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PROBLÈMES ACTUELS DE PALÉONTOLOGIE-ÉVOLUTION DES VERTÉBRÉS.

TOWARD THE ORIGIN OF THE OLD WORLD MONKEYS

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Résumé

On a suggéré qu'une espèce de *Parapithecus* était le premier ancêtre catarhinien des cynomorphes, mais les seuls caractères dérivés partagés par les deux groupes sont des couronnes molaires hautes (« hypsodontes ») et peut-être une réduction des hypoconulides et un développement fonctionnel des lophes sur les molaires supérieures. Les métaconides petits sur P_4, les M_3 courtes, l'absence de cingulum et en particulier le développement de l'aiguisage P_2/C' qui en résulte suggèrent que, bien que *Parapithecus* puisse être l'équivalent écologique des cynomorphes (ou du moins de « *Miopithecus* » *talapoin*) dans la région du Fayoum, ce singe oligocène n'est pas étroitement apparenté aux cercopithécidés actuels. Des spécimens identifiés comme *Oligopithecus* et *Propliopithecus* spp. présentent en mosaïque des caractères tels que : évidence de fusion entre l'hypoconulide et l'entoconide sur dP_4-M_2; métaconide et protoconide sub-égaux sur P_4; l'aiguisage P_3/C' bien développé; M_3 étroites; M_2 plus large et plus longue que M_1 ; et des molaires (inférieures) avec un cingulum labial, qui, s'il est incorporé dans la face labiale, produira un « évasement » du type cynomorphe. Ces spécimens partagent aussi des couronnes hautes (mais avec un relief minimal) comme dans les molaires de tous les catarhiniens du Fayoum. On peut suggérer que hors de la variabilité connue des catarhiniens anciens, une lignée pourrait allier la mosaïque des caractères ancestraux aux cynomorphes plus récents peut-être dans un milieu différent de celui du Fayoum. On peut reconnaître un tel ancêtre des cynomorphes comme « hominoïde » à cause de sa similitude totale de grade, mais cercopithécidé en terme de descendance.

Abstract

Parapithecus species have been suggested as the early catarrhine ancestors of cercopithecids, but the only derived characters shared by these groups are high (« hypsodont ») molar crowns and possibly reduction of hypoconulids and functional development of lophs on upper molars. Small P_4 metaconids, short M_3, lack of cingulum and especially the derived development of P_2/C' honing suggest that while *Parapithecus* may have been an ecological vicar of cercopithecids (or at least of "*Miopithecus*" *talapoin*) in the Fayum region, this Oligocene catarrhine is not closely related to modern Old World monkeys. Specimens allocated to *Oligopithecus* and *Propliotithecus* spp. variably present such characters as : evidence of hypoconulid fusion with entoconid on dP_4-M_2; subequal P_4 metaconid and protoconid; well developed P_3/C' honing; narrow M_3; M_2 wider and longer than M_1; and (lower) molars with labial cingulum, which if incorporated into the labial face would produce cercopithecid-type "flare" (transverse broadening from cusps to cervix). These specimens also share the high crowns (but low relief) seen in the molars of all Fayum catarrhines. It may be suggested that out of the known variability of early catarrhines, one lineage may have combined the mosaic of features ancestral to cercopithecids, perhaps in an environment different from that of the Fayum. Such a cercopithecid ancestor would be termed a "hominoid" on overall grounds of grade similitary, but a cercopithecid in terms of its descendants.

I. - INTRODUCTION

The problems of applying Hennigian or cladistic methods in paleontology have been discussed by other speakers at this meeting and elsewhere, In brief, I consider that Hennig and his colleagues have made their greatest contribution in emphasizing the value of derived *versus* ancestral conditions in determining relationships among taxa. Other aspects of "cladism" are more open to question, but systematics and comparative anatomy have long accepted the importance of derived or "specialized" features, although there has until now been little attempt to employ them exclusively.

The Old World monkeys (family Cercopithecidae) are a group of higher primates whose living members share at least one derived "key character" of adaptation : a bilophodont dentition. This adaptation is already present in the fossil forms unequivocally assigned to the family (see DELSON, 1975 a). In fact, certain authors (STRAUSS, 1953; KÄLIN, 1961, 1962) have argued that no animal can be termed a cercopithecid which does not possess this dental morphology. Although such an extreme view may not be necessary, similar criteria have been (and are still) used to define early Mesozoic mammals. What is of interest here, however, is to determine what can now be said about the possible ancestors of known Neogene Cercopithecidae.

Following HENNIG (1966), SCHAEFFER *et al.* (1972) and others, the study of morphologic diversity among the living and fossil members of a group may allow the determination of derived character states and by consequence those which are ancestral for the group. The combination of the latter conditions in a single model animal may be termed a postulated ancestral morphotype, representing those characters expected in the latest common ancestor of all known members of the group. Two additional procedures, to be considered here. are the extrapolation of this morphotype one step farther back in time and its subsequent comparison to known "primitive" fossils, which of course have the value of placing time and space constraints on our reconstructions of evolutionary history.

II. - MORPHOLOGY OF THE ANCESTOR OF CERCOPITHECIDAE

In the development of an ancestral morphotype for cercopithecid monkeys, emphasis was placed on the variation observed in modern species, although all known fossils were considered as well, in light of the increased ranges of total morphological variation thus obtained. Of hard parts available for fossilization, the dentition and less distinctively the skull provide valuable characters, but the post-cranial skeleton is much more responsive to an analysis of habitus than of heritage.

Based on the dentition, four major taxonomic-morphologic groups can be distinguished among modern monkeys, and all but a few early and possibly still-evolving taxa fit clearly into one of these. As I have detailed elsewhere (1975 a, 1973), it is thus possible to define morphotypes representing the shared (derived and ancestral) features of the Colobinae, the Cercopithecini, *Theropithecus* and the other Papionini (baboons, macaques, etc.). The last of these groups appears the least derived from a common cercopithecid ancestor in most dental characters, and the modern genus *Macaca* may be the least "specialized" of all.

