Discovery of the Oldest Known Anthropoidean Skull from the Paleogene of Egypt

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A group of primate fossils newly discovered in the Fayum badlands of Egypt is probably of Eocene age. The site is much older than the localities of previously known Egyptian early Tertiary primates. These finds include a crushed cranium that is the oldest skull found to date of a higher primate. This skull shows four characteristics of higher primates: a catarrhine dental formula, an ectotympanic at the rim of the auditory bulla, a fused frontal bone, and postorbital closure. Details of tooth structure (premolars and molars) and a possibly unfused mandibular symphysis resemble these parts in certain Eocene prosimians.

THE FAYUM BADLANDS OF EGYPT are the major site for recovery of the oldest known higher primates. Primate fossils come from the 340-m-thick Jebel Qatrani Formation. This formation consists of continental sedimentary rocks deposited on the largely marine Qasr el Sagha Formation that may in part be correlated with the middle Eocene. Although the areal extent of these fossil deposits is restricted, the primate fauna comes from a succession of deposits whose ages span several million years in time (*1*). The upper surface of the Jebel Qatrani Formation was eroded especially to the east and west of its principal exposures and then covered by the first of four basalt flows. The lowermost basalt is dated by K-Ar at 31 million ± 1 million years old (*2*); no precise dates have been determined for sediments stratigraphically below these basalts. The uppermost Fayum primates occur in stream channel deposits about 100 m below the lowermost basalt and are probably more than 32 million years old. The total 340 m in the Jebel Qatrani Formation are divided roughly equally into an upper and lower sequence (*1*).

Most primate specimens from the Fayum, almost 1000 in number, come from the upper sequence in or near quarries I and M, which are both about 245 m above the base of the formation. Below these sites in the lower sequence is quarry E, about 95 m above the base. Between 1961 and 1988 about a score of primate specimens were recovered from quarry E. None of these primates belong to the same species as do the primates of the upper sequence. In 1983, at about 47 m above the base of the Jebel Qatrani Formation, a new fossil-yielding site in a green shale unit of the upper variegated beds (*1*) was discovered and called locality 41 (L-41). Above this shale, there is a major unconformity that makes it impossible to determine the actual stratigraphic separation of L-41 from the rocks above it, including quarry E. The fossils from L-41 appear to be more primitive than species from the classic Fayum fauna of the lower sequence that were recovered mostly in the first decade of this century in and near quarries A, B, and C. These quarries overlie by a few meters the unconformity above L-41 and are themselves situated about 40 m below quarry E. The fossils at L-41 may well be of Eocene age, if the unconformity above it marks the Eocene-Oligocene boundary. Other choices for this time-boundary could be even higher in the section, at the marine-to-terrestrial transition in the Qasr el Sagha Formation, or, as has been generally accepted, at the top of the latter formation. In addition to primates, L-41 has also yielded hundreds of other mammalian fossils and fish and bird remains besides the 1987–1989 primate fossils. These primates have recently been assigned to two new genera and species that appear to represent the oldest higher primates or Anthropoidea (*3*).

The specimen described here was discovered near the south end of L-41 in November 1988. It consists of a nearly complete skull lacking only the anterior rostrum and possibly parts of the posterior margins of the cranium (Figs. 1 and 2). The specimen (DPC 8701) is flattened out with consequent distortion of the basicranial, facial, and maxillary portions. The frontal of the skull has been split by crushing, but the right side appears to pass beyond the midline. The upper teeth that are preserved are of a size and shape to belong to the species *Catopithecus browni* that has recently been described on the basis of a mandible with partial dentition and a single unassociated upper molar (*3*). The skull appears to be about the size of that of Goeldi's monkey *Callimico goeldii* or a little smaller than that of the squirrel monkey (*Saimiri sciureus*). Nevertheless, the upper cheek teeth of *Catopithecus* are rather larger than those of typical *Saimiri*.

