are not known with sufficient precision. The availability of facilities for rapid spectrochemical analysis is desirable but not essential. One can use the "single-pulse" technique.

In this article I have made only passing reference to many interesting problems now in process of solution and to several which remain to be investigated.

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Some Fallacies in the Study of Hominid Phylogeny

Poor taxonomic practice and inattention to past faunal distribution have obscured the study of man's origins.

Elwyn L. Simons

The century-long search for documentation of the fossil record of man's ancestry, which was particularly stimulated by publication of Darwin's *Origin of Species* in 1859, has by now brought in relatively abundant evidence concerning the major stages of man's lineage during the Pleistocene epoch. Accelerated discovery during the past few years confirms the view that the mainstream of human evolution in Pleistocene times evidently passed through a species of *Australopithecus* and then through *Homo erectus* and men of Neanderthaloid type to the modern varieties of *Homo sapiens* (*1*). These comparatively new findings have shifted fundamental research somewhat away from the *Australopithecus-Homo sapiens* lineage, which most students consider a plausible sequence, toward the problem of the nature and distribution of pre-*Australopithecus* hominids and hominoids (*2*). It is in this area that all new discoveries of the major stages in human phylogeny will come. Generally speaking, study of the Pleistocene section of human phylogeny has been carried out by anatomists and anthropologists, while the Miocene-Pliocene portion of the story has been investigated mainly by paleontologists. There have been, and perhaps there will continue to be, good reasons for this dichotomy. The study of Tertiary Mammalia (including nonhuman Primates) requires a more extensive background in stratigraphy, in field methods, and particularly in comparative osteology and mammalian taxonomy than is often possessed by students of man. Another factor has slowed progress in this area—the idea, expressed by some vertebrate paleontologists, that the evolution of higher Primates, and of man in particular, is too controversial

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and confused a subject to be worth much serious attention. If this view remains common among those best equipped to interpret fossil species, such lack of interest will only prolong the controversy.

In spite of the fact that there are almost no members of the Dryopithecinae of Miocene-Pliocene age for which reasonably comprehensive osteological remains are known, the actual number of specimens of this period that have been discovered is considerable (about 550), and the geographic range of the specimens is extensive. Moreover, advances in geochronometric dating techniques (potassium-argon analysis in particular) now, or shortly, will enable us to make a far more accurate temporal arrangement of man's pre-Pleistocene relatives than we have had. Many of these relatives fall taxonomically within the pongid subfamily Dryopithecinae. Although the fossil record for most dryopithecines is scanty, restudy of this osteologically limited material has now become imperative, because it is adequate to clarify the evolutionary succession of pongids and hominids.

I wish to state initially that I have carefully examined the view that *Proconsul*, from the East African Miocene, should be placed in a different subfamily from Eurasian dryopithecines and have found it unconvincing. Actually, there is hardly any morphological basis for separating Dryopithecinae (*Dryopithecus, Proconsul, Sivapithecus,* and related genera) from Ponginae (*Pongo, Pan, Gorilla*). Through the proper application of modern taxonomic principles, even without recovery of specimens more complete than those we now have, much more can be said about evolutionary relationships among the so-called dryopithecines than has been said to date. Dobzhansky (*3*) recently summed up the pertinence of good taxonomy as it applies to fossil man. His point is equally relevant to the taxonomy of earlier hominoids.

"Does it really matter what Latin name one bestows on a fossil? Unfortunately it does. It flatters the discoverer's ego to have found a new hominid genus, or at least a new species, rather than a mere new race. But generic and specific names are not just arbitrary labels; they imply a biological status. Living men constitute a single species: *Homo sapiens.* Now, *Homo sapiens* can be descended from only one ancestral species living at any given time in the past. To be sure, some plant species arise from the hybridization of two ancestral species, followed by a doubling of the complement of chromosomes, but it is most unlikely that mankind could have arisen by such a process. It follows, then, that if two or several hominid species lived at a given time in the past, only one of them can possibly be our ancestor. All other species must be assumed to have died out without leaving descendants."

Undoubtedly a much more lucid picture of the Tertiary antecedents of man could be drawn on the basis of existing evidence were it not for the questionable nomenclatural practices of past years. Clearly, and regrettably, the taxonomic significance of the new systematics has been slower in gaining wide acceptance among anthropologists and paleontologists than among most biologists studying modern taxa. Of course, paleontologists have recognized for many years that the type individual of a fossil species is merely a specimen acquired through chance circumstances of fossilization and discovery from a population of variable organisms of which it may not even be a typical member. Types of fossil origin are thus chosen primarily as name-bearers for postulated species groups (*4*). Apparently it was less generally understood, until comparatively recently, that when one makes a specimen the type of a new species, or of a new genus and species, there is an obligation laid on the proposer of the new taxon to present a good deal of morphological or other evidence of probable genetic separation from any previously described species. This point applies particularly to Hominoidea, in which there is greater variability in dental pattern and relative tooth size than there is in many other mammal groups. Distinctions in dentition in a hominid specimen, sufficient to warrant designation of the specimen as the type for a new species, must be at least as great as the distinctions that occur between species of the closest living relatives of the fossil form.

Speciation

In order to understand what fossil species were and are, it is necessary to comprehend the processes of speciation and to be familiar with modern methods of species discrimination among living animals. Thus, in the case of the dryopithecines, in order to distinguish two fossil species of a given genus, one should be able to demonstrate that forms which are roughly contemporaneous show characters that fall outside the extreme range of morphological variability to be noted in comparable parts of all subspecies of present-day pongids, such as *Pan troglodytes* or *Gorilla gorilla.* High physical and dental variability in given species of man and apes has long been known (*5*), but it is clear that this has not been taken into account by the majority of past and recent describers of fossil hominoids. Beginning with Mayr (*6*) in 1950, or slightly earlier, several experienced taxonomists have drawn attention to the extreme oversplitting of the known varieties of Pleistocene hominids. Since the late 19th century this erroneous approach to taxonomy has produced approximately 30 genera and almost countless species. At the other extreme from this taxonomic prolixity stand such workers as Mayr and Dobzhansky, who, drawing on their knowledge of modern speciation, have adduced evidence for a single line of but a few species, successive through time, in this particular lineage (*7*). To alter their view it would only be necessary to demonstrate the occurrence of two distinguishable species of hominids in a single zone of one site, but, despite much discussion of possible contemporaneity, in my opinion such contemporaneity has not been satisfactorily established. There is fair morphological evidence that there were two species of *Australopithecus* (*A. africanus* and *A. robustus*), but their synchronous existence has not been confirmed by finds of both at the same level in one site. Although the concept of monophyletic hominid evolution during the Pleistocene is now widely accepted, certain fallacies continue to affect thinking on probable pre-Pleistocene forms in this subfamily.

In the discussion that follows I attempt to outline and to clarify some of these fallacies. Changes in the taxonomy of fossil hominoids are suggested, on the basis of my direct observation of relevant original materials in America, Europe, East Africa, and India during the past 10 years (*8*). Among those acquainted with the traditional atmosphere of controversy that has surrounded the question of hominid origins there is often some reluctance to set forth an up-to-date survey of the implications of recent research on the subject. Clearly, all the points made here cannot be extensively supported by documentary evidence in this brief review. Nevertheless, it seems advisable to set some of the newer conclusions before the public at this stage.