The resultant ancestral cercopithecid dental morphotype would thus be rather similar to macaques in possessing high-crowned ("hypsodont") cheek teeth with transverse crests (as in all monkeys) linking relatively low, rounded cusps. The main notches between these cusps, especially lingually on lower molars, would not be very deep. The mesial fovea (trigonid basin — see DELSON, 1975 a for terminology and illustrations) of lower molars would be of similar size to the distal fovea, both smaller than the central fovea (talonid basin). Four cusps only would be present on dP_4-M_2, with a distal hypoconulid on M_3 and a mesial paraconid crest on dP_3. From dP_4 to M_2, the teeth would become longer and relatively wider, while the M_3 would be quite long but narrow. Four cusps and three foveas would characterize dP^3-M^3, while two subequally large cusps and a single loph (id) would be found on P^{3-4} and P_4. A honing mechanism involving C' and P_3 would involve a large mesiobuccal flange on the latter unicuspid tooth, especially in males; large upper canine teeth would also present a mesial groove from apex to root base. No cingulum would be present laterally on any cheek teeth; instead there would be a smooth "flaring" outward from the cusp apexes to the cervix on all lophodont teeth, most prominent lingually on uppers and buccally on lowers. The lower incisors would be completely sheathed in enamel and the four incisors of similar proportions, with I^2 possibly conical. In general, these are the characters found in the teeth of all cercopithecids or in macaques and baboons when there is distinct variation; the incisor region, however, has been most changed in known papionins other than *Theropithecus*, while colobines have preserved a suite of characters closer to the ancestral pattern.

In terms of other anatomical systems, there is less broad variation in the family. My studies and those of VOGEL (1966) suggest that the earliest cercopithecids had a facial morphology similar to that found today in colobines and in gibbons (Hylobatinae); the cercopithecine face is most derived among modern catarrhines. This ancestral pattern includes such features as wide interorbital region, short and broad nasal bones and a lacrimal fossa extending beyond the lacrimal bone onto the maxilla. The face in general would have been relatively short, broad and perhaps high, most similar to a modern *Presbytis*. On less secure morphological grounds, it may be expected that neither the colobine stomach specialization nor the cercopithecine cheek pouches had yet been developed; the limbs would have been of subequal length; and discontinuous ischial callosities were probably present. It may even be suggested that this early monkey possessed the presumed ancestral catarrhine diploid chromosome number of $2n = 44$ (shared today by most colobines and gibbons). Such animals might have lived early in the Miocene, and following ecological hypotheses discussed by DELSON (1975 b), may have been African arboreal or semi-arboreal quadrupeds who ate fruit when possible but supplemented their diet with leaves when necessary.

The next and more interesting step backward in time is to attempt reconstruction of the ancestor of this first cercopithecid, that is a primate lacking the Old World monkey dental specializations altogether. Many previous workers have attacked this point directly, without the above intermediate stage on which to base hypotheses. Moreover, most have become fascinated with the question of how bilophodonty developed, especially in terms of the origin of the loph(id)s themselves and of the postero-internal cusp of cercopithecid upper molars. VORUZ (1970) gave a good summary of these studies, many of which discuss the possibility that the cusp in question is not a " true " but a " pseudo- " hypocone, that is, not derived from internal cingulum. I consider that loph(id)s arose in monkeys as they did in other mammals, as an adaptation to processing of food requiring slicing as well as crushing — today bilophodonty is most strongly developed in leaf-eating colobines and grass-chewing *Theropithecus*. The rearrangement of cusps and their linkage by crests is a functional problem dependent on the relative positions of cusps (and crests) on opposing teeth. Thus, even if it can be shown (see KÄLIN, 1962, fig. 1) that the cercopithecid hypocone was never linked to the internal cingulum, I would still consider it a hypocone because of its functional relationship with trigonid cusps, so long as it cannot be shown to be a " migrated conule ", as HURZELER (1949) has suggested. KOENIGSWALD (1969) has assigned to *Victoriapithecus*, an African Miocene monkey, an upper molar which shows remnants of the crista obliqua, linking protocone and metacone. This specimen and contemporaries are now under further study, but as they are most probably cercopithecid, it would appear that ancestral populations possessed this crest more commonly. The origin of loph(id)s is not solved, but I agree with KOENIGSWALD that their development might have been relatively rapid under selection pressure for slicing occlusion, especially if a switch from fruit to leaf eating were involved.

Upper molars of pre-cercopithecids might thus be expected to have four cusps and a crista obliqua, lowers five cusps without clear talonid crests — derivation of a protolophid by strengthening the metaconid-protoconid link is simple to envisage. The presence of a hypoconulid on all lower molars (at least dP_4-M_3) is accepted as reasonable by comparison with all living and fossil primates of anthropoid grade, as well as advanced prosimians.

In addition to bilophodonty, high crowns, high relief and lateral molar " flare " characterize known cercopithecids but might have been lacking in their ancestors. It is suggestive to recall that flare seems most pronounced lingually in upper molars and buccally in lowers, as this is the distribution of cingulum in other advanced primates. It seems likely that flare developed through the incorporation of cingulum directly into the tooth face, producing a smooth surface, slightly bulged out near the cervix. Some cingulum would thus be expected in pre-cercopithecids. Because crown height and especially crown relief are greater in cercopithecid cheek teeth than in those of most other primate families, these features might be expected to be only partly developed in the ancestors of Cercopithecidae; most other characters would probably have been as described above for early cercopithecids. It is important to note that no early fossils were considered in the development of this postulated morphotype. Thus it is reasonable now to compare known fossils with the morphotype in order to seek out common features, without fear of circularity.

III. - *PARAPITHECUS* AS AN ANCESTOR OF CERCOPITHECIDAE

In a search for known fossil relatives of the ancestor of Old World monkeys, the only possible candidates at present are the early catarrhines of the Fayum Egyptian Oligocene. SZALAY (1970, 1972) has rather convincingly denied *Amphipithecus* of the Burmese Eocene any place in higher primate history. SIMONS (1972 and personal communications) has suggested that its contemporary *Pondaungia* shows closer morphological similarities to catarrhines, but the specimens have not been fully studied. Unfortunately, the same is true for the Fayum materials collected in the 1960's by SIMONS. However, he has published numerous short comments and has been most generous in allowing colleagues access to figured specimens, for which I gratefully thank him.

