rate constant to be 3×10^9 M^{-1} s^{-1} for the reaction of the oppositely charged radical ions to generate the excited singlet state (*10*). Thus, under more dilute conditions, a radical anion can diffuse some distance into the region where the radical cation exists without reaction, and a sharp reaction zone no longer exists. For example in the presence of 10 μM radical cation, the half life of the reaction will be ~25 μs, and only a portion of the radical anions will react during the 50-μs voltage pulse leading to the lower normalized λ value. Indeed, for concentrations where low values of λ are obtained, the relative number of photons produced after the cathodic pulse increases, which shows that some radical anions fail to react during the pulse. Taken together, the concentration-dependent, stochastic data illustrate the dynamic competition between the rates of diffusion and chemical reaction for a process whose rate constant is near the diffusion-controlled limit.

With sufficient temporal and spatial resolution, all bimolecular chemical reactions should have the stochastic appearance revealed in this work. However, with the exception of measurements of ion fluxes through individual channels in biological membranes (*16*), there are few other examples that so clearly reveal these fundamental events in solution. Most investigations of stochastic events involve the random actions of groups of particles as opposed to the individual events observed here (*17*). For example, the stochastic nature of the electrical noise generated by fluctuations of electrons and ions at the electrode-electrolyte interface (*18*) and the process of electronucleation of multiple atoms during metal deposition on electrodes (*19*) arise from stochastic processes. Indeed, these events for a single molecule have recently been measured with a scanning electrochemical microscope (*20*). In the measurements shown here, however, individual reaction events that can be counted and yet arise from a condition where all of the reagents are freely diffusing solution components.

The ability to observe individual chemical reactions in solution opens many new possibilities for investigation in addition to this new way to determine the rate-limiting step of bimolecular reactions. For example, although the excited singlet lifetime of DPA is too short for resolution in these experi ments, longer lived intermediates in chemiluminescent reactions, such as the excited triplet state of ruthenium trisbipyridine (*21*), should have a lifetime accessible with this technique. With a polychromator, the energy of each individual reaction could be probed. In addition, the Poisson distribution describing the results observed in these experiments defines the standard deviation for this method when used in trace analysis. In all of these applications, the stochastic nature of single reaction events adds a new dimension that can now be probed.

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11. The time-averaged photon emission is pseudo-steady state because the amount of radical cation in solution exceeds the amount of radical anion generated during the cathodic pulse. A steady-state generation rate is desirable to meet the requirement for stationarity necessary for a Poisson distribution.
12. The background in this experiment is negligible on the 50-μs time scale of each voltage pulse and is due to the dark counts of the photomultiplier tube (50/s). A suspected background count is seen at 195 μs in Fig. 2C.
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Skulls and Anterior Teeth of *Catopithecus* (Primates:Anthropoidea) from the Eocene and Anthropoid Origins

Elwyn L. Simons

Recent finds of *Catopithecus browni* at an upper Eocene fossil site in the Fayum depression, Egypt, reveal features of the earliest higher primates. This basal anthropoidean shows a set of derived cranial and dental features that first occur in combination in this fossil. Old World Anthropoidea or Catarrhini can now be traced back to *Catopithecus* in Egypt. Size, shape, orientation of incisors and canines, and other features of the teeth and skull relate *Catopithecus* both to later Anthropoidea and to the early and middle Eocene cercamoniine adapoids. Most defining characteristics of higher primates cannot be documented earlier than the late Eocene of Africa.

