" (Ibid., frontispiece).

William K. Gregory (1876-), American, Studies on the Evolution of the Primates, 1916, p. 337.

Parapithecus was regarded by Gregory as the earliest ancestor to the anthropoid pattern. From Sivapithecus the Hominidae branched away in late Miocene times while the chimpanzee-gorilla line grew out of its progenitor of this period--Dryopithecus. Many of the differences which separate living men and apes today are retrogressive changes due to dietary habits (Gregory, 1916, pp. 341-342). (See Phylogenetic Tree, p. 22.)

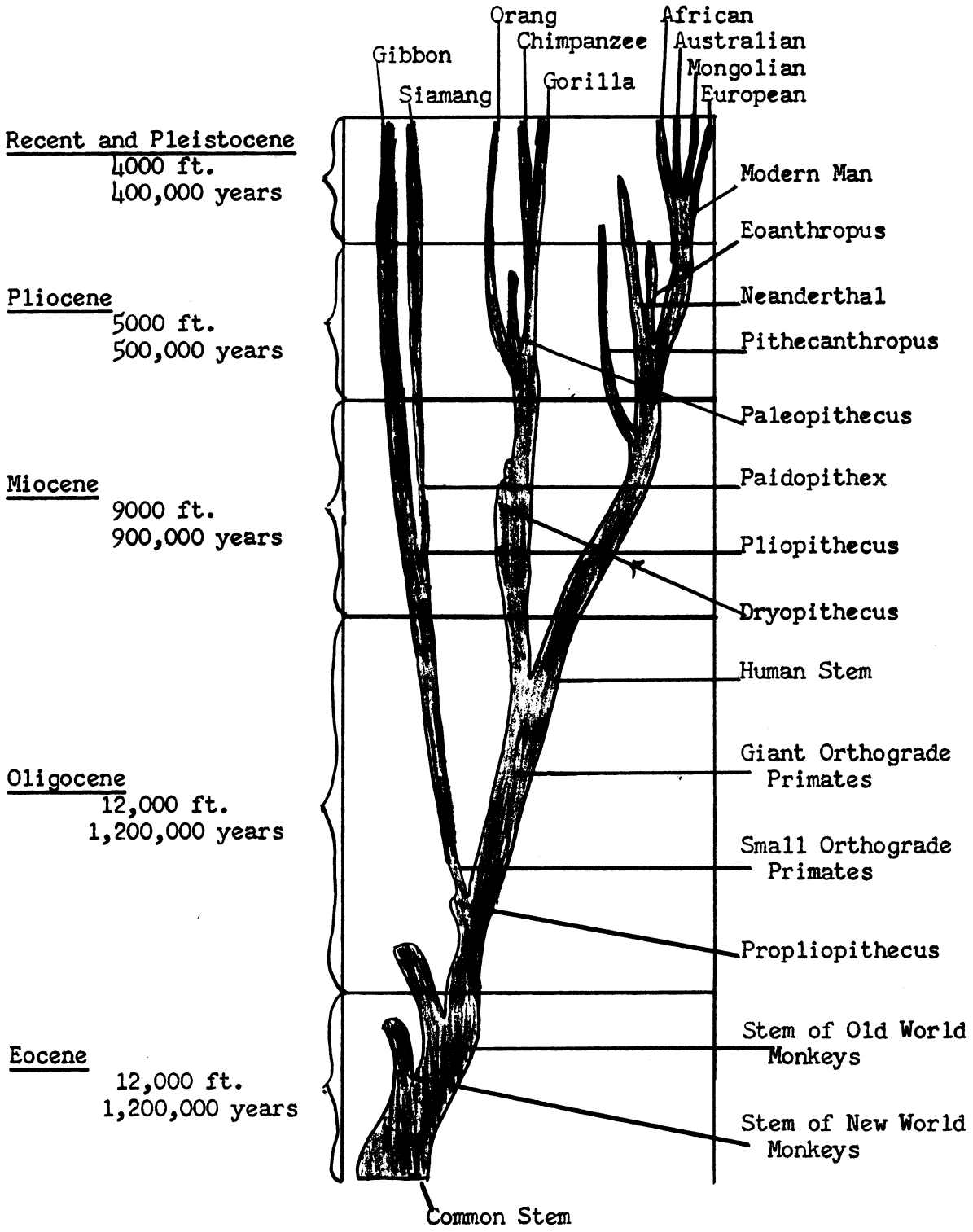
Since the separation of the Hominidae from the Simidae during the Miocene of Asia, two limbs have separated from the main human trunk--Pithecanthropines and Neanderthals. All other forms of hominids trace their relationship to the Heidelberg form. Gregory based his Phylogenetic Tree upon the dental similarities of the fossil evidence (Gregory, 1934, Chapter 2).

Richard Swann Lull (1867-1957), American, "The Antiquity of Man" in The Evolution of Man, 1923, p. 36.

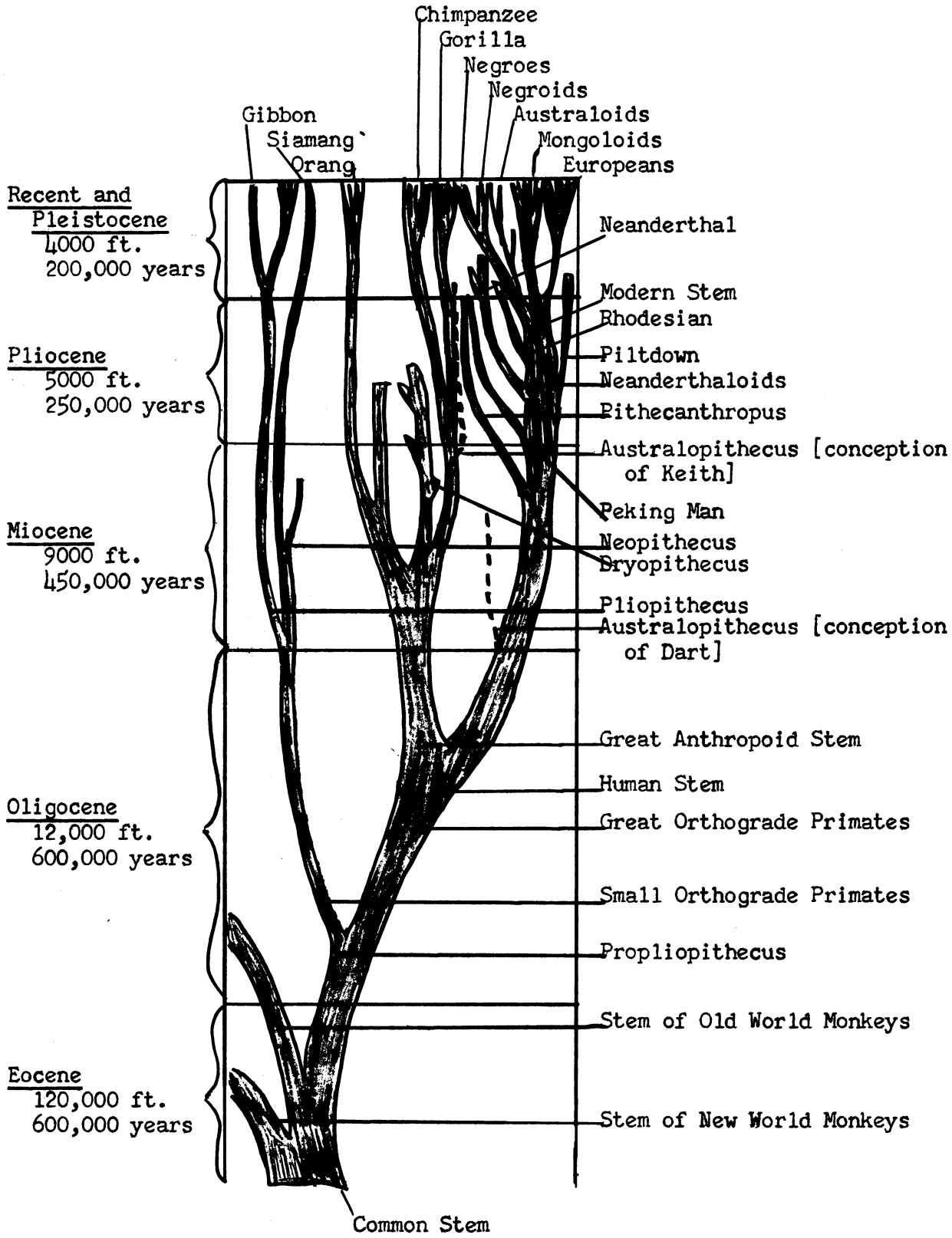
"As yet there is no actual connection with ape-like forms ancestral to both modern apes and man, but the table here reproduced gives a tentative view of implied relationships" (Lull, 1923, p. 38). The table to which he refers is a modification from Gregory's views (Gregory, 1920). Propliopithecus is called a "structural ancestor." All non-Homo sapiens fossil forms are peripheral to the main trunk which leads from this Oligocene primate to modern man. Lull sees the Miocene as the period of human origin and Asia as the place from which man diffused (Lull, op. cit., p. 38). (See Phylogenetic Tree, p. 23.)

Harris Hawthorn Wilder (1864-1928), American, The Pedigree of the Human Race, 1926, p. 270.