The right dorsal margin of the orbit is preserved and shows that the orbital opening was somewhat squared off, there being more or less a right angle between the facial end of the frontal and the supraorbital margin. The frontal, insofar as it is preserved, closely resembles that of *Apidium phiomense* (*4*) in the aforementioned details. Since no skull of *Apidium* or other parapithecid is nearly as complete as this one is, auditory and basicranial comparisons are not possible. The posterior part of the right portion of the frontal appears to extend past a hypothetical midline bisecting the frontal and therefore indicates that there was no metopic suture.

The right maxilla and jugal have been crushed up into the orbital region so that it is impossible to determine the exact shape of the orbit inferiorly. An estimate of the transverse breadth of the orbit is about 1.25 cm. The central part of the right jugal has been broken from its attachment to the frontal and somewhat displaced from the maxilla as well. It has been shifted backward over the region where the postorbital plate would have contacted it with the braincase. Nevertheless, the remaining part of the jugal is very broad and resembles the side of a postorbital plate, rather than a postorbital bar. On the left side of the skull, the jugal bone grades smoothly backward into the side of the braincase, but damage and flaking of the specimen prevent recognition of sutures and therefore determination of the exact contribution of bones to the postorbital plate. Considered overall, the evidence from this skull strongly suggests that the animal had postorbital closure.

Both maxillae are present and on each side upper third premolar (P^3) to upper third molar (M^3) are preserved. The labial half of the left M^3 has been broken away. At the anterior end of the right maxillary fragment an alveolus for a small- to medium-sized canine can be seen. The right maxilla is intact from the ventral margin of the orbit to the P^4, and it is about 6.9 mm deep above the P^4. Thus, the maxilla is slightly deeper and the cheek teeth slightly larger than in *Saimiri*. The estimated size of the orbit is much smaller than in *Callimico*, which strongly indicates that *Catopithecus* was diurnal. Just below the ventral margin of the right orbit and directly above a line between P^3 and P^4 there is a single infraorbital foramen. The type mandible of this species (*3*) demonstrates a lower dental formula of 2-1-2-3 (two incisors, one canine, two premolars, and three molars), and the skull described here, preserving the right canine alveolus, demonstrates an upper dental formula of ?2-1-2-3.

Catopithecus browni comes from the same

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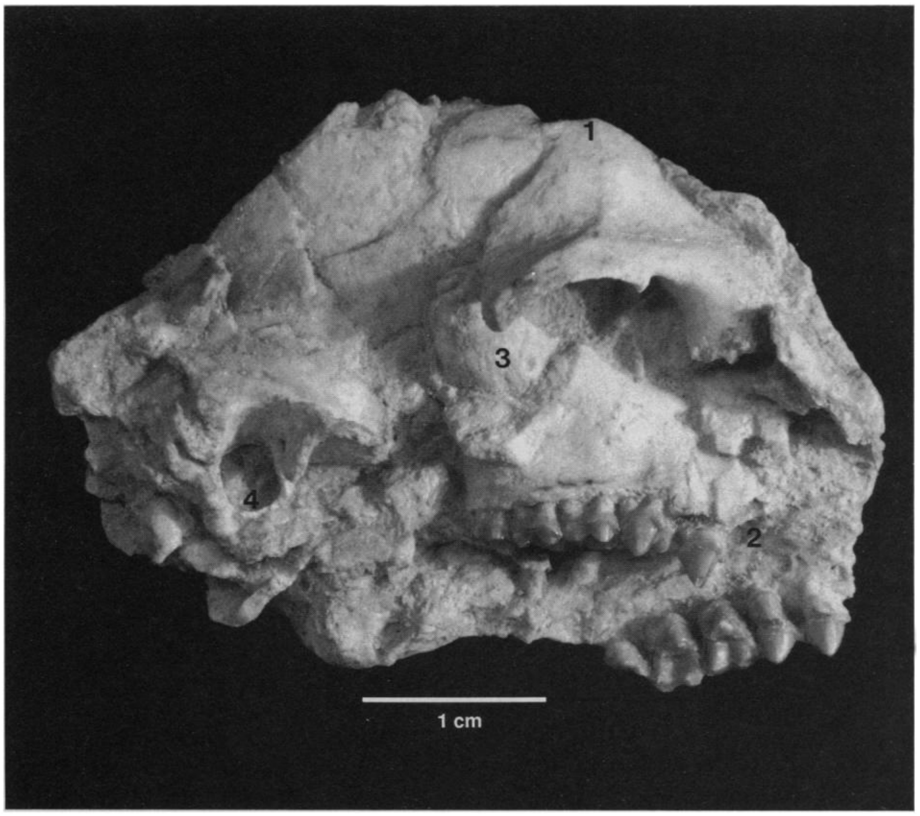