Oligocene primates from the Fayum, Egypt, show remarkable diversity. Twelve primates of five different taxonomic families have been described. Until recently, antecedents to these primates were unknown (*1*). Finds made in Egypt since 1987 of a second and different series of anthropoids from Eocene deposits give evidence about the roots of the anthropoid family tree. This second set of early higher primates comes from a site, locality 41 (L-41), situated north of Lake or "Birket" Qarun in the Jebel Qatrani Formation, Fayum Province, Egypt, which is dated at about 36 million years ago. The L-41 primates belong to seven different genera and species, one of which is undescribed (*2–4*). This brings the total of known Fayum primate species to 19. These Eocene species could belong to six or

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Department of Biological Anthropology and Anatomy, Duke University, Durham, NC 27705-5000, USA.

more families. In this report, I use dental and cranial features (2–4) to determine if *Catopithecus* and its contemporaries are definitely early anthropoids, and if they are, are they related to any earlier group at the base of our own branch of the primate family tree?

In 1992 and 1993, nearly complete specimens of *Catopithecus* were found at L-41 that together hold the entire antemolar dentition. A mandible of another contemporary L-41 primate, *Arsinoea*, also has incisors preserved. Shape and proportions in the antemolar teeth have been the subject of considerable study in hopes of identifying what Eocene primate group is related to the ancestry of apes and monkeys. Thus, unlike other specimens of Anthropoidea dating before the Miocene Epoch, *Catopithecus* finds preserve all the anterior teeth and most details of skull structure. Although the Oligocene genera *Apidium* and *Aegyptopithecus* from the Fayum are known from scores of specimens, none preserve associated upper incisors. Hence, even in these well-known primates, the most anterior upper dental arcade has been reconstructed from isolated teeth. The *Catopithecus* crania show the locale of the foramen magnum, the position of various other foramina (including the lachrymal, carotid, and postglenoid foramina), and the extent of postorbital plates and also make possible determination of the probable brain volume, 3.1 cm^3.

Some of the mandibles and cranial parts of *Catopithecus* discussed here include a partial skull at the Duke Primate Center (DPC 8701), a nearly complete but shattered skull housed at the Cairo Geological Museum (CGM 42222), and two other crania (DPC 11594 and DPC 11388). DPC 11594 holds the entire upper dentition and anterior teeth except for the right canine. DPC 11388 is the only individual higher primate from before the Miocene in which the skull and mandible are associated and is the oldest anthropoid in which all of the incisors have been preserved. These finds now document the entire dentition of one particular basal anthropoidean. In addition, the type specimen of *Arsinoea kallimos* (CGM 42310), another L-41 primate that belongs to a different primate family than *Catopithecus*, preserves most of the two left incisors.

Site L-41 reveals not only early anthropoidean anatomy but diversity of the suborder as well. *Catopithecus* is an oligopithecine propliopithecid, but there is also at L-41 a parapithecid species, *Serapia eocaena*. Two other primates found there, *Arsinoea kallimos* and *Proteopithecus sylviae*, also have dental or cranial characters of higher primates but may well belong in other unnamed families. The type mandible of *Arsinoea* preserves the entire left dental series. These discoveries imply that anthropoideans originated as very small animals: Both *Proteopithecus* and *Arsinoea* are the size of marmosets. In addition, there are two prosimian families at L-41. *Plesiopithecus teras*, regarded at the time of description (3) as of uncertain classification, is now ranked (5) as a lorisiform prosimian. Finally, another primate from L-41, a cercamoniine prosimian, has also been collected (6). All of these, when taken together with additional primate groups (a possible omomyid and a tarsier) from higher in the Fayum section, imply that Egypt was once an important center of primate evolution. Others have suggested (7, 8) that Order Primates arose in Africa, a view supported by the remarkable diversity of primates at L-41.

For many years, researchers have disagreed about the phyletic meaning of the front teeth for determination of the basic groupings among primates (9–11). There are two great groups of Eocene primates, the adapoid and the omomyid prosimians, well-documented by scores of genera and species recovered from Eocene deposits in the Northern Hemisphere. The adapoids are extinct, but there is a living descendant of the omomyids: *Tarsius*. Documentation of incisor and canine structure in these small ancient prosimians has taken a long time because the front teeth almost always fall out of the tiny mandibles, maxillae, and premaxillae.