Oversplitting of Fossil Species

Apart from the widespread temptation to be the author of a new species or genus, there are three primary causes of the oversubdivision of many extinct taxa (in the case under consideration, fossil Pongidae and Hominidae). These are, (i) uncertainties resulting from incompleteness of the available fossils; (ii) doubts concerning the identity and relative age of species (whether two or more given "types" are time-successive or contemporaneous); and (iii) questions relative to the possible, or probable, existence in the past of ecologic barriers that could perhaps have brought about speciation between populations widely separated geographically.

In view of these and other sources of uncertainty, taxonomists of fossil Primates have generally sidestepped the question of reference of new finds to previously established species, maintaining that it is unwise to assign later discoveries to species named earlier when finds are not strictly comparable or when they consist only of fragments of the whole skeleton; they frequently describe as separate species specimens which appear to come from clearly different time horizons; and they usually draw specific or generic distinctions when materials are recovered from sites that are widely separated geographically, particularly if these sites are on different continents. With continued advances in the dating of past faunas by geochemical means, and with advances in paleogeography, it becomes increasingly possible to improve procedures and practices in the taxonomy of extinct Primates, and to resolve many of the above-mentioned problems.

Generic and specific distinctions of imperfectly known forms. In the past it has sometimes happened that a taxonomist proposing a new species or genus of fossil vertebrate has maintained that, although no characteristics that would, of themselves, warrant separation of the new fossil specimen (B) from a previously known type (A) could be observed, the recovery of more complete osteological data would show the forms concerned to be different. This sort of anticipation is poor scientific practice, and such an argument should never be used in an effort to distinguish a new taxon unless (i) there is clear evidence of a marked separation in time between the previously described species A and the putative "new" form B, or (ii) there is definite geological evidence of geographic or ecologic separation—for example, evidence of a seaway or a desert—which would greatly reduce or eliminate the possibility of morphologically similar specimens A and B being members of one widespread, variable, but interbreeding, population. Some students would not grant even these two exceptions but believe that morphological distinctions must be demonstrated. Generally, some small distinction occur as a result of individual variation and can be misused as evidence of species difference. Therefore it is best to rely mainly on differences which can be shown to be probable indicators of distinctly adapted, and consequently different, species.

Abundant data on Recent and late Tertiary mammals show that many of the larger species were, and are, distributed in more than one continent, particularly throughout Holarctica. Moreover, the belief that there were fairly close faunal ties between Africa and Eurasia during Miocene-Recent times has been confirmed by the recovery and description, during the past 3 years, of new samples of continental vertebrates of this period from Kenya, Tanganyika, and the Congo (*9*, *10*). Several of the mammals in these localities show close morphological similarity to Eurasian forms, and while many African species of the period do not show extra-African ties, the types which the two land masses have in common do show that increased intercommunication was possible. The fact that some stocks did not range outside Africa cannot offset the clear evidence that many of the same genera and even of the same species occurred in both Eurasia and Africa at this time.

Taxonomic uncertainty deriving from temporal differences. Many hominoid species were proposed in the past mainly on the strength of a posited time separation from a nearly identical but presumably earlier (or later) "species." Most of the "species" designated on this basis should be reinvestigated in an effort to determine their true temporal position and taxonomic affinities. A "new look" is needed because of recent improvements in the potassium-argon method of dating, and in other geochemical dating methods (*11*, *12*) which should ultimately enable students of past species to discuss them in terms of an absolute time scale. Like other kinds of scientific evidence, dates obtained by the potassium-argon method can of course be misapplied. For instance, it must be demonstrated that dated sediments come from (or bracket) the same zones as the faunas they are supposed to date. There are other well-known sources of error in geochemical dating, but in my experience the strongest criticisms of this method come from persons relatively unacquainted with the analytical techniques involved.

One example of the application of geochemical dating techniques to the study of fossil hominoids will suffice to show what wide application such information may have. Simons (*13*) has proposed that, on morphological grounds, the primitive gibbon-like genera *Pliopithecus* and *Limnopithecus* can no longer be considered distinguishable. Newly recovered materials of *Pliopithecus* [subgenus *Epipliopithecus*] from Miocene Vindobonian deposits of Europe are closely similar, both in dentition and in postcranial structure, to "*Limnopithecus*" from the Rusinga Island beds of Kenya, East Africa. The fauna associated with this East African primate was regarded, at the time of Hopwood's proposal that a genus "*Limnopithecus*" be established, as being of earliest Miocene age and, therefore, older than the European *Pliopithecus* materials. In his fullest discussion of the generic characteristics of "*Limnopithecus*," Hopwood (*14*) was able to list only a few slight features of distinction between the tooth rows, then known, of *Pliopithecus* and of "*Limnopithecus*." These are dental variations of a degree which have repeatedly been shown to occur even within members of one small population of such living pongids as *Pongo pygmaeus* and *Gorilla gorilla*. Hopwood further bolstered establishment of his new genus by remarking that additional bases for distinguishing the genera concerned "are the various ages of the deposits in which they are found and their widely separated localities." But he did comment, "apart from convenience neither reason [for placing the African species in a new genus] is particularly sound. . . ." The point I stress here is that taxonomic separations such as Hopwood proposed are not "convenient," for they create complexity where it does not exist.

Recently, Evernden and his associates (*12*) have reported a date of 14.9 ± 1.5 million years obtained by the potassium-argon technique from biotite samples of tufaceous sediments in the Rusinga Island series. Admittedly this is only a single datum, but if this sample is truly satisfactory for dating by the potassium-argon method, and if it does come from the same horizons as the "*Proconsul* fauna," it shows that the fauna which contains "*Limnopithecus*" *legetet* and "*L.*" *macinnesi* could be contemporary with the European Vindobonian materials. Nevertheless, more dating of this fauna will be necessary before we have proof that it is as young as this. If this younger age becomes established, species of "*Limnopithecus*" may well fall entirely within the known temporal distribution of European members of *Pliopithecus*. Evernden and his coworkers also state that the evidences from relative faunal dating suggest a middle or late, rather than an early, Miocene age for the Rusinga fossils. In my opinion this view is supported by close similarities between three other Rusinga primate species (which I discuss later) and forms which occur in the Siwalik deposits of India, of probable middle or late Miocene age.

Finally, it should be stressed that Hopwood did exhibit considerable foresight in recognizing the basic unsoundness of attempting to reinforce a taxonomic separation by the argument of possible (but not proved) temporal difference. The foregoing example, and others which could be noted, show the danger of using the temporal argument when separating closely similar fossil specimens taxonomically. Moreover, it has been demonstrated that many extant mammalian genera have time ranges greater than the entire Miocene epoch, as estimated at present. Numerous instances of genera with long time ranges could be adduced. For instance, the perissodactyl genera *Tapirus* and *Dicerorhinus* in all probability extend back to the early Miocene or late Oligocene, about 25 × 10^6 years ago; members of some genera of carnivores (*Ursus, Bassariscus, Lutra, Felis,* and others) have all been described from deposits of late Miocene or early Pliocene age (10 to 15 × 10^6 years ago). Of course, we do not know that any hominoid genera survived as long as the genera in these categories, but most hominoid genera probably endured for at least 3 to 7 million years without much change of form. Consequently, even if it were known that European and East African *Pliopithecus* differed in absolute age by 4 or 5 million years, taxonomic separation at the generic level could not safely be based on this fact alone.