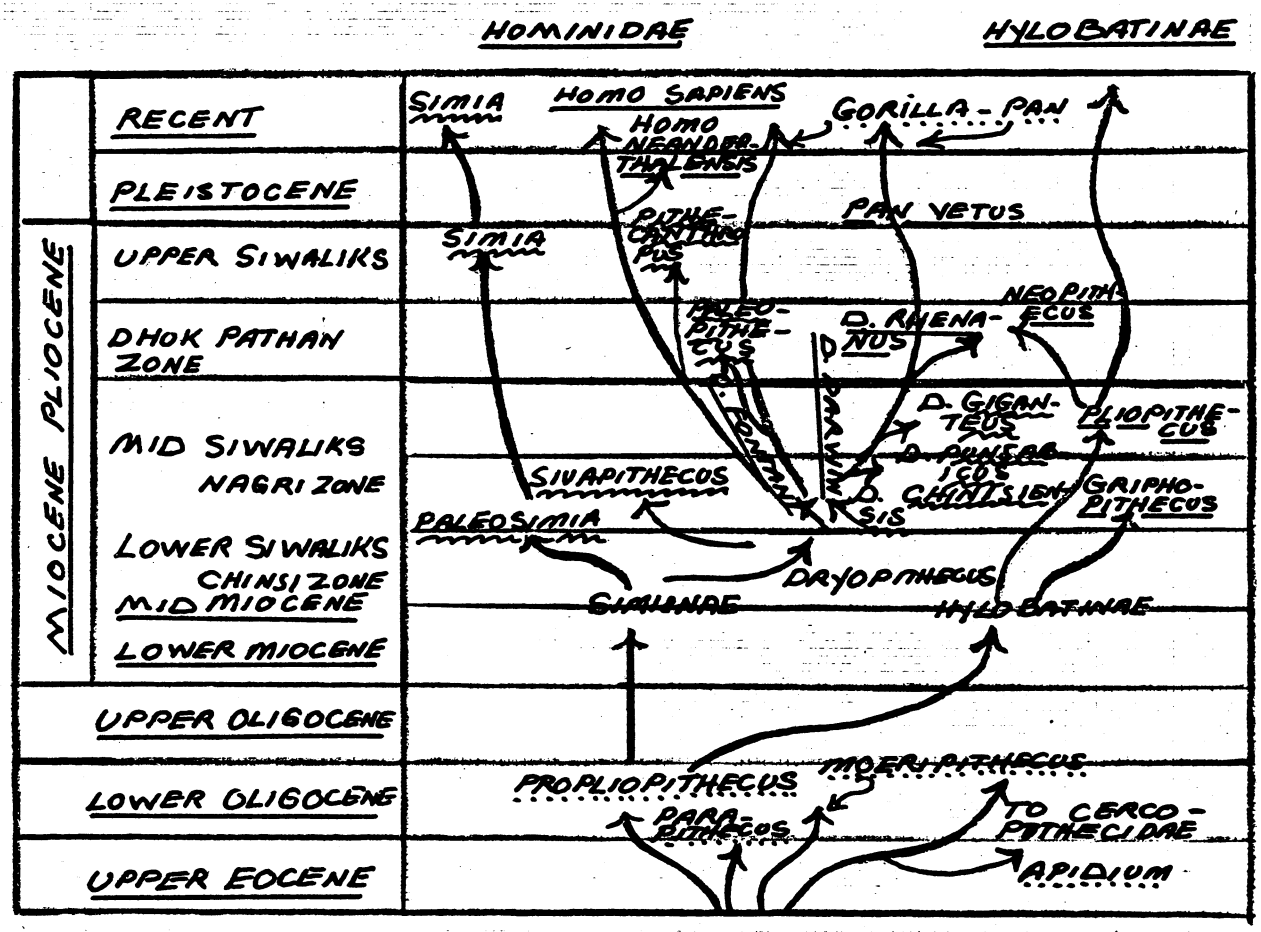
From a branch collateral to that of Dryopithecus three lines of primate specialization evolved: (1) a gibbonoid line which most closely preserved the morphological characteristic of the progenitor, (2) a main simian line which ramified into the three great apes, (3) a hominid line early represented by Pithecanthropus. From the Pithecanthropines was evolved Eoanthropus, which stands, in regard to its mandible, intermediate between the Javanese fossils and the Heidelberg form. But because its cranium is most like that of modern



Keith, 1915, p. 509



Keith, 1931, frontispiece



LEGEND:

~~~~ - FOUND IN ASIA
..... - " AFRICA
———— - " EUROPE

GREGORY, 1916, p. 337
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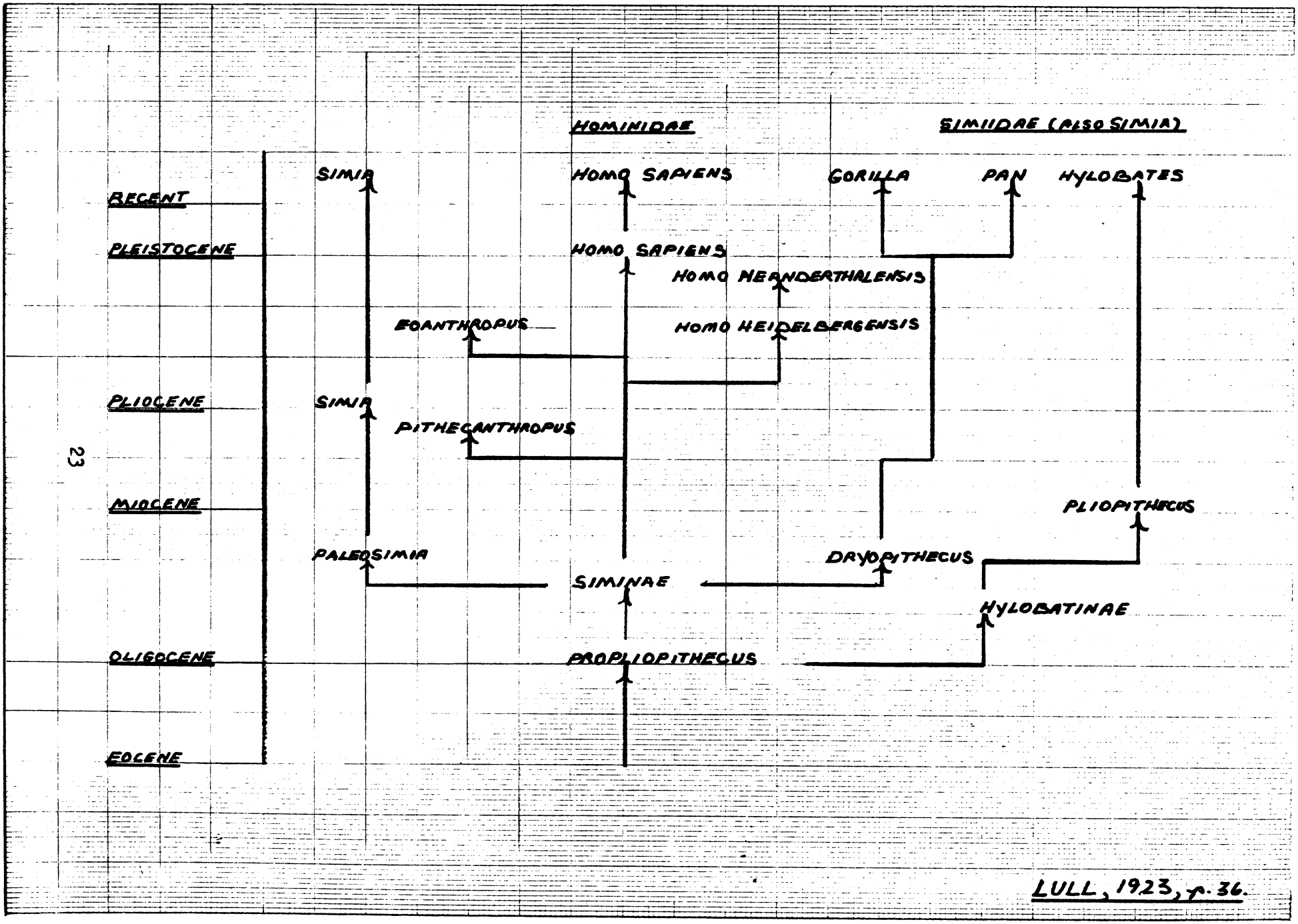


LULL, 1923, p. 36.

man, it can only be regarded as a direct human ancestor. Neanderthaloids form a collateral branch. Wilder does not place the newly discovered Australopithecus skull on his tree, but mentions in the text that it may be positioned on the human line a little lower than Pithecanthropus (Wilder, 1926, pp. 271-272).

Wilder omits a time scale from the Phylogenetic Tree, but reproduces in the text the tree designed by Dubois (1896) upon which a time scale does appear. Here Dryopithecus is shown in the Mid-Miocene and Pithecanthropus in Mid-Pliocene. Wilder agrees with Dubois' sequence, merely adding to it the fossil forms discovered since Dubois' publication.

G. Elliot Smith (1871-1937), British, The Evolution of Man, 1927, p. 3.

> The object of [the diagram] is to indicate the fact that all these Lemurs, Monkeys, and Apes, which have become specialized in one way or another, should be regarded as having departed from the main stream of development that leads straight up to Man, and by doing so, lost something of the primitive structure and plasticity that were necessary for the attainment of the high powers of adaptation which represent one of the most distinctive characteristics of the human family (Smith, 1927, p. 16).

The hominid on the main stem that was the progenitor of the human family was placed in the Pliocene by Smith on the grounds that

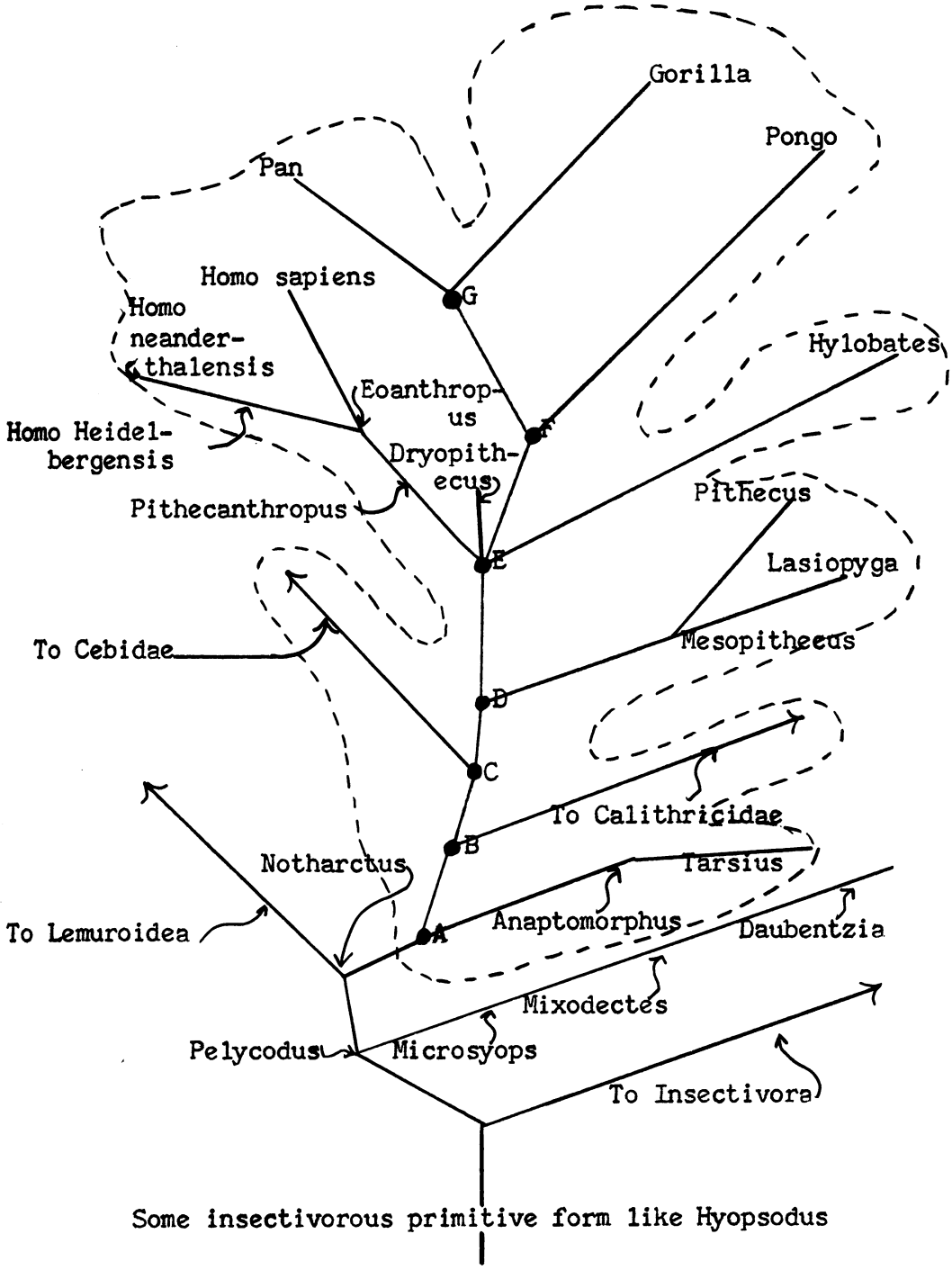
> . . . the marked contrast between Pithecanthropus and Eoanthropus, a separation which is not only structural but geographical, makes it quite certain that Man must have existed in the Pliocene and probably still earlier (Ibid., p. 6).