Also, there are two schools as to how to divide Order Primates into suborders. The two suborders are either Prosimii and Anthropoidea or, differently defined, Strepsirrhini and Haplorhini. In diagnosing the latter category, *Tarsius* is joined with the higher primates (monkeys, apes, and humans) to make up the haplorines, but in the former choice of subordinal arrangement, this genus stands among the Prosimii. Fossils can contribute to resolving whether tarsiiform omomyids are particularly close to Anthropoidea. For those who consider *Tarsius* and its omomyid relatives to be allied to anthropoids, in Haplorhini, there has been a problem in dealing with anterior tooth morphology, which is not like that of early anthropoideans. Among omomyids and *Tarsius*, the front teeth are all rather homomorphic with conical apices on the anterior premolars, small conical canines, and conical incisors, whereas in anthropoids, the premolars, canines, and incisors are all quite different from each other in morphology (heteromorphy). A survey of early fossil primates and living non-anthropoideans demonstrates that pointed incisors are primitive in both Proprimates and Primates. Therefore, the spatulate incisors, heteromorphic anterior tooth groups, and relatively large canines are shared-derived features held in common between cercamoniine adapoids and the anthropoids.

Lower incisors of *Catopithecus* and *Arsinoea* are illustrated here (Fig. 1). *Catopithecus* had large upper canines and an upper dental formula of 2·1·2·3, the same as in later catarrhines (Fig. 2). The mandible of DPC 11388 shows the same lower dental formula. These specimens demonstrate that, as in later higher primates, *Catopithecus* had upper central incisors larger than the laterals (Fig. 2) and had lower central incisors that were smaller than the laterals (Fig. 1A). This is a characteristic of both Oligocene-Miocene Anthropoidea and members of the earlier family Adapidae. Omomyid prosimians typically have the reverse condition in incisor size (that is, the lateral upper and lower central incisors are larger) and usually have relatively small canines compared with adjacent teeth. In con-

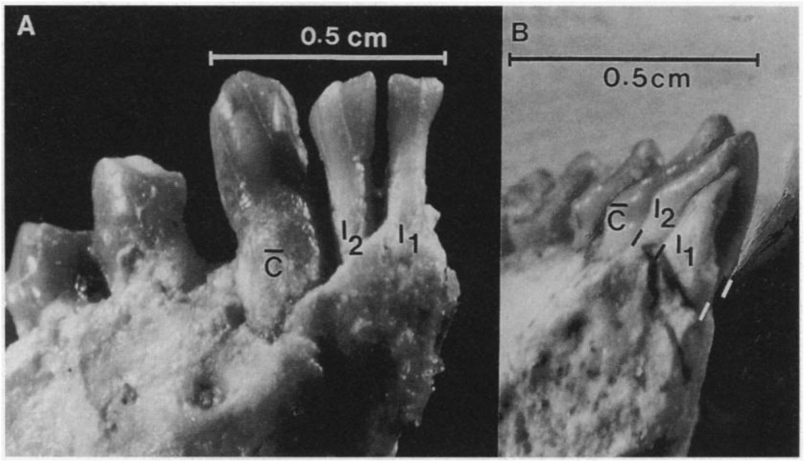

Fig. 1. Lower incisors of earliest anthropoideans. (**A**) Close-up view of the right incisors (I) and canine (C) of *Catopithecus* DPC 11388. Note the broad, chisel-edged incisor crowns and that, as is typical of all basal anthropoids, I/1 is much smaller than I/2. (**B**) View of the left I/1 and I/2 of *Arsinoea kallimos* type CGM 42310. Note how the central base of the middle incisor, I/1 marked by lines, is much smaller in anteroposterior diameter than is I/2, thus demonstrating the characteristic smaller central incisor pair of Oligocene-Miocene anthropoids.

trast, the upper and lower canines of *Catopithecus* are large and long. *Catopithecus* also has the anthropoidean type of spatulate and relatively vertically emplaced incisors above and below. Its incisors have no resemblance in shape or orientation to the forward-jutting front teeth that are typical of omomyids. Thus, it seems unlikely that the basal higher primates arose from the latter group as some have suggested (*10, 12*).