Fig. 1. Right side view of the skull of *Catopithecus browni* showing at 1, the lack of the frontal metopic suture; at 2, the presence of a canine alveolus; at 3, the expanded jugal; and at 4, the raised ectotympanic rim of the auditory aperture.

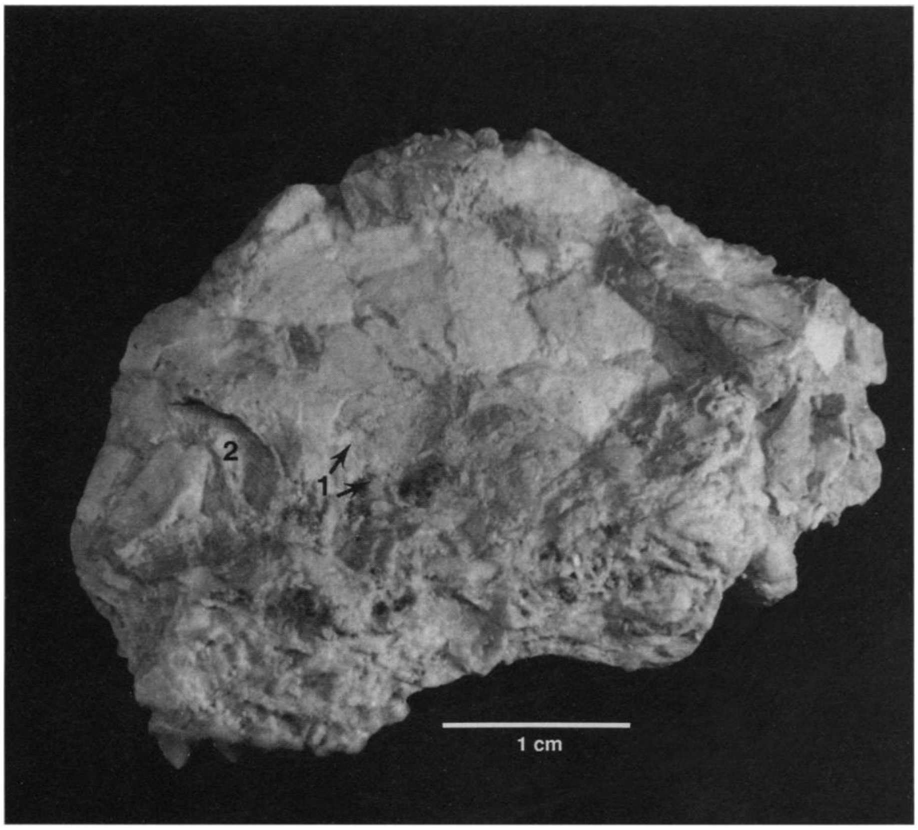

Fig. 2. Left side of the skull showing at 1, the presence of continuous bone from the orbital margin onto the anterior face of the braincase, thus indicating postorbital closure. The dorsal rim of the orbit is shown at 2.