Migration, paleogeography, and past restrictions of species ranges. One of the most widespread assumptions in the study of the antecedents of man is that at some early period (Miocene, Pliocene, or "Villafranchian," depending on the author concerned) the species ancestral to *Homo sapiens* was restricted to a comparatively small geographic area. This restriction is taken by many scientists to account for the supposed "failure" to find pre-Pleistocene human forerunners. Such an assumption may be referred to as the "Garden of Eden illusion." Insofar as this widespread view is held as a scientific theory by some persons interested in the evolutionary history of man, it appears to be based on analogy with the restricted ranges of various recent mammal species, particularly, in this case, of higher Primates with limited distributions, such as orangutan (*Pongo pygmaeus*) or mountain gorilla (*Gorilla g. beringei*).

Place of Man's Origin

Some people believe that the place of hominid or human origin has not been discovered; conjectures, by others, as to its location have followed shifting vogues. Thus, when the first materials of "*Meganthropus*" were recovered in Java from levels lower stratigraphically than those at which "*Pithecanthropus*" remains were recovered, many students favored the view that differentiation of the ancestral stock of mankind occurred in Southeast Asia. Later, with the realization that *Australopithecus* finds from the Transvaal were hominid remains, a case was made for initial hominid differentiation in South Africa (*15*). Now, new additions to our knowledge of early Hominidae, made in East Africa by Leakey and his associates, have shifted attention northward to that quadrant of the African continent.

It should be obvious that the oldest *known* localities of occurrence of human tools, or of given species of higher Primates, are probably not the first places where these technical developments or species arose. In order to report with confidence the exact regions of origin of the human species and of earliest cultural items, we would need 100 times the archeological and paleontological evidence that we now have, with absolute dates for all sites.

There are a number of possible reasons for the persistence of the "Garden of Eden" concept among scientists, but here I mention only a few of the misconceptions through which this point of view appears to have been initiated and sustained. Students who believe that ancestral species occurred in restricted areas may have in mind four well-known kinds of diffusion from local centers: (i) spreading of cultural items from specific places of invention; (ii) wandering of tribes, both historic and prehistoric, over great distances; (iii) spreading of advantageous gene mutations from individuals or local populations outward throughout an entire species population; and (iv) intercontinental faunal migrations across land bridges at various times in the past.

All these, and other, similar concepts, while pertinent in their own right, do not in my opinion validate the illusion that, through time, each species, as a unit, wanders widely from one region to another. Such a picture is particularly inaccurate in the case of Late Tertiary land-mammal species, such as species among the dryopithecines, whose main area of distribution was the tropical and warm-temperate portion of the Old World. Of course, given sufficient time, species ranges, particularly among the large Mammalia, do expand and contract, and do occasionally shift from one continent to another in response to environmental change. Nevertheless, movement of subpopulations is much greater than the range shifts of an entire species. Even within an evolving species lineage, time-successive species apparently do not appear from one of several populations of the antecedent species; in general, all populations of a single species tend to evolve together, the species changing as a whole because, as the environment changes, newly advantageous genes originating in various sections of the group spread through the species. Of course, if these streams of gene flow are broken for sufficiently long periods, speciation will ultimately occur. A single species, however, *is* a single species just because gene flow throughout all its members is (or recently has been) taking place.

Range of Large Mammal Species

Now, in applying these ideas to the evolution of large mammals in the Miocene-Recent period, primarily to mammals of the tropical and warm-temperate regions of Palearctica, certain points extremely relevant to the interpretation of dryopithecine evolution emerge. The first of these is illustrated in Fig. 1, which shows a hypothetical model of the range of a large mammal species-series at three periods in the earth's history. The diagram is given as an abstraction because limitations in the distribution of sites yielding fossil land mammals (limitations that result from erosion of sediments or from non-deposition) are such that exact species ranges for past forms cannot now be drawn (and probably never can be). Nevertheless, this is the sort of distribution which recovered fossils indicate was characteristic, during the period with which we are concerned, of certain species of groups such as elephants, hyenas, the big cats, and ruminants. In this context it should be pointed out that the early supposition that many surviving species of large mammals have diminished ranges owing primarily to climatic fluctuations during the Pleistocene and to the activity of human hunters has, by now, been abundantly confirmed. Two examples, taken from dozens, illustrate this point. The lion, *Felis leo*, is now extinct in Eurasia except for a few small surviving populations in India. However, 15,000 to 20,000 years ago, *Felis leo* occurred widely in Europe and the Near East and was, presumably, then abundant in the Indian subcontinent and perhaps even further east. Ewer (*16*) has reported fossil remains closely resembling *Felis tigris* (but from a mammal slightly larger than the largest of modern tigers) from Olduvai Gorge in Tanganyika. Today, of course, the tiger exists only in Asia.

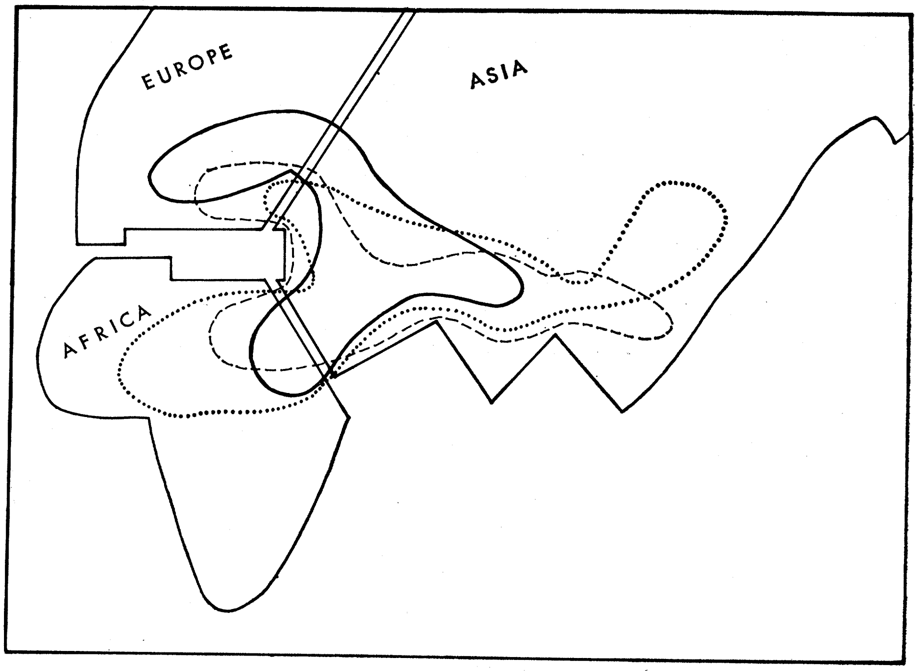

Fig. 1. Three species ranges, successive through time, of a hypothetical lineage of a large mammal, as they might have appeared in (dashed lines) the late Miocene, (dotted lines) the early Pliocene, and (solid lines) the late Pliocene.