I must preface all further remarks by accepting the limited nature of the Fayum record, both in small numbers of specimens of most primate taxa and as representing only a fraction of the area of Africa, much less the Old World, during only part of the Oligocene. However, these several species existed and need to be interpreted, and they may aid in the search for the origins of the Cercopithecidae and other modern groups.

As described by SIMONS (e.g., 1972), the Fayum primates are known from all three fossiliferous horizons. The unique holotype of *Oligopithecus savagei* is from the oldest level, the Lower Fossil Wood Zone. The many specimens of *Apidium moustafai* and perhaps SCHLOSSER's holotypes of *Parapithecus fraasi*, *Propliopithecus haeckeli* and " *Moeripithecus* " *markgrafi* are derived from an intermediate horizon. The youngest beds, known as the Upper Fossil Wood Zone, have yielded large series of *Apidium phiomense* and *Parapithecus grangeri* (SIMONS, 1974; see page 843), as well as specimens of *Aegyptopithecus zeuxis* and the unique type of *Aeolopithecus chirobates* (and perhaps *Propliopithecus*, see below). The species of *Apidium* and *Parapithecus* differ by about 15 % in size, the younger populations being larger.

Since the first finds early in this century (OSBORN, 1908 and SCHLOSSER, 1910, 1911), authors have claimed ape or monkey status for each Fayum primate, often without close study. Because of his major accomplishments in raising our knowledge of these animals from four specimens in 1959 to hundreds today, the opinions of E. L. SIMONS are the most important for further consideration. As expressed in several papers since 1967, SIMONS argues for special, indeed direct ancestral relationship between cercopithecids and the Fayum primate *Parapithecus*. It must be assumed that the total body of evidence in support of this view is eventually to be published as a coherent unit, perhaps in the manuscript cited as in press in SIMONS, 1972. As yet, however, these arguments have not been presented in full, but on the basis of previous papers by and

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FIG. 1.* — Occlusal (and distal) views of selected Fayum primate specimens. A. *Parapithecus* sp., C.G.M. 26912, P$_3$-M$_3$. B. *Parapithecus* sp., Y.P.M. 23796, dP$_3$-M$_2$ (photographically reversed). C. *Parapithecus fraasi*, type, S.M.N.S. 12639a, R C,-L M$_3$. D, E. *Propliopithecus haeckeli*, type, S.M.N.S. 12638, P$_3$-M$_3$ and C,-M$_3$ (E photographically reversed). F, G. *Propliopithecus* (= « *Moeripithecus* ») *markfrafi*, *type*, S.M.N.S. 12639b, M$_{1-2}$; distal and occlusal view (G reversed photographically). H. *Oligopithecus savagei*, type, C.G.M. 29627, C,-M$_2$. All at approximately three times natural size, except H about four times natural size. A is type *P. grangeri* Simons, 1974.

(*) Photographs by the author except 1H and 2J-K courtesy of E.L. SIMONS. Thanks are due to Dr. SIMONS and Dr. K. D. ADAM for permission to study and photograph Yale and Stuttgart specimens, respectively. Abbreviations used for museums :

C.G.M. : Cairo Geological Museum;

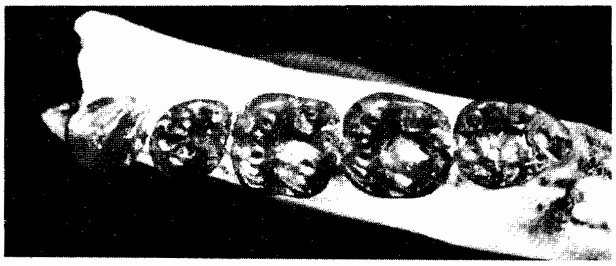
S.M.N.S. Staatliches Museum für Naturkunde, Stuttgart;

Y.P.M. Yale Peabody Museum, New Haven.


A


B


C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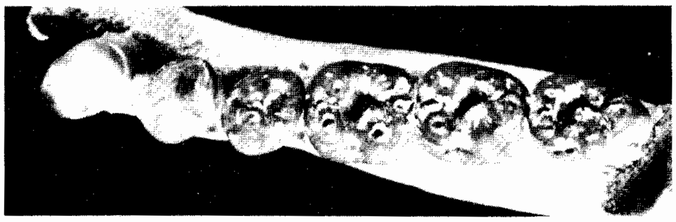
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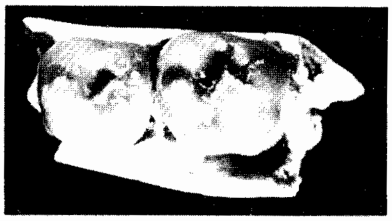
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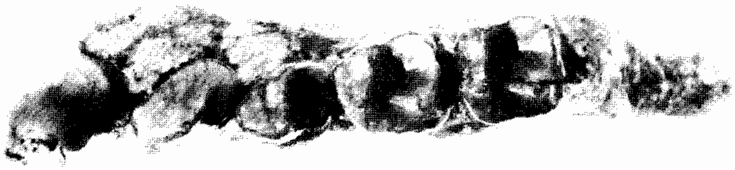
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communications from Dr. SIMONS as well as my observations of the fossils, a brief description of the characters of *Parapihtecus* may be given (see also KÄLIN, 1961). (See note added in proof, p. 862).

