A frotarsius chatrathi, first tarsiiform primate (? Tarsiidae) from Africa

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sharp resonances, which would have been readily detectable above the broad band of unsaturated carbon in fulvic acid when present as only 1% by weight of fulvic acid. Thus, benzene carboxylic acids, or any similar aromatic system with sharp resonances, would have been readily detected in the original fulvic acids. We conclude that the sharp peaks observed[7] in diazomethane-treated humic preparations must arise either from aromatic contaminants, or from reaction products of diazomethane with the fulvic acid. Also, there is no good reason to reject the ^{13}C-NMR evidence that fulvic acid does not contain all the benzenoid structures which appear in the oxidation products[4], there being nothing in the nature of fulvate solutions which would obscure their presence. In particular, a suggestion[1,7] that benzene and hydroxybenzene polycarboxylic acids exist as such in fulvic acid can now be discounted.

As the oxidation products of diazomethane-treated humic materials have been used to infer their structure[1-3], we have examined the literature to estimate the contribution of the artefacts or contaminants now shown to be present and to determine whether there may be other contributions to the oxidation products arising from the complex procedures used. There is considerable independent evidence that diazomethane reacts with humic materials to produce byproducts of the desired methylation of hydroxyl groups. Preston and Schnitzer[7] reported that treatment of humic and fulvic acids with diazomethane caused increases in weight of 20 and 40% respectively. As methylation alone would account for only 8 and 14% respectively, there must be substantial amounts of other reaction products, for example, polymethylene, which has been reported in diazomethane-treated humic acids[8] and which can be correlated with a peak at 29.7 p.p.m. in ^{13}C-NMR spectra of diazomethane-treated humic and fulvic acids[7]. Indeed, polymethylene is a probable source of the straight-chain mono- and di-carboxylic acids that appear among the oxidation products of diazomethane-treated fulvic acid[1].

Diazomethane is highly reactive towards α,β-unsaturated acids with which it can form a great variety of addition and insertion products[9]. Such α,β-unsaturated acids have been shown to constitute a major proportion of the total acidity of a peat humic acid[8]. Reaction of diazomethane with humic acids to form pyrazole derivatives has been established[10]; other nitrogen-free reaction products are not improbable. These artefacts cannot, however, be the source of the benzene polycarboxylic acids that appear in the oxidation products of methylated humic materials, as there is no significant difference in yield between methylated and non-methylated humic and fulvic acids[11,12]. Moreover, reaction of diazomethane with double bonds in humic material is unlikely to create benzene rings of well-defined type, so that the four sharp aromatic resonances mentioned above are more likely to arise from contaminants such as benzenoid plasticizers and anti-oxidants. This is consistent with the absence of the resonances in one fulvic acid preparation and with their uniformity among the other diverse humic and fulvic acids.

Contaminants arising from synthetic polymers and their associated plasticizers and anti-oxidants are difficult to avoid in the laboratory, given the widespread use of plastic vessels and tubing and of polymer-based ion-exchange and chromatographic materials. These contaminants are eliminated by purification procedures in small-molecule organic chemistry, as are unwanted byproducts of reactions. All these substances accumulate in the reaction products of humic materials; for example, the long-chain fatty acids isolated from the $Cu_2O/NaOH$ oxidation and from the NaOH hydrolysis of fulvic acids[13,14] must be contaminants, as their $(CH_2)_n$ chains would have been detected readily as major features of the ^{13}C-NMR spectra of fulvic acid. Infrared spectra of fulvic fractions isolated by gel chromatography show di-alkyl phthallate plasticizer contaminants in amounts which are clearly not present in the starting material (see Fig. 4.8 of ref. 15). We conclude, therefore, that laboratory contaminants are picked up commonly during the manipulation of humic materials and their derivatives.

Given, then, that ^{13}C-NMR spectroscopy establishes that fulvic acid does not contain benzenoid structures in sufficient amounts to account for the high yields of benzene and hydroxybenzene polycarboxylic acids in its oxidation products, it remains uncertain whether these arise as artefacts of the oxidation procedures or as contaminants in subsequent manipulations. Martin et al.[16] concluded that they were probably artefacts, as they obtained benzene polycarboxylic acids by various oxidations of a polymaleic acid containing little unsaturated carbon. However, they found no phenolic acids among their oxidation products, whereas Spiteller and Schnitzer[6] did find hydroxybenzene polycarboxylic acids in the oxidation products of polymaleic acid. The difference between the two laboratories suggests a laboratory source of these products.