From the main trunk the Pithecanthropus form departed the earliest. Because the Heidelberg mandible "fits" the Rhodesian calvaria, Smith placed them near together at the point of departure from the human line. At the point where Neanderthals arborize, the species of modern man makes its appearance.

Modern races were arranged by their degree of removal from the primitive forms of hominids and great apes on the basis of skin pigmentation and brow ridge development. The former trait was represented on the Phylogenetic Tree by the arrangement of the races around the Nordic limb. Brow ridge development is greatest among those races to the right of the Nordic branch. Smith hastens to add in the text that brow ridge development is not an exclusively primitive character nor an accurate index of race (Ibid., pp. 9-10).

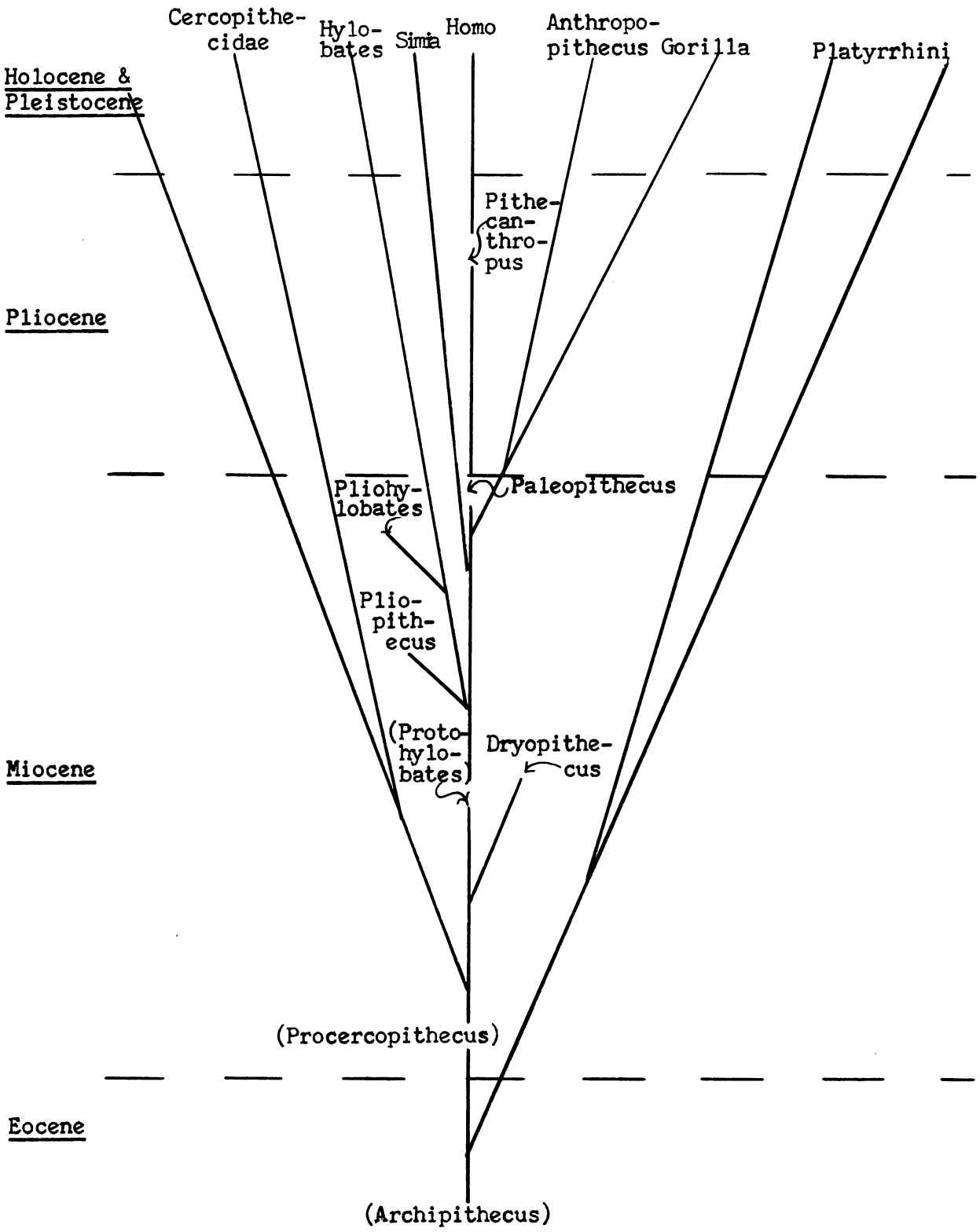
Othenio Abel (1875-), German, Das Verwandschaftsverhältnis zwischen dem Menschen und den höheren fossilen Primaten, 1934, p. 1.

Abel favored Africa as the place for human origin, the arid regions rather than the tropics being most conducive for his survival and early differentiation. The Dryopithecines form the basic human stock from which arose the great apes and man. Australopithecus is considered a questionable offshoot of the gorilla limb. All hominid fossils are brought into a uniserial order from Pithecanthropus to Homo. Abel expresses the view that man stands somewhere

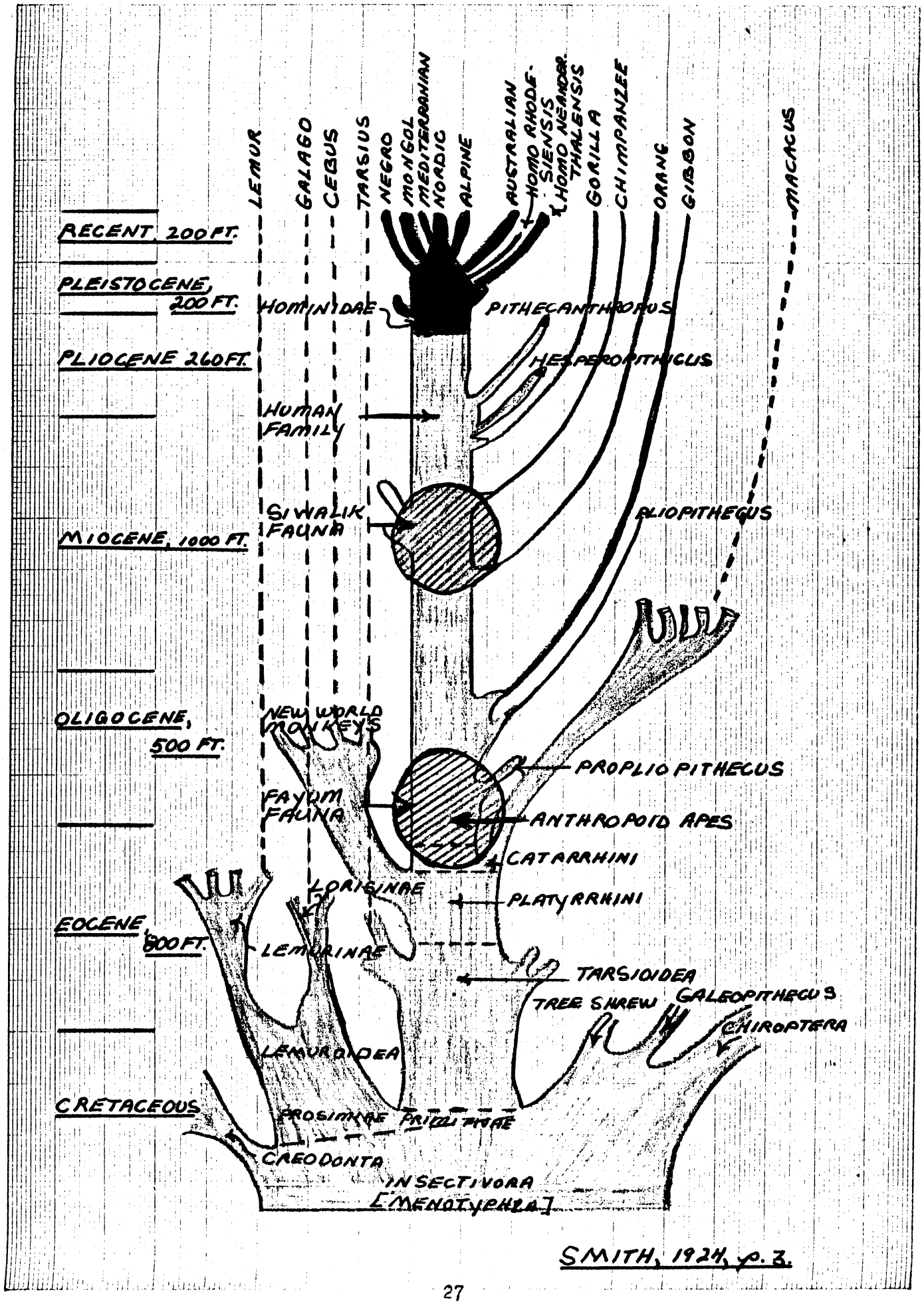


A = Primordial anthropoid
B = Archipithecus
C = Last ancestor of Cebidae
D = Procercopithecus
E = Primordial simian ape
F = Last ancestor of living apes
G = Direct ancestor of living apes

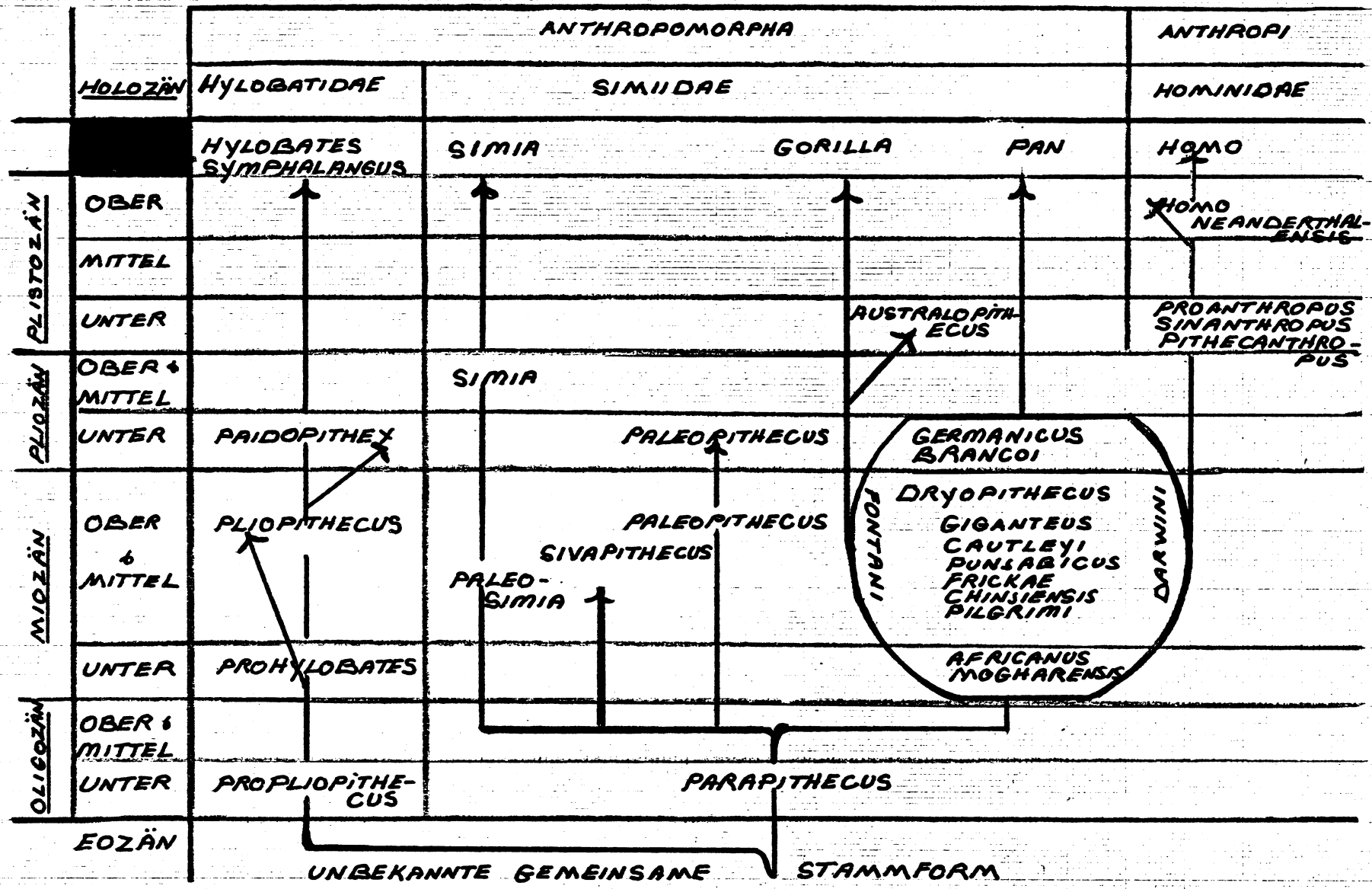
Wilder, 1926, p. 270



Dubois [Wilder, 1926, p. 266]



SMITH, 1924, p. 3.