The lower molars of *Parapithecus* species each have five cusps with a relatively small but distinct hypoconulid on the midline. The molars are relatively high-crowned, but the lingual intercusp notches are shallower even than in cercopithecines. Paraconids are reduced to a crest perhaps confluent with the mesial margin in molars, but are distinct on dP_4 (and probably dP_3). There are no lophids crossing the teeth, but the median buccal notch does angle inward as in cercopithecids to constrict the tooth between trigonid and talonid; unpublished upper molars may functionally approach a lophodont condition through incorporation of conules. There is no indication of a cercopithecid-type distal fovea, set off between distal margin and rear cusps, in the lower teeth of *Parapithecus*, nor would one be expected because of the omnipresent hypoconulid. All three permanent molars are rectangular and rather wide, and the M_3 is slightly or even considerably shorter then M_2. Unworn teeth of *P. grangeri* are more crest-oriented than in the bulbous cusped *P. fraasi*, but rapidly flatten with wear. The lower premolars increase in size but decrease in complexity from P_4 to P_2 : a talonid basin and low metaconid are present on P_4 and less clearly on P_3, but P_2 is a simple, unicuspid tooth which appears to have been incorporated in some form of canine honing, as in modern platyrrhines. These features may be discerned on figures 1 A-C and 2 B, D.

As SIMONS has argued (1967a, p. 599 and later), the new finds clearly show that two incisors and accompanying alveolar bone were lost from the type mandible of *P. fraasi* (fig. 2A). It is less certain that both remaining teeth are I_1; they seem slightly different in morphology, and as no specimen of *Parapithecus* (or *Apidium*) has yet been recovered with both I_1 and I_2 *in situ*, the question remains open. It may finally be noted that while the mandibular corpus of *Parapithecus* is rather shallow, the bone is much deeper in the closely related *Apidium*, which differs further in possessing a long M_3, premolars relatively smaller by comparison to molars and accessory cuspules on molars, notably a centroconid (mesoconid) on all lowers.

SIMONS has selected certain of the listed characters which are similar to those in cercopithecids in order to promote *Parapithecus* as an Old World monkey ancestor. It is of interest to review the way his views have changed with increasing information and study. At the last C.N.R.S. colloquium in 1966, he argued that the parapithecids (*Parapithecus* and *Apidium*) were anthropoidean and suggested them as possible ancestors for Old World monkeys, noting that this would imply independent loss of P2 in Cercopithecoidea and Hominoidea (1967a, p. 599). A later paper that year (1967b) compared unworn M_{1-2} of a new *Parapithecus* species to those of living *Cercopithecus* (*Miopithecus*) *talapoin*; this is still the closest similarity yet demonstrated. SIMONS wrote (1967b, p. 321) : " preliminary work suggests that some of these creatures (*Apidium* and *Parapithecus* species) may be related to the Old World monkeys. " Further study allowed the statements that : " *Parapithecus* is extremely close in a number of dental and mandibular details to the smallest (and possibly most primitive) living African monkey *C. talapoin*... In order to derive the dental-mandibular morphology of the talapoin from that of *Parapithecus* it would only be necessary to reduce lower molar hypoconulids from a small cusp to a flat platform... and eliminate the P_2 " (SIMONS, 1969b, p. 323). In terms of formal taxonomy, SIMONS proposed (1970, p. 100) that " *Parapithecus* and *Apidium* should no longer be considered as representing a distinct primate family, Parapithecidae, but instead should be classified as the Parapithecinae, a primitive subfamily of the Cercopithecidae. "

In his most recent work (1972), SIMONS appears to waver somewhat in his assertions. In a formal classification (p. 288), the Parapithecinae is one of three subfamilies of Cercopithecidae, of equal rank with Colobinae and Cercopithecinae. In discussing reasons for the lack of Miocene cercopithecid fossils (pp. 185-186), SIMONS argues for (and I concur in) a late diversification with only a few (Early and Middle) Miocene species. He doubts that apes were more successful than monkeys at this time, mostly because of the abundance of Fayum parapithecines by comparison to contemporary " apes ". On a more plaintive note, he writes (p. 189) : " it does seem unlikely that such abundant and adaptively successful primates as *Apidium* and *Parapithecus* were aberrant side branches, doomed to eventual extinction. " Finally, SIMONS concludes his discussion by noting (1972, p. 191) : " The similarity between the teeth of *Miopithecus* and *Parapithecus* is remarkable, but may be due to parallel evolution. In any case, *Apidium* and *Parapithecus*, with symphyseal and frontal fusion and with post-orbital closure, have reached the anthropoid grade and qualify to be considered monkeys. "

It is at this point that a confusion is revealed which has affected all of SIMONS' argument. It is evident to anyone who has considered the evidence that the parapithecids (or -cines) are at a *grade* level equal to that of monkeys in the vernacular sense, perhaps more " progressive " in some characters than the marmosets (Callitrichidae) of South America (see SIMONS, 1970, p. 102). But this is not proof of taxonomic placement, much less ancestry, by comparison to other forms, living or extinct. Success in terms of numbers in one time interval does not guarantee evolutionary survival or advancement, as witness the extremely successful primate *Plesiadapis*, the equid *Hipparion* and innumerable other " dead-ends ". If the parapithecids were not ancestral to later cercopithecids, the success of the former is not (directly) relevant to the rarity of the latter. Only a more detailed analysis of the morphology involved can demonstrate or " prove " relationships, and even then, not necessarily ancestry.

It is to be recalled that SIMONS' most convincing display of morphological similarity between *Parapithecus* and a monkey was with *C.* (*M.*) *talapoin*, which he termed " possibly most primitive ". Only brief comparison was made with the earliest fossil cercopithecids and none with the suite of characters expected in a pre-cercopithecid ancestor. Moreover, my analysis indicates that in both dental and cranial form, the talapoin is a member of the highly derived Cercopithecini, which have lost M_3 hypoconulids, reduced lateral flare and increased relative length in all cheek teeth. Further, as shown by VERHEYEN (1962) and others, the skull of the talapoin is probably derived (through neoteny ?) by comparison to typical *Cercopithecus*. Only the (unrelated) character of female sexual swelling may be an ancestral trait retained by *C.* (*M.*) *talapoin*.