Whether or not these benzene and hydroxybenzene polycarboxylic acids appear in the oxidation products of fulvic acids, or are introduced in further manipulations, can now be resolved by applying ^{13}C-NMR spectroscopy to the unfractionated oxidation products, as they would be readily recognized there if present even as a few % by weight of the starting material. Schnitzer[1] has estimated that they amount to 50% of the starting material, allowing for plausible losses during the complex separations. If they are indeed artefacts of the oxidation procedures and present in such amounts, they are important clues to the structure of fulvic acid.

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Afrotarsius chatrathi, first tarsiiform primate (? Tarsiidae) from Africa

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Tarsiiform primates have long been regarded as a Laurasian group, with an extensive fossil record in the Eocene of North America and Europe[1-4] and two important but less well-known records from Asia[5,6]. The only living genus is Tarsius (Tarsiidae), whereas all of the fossil tarsier-like primates are usually placed in the extinct family Omomyidae[3]. We now report the discovery of Afrotarsius chatrathi from early Oligocene rocks of Fayum Province, Egypt. This is the first known tarsiiform primate from Africa. Compared with fossil primates, the molar tooth morphology of this diminutive prosimian is most similar to that of the European Eocene microchoerine Pseudoloris; however, the closest similarity is to the

molars of *Tarsius*. Because the phylogenetic relationships among living *Tarsius* and the omomyids remain unclear[7,8] and because of the fragmentary nature of the only known specimen of this new primate, allocation of *Afrotarsius* to either Omomyidae or Tarsiidae is necessarily provisional. As we believe that its molar teeth are more like those of *Tarsius* than of any omomyids (including *Pseudoloris*), we tentatively assign the new genus to the extant family Tarsiidae as its only known fossil representative. Recovery of a *Tarsius*-like primate from Africa suggests that it or its ancestors might have been immigrants from Europe, may have been derived from an unknown Asian stock related to the ancestry of *Tarsius*, or may have originated in Africa.

Order Primates
Suborder Prosimii
Infraorder Tarsiiformes
Family Tarsiidae?

Afrotarsius, gen. nov.

Type species: *Afrotarsius chatrathi*, sp. nov.
Diagnosis: Differs from *Tarsius* in having a more posteriorly placed entoconid and thereby relatively longer distance between the M_{1-2} entoconid and metaconid; in having a relatively larger and slightly more labial M_2 paraconid; in lacking a distinct entoconid and in having a smaller, less posteriorly extended posterior cusp on M_3; and in having M_3 with a shorter talonid and a relatively smaller crown with respect to M_2. The specimen differs from all anaptomorphine and omomyine omomyids in the combination of labiolingually broad and shelf-like molar paraconids separated from metaconids and protoconids by a deep notch, and from all omomyids in having a raised, wall-like ridge between the entoconid and metaconid (both features as in *Tarsius*). It differs from all omomyids (except possibly *Hemiacodon* and *Macrotarsius*) in having M_1 metaconid lingually opposite to protoconid, not placed more posteriorly, and in having a smooth posterior wall on the M_1 trigonid. It differs from all omomyids and *Tarsius* in having an indistinct talonid notch on molars and in having $M_1 > M_2 > M_3$.

Afrotarsius chatrathi, sp. nov.

Etymology: For Prithijit S. Chatrath, collector of the type and only known specimen.
Holotype: CGM (Cairo Geological Museum, Ma'adi, Cairo) 42830, fragment of right mandibular ramus with M_{1-3}, lower parts of crowns of P_3 and P_4 (Figs 1, 2).
Locality: Fossil vertebrate quarry M, 249-m level of Jebel Qatrani Formation (Oligocene), Fayum Province, Egypt. Older than 31.0 ± 1.0 Myr[9].
Diagnosis: Only known species; same as for genus. Measurements (mm) are: P_4-M_3 (in series trigonids overlap talonids), 8.70; P_4 length, 1.90; P_4 width, 1.60; M_1 length, 2.45; M_1 trigonid width, 2.00; M_1 talonid width, 2.10; M_2 length, 2.30; M_3 length, 2.20; M_3 trigonid width, 1.80; M_3 talonid width, 2.65; depth of horizontal ramus beneath anterior root of M_2 (lingual side), 3.25.
Description: CGM 42830 is a right lower jaw fragment preserving parts of P_3-M_3 (Figs 1, 2). The top of the crown of P_3 and most of P_4 are missing, as is much of the labial margin of M_2. In addition, the protoconid of M_1 and the metaconids of M_1 and M_3 are broken. Anterior to P_3, part of the distal border of an alveolus is preserved. The lower jaw is slender and shallow and maintains a fairly even depth of 3.25 mm beneath M_{1-3}, shallowing to about 2.90 mm beneath P_3. A tiny mental foramen is present about 1.20 mm above the inferior border of the jaw and slightly anterior to the anterior root of P_4.