Taken altogether, known specimens of *Catopithecus* confirm another characteristic of later anthropoids, and of certain adapoids, namely sexual dimorphism in canine size (Fig. 3). Such dimorphism is not found in modern prosimians. Its first occurrence is in the Eocene adapoids (*13, 14*). Unlike earlier Eocene primates, in which incisors jut forward, the roots of central upper incisors of *Catopithecus* appear to fit closely together: Their orientation is apparently more vertical (orthal), and the upper canine has a vertical groove on its anterior side. These additional features are all resemblances to Eocene adapoids (*13*) and to most Oligocene-Recent anthropoids.

The *Catopithecus* skulls establish the antiquity of a range of other anthropoid cranial characters. The first of these concerns sutural fusion in the face. DPC 11594 and 11388 show the loss of the metopic suture between the frontals but not sutural fusion between the two halves of the mandibles (DPC 11388). Closure of both sutures has always been found together in subsequent, Oligocene-Holocene, anthropoids. It has been thought that fusion of these two sutures uniquely occurred in earliest anthropoids perhaps as a response to facial stresses in chewing, but the *Catopithecus* specimens show that these two events were not coeval.

Postorbital closure of the eye region into an eye socket is a second higher primate characteristic. This feature never occurs in prosimians but is partially developed in species of *Tarsius*, owing, perhaps, to a coincidence arising from the large size of the eyeballs compared to the size of the brain. In species of this latter genus, eyeball size ranges from 81 to 116% of brain size (*15*). In tarsiers, in order to hold in this huge eyeball, a flange-like rim extends far out beyond the skull around the edge of the orbit. Most of the seemingly broad area of postorbital closure is made up of this flange projecting away from the braincase. Similar flanges are extended inward, giving the appearance of closure behind the eyeball, but typically there remains a large postorbital fenestra. The orbital region of *Catopithecus* shows no special resemblance to that of *Tarsius*, and the degree of postorbital closure is greater. Specimens such as the Cairo skull (CGM 42222) confirm postorbital closure of a degree equivalent to that seen in *Aegyptopithecus*. The ectotympanic of *Catopithecus* encircles the rim of the auditory opening, a condition seen also in *Aegyptopithecus*, living lorisoids, and platyrrhine primates. Even though both CGM 42222 and DPC 11594 are crushed flat, they show that the foramen magnum was shifted forward on the underside of the cranial vault, a location more anterior than usual for early prosimians but typical of higher primates. On the right side of DPC 11594, the outline of a crushed but uninflated middle ear can be made out, and on its mesial side, an anteriorly shifted carotid foramen, another derived anthropoidean feature first seen in *Catopithecus* (*16*).

The earliest well-documented Anthropoidea occur only in the Fayum, Egypt. Their retention of some prosimian features indicates that *Catopithecus* and other Fayum genera and species are probably close in time to the initial differentiation of higher primates. Analysis of the teeth of *Catopithecus* and the other anthropoideans from L-41 shows that it would be difficult, if not impossible, to prove on the basis of morphology of fragmentary and partial dentitions alone that a particular Paleogene primate belonged to Anthropoidea. Primate species that may or may not be anthropoideans and that could be 10 to 20 million years older than those of the Fayum have recently been reported from Morocco and China. In the first instance (*Altiatlasius*), the material is composed of isolated unassociated teeth (*17*), and the second (*Eosimias*) (*18*) consists of two jaw fragments: one with one tooth and the other with three. As a general rule, early material of this fragmentary sort cannot with confidence be assigned to the higher primates (*17*). *Eosimias* (*18*) has recently been made the basis of the assertion of the existence of an anthropoidean radiation in the middle Eocene of China. The two described specimens do not belong to the same species and the type is without any defining characters of anthropoideans. Why is this so? *Eosimias* lacks the defining set of features that char-