In the sort of species succession through time that is diagramed in Fig. 1, is it not possible to say where the paleontological "species" came from—the population during, for example, the late Pliocene did not come *from* any one place and, strictly speaking, does not have a known place of origin. As nearly as can at present be determined, from the literature and from direct study of the relevant fossils in East Africa and in India in Miocene-Pliocene times, Eurasia and Africa had over 35 genera of land mammals in common. These included insectivores, anthracotheres, rodents, ruminants, monkeys, apes, hyracoids, hyenas, felids, mastodonts, deinotheres, and several other groups of mammals. Members of over 15 additional mammalian genera that now occur in Africa but have not yet been found in fossil sites on that continent have been found in Pliocene deposits of the Indian Siwalik Hills (*17, 18*). This total figure of half-a-hundred genera stands in spite of the early tendency to separate, at the generic level, African mammals from allied forms found elsewhere, just because they are of African provenance. Nevertheless, there are some distinct differences in African and Eurasian faunas of Miocene and Pliocene times.

Although numerous groups do appear to have been prevented from crossing between the two areas, there is now evidence that certain mammal species had no difficulty in getting across whatever partial ecological barriers may have existed between the two regions in Pliocene times. One of these is the proboscidean species *Trilophodon angustidens*, which has been found as far east as Baluchistan, occurs in the Kenya Miocene, and has recently been reported by Hooijer from the Congo (*10*). There are enough such occurrences to indicate to me that there was reasonably free faunal interchange between these two major regions of the Old World at some time in the Miocene. I see no reason why certain species of dryopithecines or early hominids, or both, could not have participated in this interchange.

Nevertheless, one may ask whether higher Primates ever had range distributions as extensive as those of such later Tertiary Mammalia as I have mentioned. Clearly, the range distribution of most present-day great apes is a restricted or relict distribution, but the fossil record of the pongids for the Miocene through the Villafranchian, as it now stands, is ample indication that certain varieties of these animals had much wider range distributions formerly than they have now. This also appears to be true for many animals of the later Pleistocene. For instance, *Pongo pygmaeus*, now restricted to the islands of Borneo and Sumatra, was then present in South China, and if the Siwalik Pliocene fossils reported by Pilgrim (*19*) are truly ancestors of this species, it probably had, at an earlier date, an extended range through the Malay Peninsula and Burma into India. Probable antecedents of the gibbons (*Pliopithecus*) are known from several scattered localities throughout Europe and northern and eastern Africa; at one time they must have been distributed (in suitable habitats) between these areas and the present range of members of this genus, in Southeast Asia. Evidently the ranges of modern species of great apes have dwindled greatly as a result of environmental changes in the relatively recent past. Among such changes was shrinking of the type of forest cover that was necessary for their existence. In certain populations, such as those of *Pongo* in South Asia, extermination or restriction of isolated enclaves on offshore islands surely came about as a result of hunting by human beings.

One of the varieties of primates least affected by these types of constriction are the present-day species of the genus *Macaca*. Distribution of members of this genus (Fig. 2) illustrates the extremes of geographic range which members of a single stock of a prehominoid grade of partly arboreal primates have been able to achieve. It need not be assumed that man's ancestors had limited species range until they became terrestrial bipeds. In late-Pliocene and Villafranchian times, *Macaca* was nearly twice as widespread geographically as it is today. An acceptable evolutionary interpretation of this distribution would be that the ancestors of present-day *Macaca* reached the present extremes of their range (Japan, Gibraltar, and so on) when continental shelves were exposed during one of the Pleistocene glaciations, and that the far-flung present-day populations are descendants of perhaps no more than one widespread species that existed 1 to 3 million years ago. Of course, this species could have been already differentiating into genetically diverse populations (subspecies), with only moderate gene exchange between them, before and while the total range of the species was approaching its greatest extent. But it seems more probable that such species distinctions as exist in *Macaca* came about through relatively recent cessation of gene flow between various populations within the entire genus range (*20*). This would be particularly the case for populations isolated on islands since the last glaciation, or separated by late disappearance of suitable habitat, as between the western population of North Africa and its eastern allies. Members of *Macaca* appear to have been able to achieve such broad distribution mainly because its species have been ecologically plastic. Some varieties, such as the Japanese monkey, have remained relatively arboreal, while others, like the Barbary ape of Gibraltar, are almost entirely terrestrial. Conceivably, from the late Miocene on, the earliest hominids were at least as capable of extending their range as the species of *Macaca* evidently were at a somewhat later date.

Thus, it can no longer be argued with confidence that the reason no pre-Pleistocene forerunners of man have been discovered is that these prehominids lived only in a limited geographical area of the Old World, and in a region (perhaps of tropical forests) which has yielded no fossil remains. It is now quite clear that the early hominoids as we know them from fossil remains ranged widely in the Old World in Miocene and Pliocene times. In Fig. 3 the scattered occurrences of the hominoid genera are connected by straight lines, forming rough approximations to range diagrams. Particulars of the sites and species upon which Fig. 3 is based can be found in Piveteau (*21*).