site that has yielded the type of *Proteopithecus sylviae*, a slightly smaller primate species known from a single maxilla (*3*). Although the latter species is more poorly known than *Catopithecus browni*, it appears to be related to it, but is characterized by a larger hypocone, a smaller M^3, and teeth that are narrower anteroposteriorly. Both these early African species are related to *Oligopithecus savagei* that was described from quarry E in 1962 (*5, 6*). *Catopithecus* differs from *Oligopithecus* in having lower molars that decrease in size posteriorly, upper molars that have a small mesostyle nodule lacking in *Oligopithecus* and all later Fayum primates, in showing a weak paraconid on M_2 and a weaker metaconid and smaller talonid basin on P_4, and a P_3 that is less elongate mesiodistally and small relative to P_4. It differs from parapithecids in having lost the second premolars, in having anterior honing facets on the premolars, and in lacking para- and metaconules on the upper molars and conules on the upper premolars. Tooth crown comparisons show that there is little similarity with the highly derived dental anatomy of parapithecids. *Catopithecus* resembles propliopithecids in that P_3 is distinctly higher than P_4, but differs from them in having a relatively much shallower mandible. Study of the upper teeth in this skull, together with the lower teeth of several jaws of *Catopithecus* (*3*), shows that their dental anatomy (and that of *Oligopithecus* (*6*) is almost as close to that of certain Eocene adapids as it is to that of propliopithecids.

On both sides of the skull (DPC 8701) the parietals are shattered. On the right side, part of the squamosal surrounding the auditory aperture is preserved. This shows a broad and long glenoid fossa for the articulation of the mandible, with a postglenoid process behind it. To the rear of this process is a distinct postglenoid foramen. The bullar area appears to lie rather close to the foramen magnum, which may thus have occupied a relatively anterior position. Nevertheless, the general crushing of the whole skull makes it impossible to accurately determine basicranial relationships. On the right side, the auditory opening is clearly seen and can also be located on the left side, but more obscurely. The right auditory aperture is surrounded by a slightly elevated rim that appears to represent the ectotympanic, thus situated at the bullar margin as in lorises, platyrrhines, and in the archaic catarrhine *Aegyptopithecus*. An ectotympanic tube characteristic of omomyids could not have been present. The degree of crushing of the skull makes it impossible to suggest anything about the size of the brain or shape of the braincase.

The auditory region of *Catopithecus* neither resembles that of omomyids, which (where it can be documented) show an ossified external auditory meatus formed by the ectotympanic, or that of adapids, where the ectotympanic forms a free ring within the bulla. As indicated above, the ring appears to be situated in the margin of the auditory opening as in primitive Anthropoidea and in Lorisiformes.

In sum, the combination of characters seen in *Catopithecus* (*7*) indicates that it is a very primitive anthropoidean near the evolutionary transition from Prosimii, because (unlike Prosimii) it has already acquired frontal fusion, postorbital closure, an ectotympanic in the lateral wall of the bulla, and a catarrhine dental formula. *Catopithecus* together with *Oligopithecus* and *Proteopithecus* constitute the new subfamily Oligopithecinae (*3*). Similarities in the morphology of the upper and lower molars and the dental formula in particular argue strongly for placing this subfamily in the family Propliopithecidae. The lack of accessory upper molar cuspules in oligopithecines resembles propliopithecines as does the presence of M^{1-2} hypocones, a twinned entoconid-hypoconulid pair in the lower molars, and in an incipient distal fovea in *Oligopithecus* that closely resembles features of the lower molars of the early propliopithecine, *Propliopithecus markgrafi*. The type mandible of *Catopithecus* (*3*) is separated more or less through the midline of the symphysis. Convoluted rugosities on this surface show that the two mandibular rami must have been strongly interlocked, but the condition at the symphysis of the one known specimen does not clearly show that symphyseal fusion had yet been attained.

Analysis of the upper teeth of this skull and unassociated lower dentitions of *Catopithecus* (*3*) reinforces the conclusion already drawn for *Oligopithecus* (*6*) that oligopithecines link the later Fayum propliopithecines with certain Eucene adapids and not with any omomyid. Among the strongest lines of evidence for an adapid relationship for *Catopithecus* are the absence of a tubular ectotympanic, the relatively small incisor alveolae compared to the canine, the possession of lateral incisor alveolae that are larger than those for the central incisors, and similarities of structure in the upper and lower premolars and molars.