A direct comparison of the morphology of *Parapithecus* and the pre-cercopithecid morphotype postulated above reveals that they share high-crowned molars and the less definite features of deep mandibular corpus (in *Apidium*) and slightly rotated P_4 (in some Miocene monkeys). The retention of rather large hypoconulids and of a paraconid on dP_4 are probably ancestral catarrhine (Old World anthropoid) features, as is retention of three premolars. However, the development of canine honing on P_2 is derived, and it seems unlikely that such a specialization would be lost and then redeveloped on P_3 if P_2 were dropped, nor is it likely that the P_3 of *Parapithecus* might be lost, leaving only P_2 and P_4. The low metaconid on P_4, short M_3 and general lack of cingulum are additional important differences between this fossil and the hypothesized pre-cercopithecid condition.

It would seem best at present to consider that *Parapithecus* and *Apidium* represent a group of early anthropoids of " monkey " grade which may have been the ecological vicars of cercopithecids and whose environment might have been specially similar to that of talapoins, causing further parallels. In some dental characters, notably increased crown height and perhaps a tendency toward lophodonty by a different route, this group converged on cercopithecid morphology, while in other ways they modified ancestral conditions in parallel. Several of SIMONS' above-cited statements are more easily interpreted in this light as well. Finally, the dangers of searching only for ancestors are clearly revealed, for if parapithecids are not the ancestors of cercopithecids, where are they to be placed in primate phylogeny ?

IV. - AN ALTERNATIVE APPROACH TO MONKEY ORIGINS

Having rejected SIMONS' interpretation of cercopithecid ancestry as unsatisfactory, the most prudent course might be to claim that the incompleteness of the fossil record allows no further conclusions at this time. But hypothesis-formulation and prediction are among the essential aspects of the scientific method, and paleontology is built around fossil evidence. Therefore we may ask if any other known fossils are better candidates for having shared recent common ancestry with the progenitor of Cercopithecidae. All of the non-parapithecid Fayum primate species are at present considered "apes" by SIMONS (1972). One immediately obvious feature of this adaptive-taxonomic complex is the variation observed at what appears to be an early stage of catarrhine evolution. *Aegyptopithecus* is known from a skull, several partial mandibles and isolated teeth; of all the Fayum species, it seems most similar in morphology to early African species of *Dryopithecus* (and perhaps "*Limnopithecus*", with which it has been compared by ANDREWS, 1970). *Aeolopithecus* is represented by a single mandible whose precise dental morphology cannot be evaluated due to its erosion, but it does afford further evidence of Fayum primate variability. The three remaining named species, including only five or six specimens with certainty, are of greater interest to this discussion.

Oligopithecus savagei, the oldest Fayum catarrhine (figs. 1 H, 2 J & K), is known from a single mandibular fragment with C-M_2, presumably of a male because of the well-developed C′ honing facet on P_3 (see also SIMONS, 1971 a). *Propliopithecus haeckeli* has as holotype two portions of (probably) a single mandible, preserving both $C_{,}$-M_3 (except the left $C_{,}$ – figs. 1 D & E, 2 H & I). SIMONS (1967 a, 1971 b) has reported but never described isolated teeth of similar morphology and size from the middle faunal horizon, suggesting a similar (or older) age for the type. Two incompletely described specimens from the upper horizon also present similar morphology : a juvenile mandible with $dC_{,}$-M_2 (fig. 2 C & E; see 1967 b) and a specimen with P_3-M_3, previously figured and identified as *Aegyptopithecus zeuxis* (1971 a, b, 1972). Simons now (personal communication) identifies the latter as *Propliopithecus* sp. because of its short M_3 - I suggest it to be a male, with a large P_3, while the type is presumably female. The final specimen of interest is that which SCHLOSSER (1910, 1911) termed *Moeripithecus markgrafi*, a mandible fragment with $M_{1\text{-}2}$ (figs. 1 F-G, 2 F-G). SIMONS (1967 a, 1971 b, 1972) has argued convincingly that this specimen is a juvenile best considered as representing a distinct species of *Propliopithecus*. It certainly appers referable to that genus, and its juvenile character is further emphasized by the open distal root on M_2 (see fig. 1 F) (1).