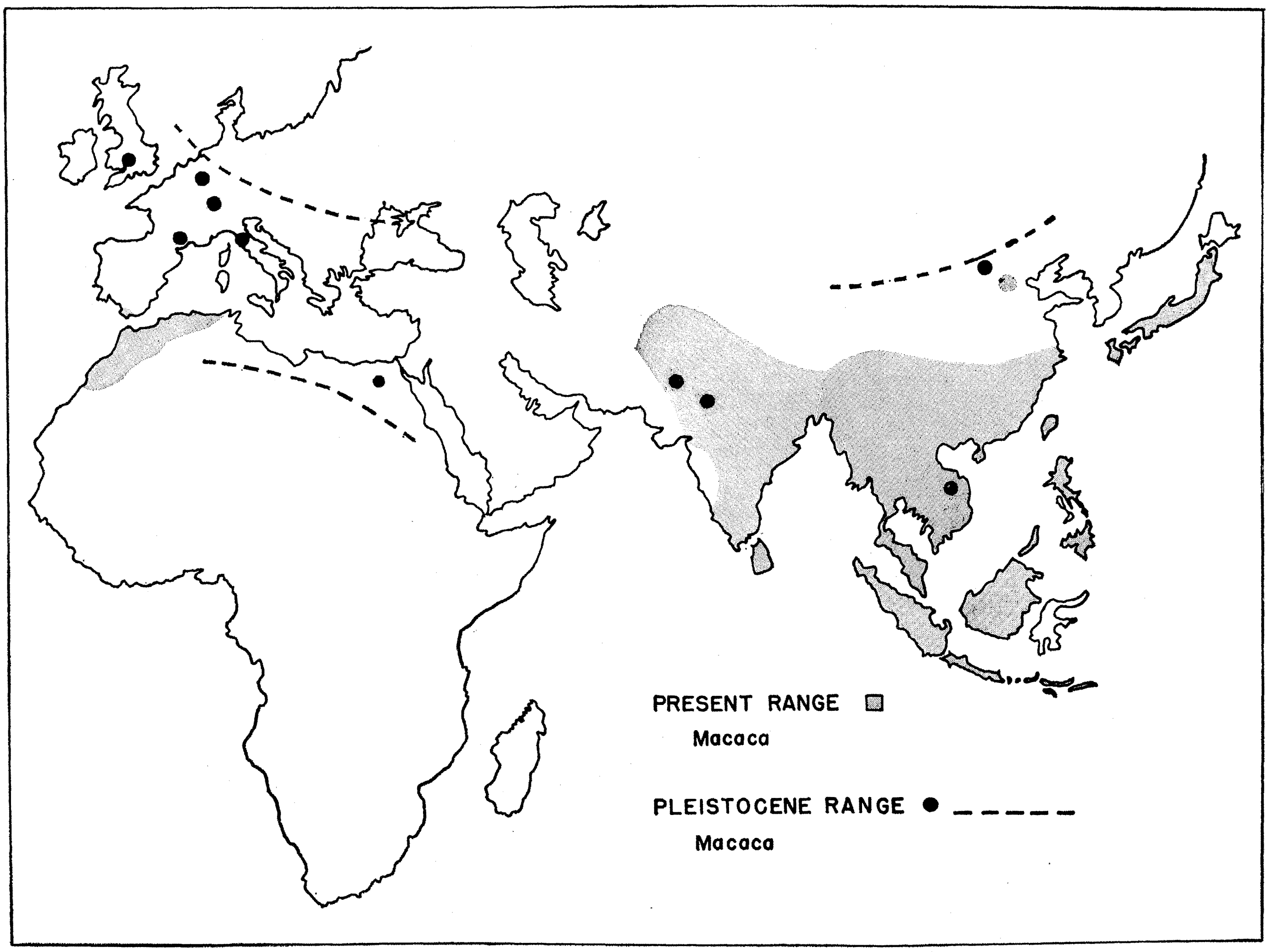

Fig. 2. Recent and fossil distribution of the species of *Macaca*.

In spite of three contrary factors—the rarity of fossil Primates, the enthusiasm of certain taxonomists for subdividing at the generic level, and failure to discover fossil-bearing localities in relevant areas—each of several "generic" units among Anthropoidea of this period have now been reported from at least two Old World continents, and some have been discovered in all three. That ancestors of man are not included among these extensive materials is, in my opinion, no longer an easily defended viewpoint. Moreover, the idea is equally controverted on morphological grounds. Some dryopithecines do show hominid features. The argument that human antecedents lived during pre-Pleistocene times in a restricted area which remains undiscovered has another rather unlikely consequence. This assumption implies that apes and even some monkeys (*Dryopithecus, Pliopithecus, Macaca*), although largely or partly arboreal, were able to spread their range widely, while the forerunners of man were somehow unable to do this. We are here concerned with a stock which, by the early Pliocene, was probably experimenting with terrestrial living and bipedal locomotion. If, at this time, man's predecessors were not able to distribute themselves as readily as their contemporaries among the monkeys and apes could, then it becomes necessary to conclude that man's evolutionary emergence from his pre-human past was truly explosive. This conclusion becomes all the more necessary if we assume that our supposedly poorly distributed antecedents suddenly outdistanced their more "primitive" contemporaries in the matter of species-range extension.

Species Distinctions

It should be noted that, although the particular specimens assigned by one or more competent authorities to the genera indicated in Fig. 3 are adequately known for purposes of generic placement, students cannot tell definitely whether the specimens assigned to a genus were members of the same or of different species. The common practice has been to regard European, Asian, and African finds of later Tertiary fossil Mammalia as belonging to different species, presumably in part because of the tacit assumption that ecologic barriers would, in nearly all cases, have prevented members of a species from reaching all three areas. Nevertheless, since these fossil forms are known primarily from fragmentary dentitions, it remains as difficult to prove that members of populations discovered in different continents represent distinct species as to demonstrate that they are members of the same species. Consequently, it will not be possible to test the validity of species distinctions among many such extinct mammals until much greater numbers of fossils of particular groups are known. In the case of these fossil "apes," for instance, when enough material has been recovered, statistical methods may be used in making species distinctions.

In connection with Fig. 3, it should also be pointed out that leading taxonomists of fossils differ as to the generic