ANTHROPOMORPHA
ANTHROPI
HOLOZÄN
HYLOBATIDAE
SIMIIDAE
HOMINIDAE
HYLOBATES SYMPHALANGUS
SIMIA
GORILLA
PAN
HOMO
PLISTOZÄN
OBER
HOMO NEANDERTHALENSIS
MITTEL
UNTER
AUSTRALOPITHECUS
PROANTHROPUS
SINANTHROPUS
PITHECANTHROPUS
PLIOZÄN
OBER & MITTEL
SIMIA
UNTER
PAIDOPITHEX
PALEOPITHECUS
GERMANICUS
BRANCOI
MIOZÄN
OBER & MITTEL
PLIOPITHECUS
PALEOPITHECUS
SIVAPITHECUS
PALEO-SIMIA
DRYOPITHECUS
GIGANTEUS
CAUTLEYI
PUNJABICUS
FRICKAE
CHINSIENSIS
PILGRIMI
FONTANI
DARWINI
UNTER
PROHYLOBATES
AFRICANUS
MOGHARENSIS
OLIGOZÄN
OBER & MITTEL
UNTER
PROPLIOPITHECUS
PARAPITHECUS
EOZÄN
UNBEKANNTE GEMEINSAME STAMMFORM

ABEL, 1934, p. 1

between gorilla and chimpanzee in his morphology by placing this trinity in a group apart from the other Anthropoids (Abel, 1934, pp. 1-2).

Franz Weidenreich (1873-1948), German, Apes, Giants and Man, 1946, p. 30.

Weidenreich's diagram of phylogenetic relationships approached a chart more closely than a tree. The grouping of fossil and living hominids according to their location in the evolutionary sequence was represented by vertical lines. Their geographical distribution into four groups was shown by horizontal lines. Cross lines indicated interchange of genes between populations. Weidenreich conceived of ten evolutionary phases (vertical divisions I-X), which were listed according to the "morphological age" of the fossil specimens. These were classified into three groups: Archanthropinae (Pithecanthropus-Sinanthropus), Paleoanthropinae (Neanderthal), Neoanthropinae ("recent man"). The empty spaces, ". . . reveal how little we know of the intermediate forms which must be expected from what the known types indicate" (Weidenreich, 1946, pp. 29-31).

The criterion for assessing the "morphological age" of the fossil specimens is development of the brain case, to which is related the nature of the cranial shape, thickness and musculature (Ibid., pp. 31-46). His horizontal differentiation of the human pedigree has gained the respectability of a name--the Polyphyletic School. Members of this cult see human evolution progressing independently in each corner of the world, but the final product being of the same genus and species--an amazing example of phylogenetic parallelism! This theory is similar to that of Klaatsch (1910), but Weidenreich saw all living hominids as members of a single species and interrelated in spite of regional variations, thus avoiding the difficulties that sprang up for his elder colleague (Dobzhansky, 1944, p. 260).

Ruggles Gates (1882-), British, Human Ancestry from a Genetical Point of View, 1948, pp. 56, 161.

The Siwalik Hills of India are regarded as an area of differentiation and dispersal of early hominids and pongids out of a parent Dryopithecine population. A similar center is in Africa where pre-hominids evolved from Australopithecines whom Gates regards as regional variants of such Dryopithecine genera as Ramapithecus (Gates, 1948, pp. 53, 72). This isolation of pre-hominids in the Miocene-Pliocene period led to the evolution of two separate stocks:

> Meganthropus and Eoanthropus-Homo kanamensis stock, being at opposite ends of the scale in their skull characters and widely separated geographically, there is no reason to suppose that they had a common ancestor. They probably originated independently at the Dryopithecine level, just as the Australopithecines may have had a separate origin from other Hominidae (Ibid., p. 229).

On the basis of brow-ridge development, Gates defines a rugged-browed gorilloid strain and a smooth-browed orangoid strain in early man which crossed at the Neanderthal level. The absence of brow ridges in Europe before the Würm

PEDIGREE OF THE HOMINIDAE

	Phase	Horizontal Differentiations 1 Australian Group	2 Mongolian Group	3 African Group	4 Eurasian Group
Neoanthropinae	X Hos	Australian	Mongolian	South African	Eurasian
	IX Hof	Wadsak	Chookoutien [Upper cave]	Boskop	Cro-Magnon
Paleoanthropinae	VIII Pae	?	?	?	Skhul [Palestine]
	VII Pan	?	?	?	Tabun [Palestine]
	VI Par	?	?	Paleoanthropus rhodesiensis	
Archanthropinae	V Pis	Pithecanthropus soloensis		?	?
	IV Pie	Pithecanthropus erectus	Sinanthropus pekinensis	?	?
	III Pir	Pithecanthropus robustus		?	?
	II Mes	Meganthropus		?	?
	I Gig		Gigantopithecus	?	?
	—				

Weidenreich, 1948, p. 30.

Glaciation, i.e. before the arrival of the gorilloid Neanderthals, and their continued absence in southeastern Asia, ancient home of the orang-utan, explains an orangoid strain in Eoanthropus which is not a characteristic of Pithecanthropus and his descendants who are derived from the gorilloid strain (Ibid., p. 6):

> . . . beginning with Eoanthropus in the orangoid series and Neanderthal man in the gorilloid series we have traced descent to modern Homo partly through crossing of different human species and genera, partly through influx of human types from other continents and partly through multalineal changes in particular races and species (Ibid., p. 274).

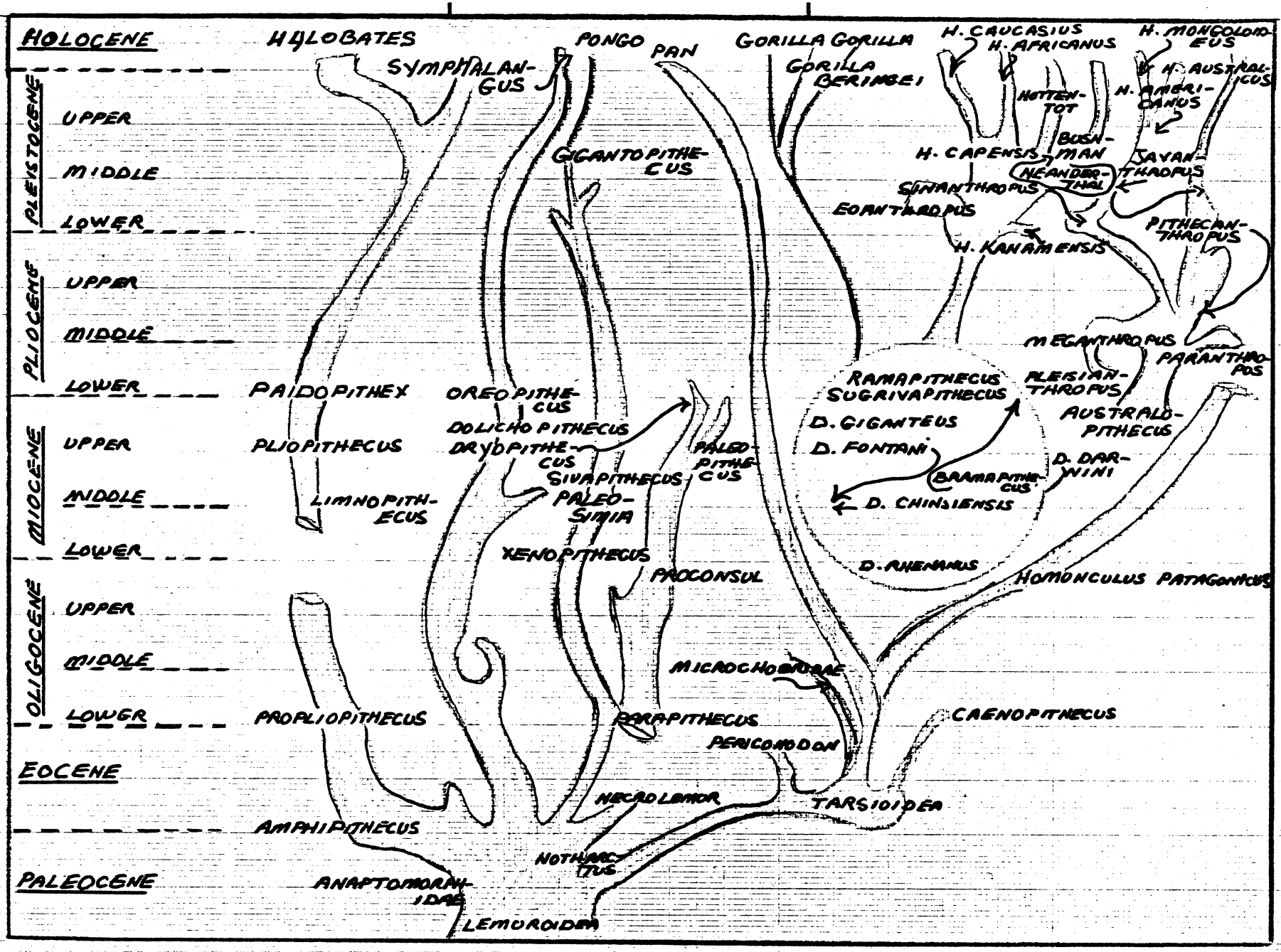
All these pre-hominid varieties are considered to be interfertile, but Gates continues to speak of them as differing on species and even genus level (Ibid., p. 114).