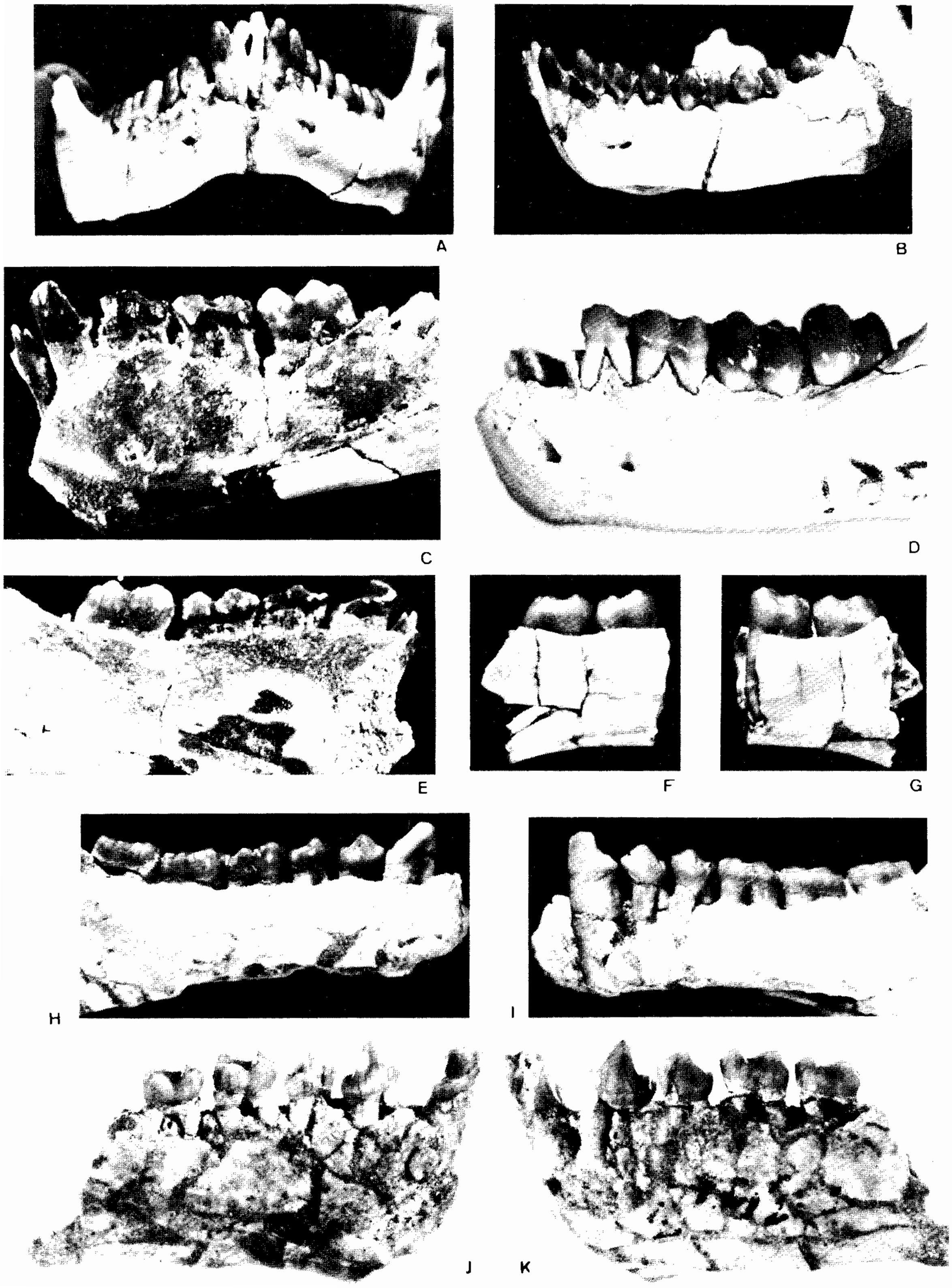
If these several specimens are considered together as representing a pool of morphological variability known to be present in the Oligocene of northeastern Africa, it is possible to discern a mosaic of features similar to those postulated for a pre-cercopithecid of similar age. These include : the presence of only two premolars, the P_3 with well-developed upper canine honing facet, the P_4 with subequally large metaconid and protoconid and two large foveas; a cingulum, especially bucally, around the lower molars, which have lost the paraconid and moderately enlarged the trigonid, separating the protoconid and metaconid but linking them by a crest (this feature only in *Propliopithecus* spp.); the tooth crowns are high, but the lingual notches relatively low; hypoconulids are present and of moderate size, but with evidence of appression to the entoconid — this is clearest in *Oligopithecus* and on M_1 more than M_2, while it is strongest on dP_4 of *Propliopithecus* sp. The molars are rounded, with flat wear of thin enamel in *Propliopithecus* : in *P. haeckeli,* the M_3 is narrow, but $M_{1\text{-}3}$ are subequally long; the M_2 is wider and longer than M_1 in "*Moeripithecus*", in which the buccal cingulum slopes outward almost in a "flare", and the trigonid basins are longer.

It has already been suggested that the lower buccal cingulum could have developed into cercopithecid flare are in P_4-M_3, and the high crowns of these teeth are similar to those expected in premonkeys; shallow intercusp notches are also expected in ancestral forms, especially as they seem to have deepened independently in both subfamilies (compare colobines and *Theropithecus*). The large P_4 metaconids of Fayum "apes" are more cercopithecid-like than those of *Parapithecus,* and as VORUZ (1970) has also observed, it is quite conceivable that the hypoconulid on dP_4-M_2 could have been lost through fusion with the entoconid due to interference with upper molar occlusion, in much the same way that many lineages lost the paraconid through interference with a developing hypocone. Hypoconulids were retained on M_3 to occlude with the M^3 distal fovea. Few upper molars of Fayum non-parapithecids are known (or published), and these are quite wide with lingual cingular shelves, but with cingular incorporation into the lingual surface, a moderately flared tooth would result.

In his original description of *Oligopithecus,* SIMONS (1962) suggested possible similarities to cercopithecids, but later abandoned this view in favor of a parapithecid ancestry. KÄLIN (1961 and especially 1962) discussed the possibility that "*Moeripithecus*" might be a monkey ancestor, but rejected this relationship while concentrating on questions of cusp and loph(id) homology. He also agreed with SCHLOSSER that the shallow jaw would imply a long face, but this shallowness is a function of its juvenile state, not a definitive character. ABEL (1931) found "*Moeripithecus*" difficult to place phyletically, but thought it might be somehow linked to *Apidium*, which he considered a cercopithecid forerunner. Even earlier, REMANE (1924) had noted some similarity between *Propliopithecus* and *Prohylobates tandyi,* an (early ?) Miocene Egyptian fossil which SIMONS (1969 a) has shown to be one of the earliest identified cercopithecids. Simons emphasized the distal wear facet on M_2 of the type specimen, suggesting it to be a true hypoconulid, on the midline and thus similar to

(1) More detailed descriptions, illustrations and different interpretations of SCHLOSSER's three types are given by KÄLIN (1961).

FIG. 2. — Lateral views of Fayum primates. A, B. Same as 1C, frontal and left labial views. C, E. *Propliopithecus* sp., Y.P.M. 23804, $dC_{,}$1M_1, photographically reversed right labial and lingual views. F, G. Same as 1F, G, photographically reversed right lingual and labial views. H, I. Same as 1E, photographically reversed right lingual and labial views. AB, F-I at approximately twice natural size; C-E, J-K at approximately three times natural size.


A
B
C
D
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K

Parapithecus. This may indeed be a remnant hypoconulid, as might be expected in light of the remnant crista obliqua in roughly contemporary *Victoriapithecus*; but similar facets are found on M_2 of some *Theropithecus* individuals, representing merely an accessory cuspule. Finally, KURTEN (1972) has recently argued that *Propliopithecus* could be an early hominid, a view held previously but since dropped by both SIMONS and PILBEAM. Much of KURTEN's argument is based on the small P_3-C' complex in the type specimen of *P. haeckeli* – the value of this point diminishes greatly if it is accepted that this individual is female, a previously unconsidered possibility.