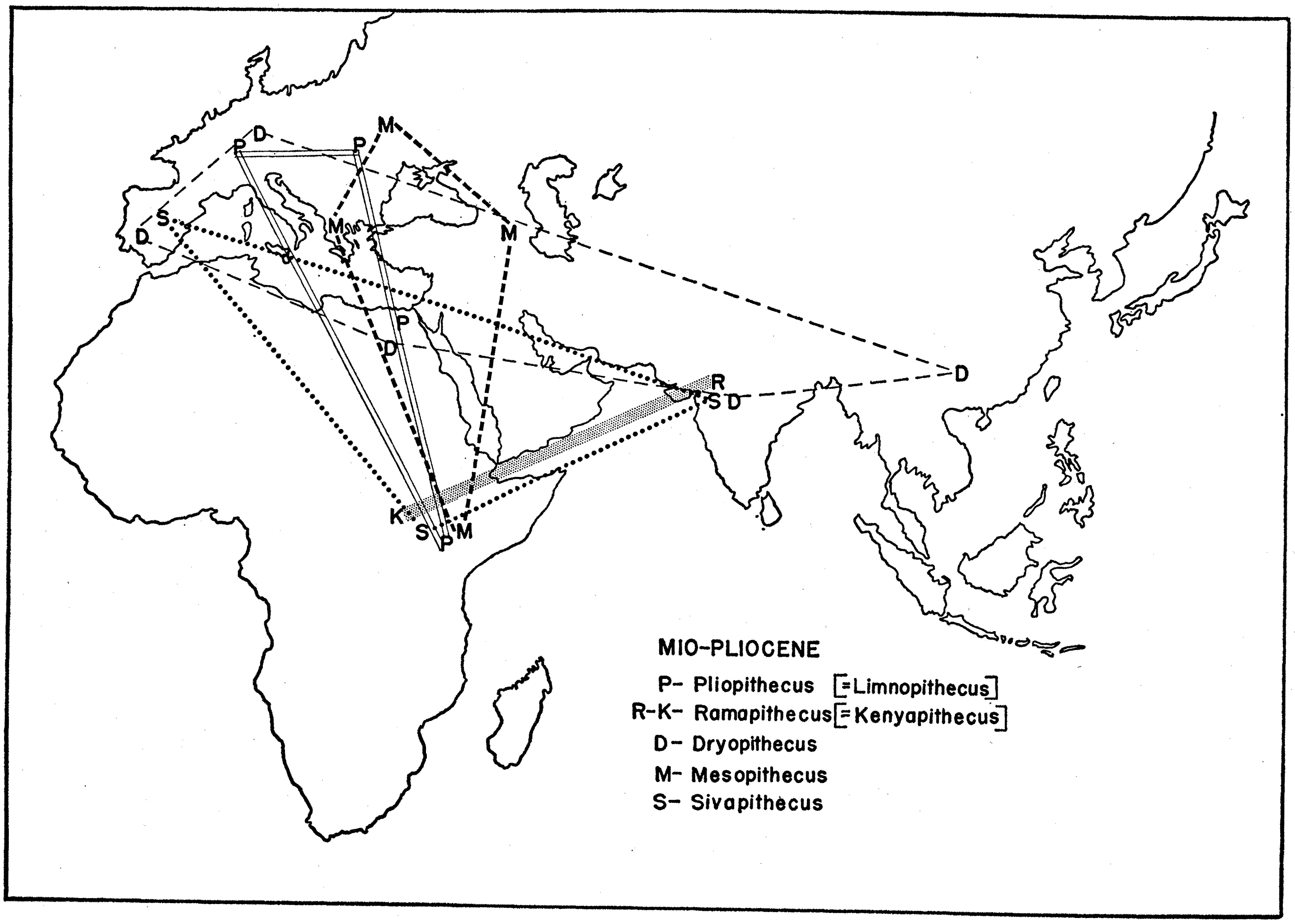

Fig. 3. Occurrence and range distribution of some Miocene-Pliocene Hominoidea.

assignment of some of the species represented. For instance, after initial assignment of certain Spanish dryopithecine remains to the genus *Sivapithecus* (*22*) (an assignment followed here), this material was later referred elsewhere. On the other hand, Lewis (*23*) believes that materials currently assigned to *Dryopithecus* from the Miocene of Czechoslovakia should be placed in the genus *Sivapithecus*.

Consequently, I doubt that it has been established that *Sivapithecus* does not occur in Europe. Conversely, Fig. 3 does not indicate a range extension of *Pliopithecus* into Southeast Asia, but it seems entirely possible that the very fragmentary type of "*Hylopithecus*" from the Siwalik "series" may represent a primitive gibbon, perhaps assignable to *Pliopithecus*. With reference to this specimen, it seems instructive to quote what must be one of the most amazing passages in the history of bad taxonomic practice. This remark occurs as a conclusion to the description of the type species of "*Hylopithecus*" (*24*): "In preference to leaving the tooth now described without a generic name and so increasing the difficulty of reference I am giving it the name of *Hylopithecus*, although I am conscious that my material is quite insufficient for diagnosis."

Origin of the Hominidae

In 1910 Pilgrim was ready to state that Hominidae are descended from *Sivapithecus* (*25*). Later, in 1922, W. K. Gregory observed (*26*) "that man is a late Tertiary offshoot of the *Dryopithecus-Sivapithecus* group. . . ." Discoveries of hominoids during the half century which have elapsed since Pilgrim's writing have reinforced his viewpoint. Entirely apart from morphological considerations, such conclusions gain strength in the light of the taxonomic procedures and zoogeographic examples that I have discussed. It is curious that, in spite of numerous suitably cautious demonstrations in paleontological papers that the origins of man lay among the dryopithecines, it is still widely held by experts that next to nothing of definite value is known about the pre-Pleistocene forerunners of man (*27*). One is reminded of a possibly apocryphal comment said to have been made in 1860 by the wife of the Bishop of Worcester. On learning from her husband that T. H. Huxley had then recently argued that man had apelike ancestors, she observed (*28*): "Descended from apes! My dear, let us hope that it is not true, but if it is let us pray that it will not become generally known." Although the fact of human evolution is no longer doubted, the phyletic sequence before the Pleistocene has never been elucidated during the more than 100 years which separate us from the pronouncements of T. H. Huxley.

Briefly, the following relevant facts as to the origin of the family of man are known. Fossil "apes" of the *Dryopithecus-Sivapithecus* type have now been recovered from deposits distributed throughout a vast area of warm-climate regions of the Old World, including sites in Spain, France, central Europe, Turkey, Georgia, the U.S.S.R., Egypt, Kenya, Uganda, Pakistan, India, and China. Without undertaking a taxonomic revision of these forms at this juncture, but assuming for the moment that all these occurrences do in fact pertain to dryopithecines, I must point out that far too many genera have been proposed for them (*29*). Some of the genera which have been named are *Ankarapithecus, Austriacopithecus, Bramapithecus, Griphopithecus, Dryopithecus, Hylopithecus, Indopithecus, Kenyapithecus, Neopithecus, Paidopithex, Proconsul, Paleosimia, Ramapithecus, Rhenopithecus, Sivapithecus, Sugrivapithecus,* and *Udabnopithecus* (*21, 30*).

Such a large number of distinct genera implies an extensive adaptive radiation of sudden appearance in the early or middle Miocene, but in the case of the dryopithecines this diversification probably occurred more on paper than in reality. Direct study of nearly all of the original specimens of these Primates suggests to me that the dryopithecines should probably be assigned to only three or four distinct genera, perhaps even fewer.

Species of four of these "genera" (*Dryopithecus, Sivapithecus, Proconsul,* and *Ramapithecus*) are now fairly well known. To date, however, no student has adequately dealt with the possibility that not even all of these genera may be separable from each other. This is an important issue, for it now appears that the direct hominid lineage passed through members of at least two of these taxa.

Starting with the more *Australopithecus*-like of these forms and working backward through time, we can now draw some fairly clear inferences about the evolutionary appearance of Hominidae. *Ramapithecus brevirostris*, of probable early Pliocene (Pontian) age, from the Nagri zone of the Siwalik Hills of India, has long been known to possess several characters in the upper dentition and maxilla which significantly approach the dental conformation of Pleistocene species of tool-making man. Briefly, these characters, which distinguish the forms from typical pongids and suggest hominid ties, are a parabolic (not U-shaped) dental arcade, an arched palate, a canine fossa, low-crowned cheek teeth, small incisors and canines, a low degree of prognathism, and a short face. Separately, almost all of these features can be found among pongids, but their occurrence in combination in *R. brevirostris* is a strong indication of hominid ties. Recently, Leakey has described a new East African primate specimen, "*Kenyapithecus wickeri*," probably from about the same period or a little earlier, which is exactly like *R. brevirostris* in these and other features. In fact, in my opinion, not one *significant* character of difference exists between the two specimens (both are maxillae). This being so, the new form from Kenya should be assigned tentatively to *R. brevirostris*, at least until such a time as further material provides a basis for demonstrating that the two are different species. The conclusion that these two specimens are at least of the same genus has recently been supported by Frisch, who has also studied them directly (*31*). Perhaps the most extraordinary thing about Leakey's Fort Ternan, Kenya, specimen is its extreme similarity to the type specimen of *R. brevirostris*—an important and very significant fact that "generic" splitting only obscures. Greater differences than are to be noted here typically occur among members of a single-family social group within nearly all species of present-day hominoids. These two specimens indicate to me a considerable probability that in early Pliocene or latest Miocene times, or both, a single species of progressive (?)dryopithecine ranged all the way from northern India to East Africa, and perhaps farther. Personal examination of the specimens concerned also indicates that a third individual of this species, from the Nagri zone of the Siwalik Hills, in the Haritalyangar area, is represented by Pilgrim's specimen No. D185—the right maxilla of "*Dryopithecus punjabicus*"—in the Indian

Museum, Calcutta. This specimen agrees with the other two in significant details of dental morphology, and in the possession of a much-reduced rostrum and an extremely short canine root (alveolus). These three specimens of *Ramapithecus* strongly reinforce each other in indicating a valid species group. Moreover, all three specimens come from a stratigraphic level higher than that at which most of the more generalized dryopithecine remains are found.