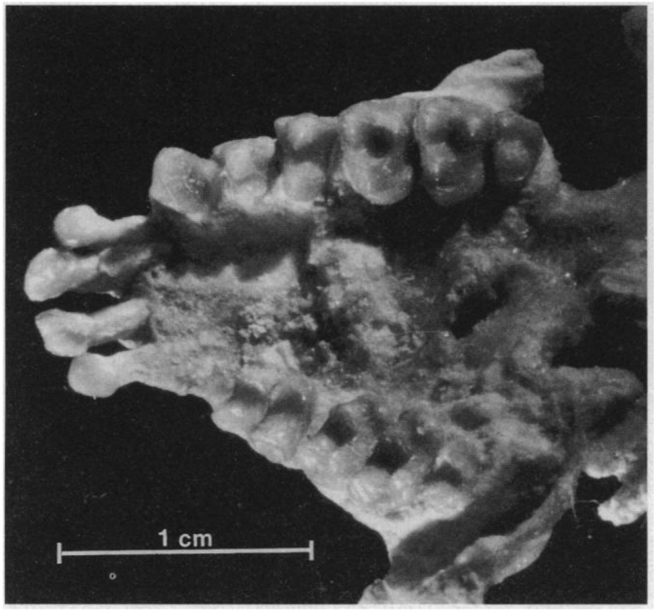

Fig. 2. The upper teeth of *Catopithecus browni* showing relative proportions. At the posterior base of the upper central incisors is a central boss or cusp edged laterally by faint cingula. Upper central incisors show a midline interstitial wear, or contact, facet. It appears from the shape and position of the complete left premaxilla that these two central teeth had closely approximated roots. The left premaxilla, in which the two incisors are firmly rooted, has slipped somewhat out of position so as to tilt the incisors forward into a more procumbent position. When this is corrected for, incisors are directed downward (or more orthally), as in modern Anthropoidea. *Catopithecus* is just as different in its anterior dentition from omomyids, or from *Tarsius*, as are later higher primates, and structural details of *Catopithecus* premolars and molars link cercamoniine upper molar anatomy with that of *Aegyptopithecus*.

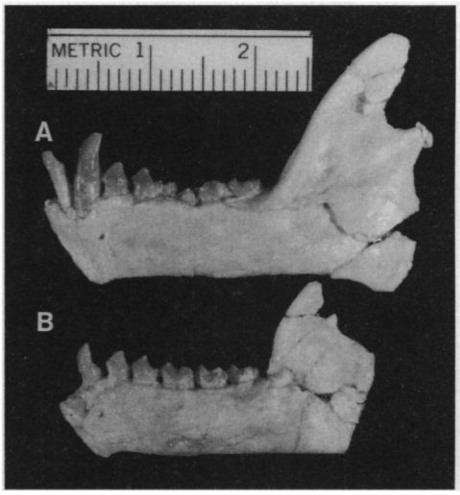

Fig. 3. Sexual dimorphism in *Catopithecus*. (**A**) Lateral view of left mandible of male *Catopithecus* DPC 7342 showing large lower canine. Although this tooth and the lateral incisor have slipped partly out of their sockets, this canine is almost 20% larger than the canine of DPC 11943 in (B). (**B**) Lateral view of left mandible in female *Catopithecus* DPC 11943 showing small lower canine. The combined height, anteroposterior length, and buccolingual breadth of this canine is 82% of the same measures in DPC 7342, although in both, the lengths of postcanine teeth are subequal.

acterize primitive anthropoids. There are also other possible Asian claimants to higher primate status, such as *Pondaungia*, *Hoanghonius*, or *Amphipithecus* (*19*), for which, unlike *Eosimias*, ranking in Anthropoidea might be a possibility. Paleogene faunas and floras show that some sort of interconnection existed then between northeast Africa and southern Asia, and thus, this suborder could have reached both regions in the Eocene. Nevertheless, neither *Hoanghonius* nor the Burmese Eocene fossils preserve the skull and front teeth, which, if they existed and were like those of Anthropoidea, would make their ordinal or subordinal ranking certain. Even if the Burmese forms were to prove to be definite anthropoideans, they could just as well be outmigrants from Africa as from anywhere else.