Earnest A. Hooton (1887-1954), American, Up From the Ape, 1949, p. 411.

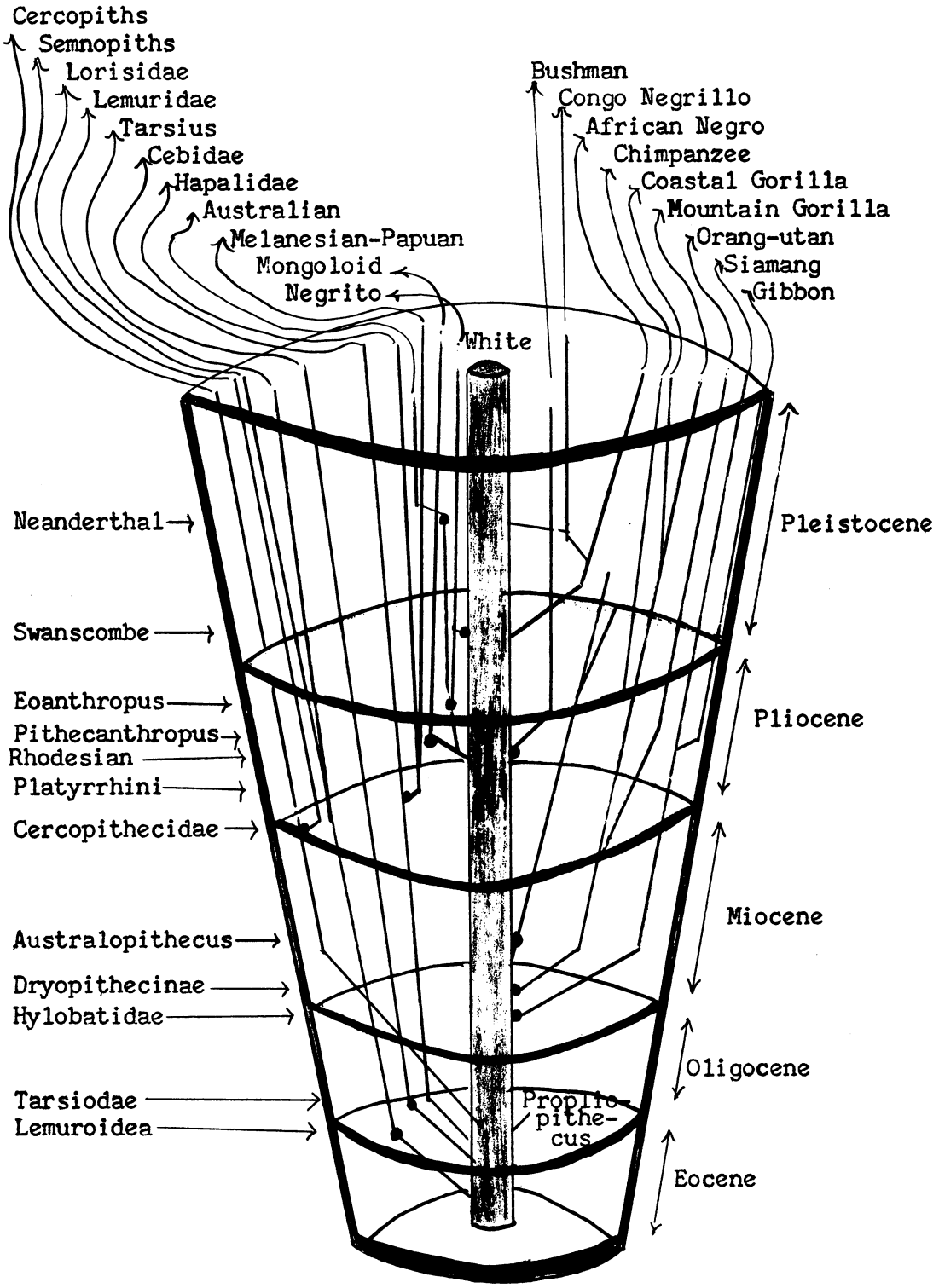
The common ancestor to living pongids and hominids came into being during the Miocene. From this main trunk diverged the Dryopithecinae, ancestor of the pongids, and the Australopithecinae, an extinct branch which had originated higher on the main trunk and had pursued an evolutionary course that brought them close to the progenitors of early hominids. Hooton regarded the main trunk as leading directly to modern Homo sapiens, indeed to a "Basic White" race! Hence the Pithecanthropus-Sinanthropus-Neanderthal forms are relegated to side branches. He accepts Weidenreich's view that Australians have descended from a Pithecanthropus-Solo-Wadjak line. The ancestor of the Neanderthals becomes Sinanthropus. As for living races, Hooton was sure only of the ancestry of his "Basic White" line which could be traced back to Eoanthropus. He did not follow Weidenreich, however, in relating Mongoloids to Sinanthropus. Rather, for lack of good fossil ancestors for Negroids and Mongoloids these racial groups are placed as offshoots from the main trunk at the Eoanthropus level (Hooton, 1949, pp. 410-414). No limb of the tree is unattached to other limbs, this winding about of branches representing crossings of various races. Gigantopithecus and Meganthropus are omitted, but Hooton would place them below Pithecanthropus, if they can be proven to be hominids (Ibid., p. 421). There is no time scale on the tree, but a section on "The Stages and Status of Human Evolution" appears elsewhere in the text (Ibid., pp. 694-697).

George G. Simpson (1902-), American, The Meaning of Evolution, 1949, p. 91.

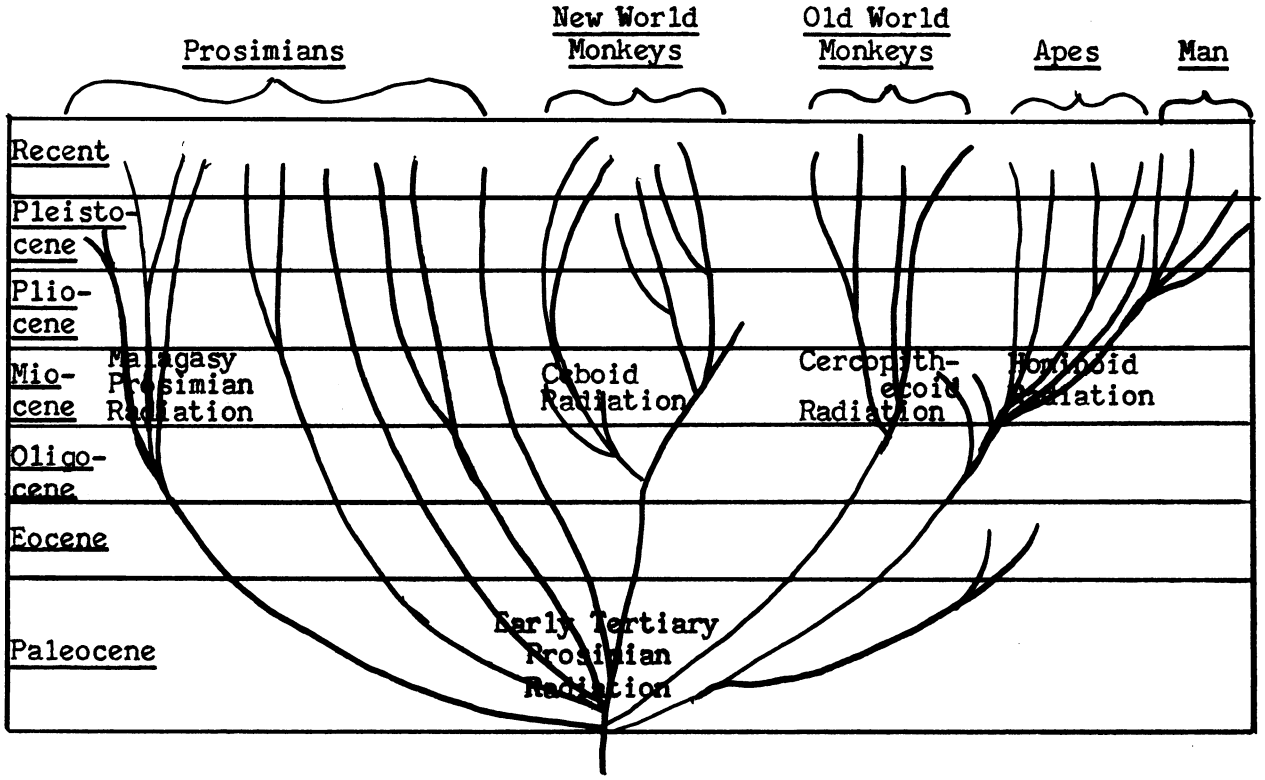
Simpson's diagram is closer to the conformation of a bush rather than of a tree. Hominoid radiation reached its climax in the Miocene. This was followed by a reduction of generic lines which might well have accompanied an actual increase in the number of animals (Simpson, 1949, pp. 92, 95). Simpson argued that the classic division of Anthropoidea into Platyrrhini and Catarrhini should be replaced in favor of a three-fold division: Ceboidea, Cercopithecoidea, Hominoidea. All may be of equal antiquity and the latter two groups not an isolated unit (Simpson, 1945, p. 184).



GATES, 1948, p. 56



Hooton, 1949, p. 411.



Simpson, 1949, p. 91

The line leading to man pre-empted the way of life of the Australopithecines and others at different times in the Pliocene-Pleistocene (Simpson, 1949, pp. 95-96). Simpson is most concerned with primate evolution at this level, but refrains from speculating on the interrelationships of early hominid forms.

Camille Arambourg (1885-), French, La Genèse de L'Humanité, 1952, p. 131.

A Catarrhine stock is represented as the progenitor of all living primates. Parapithecus and Propliopithecus are considered to be sufficiently generalized morphologically to lie at a point of differentiation from Catarrhine stock during Eocene-Oligocene period. The Homidae early separated from a group of Anthropoidea during the Miocene-Pliocene (Arambourg, 1952, pp. 123-125).

Arambourg believed in a uniserial Phylogenetic Tree. Homo sapiens were derived from Neanderthals as exemplified by the Mount Carmel finds. He did not accept the views of the Pre-sapiens School (Ibid., p. 129). Associated with the phylogenetic scheme is a scale of psychic progress which Arambourg had conceived on the typological sequences of tools: "Ainsi done, chaque étape du progrès technique est etraitement lié a étape du perfectionnement cérébral" (Ibid., p. 21).

L. S. Palmer (1891-), British, Man's Journey Through Time, 1957, pp. 19, 145.

The charts that Palmer devised had as their aim

> . . . to collect, to measure, and to arrange chronologically enough evidence, physical and cultural, to enable man's development to be seen graphically and thus to be more clearly appreciated than is possible from qualitative descriptions of his physical appearance and cultural status (Palmer, 1957, p. 20).