It seems clear that known *Propliopithecus* spp. are morphologically close to *Aegyptopithecus,* and *Aelopithecus* and *Oligopithecus* probably also shared recent common ancestry with these genera. The purpose of the present discussion is not to prove that any known population is *the* ancestor of the Old World monkeys, but merely to clarify some of the geometry of phylogenetic relationships. The search for ancestors alone is generally counter-productive, more so in this case where the parapithecids may have been the ecological replacements of cercopithecids in the Fayum region. On the other hand, the variability seen in known Fayum "apes", especially *Oligopithecus* and *Propliopithecus* spp., suggests that perhaps in a different environmental zone, some early catarrhines combined in a single animal the mosaic of cercopithecid-like features found above in several species. This ancestor might be termed a "hominoid" on overall grounds of grade similarity, but a "cercopithecid" in terms of its descendants. In less precise terms, one can almost facetiously say that monkeys did not give rise to apes, but that (some) "apes" gave rise to (Old World) monkeys.

V. - OTHER RELATIONSHIPS WITHIN ANTHROPOIDEA

This study has suggested that the Old World monkeys developed as a specialization from an Oligocene catarrhine stock already possessed of an "apelike" dentition. Additional derivatives of this stock became known forms of apes and men, among other groups. But then to return to an earlier question, what is the position of the Parapithecidae ? If the above analysis is correct, they would seem to represent a group rather distinct from the living catarrhines and their ancestors. In cladistic terms, the Catarrhini *sensu stricto* (inluding *Oligopithecus*, etc.) and the Parapithecidae are sister groups descended from a common ancestor, unknown and of uncertain grade. The step of constructing a morphotype for this ancestor is of great interest, although beyond the scope of this paper (but see SZALAY, 1970, 1972). Such an ancestor, however, may not yet have developed a canine honing mechanism : that of parapithecids seems weak on the retained P_2, while the strong hone on *Oligopithecus* has cut through the as yet unthickened enamel, suggesting a recent, "unperfected" adaptation.

Classification at family-group level among the Anthropoidea is quite unsettled, but one possibility which merits consideration is to place Cercopithecidae, perhaps Oreopithecidae, and one to three families of apes and men in a single superfamily (2). Parapithecidae might be placed in such a superfamily by a classical systematist (e.g., MAYR or SIMPSON) on grade ("horizontal") grounds, but would certainly be excluded by a strict cladist. In the latter case, the infraorder Catarrhini could include two superfamilies, rearranging their contents while retaining the present concept of this monophyletic group.

Finally, the question of a possible Old World origin of South American Platyrrhini has been reviewed by HOFFSTETTER (1972). I remain unconvinced by either the morphological or paleogeographical arguments presented to date, but recently GINGERICH (1973) has shown that *Apidium* had the same annular ectotympanic development as *Aegyptopithecus* (SIMONS, 1972), *Pliopithecus* and modern ceboids. This is presumably the ancestral condition for anthropoids, as opposed to the tubular meatus of later catarrhines. Parapithecids are again seen to be extremely conservative animals, and it is morphologically conceivable that a West African primate group may have existed which was related both to the known Fayum genera and to ceboids.

More African Paleogene fossils and detailed analysis of extant and extinct anthropoideans will provide the only meaningful solutions to these problems.

(2) The vicissitudes of nomenclatural priority lead to this superfamily being named Cercopithecoidea, a sidelight which may delay serious consideration of its utility as a concept.

BIBLIOGRAPHY

Abel O., 1931. — *Die Stellung des Menschens im Rahmen der Wirbeltiere.* G. Fischer, Jena, 398 p.

Andrews P., 1970. — Two New Fossil Primates from the Lower Miocene of Kenya. *Nature*, **228**, 537-540.

Delson E., 1973. — Fossil Colobine Monkeys of the Circum-Mediterranean Region and the Evolutionary History of the Cercopithecidae (Primates, Mammalia). University Microfilms, Ann Arbor, 856 p.

Delson E., 1975 a. — Evolutionary History of the Cercopithecidae. In *Approaches to Primate Paleobiology*, ed. F. S. Szalay. *Contrib. primat.*, **5**. 167-217. Karger, Basel, New York.

Delson E., 1975 b. — Paleoecology and Zoogeography of the Cercopithecidae. In *Antecedents of Man and After*, vol. 1, ed. R. Tuttle. *World Anthropology* : Proc. IX Int. Cong. Anth. Ethn. Sci. Mouton, the Hague.

Delson E. and Andrews P., 1975. — Evolution and Interrelationships of the Catarrhine Primates. In *Phylogeny of the Primates : A Multidisciplinary Approach*, ed. W. P. Luckette and F. S. Szalay, Plenum, New York.

Gingerich P. D., 1973. — Anatomy of the Temporal Bone in the Oligocene Anthropoid *Apidium* and the Origin of Anthropoidea. *Folia primat.*, **19**, 329-337.

Hennig W., 1966. — *Phylogenetic Systematics.* Chicago, Univ. Illinois Press, 263 p.

Hoffstetter R., 1972. — Relationships, origins and history of the ceboid monkeys and caviomorph rodents : a modern reinterpretation. *Evolutionary Biology*, **6**, 323-347.

Hürzelier J., 1949. — Neubeschreibung von *Oreopithecus bambolii* Gervais. *Mem. Paleont. Suisses*, **66**, 1-20.

Kälin J., 1961. — Sur les Primates de l'Oligocène inférieur d'Egypte. *Ann. Paleont.*, **47**, 3-48.

Kälin J., 1962. — Über *Moeripithecus markgrafi* Schlosser und die phyletischen Vorstufen der Bilophodontie der Cercopithecoidea. *Bibl. primat.*, **1**, 32-42.

Koenigswald G. H. R., von, 1969. — Miocene Cercopithecoidea and Oreopithecoidea from the Miocene of East Africa. *Fossil Vertebrates of Africa*, **1**, 39-51.

Kurten B., 1972. — *Not From the Apes.* Random House, New York.