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7. The name comes from the Greek "cato" meaning "below" and "pithecus" meaning "trickster" or "ape."
8. I thank D. T. Rasmussen, F. A. Ankel, and P. Holroyd-Vychodil for assistance in preparation of this manuscript, P. S. Chatrath and P. Holroyd-Vychodil for help in cleaning the skull, and A. Benson for the photographs. Supported by NSF grants BNS-86-07392 and BNS-88-09776. This is Duke Primate Center publication 467.

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Intragranular Diffusion: An Important Mechanism Influencing Solute Transport in Clastic Aquifers?

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Quantification of intragranular porosity in sand-size material from an aquifer on Cape Cod, Massachusetts, by scanning electron microscopy, mercury injection, and epifluorescence techniques shows that there are more reaction sites and that porosity is greater than indicated by standard short-term laboratory tests and measurement techniques. Results from laboratory and field tracer tests show solute nonequilibrium for a reacting ion consistent with a model of diffusion into, and exchange within, grain interiors. These data indicate that a diffusion expression needs to be included in transport codes, particularly for simulation of the transport of radioactive and toxic wastes.

SOLUTES IN GROUND WATER MOVE BY advection and diffusion. In most aquifer systems rates of solute movement by diffusion are typically four orders of magnitude less than advective velocities. It has therefore generally been assumed that diffusion plays a minor role in solute transport in systems where ground-water velocity is greater than the rate of movement by diffusion. Most studies documenting the effects of diffusive transport in ground water have been carried out in shale and clay systems, which exhibit low (<1 mm/day) fluid advective velocities. Diffusion has also been proposed as a control on solute transport from fractures into surrounding rock (*1–3*). In this report, we present laboratory and field data suggesting that diffusion can significantly affect the transport of solutes in sand and gravel aquifers where advective velocities are high (>0.4 m/day).

A solute diffuses into an individual grain in response to the difference between its chemical potential in the interstitial pore fluid and in the interior of the grain. Because the diffusion distances are short, concentration gradients are large; because the effective surface area of a granular aquifer is large, a significant diffusive flux can enter the grains (*4*). If the solute concentration in the interstitial pore space changes rapidly relative to the rate of diffusion into the grain, disequilibrium can occur between the fluid and grains, resulting in an increase in apparent dispersion. This apparent dispersion is larger for a reactive solute, because it takes longer to diffuse than a nonreacting one.

We used sediment obtained from an excavation 2 m deep in the unsaturated zone of Pleistocene glacial outwash on the southern border of Otis Air Base, Cape Cod, Massachusetts (41°36′N, 70°32′E), to investigate the significance of intergranular diffusion in the laboratory. The sediment was approximately 91% sand (grain size >63 μm but <2000 mm), 8% gravel (>2000 μm), and 0.1% silt and clay (<63 μm). The sand-size grains were separated into three groups by use of heavy liquids: <2.58 g/cm^3 (5%), mostly feldspar; >2.58 to <2.70 g/cm^3 (92%), mostly quartz; and >2.70 g/cm^3 (3%), mostly weathered biotite and muscovite. There was no carbonate or organic material, but grains were coated with iron oxides or hydroxides.

A scanning electron microscope (SEM) was used to image both the exterior and the interior (thin sections) of sand-size grains. Most feldspar (Fig. 1A) and many quartz grains (Fig. 2A) exhibit a porous-looking exterior indicative of intragranular porosity. In cross section the porosity observed on the surfaces of the grains was also clearly present in the interiors (Figs. 1B and 2B) (*5–8*). The development of intragranular porosity on weather mica was not as graphic as that on quartz and feldspar, but samples had an expanded "puffy" texture relative to fresh, unweathered samples.

We analyzed samples from the three density fractions by mercury porosimetry and ultraviolet epifluorescence to quantify the amount of observed internal porosity. Results of mercury injection analyses suggest that internal porosity is, on average, ~11% (from 5 to 19%) for the feldspar grains, 9% (from 5 to 14%) for the quartz grains, and

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