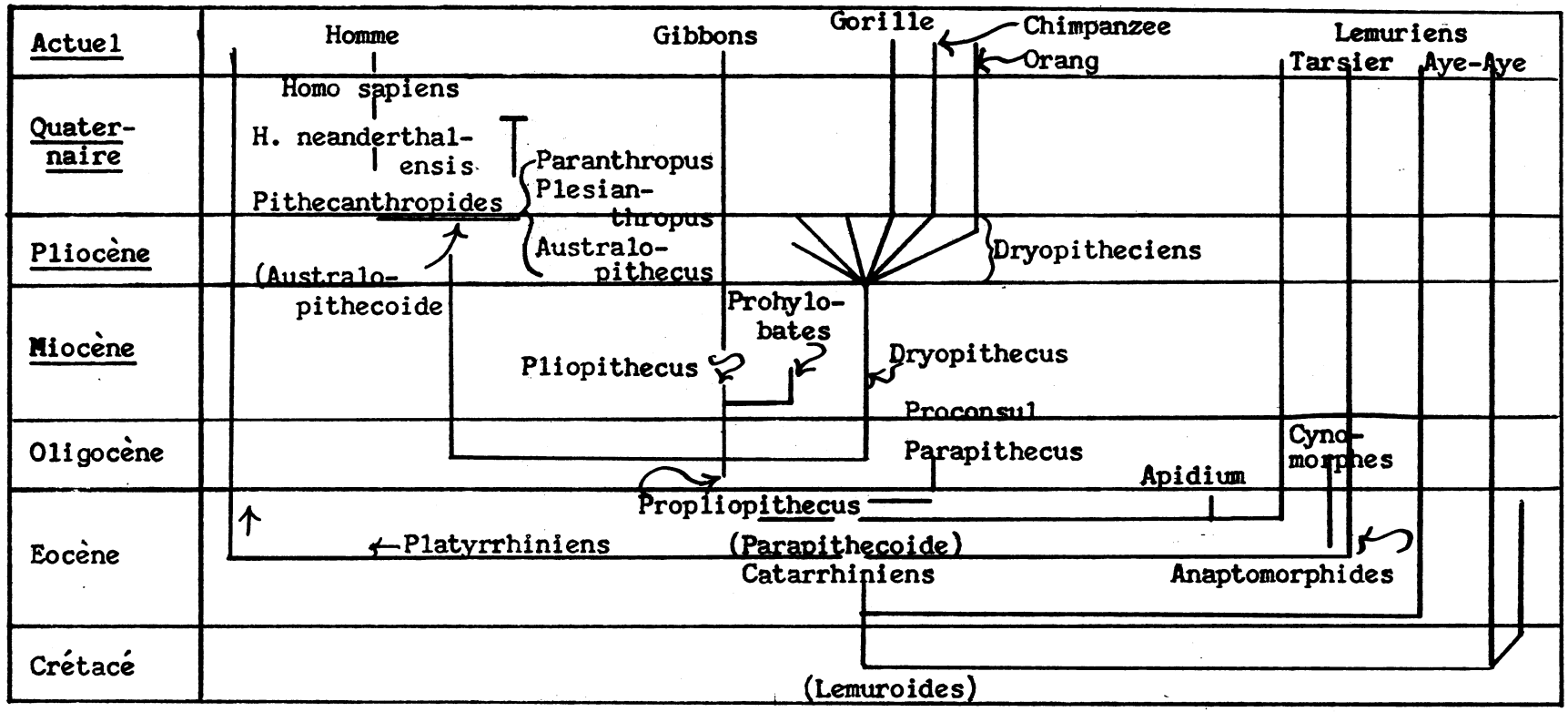
This ambitious if not oversimplified kind of problem is considered here because of its unique handling of fossil evidence. The trees were based upon metric data and the connection by lines of the series of points which relate to different fossil specimens did not imply a genetic relationship between the specimens. Because the graphs are initially (for remote times) only single lines the ideas of orthogenesis or common origin are not implied, but Palmer favors an orang-Asiatic line and a gorilla-African line of evolutionary development in these separate areas (Ibid., p. 146). Reproduced here is his Phylogenetic Tree which is based upon Simpson (1955).

Summary

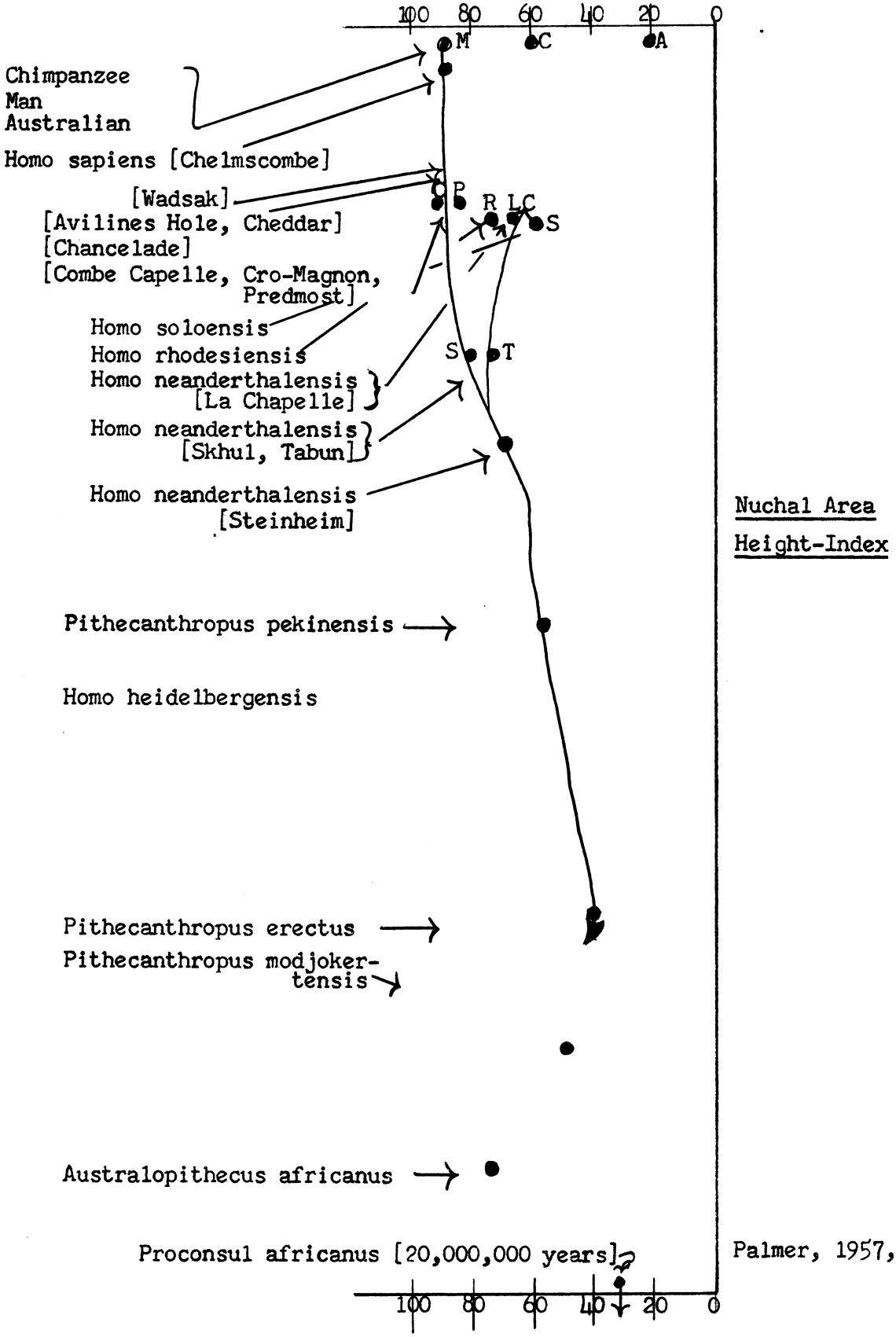
The aim of this paper has been to discern the nature of the Phylogenetic Tree and to examine the use which this diagrammatic tool has undergone in the hands of particular students of human evolution.

This thesis is treated in the three preceding sections of the paper:

1. A preface which defines in detail the limits of the problem.



Arambourg, 1952, p. 131.



Palmer, 1957, p. 144

2. Part I which discusses the historical development of phylogenetic theory with respect to the increasing amount of fossil hominid material during three time periods: 1856-1890, 1891-1924, 1925-1958.

3. Part II which analyzes and reproduces the Phylogenetic Trees of German, French, British and American scholars whose diagrams are representative of particular schools of thought.

Following the Summary and Conclusion of the paper is an Appendix:

1. Section A discusses the major historical issues of taxonomy prior to the Darwinian period with the view that while these concepts were outside the problems of human phylogeny they were in part influential in establishing a basis for present-day evolutionary theory.

2. Section B contains the taxonomic tables of the Hominidae as conceived by some pre-Darwinian classifiers.

Conclusion

From the foregoing data two trends of phylogenetic theory are perceptible:

1. The course of human evolution has been steadily divergent, producing a Phylogenetic Tree of many branches. Known fossils represent a few of these branches, but only rarely are they depicted on the main trunk. All these branches are withered, save for the one supporting *Homo sapiens* and the living anthropoids. The extremists of this view advocate uniserial evolution; the moderates hold a wide range of opinions as to which particular fossil forms had their loci on the main human trunk and which were ineffective aberrations branching away from it.

2. The process of evolution has run a parallel course among different strains of human species (or races) in different regions of the world. The speeds through which each population independently underwent the evolutionary stages varied, but today all men are of the same genus (and species). The extremists of the Polyphyletic School hold that races are on a species level: the moderates regard no more than one human species as having existed at any given time period: "All the phylogenetic transformations in Hominidae were always taking place within a single genetic system, a species consisting of geographically but not reproductively isolated races" (Dobzhansky, 1944, p. 262).

The problem of the placement of the Hominidae in relation to the larger matrix of living and fossil primates has been approached through three theories:

1. Man stands in close relationship to the Anthropoids, both together forming a common branch which has long been separated from the Cynomorphs who evolved from a basic Catarrhine stock (Abel, Smith, Arambourg, Keith, Gregory, Dubois).

2. The human group is an early autonomous ramification away from the mother branch of the various primate families.

a. Catarrhine branch (Darwin, Haeckel, Huxley).
b. Platyrrhine branch (Vogt, Ameghino).
c. Lemuroid branch (Cope).
d. Tarsiioid branch (Jones).

3. The human group has its place within the Anthropoid branch (Klaatsch).

With regard to the criteria which phylogenists have used in ascribing fossil finds to particular branches of the Phylogenetic Tree, a shift has occurred since the turn of the Century. The idea of an Archetype persisted from pre-Darwinian times and led some students of human evolution to base their classifications upon single morphological characteristics (Gregory used teeth, Owen used the brain, Haeckel used the placenta, Smith used brow-ridge development, etc.). With the expansion of the fossil record, taxonomists no longer regarded this Archetype as the reality of the class nor explained away morphological differences on the basis of environmental pressures. Rather, fossil material became viewed in terms of populations and the gene pool for a given group was recognized as the real focus for investigation. It was further realized that while comparative anatomy of modern man and living apes might render a gradational series of morphological types suggestive of an actual temporal sequence in evolution, any such system demanded validation by direct evidence from paleontology. Similarly uncertain would be the positioning of a fossil specimen in the Phylogenetic Tree on the basis of its "morphological age" since ancestor and descendant must appear in proper chronological sequence paleontologically. A combination of "primitive" and "modern" traits may appear in any phyletic line.