The transitional nature of these specimens of itself raises the question of arbitrariness in separating the families Pongidae and Hominidae—a problem which has also been posed recently in connection with another event, the discovery of close biochemical similarities between man and the apes, in particular the African apes (*32*). Nevertheless, there do seem to be fairly good reasons for continuing to view the Pongidae and the Hominidae as distinct enough to be considered separate families. What I want to stress is the fact that the transitional nature of the *Ramapithecus* materials is such that they cannot be placed with finality in either group. Personally I do not see that it very much matters whether members of this genus be regarded as advanced pongids or as primitive hominids, but perhaps considerations of morphology slightly favor placement among the hominids. There is certainly no need to produce a new, higher category for such links—an alternative which has sometimes been resorted to in the past when a fossil taxon was determined to be roughly intermediate between two others.

Two Series of Dryopithecines

To date, the most extensive series of dryopithecines come from two main areas, the Rusinga Island and Fort Ternan beds of Kenya and the Siwalik Hills of India and Pakistan. A primary difficulty in understanding the actual significance of these two series of Primates arises from the fact that the Indian dryopithecines were studied and described primarily in the period between 1910 and 1937, while the dryopithecines of Kenya have been dealt with mainly since 1951. No one has ever published the results of extensive comparative study of the two sets of materials. Lewis, in the most recent taxonomic treatment of the Siwalik "apes," in 1937, reduced the number of genera to four (*Bramapithecus*, *Ramapithecus*, *Sivapithecus*, *Sugrivapithecus*), with ten contained species (*33*). Members of the first two of these genera he regarded as more manlike than members of the other two; *Sivapithecus* and *Sugrivapithecus* he regarded as being closer to the present-day great apes. Unfortunately, there was a lack of associations between upper and lower dentitions in the Siwalik material, and knowledge of some of these genera—such as *Bramapithecus*, known only

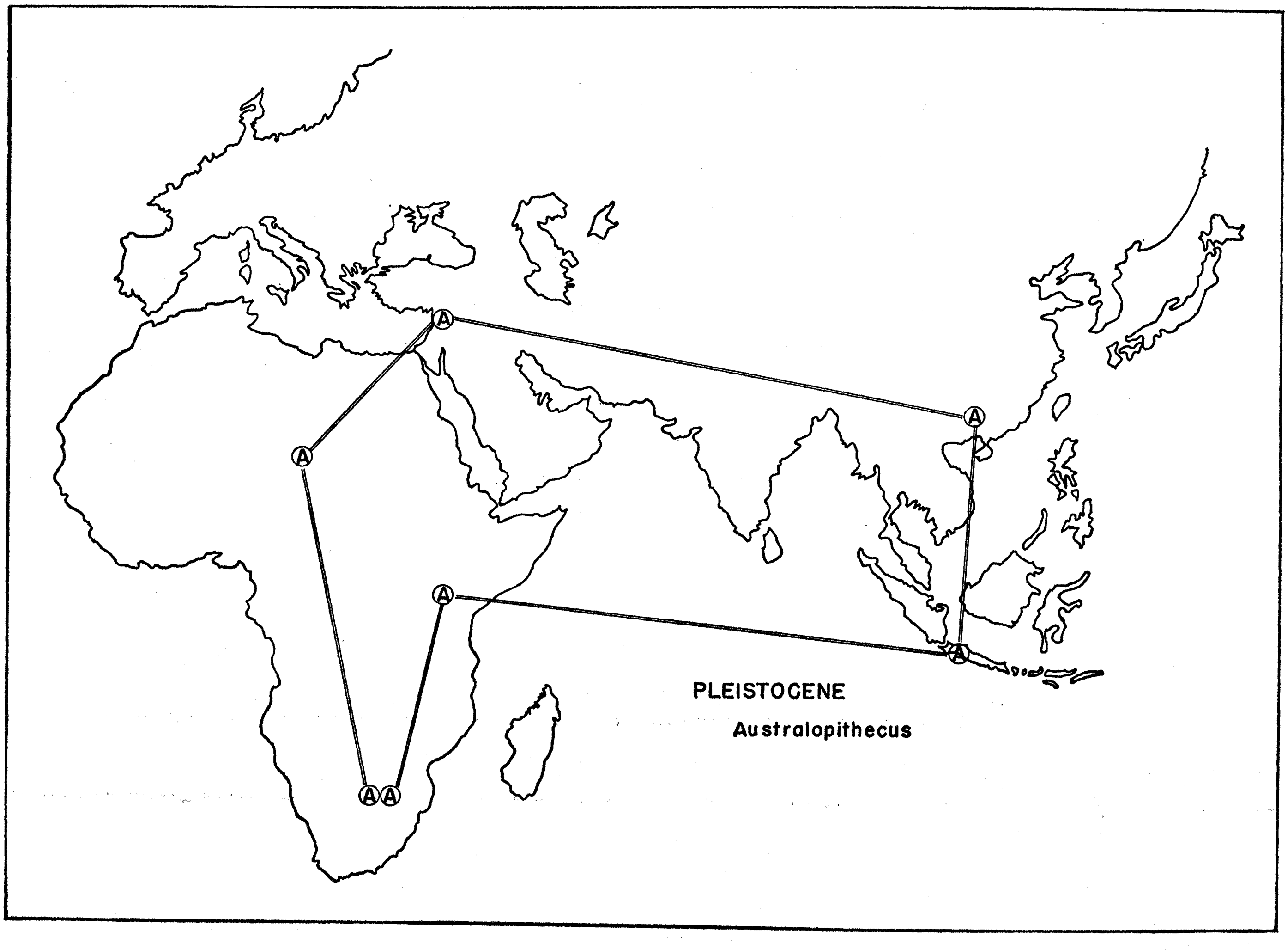

Fig. 4. Reported range of *Australopithecus* species.

from jaw fragments containing the last two molars—was very limited. There were no whole or nearly complete dentitions in which to study the range of variability. This situation has now changed, because of the recovery in Africa (1948–1962) of relatively complete portions of skulls, maxillae, and mandibles of several individual dryopithecines, together with postcranial bones and, in some cases, associated upper and lower jaws. Comparison of these two series of data indicate the following problems.