Fayum mammals also indicate that there was faunal interchange with Europe, but Europe lacks evidence of early anthropoideans. Recent discoveries at Glib Zegdou in Algeria described as *Algeripithecus* (*20*), *Tabelia* (*21*), and a form called *Djebelemur* from Chambi, Tunisia (*22*), are all forms that resemble in various ways the Fayum L-41 primates but are earlier in age. There is some evidence that the Algerian and Tunisian forms either are primitive anthropoideans or, in the case of the mandible of *Djebelemur*, relate to the cercamoniine group. Together, these latter primates and those from L-41 appear to root the earliest higher primates in the cercamoniine radiation. There have often been differences in deciding whether *Oligopithecus*, *Hoanghonius*, or *Algeripithecus* should be ranked as adapoids or as anthropoids (*6*, *8*, *21*). This is because of the high degree of similarity in the cheek tooth crowns of both groups, especially now that we understand the L-41 anthropoideans so fully. Thus, these shared-derived features do not involve just the front teeth but the entire dentition. The approximation of these two groups, which makes their molars difficult to tell apart, extends also to time and place, because a cercamoniine has been found at L-41 (*6*). The foregoing conclusions bring into question the existence of an haplorhine clade. The best evidence is that the origin of Anthropoidea was in Africa. Anthropoids either arose from a cercamoniine-like ancestor or from a similar endemic African group.

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A Scattered-Wave Image of Subduction Beneath the Transverse Ranges

J. Revenaugh

Over 5600 short-period recordings of teleseismic events were used to create deterministic maps of *P*-wave scatterers in the upper mantle beneath Southern California. Between depths of 50 and 200 kilometers, the southern flank of the slab subducting beneath the Transverse Ranges is marked by strong scattering. The marked scattering indicates that the edge of the slab is a sharp thermal boundary. Such a boundary could be produced by slab shearing or small-scale convection in the surrounding mantle. The northern limb of the slab is not a strong scatterer, consistent with thicker lithosphere north of the Transverse Ranges.

The Transverse Ranges comprise a distinct physiographic province that cuts across the dominant, north by northwest, tectonic fabric of Southern California and showcases some of the most spectacular topography in North America. The mantle beneath the ranges, home of a 60-km-wide tabular velocity anomaly to depths in excess of 200 km (*1*, *2*), is no less spectacular. This curtain of high *P*-wave velocity draped from the Transverse Ranges is commonly believed to be subducted subcrustal lithosphere resulting from $\geq 5 \times 10^6$ years of oblique convergence across the San Andreas fault zone (*3*, *4*), but the details of the anomaly are unclear. For instance, is subduction one-sided or two-sided (*3*–*5*)? Does the anomaly extend from the base of the crust, or does it only appear at greater depths (*2*, *6*)? And where does the slab detach from the crust? The subhorizontal crustal detachments beneath Los Angeles and the Ventura Basin—poorly understood but capable of great earthquakes (*7*)—are tied to deeper detachments of the Transverse Ranges.

In this study, I present a mode of imaging crust and upper mantle structure that uses singly scattered energy within the coda of teleseismic *P*. The method, known as Kirchhoff coda migration (KCM) (*8*), allows imaging of short length scale (≤ 2 km) velocity and density heterogeneity and structures transparent to travel-time tomography. The scattered-wave images are not as intuitive as tomography's, but the combination of the two methods is powerful. I applied KCM to 13 years of teleseismic seismicity recorded by the Southern California

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Earth Sciences–Crustal Imaging Laboratory, University of California, Santa Cruz, CA 95064, USA.