Osborn H. F., 1908. — New fossil mammals from the Fayum Oligocene, Egypt. *Bull. Amer. Mus. Nat. Hist.*, **24**, 265-272.

Remane A., 1924. — Einige Bemerkungen über *Prohylobates tandyi* R. Fourtau und *Dryopithecus mogharensis* R. Fourtau. *Cbl. Min., Geol. Paläont.*, 220-223.

Schaeffer B., Hecht M. and Eldredge N., 1972. — Phylogeny and Paleontology. *Evolutionary Biology*, **6**, 31-46.

Schlosser M., 1910. — Über einige fossile Säugetiere aus dem Oligocän von Aegypten. *Zool. Anz.*, 500-508.

Schlosser M., 1911. — Beiträge zur Kentniss der Oligozänen Landsäugetiere aus dem Fayum, Aegypten. *Beitr. Paläont. Geol. Öst.-Ung.*, **24**, 51-167.

Simons E. L., 1962. — Two New Primate Species from the African Oligocene. *Postilla* (Yale), **64**, 1-12.

Simons E. L., 1967 a. — Review of the Phyletic Interrelationships of Oligocene and Miocene Old World Anthropoidea. *Coll. Int. Cent. Nat. Rech. Sci.*, 163, *Problèmes Actuels de Paléontologie* (*Evolution des Vertébrés*), 597-602.

Simons E L., 1967 b. — The Significance of Primate Paleontology for Anthropological Studies. *Amer. J. Phys. Anth.*, NS, **27**, 307-332.

Simons E. L., 1969 a. — Miocene Monkey (*Prohylobates*) from Northern Egypt. *Nature*, **223**, 687-689.

Simons E. L., 1969 b. — The Origin and Radiation of the Primates. *Ann. N. Y. Acad. Sci.*, **167**, 319-331.

Simons E. L., 1970. — The Deployment and History of Old World Monkeys (Cercopithecidae, Primates). In *Old World Monkeys*, ed. J. R. and P. H. Napier, Academic Press, New York, 97-147.

Simons E. L., 1971 a. — Relationships of *Amphipithecus* and *Oligopithecus*. *Nature*, **232**, 489-491.

SIMONS E. L., 1971 b. — A Current Review of the Interrelationships of Oligocene and Miocene Catarrhini. In *Dental Morphology and Evolution*, ed. A. A. Dahlberg, Chicago, Univ. Chicago Press, 193-208.

SIMONS E. L., 1972. — *Primate Evolution : An Introduction to Man's Place in Nature*. Macmillan, New York, 322 p.

SIMONS E. E., 1974. — *Parapithecus grangeri* (Parapithecidae, Old World higher primates new species from the Oligocene of Egypt and the initial differentiation of Cercopithecoidea. *Postilla* (Yale), **166**, 1-12.

STRAUS W. L., jun., 1953. — Primates. In *Anthropology Today*, ed. A. L. Kroeber, Wenner-Gren Foundation, New York.

SZALAY F. S., 1970. — Late Eocene *Amphipithecus* and the Origins of Catarrhine Primates. *Nature*, **227**, 355-357.

SZALAY F. S., 1972. — *Amphipithecus* Revisited. *Nature*, **236**, 179-180.

VERHEYEN W. N., 1962. — Contribution à la crâniologie comparée des Primates. *Ann. Mus. Roy. Afr. Centr., Sci. Zool.*, sér. 8°, **105**, 1-247.

VOGEL C., 1966. — Morphologische Studien am Gesichtsschädel Catarrhiner Primaten. *Bibl. primat.*, **4**, 1-226.

VORUZ C., 1970. — Origine des dents bilophodontes des Cercopithecoidea. *Mammalia*, **34**, 269-293.

INTERVENTION DE M. VASSEROT
après la communication de M. Delson

Vous estimez qu'un rameau détaché de la souche des Anthropoides a donné naissance aux Singes de l'Ancien Monde ?

RÉPONSE DE M. DELSON

Cela dépend de votre définition des «-Anthropoïdes ». La dichotomie de base parmi les « Primates supérieurs » est celle entre Platyrhiniens et Catarhiniens,' qui ensemble composent les Anthropoidea (ou les Simiiformes du Prof. HOFFSTETTER). Puis, parmi les Catarhiniens, la dichotomie principale me paraît être entre les Parapithécidés et les « Catarhiniens modernes », les Cynomorphes (Cercopithecidae) et les Anthropomorphes (« Hominoidae » de la plupart des auteurs). L'ancêtre commun des « Catarhiniens modernes » a pu avoir des dents de type anthropomorphe dans un crâne de type gibbon (ou colobiné) situé sur un corps de type « singe inférieur » (monkey-like) : ce sont les conditions ancestrales pour le groupe. Enfin, les Cynomorphes sont forcément distingués des Anthropomorphes et ceux-ci peuvent être divisés d'une manière ou d'une autre d'après l'interprétation de la phylogénèse des gibbons.

NOTE ADDED IN PROOF

In an article published while the present paper was in press, SIMONS (1974) formally described and named *Parapithecus grangeri* — this name is therefore used in the text as it is no longer a *nomen nudum*. Unfortunately, the distinctions between the species of *Parapithecus* and between this genus and *Apidium* remain incompletely documented — the relatively larger premolars in *Parapithecus* are especially diagnostic. Essentially, SIMONS has reiterated his arguments as summarized above, concluding in part (pp. 9-10) : "there can no longer be any doubt that Parapithecidae are monkeys, not prosimians; zoogeographic considerations ally them with cercopithecoids — not ceboids." This is still the grade argument I have discussed. SIMONS (1974, p. 10) continues to classify *Parapithecus* and *Apidium* in the Cercopithecoidea, but has returned them to family rank. "Their ranking among the Cercopithecoidea need in no way imply that the parapithecids would or could have been directly ancestral to any surviving Old World Monkey group but does leave open the possibility that *Parapithecus* may well prove to have been such an ancestor." This purely phenetic approach to taxonomy is unsatisfactory, as no special relationship has been shown to exist between Cercopithecidae and Parapithecidae.