1) In both the Kenyan and the Indian sites (in the lower part of the section, in particular) is found a large form with large snout, protruding incisors, slicing anterior premolars, and rather high-crowned teeth. In the East African material the lingual molar cingula are more pronounced, but otherwise, characters of dentition, snout, and jaw do not differ significantly. Mainly, these Miocene varieties have been called *Sivapithecus indicus* (Siwaliks), and *Proconsul major* (Rusinga). May it not be that these two sets of fossils represent a single species that ranged fairly widely, and perhaps over a long period, but which in known populations (even from far-flung portions of its range) is not particularly variable? This large-snouted type of ape is temporally distributed from early or middle Miocene (Rusinga; Chinji, in the Siwaliks) to latest Miocene or early Pliocene (Fort Ternan; Nagri, in the Siwaliks), as is evidenced by a very large upper canine recovered at Fort Ternan, at the same level as "*Kenyapithecus*," reported by Leakey (*9*); perhaps by other teeth found at Fort Ternan, that have not been described; and by several discoveries in the Nagri Zone. Differences in the molar-crown patterns of the two populations are about as great within each area as between the two groups. A few successive species may be indicated by this material, or only a single species may be involved. This species could well be ancestral to the gorilla and chimpanzee. Ancestors of the African apes certainly need not always have been restricted to that continent.

2) A second primate form common to the Kenya and Indian areas in the Miocene is represented by the *Sivapithecus africanus* material (Kenya) and the "species" *Sivapithecus sivalensis* (India). In this group the teeth, particularly the canines, are relatively smaller than in "*S.*" *indicus*, and lingual cingula on upper molars apparently occur less frequently. The possibility remains high that other East African and Siwalik species, of the 15 accepted as valid in the more recent literature, will fall into synonymy with these two species as new data are recovered, or as a result of a fuller comparative study now in progress. The main distinction in dentition (and almost the only difference in known parts) between some *Sivapithecus* and modern *Pongo* is the higher degree of crenulation of the crowns of cheek teeth in *Pongo*. Several specimens of Indian *Sivapithecus* show rather crenulate molar crowns, and this may be assumed to indicate something about the origin of the orangutan. Such crenulations are particularly developed in the upper molar described by Pilgrim as "*Paleosimia*," which may be a valid genus. In view of these crenulate teeth, it appears probable that a species that differentiated toward the Bornean great ape is represented in the Siwalik material, but this form has not been fully distinguished in taxonomic work to date. The probability that *Proconsul* cannot be separated generically from *Dryopithecus* is worth mentioning here. Both these genera, if indeed they are two rather than one, appear to be restricted to the Miocene. *Sivapithecus* apparently crosses the Mio-Pliocene boundary but is not easily separated from *Ramapithecus*, a conclusion indicated by Leakey's report on the East African materials (*9*) and by my own studies on the Indian dryopithecines.

Conclusion

In concluding it seems advisable to make several observations as to the current state of knowledge of the origins of advanced hominoids.

The fossil hominoids of the Miocene of Kenya do not now appear to belong to the early part of that epoch, as had been previously believed, but may be of middle or, less probably, late Miocene age. Similarities between hominoids of the Miocene in India and Kenya, together with resemblances in other members of the two faunas, suggest that the Chinji Zone of the Siwaliks may be middle or late Miocene, as originally suggested by several early workers (see *18*). At this time the "radiation" which produced the great apes of today and man seems barely to have begun. The possible occurrence of *Dryopithecus* in early Miocene equivalents of Egypt requires further investigation (*34*). There is now nearly universal agreement among those most competent to judge that *Oreopithecus* does not stand in the ancestral line of later pongids and hominids, although it is related to them (*35*). In view of these conclusions, the origins of man and of the great apes of Africa and Borneo are seen to lie directly among the dryopithecines. This conclusion supports the extensive discussions of Gregory as to the significance for human phylogeny of the *Dryopithecus* molar pattern and LeGros Clark's analysis of the morphological evidences favoring the occurrence of secondary canine reduction in the ancestry of Hominidae (*36*).

There is now adequate fossil evidence to indicate, (i) that, from about middle Miocene times, a few widely distributed species of the larger hominoids were present in both Eurasia and Africa and that successive differentiation of these species, through time, has occurred, with little branching or radiation; (ii) that the primary center of speciation among these animals was outside of Europe; (iii) that some dryopithecines in known parts entirely close the slight morphological gap between Hominidae and Pongidae; and (iv) that, if reports as to localities of *Australopithecus* (*37*) by several serious students be accepted, the data now show that this earliest generally accepted antecedent of man was widely distributed in tropical regions of the Old World in the early Pleistocene (Fig. 4). Present archeological evidence does suggest that the use of tools may have occurred first in Africa, but this is not the same as to suppose that the initial species of man differentiated there, unless man be defined solely as a tool-manufacturing primate. To date, the latter supposition is an inference primarily supported by negative evidence—namely, the scanty recovery of australopithecines and of pebble tools in Southeast Asia and China. It must be remembered that one creditable occurrence is all that is needed to demonstrate the early presence of *Australopithecus* in the East. Such an occurrence apparently has now been confirmed by von Koenigswald, through his description of about a dozen teeth, assigned by him to a new genus, "*Hemianthropus*," in materials recovered from Chinese drugstores (*37*). In my opinion these teeth are from members of the Australopithecinae assignable to the subgenus *Paranthropus*, but Woo (*38*) suggests that some of these teeth could belong to *Gigantopithecus* (*39*).

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News and Comment

Appalachians: How a Have-Not Region and People Got That Way Conditions Development Efforts

A book written with indignation and rhetoric reminiscent of the muckraker journalists who attacked injustice, indifference, and "the interests" earlier in the century has helped to call attention to the perennial problems of the Appalachian region, which has been generally left behind in the advance of American science and industry.

Night Comes to the Cumberlands (Atlantic–Little, Brown, Boston, 1963. $6.75) is a book about the mountain counties of eastern Kentucky, the 10,000 square miles of rugged hills and narrow valleys on the Cumberland Plateau bordering Virginia, West Virginia, and Tennessee, a land of persistent hard times shared by similar areas in states lying north and south along the Appalachian range.

The author is Harry M. Caudill, an attorney who lives in Whitesburg in Letcher County on the plateau. Caudill was raised in the mountains, he has practiced law on the county courthouse circuit, and he has served in the Kentucky legislature, where he made education and conservation his cause.

Caudill writes from inside, and he writes with his eye unwaveringly on the people of the area, particularly the miners and their families, for the story of eastern Kentucky for the last half century in good times and bad has been the story of coal.

The subtitle of the book is "A Biography of a Depressed Area," and Caudill starts with the beginning, tracing the troubles of the present to the conditions of the settlement of the region which began more than 200 years ago. Caudill writes like a cured romantic, and his pioneers are not Arcadians. The mountaineers of today are the descendants of the men and women who started the western migration from Virginia and North Carolina. For the most part, says Caudill, these people were of English and Scottish stock, but they were the strays and outcasts—orphans, debtors, fugitives—the transported criminals or indentured servants who came to work on the plantations to fill the same need for labor that kept the slave ships coming from Africa.

Many of these people who had worked out their indentureships, or had simply run away, went to the foothills of the Piedmont, and by the latter half of the 18th century were established in the fringes of the Appalachians.