Associated with the problem of establishing particular or general criteria for genetic affinities between fossil materials--a problem true for any biotic form with which paleobiology might be concerned--is the specific difficulty of finding phylogenetic ties between fossil and living Hominidae. Construction of a Phylogenetic Tree for non-hominids is comparatively easy if the fossil and living forms are ample. Animal species are geographically circumscribed through adaptation to particular conditions of their ecology which are favorable for speciation if isolation is long and continued. Man, however, has always been capable of surviving under a variety of conditions. The resulting nomadism has hindered the rise of new human species since the Mid-Pleistocene. Some ancient populations have contributed more to the present world gene pool than others, but the notion that all fossil forms can be found among living populations is as unrealistic as the older view that there are races who have maintained their purity through time. Along with the racial crossing, modern phylogenists look to the processes of genetic drift and natural selection, but the peculiar problems involved in hominid development give these evolutionary features a limited significance, particularly for the time following man's possession of culture.

An additional problem lies in the taxonomic classification of the Hominidae. The flare for eighteenth century liberalism that led Linnaeus to lump the Hominidae with the other primates initiated the present difficulties of giving fossil forms a biologically significant nomenclature. Confusion has resulted from (a) a difference of taxonomic standards at different periods of time, (b) an exaggeration of every morphological peculiarity, and

(c) the general state of ignorance of some scholars about the rules of taxonomy. Hence, the kind of criteria that include the six hundred species of Drosophila within a single genus rank as an order among the primates. No doubt many of the morphological features now distinguishing fossil forms rest upon sex rather than species difference. Realization of these problems has encouraged phylogenists to reduce the taxonomic categories for the Hominidae and to regard the familiar fossil specimens with generic and/or specific titles as racial components of a single species. Man attained genus status when he reached a new adaptive plateau apart from other anthropoids.

The finding of abundant fossil material in Africa, particularly the hominid finds at Taungs and Broken Hill, caused scholars to regard this continent as the place of man's origin. Formerly, Asia was deemed the favorable center for hominid dispersal on the basis of discoveries in Java, China, and northern India.

Nationalism has played a wider part in the fate of Phylogenetic Trees than was recognizable from this brief outline. The ill favor that the Piltdown material received in Germany was matched only by the late acceptance of the Heidelberg mandible in France and England. Various fossil discoveries were omitted from Phylogenetic Trees, as observable above, because national biases were plaguing the taxonomist.

The advantages and defects of the Phylogenetic Tree which have been discussed above may best be summarized by von Koenigswald:

> The most vivid way of presenting relationships between allied forms from different geological periods is probably the much-praised and much-maligned family tree. It is an auxiliary--no more: its touching simplicity may all too easily blind us to the complexity of the interconnections. It must not be forgotten that in the family tree we bring together forms that lived in different regions, often in different climates, and which must certainly have unfolded at very different rates. In most genealogical tables the various forms are simply connected by a straight line, tending to create the illusory impression of rectilinear evolution. These lines should really be curved and this means, metaphorically speaking, that looking backwards we cannot see our forerunner who is hidden behind a bend: hence man all too readily gains the impression that he has always existed. . . (von Koenigswald, 1956, p. 19).

Appendix

Pre-Darwinian Taxonomy

The earliest systematizers of biotic phenomena were unconcerned with physiological and ecological distinctions: rather, their criteria for setting apart the different varieties of plants and animals were based upon economic usefulness, as exemplified by certain Assyrian tablets (Menant, 1880), by dietary taboos (Leviticus XI), and for a plethora of factors relating to the totemic and panthionic hierarchies. The Greek thinkers of the fifth century, B.C. were impressed by the continuity of living forms and the uninterrupted

merger in the Scala Natura of the inanimate with the divine. Thus Democritus conceived of all life arising from the primal slime with differences between forms being only a matter of degree (Sikes, 1914, p. 59). Plato included within this Chain of Being not only that phenemenon known to man, but all possible entities, the reflection of the real essences in the World of Ideas. This universe, once established, tolerated no transformations or extinctions of its parts. The qualities of perfection were completeness and immutability (Plato, Timaeus).

The mechanisms responsible for biological variation, operative at the time of Creation, were (1) spontaneous origin or (2) the act of a god. The ruling classes of Greece traced their lineage to the latter source, and speculation wavered as to the position of the citizenry as well as of the lower forms of plant and animal life within this classification. Archelaus favored a different classification in which man was set apart from the beasts at the time of Creation by virtue of his intellect (Ritter & Preller, 1898, p. 217). But it is to Aristotle that the idea of classification of animals on the basis of physiology and ecology is attributed. The criteria of rank in his plan for arranging all animals in a single graded Scala Natura according to their degree of "Perfection" are several, a particular criterion being adopted as the occasion demanded. Among the major determinants: (1) the presence of blood or a nutritive fluid analogous to it (Sanguinous and Bloodless animals); (2) body size; (3) longevity; (4) temperature; (5) brain size; (6) condition of the embryo; (7) bodily attitude (erect posture in man and quadrupedal posture for lower forms); (8) degree of anatomical complexity; (9) presence of lungs which, with the brain, regulate the heat emanating from the blood. Souls, which are the seat of Aristotle's teleological mechanism, differ in their possession and/or degree of development for each of these criteria, and hence vary in their status of perfection (Ogle, 1882, pp. XXII-XXVI). Aside from the philosophical aspects of this problem, Aristotle recognized the practical value of developing a logical nomenclature for zoology, and he attempted to refer to groups of like-animals by collective names, his criterion here being somewhat different from those just described--animals with manes, hoofed and nailed animals, etc. Aristotle, borrowing from Plato, used only two systematical terms: "eidos," or species, and "genos," the family (Gregory, 1910, p. 10).

By selecting these various groupings out of their contexts, the scholars of the Middle Ages established a super-classification which Aristotle had never anticipated; and, with the dawn of the Renaissance, this compilation of systems attained the status of ecclesiastical dogma (Whewell, 1847, pp. 382-383). More intimately Aristotelian are two tenets of seventeenth century natural history: (1) the idea of a hierarchy of beings; (2) the postulate that between natural phenomena the transitions are insensible and quasi-continuous (Lovejoy, 1936, p. 61). But the more elaborate the groupings of terms became in post-Classical times, the more abstract became the results: the higher one climbed the Ladder of Perfection, the further away one came from the basic tenets of classification.

The impetus for a revision and expansion of the Aristotelian system came from the increasing knowledge of plants used for pharmacological purposes in the late Middle Ages. The botanical data compiled by the younger Pliny from works of Theophrastus and other systematists proved inadequate in the

encompassment of flora in Western Europe, and by the fifteenth century new systematists appeared. Of these, Andreas Caesalpinus of Arezzo (1519-1603) assigned monomial titles to ten great classes of plants based upon number, position, and configuration of their reproductive parts and so made obsolete the earlier used descriptive phrases of classification (Nordenskiold; 1929; pp. 192-194). Caesalpinus' system, the first taxonomic study based upon a comparative study of form, established botany as an independent science which, except for stimulating the older but less advanced discipline of zoology, proceeded to follow an original course in the history of biology.

The success of the improved botanical techniques, assisted by the high frequency of known plant species and the definite character of their numerical relationships, was carried over into zoology by John Ray (1627-1705). With the collected data from Wotton (1492-1555), who had been concerned with the ecological setting of animals (Gregory, 1910, pp. 14-15), from Conrad Gesner's (1516-1565) illustrations and descriptions (Brooks, 1895), and from his early training in botany, Ray produced the Synopsis (1693). Like Aristotle, he was concerned with the lack of an existing terminology and he similarly distinguished between a genus or substantive name and the specific or modifying terms included within its scope. The prime criterion for this dichotomous system was the nature of the feet--hoofed, clawed, and nailed--but some of Aristotle's standards were retained as well (Whewell, 1847, pp. 312-320). Linnaeus found Ray's work basic to his own zoological scheme which did not rapidly replace it.

In all the classifications thus far described, man is regarded as the link between the animal and spiritual realms--a Homo duplex. Not only could the Anthropoidea stand on a step of the ladder close to man, but a multitude of as yet undiscovered ape-men were regarded as filling the space between these levels. Yet man was distinct from these parodies of his nature and no transformation between species was admissible in an immutable system. Of these anthropoids known to early classifiers, the macaque and Semnopithecus were most familiar, the only ape being the chimpanzee which Hanno of Carthage encountered at Sierra Leone (470 B.C.) (Hartman, 1904, p. 1; Zaborowski, 1880, p. 544). Aristotle distinguishes three types of primates, all from North Africa: (1) Pithecus, tailless ape; (2) Cebus, tailed monkey; (3) Cynocephalus, tailed and dog-faced monkey (baboon) (Aristotle, De Animalibus Historia, C, VIII). The identification of particular species with these classes of primates is highly speculative, for in antiquity the primates were referred to as satyrs and a name may be applied to several different forms. The Middle Ages saw no advance in classification of primates until after 1590, when explorers discovered the gorilla and other primate forms in West Africa. The orang-utan and gibbon were known after 1650, when some animals were brought alive to Europe. It was not until well after the turn of the eighteenth century that the confusion between the true anthropoid apes, hybrid "wild man-apes," satyrs, and hominids could be resolved (Wendt, 1956, pp. 75-76). Then accurate descriptions of anatomical structure could be made available.

When in the seventeenth century the Book of Genesis, and thereby the concept of Special Creation, attained the status of church dogma as a result of the conservatism of the Reformation and its Catholic counter-reform, a classification of life such as that offered by Linnaeus in 1735 was welcomed as a graphic illustration of the origin and immutability of each species (Osborn,

1929, pp. 11-12; Eiseley, 1958, p. 24). However, the ideas of Linnaeus were anything but static, and the twelve editions of the Systema Naturae, which ranged from an original dozen to twenty-four hundred pages within the years 1735 to 1766, were the stepping stones across the seas of Aristotelian Scholasticism to the headlands of Darwinian biology. To trace this development of ideas is essential for an understanding of modern phylogenetic theory.

In the first editions of the Systema Naturae, Linnaeus (1707-1778) sought to describe a natural system of groupings of animals sharing similar traits and affirmed that "We count as many species as have been created from the beginning," and all species are descended from an original pair of that species (Nordenskiold, 1928, p. 210). Drawing from the works of Ray and Gesner and from traveler's accounts he borrowed generic names for a monomial system, but with the tenth edition of his work (1753) a binomial taxonomy was substituted, the short descriptive ordinal word serving as a species designation. Linnaeus used a wider range of taxonomic criteria than his predecessors and these were based upon activity of the animal in its environment, internal organ structure, superficial features, dentition (from Ray), mode of sustenance, and type of clavicle (the single osteological feature used by Linnaeus in ordinal definitions). He also recognized the value of varieties or subspecies, the limbo into which he poured the remainder of Ray's 18,000 species after selecting some 7,300 for a species status of his own (Gregory, 1910, pp. 31, 34; Glass, 1959, p. 145).

The tenth edition of the Systema Naturae had been in circulation for only six years before Linnaeus presented his views on the mutability of species. This concept, the keystone of phylogenetic theory, had been the concern of Sprenger, an apothecary of Heidelberg, in 1590 (Glass, 1959, p. 147), but the earliest written treatise was in Sir Walter Raleigh's five-volume work on world history (1603-1616). Raleigh decided that only the animals of the Old World could have been rescued from the Flood and these survivors later migrated to America where they underwent morphological change (Wendt, 1956, p. 26). Matthew Hale (1609-1676), Lord Chief Justice of England in 1660, to alleviate the tonnage of the Ark, suggested that only rudimentary forms of life had been initially created, later forms arising from this nucleus of breeding stock. This same idea came to Linnaeus by way of the writings of Marchant of Paris who in 1719 saw this nucleus as the genera of the varieties derived from interbreeding (Glass, 1959, p. 147). Quite apart from these literary sources, Linnaeus might well have arrived at an independent conviction of the mutability of species on the basis of his own observations of morphological affinities between certain species and from knowledge of breeding experiments. The original dictum that no new species can arise was omitted in the final edition of the Systema Naturae after the classifier recognized the plant "Peloria" as a mutation from the familiar "Linarea." Henceforth he regarded only the genera as originally created and immutable, with new species developing from crossings of genera: "Life originated from a single initial point from which creation began and gradually spread" (Wendt, 1956, pp. 70, 72). But this concept, first presented in Plant Metamorphosis (1759) went unheralded for a full century until reworked and reintroduced by Darwin.

For the study of human phylogeny, the major contribution of Linnaeus has been expressed by Gregory:

> The primates were . . . regarded as chiefs of the graded hierarchy of terrestrial beings, and consequently, as in nearly all subsequent schemes down to the Darwinian epoch, head the classical legions of creatures. This placing of mankind under the order Primates was surely another instance of Linne's genius in surmising the true affinities of puzzling animals. It led the way to the modern generalization that man is knit by ties of blood, kinship to the Primates and more remotely to the whole organic world (Gregory, 1910, p. 29).

This placement of Homo within the Primate Order first appeared in the tenth edition of the classification as a result of Linnaeus' greater familiarity with Perrault's work on primate anatomy (Perrault, 1671-1676). In the earlier editions Homo was listed as Anthropomorpha. The primates of which Linnaeus was aware included the chimpanzee, mandrill, and lemur plus four races of Homo. To the latter genus were added feral creatures and abnormals, and a fourth genus--Vespertillo (bat)--was included. Friedrick Martinus of Berlin ramified this scheme by defining two groups of "wild" Homo (Wendt, 1956, pp. 76-77). Criteria for primate status included,

> Inferior front teeth IV, parallel, laniary teeth solitary (a single pair above and below). Mammae pectoral, one pair. Anterior extremities are hands. The arms separated by clavicles. The gait usually on all fours. They climb trees and pluck the fruit thereof (Gregory, 1910, p. 30).

Homo was intergraded so intimately into this classification that Linnaeus could question, "Show me a generic character by which to distinguish Man and Ape; I myself know of none" (Bryson, 1945, p. 60).

While Linnaeus never formulated a theory of biology, he did perceive the basic principles of the phylogenetic process. He was aware by 1779 that "Species are the work of time" (Glass, 1959, p. 150) and was certain that the gaps in his classification would be covered as new animals in remote parts of the world were found, but toward the fossil record, although inconsiderable then by present standards, Linnaeus had no interest and inserted Fossilia into the mineral kingdom, "Regnum lapideum." Thus paleontology was relegated to a study of stones and "zooliths."

The century between the tenth edition of the Systema Naturae (1759) and the first appearance of Darwin's Origin of the Species (1859) saw the metamorphosis of taxonomy from a classification of immutable species to an incipient phylogenetic arborization. This change was due to the following factors which will receive further comment in the text:

1. The increase in the paleontological record.

2. The coming into maturity of comparative anatomy and zoology.

3. The popularization of "Natural Philosophy."

4. The rejuvenation of the evolutionary concept from Antiquity to scientific respectability.

5. A recognition of the superficiality of the taxonomic systems and the search for hidden affinities between the levels of biotic organization.

The torch which had been lit at Uppsala did not pass immediately into the hands of the Parisian naturalists. Buffon (1707-1778) saw the Systema Naturae as artificial and he set up his own classification on the basis of Daubenton's anatomical labors which he utilized in the Histoire naturelle des animaux (1753). Buffon set man apart from the other primates only on the basis of his "physic nature" while biologically recognizing man as a part of nature--a Homo duplex (Nordenskiold, 1928, p. 226). He seems to have glimpsed the necessity of filling in the gaps in the taxonomic record with "ancestral forms," but such extinct or undiscovered links were purely speculative and living animal forms remained the key to understanding morphological change (Barr, 1807, Vol. 9, p. 137).

In Germany a third taxonomic classification based on Linnaeus and Ray had a vogue. Blumenbach (1741-1811) set man apart from his primate relatives on the basis of morphology alone. Of the dozen distinctive features he lists, the use of two hands is most striking and thus Homo is set into a genus of his own--Bimana (Inermis of earlier editions)--apart from the quadrumanal primates. Human races are regarded as synonymous with varieties of domesticated animals, and corrections are made in Linnaeus' system respecting the popular names for the apes and the removal of the bats from the Primates into an order of their own--Chiroptera (Blumenbach, 1825). The original human pair was of the Caucasian race and other varieties due to the degeneration from climatic fluctuations. With the assistance of Pennant (1726-1793), Blumenbach arranged the non-human living forms in a gradation representative of natural succession to be explained by parallelisms of similar adaptive needs.

Based on Blumenbach's work, Cuvier (1769-1832) and Geoffrey Saint-Hilaire (1772-1844) published a classification of mammals, but in spite of Cuvier's knowledge of taxonomy, comparative anatomy, and paleontology, no successful wedding of these disciplines was attempted in the Lecons d' Anatomie (Cuvier, 1805), his most comprehensive work. The ideas which Blumenbach had engendered concerning the role of analogous adaptations among species were now taken up by de Blainville (1777-1850). He saw that hidden bonds of affinity joined dissimilar animals, and until taxonomy lost its artificiality the links could not be examined. This concern for adaptational similarities opened the way for explaining morphological similarities by (1) common descent and (2) parallelism and convergence. De Blainville set up a classification based upon similarities of adaptation--groups adapted "pour le vol," "pour nager," etc. (De Blainville, 1817; see Gregory, 1910).

From the ranks of the "philosophical zoologists" or "natural philosophical zoologists" or "natural philosophers" arose classifications based upon homological resemblances of particular mammal organs. The most famous example is the argument as to whether man lacks an os maxillae and, if so, how it places him apart from the animal kingdom. The question was first raised by Jacobus Sylvius (1400-1500) in the early sixteenth century and revived by von Camper (1722-1789) who had found the bone present in a dissected orang-utan. The question was finally settled by Felix Vicq d'Azyr (1748-1794) and Goethe (1749-1832) (Wendt, 1956, p. 77). Owen (1771-1858), an anti-evolutionist, speculated upon a common "Archetype" for all animals to which the homologies of various animals are referred (Nordenskiold, 1929, p. 416).

It is within this matrix of numerous artificial classifications and incipient evolutionary theories that the early phylogenetic trees first appear. Two schemes were published within the same year--1766--but independent of one another--the "Arbre geneologique" of Duchesne (1747-1827) (Duchesne, 1766) and the pictorial representation of zoophytes with ascending forms sent to Blumenbach by Pallas (1741-1811) (Wendt, 1956, p. 173). It is to Lamarck (1744-1829), however, that the earliest discussion of phylogenetic trees may be attributed. In the Recherches sur l'organisation des corps vivant (1802), Lamarck argues for a linear series of species or genera with shaded gradations and "Lateral ramifications in many, the extremities of which are truly isolated points" (Lamarck, 1802, pp. 40-41). Seven years later in the Philosophie zoologique, he conceived of a tree of life not as radiating from a single central stem, but as a system of branches coming from the very roots and ramifying into finer and finer stems. When Lamarck realized that many animal forms had become extinct he knew that phylogeny was possible:

> The existing animals. . . form a branching series irregularly gradated, the gaps having been filled by lost forms. It follows that the species which terminates each branch of the series are related, upon one side at least, with others which shade into them (Lamarck, 1809, Vol. I, Chap. 3).

In harmony with this view that the inheritance of acquired characteristics is the mechanism of evolution, Lamarck believed that apes could be "improved" through proper training, since man became as he is today through habit. However, he accepted spontaneous generation of lower animal forms and argued that no species could become extinct, fossils, whether known or not yet discovered, being ancestral to the transformed species now existing (Nordenskiold, 1928, pp. 324, 326). Lamarck was a Deist and visualized the Ladder of Being as an escalator--emergent evolution with persistence of simple life forms with the complex (Eiseley, 1958, p. 50).

Aside from biologists and natural historians, support of phylogenetic theories came from the camps of the "Natural Philosophers," the title of those writers primarily occupied with assimilating Newton and popularizing his system, but also concerned with deistic views of discovering a Divine Process in nature. In Germany, Kant (1724-1804) and Schopenhauer (1788-1860) were most influential. The former described a Chain of Being ranging from mosses to man with polyps standing at the crossroads of plant and animal. Alterations occurred through changes in environmental conditions:

> It is possible for a chimpanzee or an orang-utan, by perfecting its organs, to change at some future date into a human being. Radical alterations in natural conditions may force the ape to walk upright, accustom its hands to the use of tools, and learn to talk (Wendt, 1956, p. 141).

Schopenhauer saw change occurring through mutation, thus disregarding the maxim that "Nature makes no leaps": "We must imagine the first human beings of having been born in Asia of orang-utans and in Africa of chimpanzees, but not born as apes but as full-fledged human beings" (Ibid., p. 142).

The concepts of environmental determinism and mutation were wed in Robert Chambers' Vestiges of Creation (1844), one of the strongest influences

upon Darwin along with Lamarck, Malthus (1766-1834) and Lyell (1799-1875). Chambers believed that there were several distinct foci of organic production throughout the earth wherein new forms of class level or above are constantly rising as a result of environmental pressures and minute inappreciable causes. One quality of development was the rule and some geographical areas had forms of life more advanced than others (Chambers, 1887, pp. 193-194).

Until the theory of evolution could be supported by the concept of natural selection, i.e., until species were conceived as mutable and subjective to a uniform mechanism of biotic change, phylogenetic trees were divorced from ideas about: (a) descent of species through common ancestors, (b) a correlated time scale. Such lists were surely classificatory and based upon comparative anatomy. The pre-Darwinian period had developed a scientific taxonomy and hesitantly admitted the mutability of species, but is set apart from the events of the Darwinian and post-Darwinian periods by its lack of phylogenetic theory--the idea that species descended from one another and shared certain common ancestors in the past.

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