P_{3-4} are two-rooted teeth, P_3 being the smaller. Both teeth seem to have been essentially unicuspid. A small cristid connects the base of the P_4 protoconid with the tiny hypoconulid on the posterior margin of the tooth. A well-developed labial cingulid becomes confluent posteriorly with this raised distal heel.

In area and length of the molar crowns, $M_1 > M_2 > M_3$. The molars are simple tribosphenic teeth, each with a large, shelf-like paraconid separated from the metaconid and protoconid by a
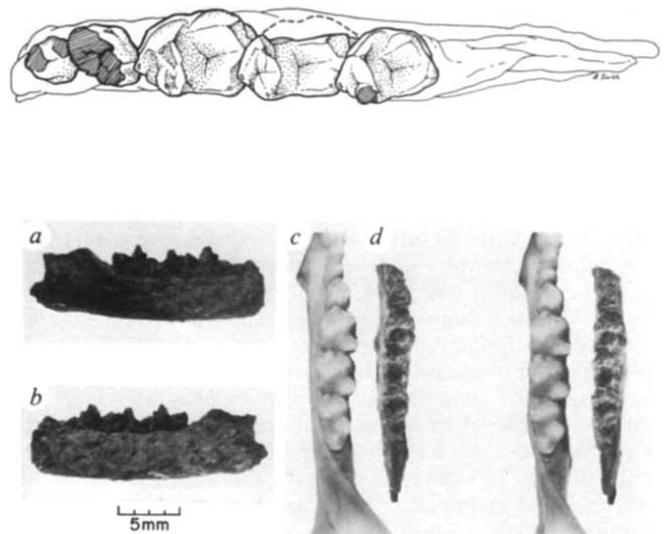

Fig. 2 Labial (*a*), lingual (*b*) and occlusal (*d*) aspects of CGM 42830, holotype of *Afrotarsius chatrathi*, and occlusal aspect (*c*) of FMNH 57281, *Tarsius syrichta*; *c* and *d* are stereo photographs.

deep, curved, posteriorly convex sulcus. On M_{1-2} the paraconids are lingual to the midline mesiodistal axis of the crown and project mesially, giving the trigonid an almost equilateral triangular shape in occlusal view. On M_3 the paraconid is more lingual in position and is slightly closer to the metaconid than on M_1 or M_2. The M_{1-2} talonids are broad, deeply basined, bounded by hypoconids and entoconids of approximately equal size, and closed posteriorly by small but distinct hypoconulids. The entoconids are located on the distal border of the talonids, with the result that the talonid basins are long mediodistally. The high wall connecting the entoconids with the bases of the metaconids has an even crest, causing the talonid notch to be indistinct.

M_3 has a somewhat narrower talonid than M_2, caused by the sharp posterolabial inflection of the entocristid, and possesses only two talonid cusps, a large hypoconid at the posterolabial margin of the crown, and a second cusp (hypoconulid or entoconid) at the centre of the posterior margin of the crown. A high oblique wall connects the hypoconulid with the base of the metaconid. As on M_{1-2}, there is no distinct talonid notch. The M_3 post-hypocristid reaches distally into a sharp notch at the base of the hypoconulid.

The M_{1-3} hypoflexids are shallow, the cristids obliquae reaching the bases of the trigonids slightly lingual to the protoconid. M_1 and M_3 have strong labial cingulids that cross the hypoflexid and merge with strong precingulids and weaker post-cingulids (this part of the crown is missing on M_2).

Afrotarsius chatrathi shows a mosaic of dental similarities to the late Eocene microchoerine *Pseudoloris* and to living South-East Asian *Tarsius*. Traditionally, *Tarsius* has been considered to be a living remnant of some early lineage of omomyid primates, which were diverse and abundant during the Eocene in North America and Europe. More recently, several authors have suggested that *Tarsius* has a closer phyletic relationship with living and fossil higher primates than with omomyids[10-12]. Nonetheless, the morphology of the teeth of *Afrotarsius* is clearly closest to that of living *Tarsius* and, among fossil forms, the Omomyidae. We therefore believe, in the absence of other evidence, that the affinities of *Afrotarsius* lie with these animals.

Development of a linguolabially broad and shelf-like molar paraconid separated from the other cusps of the trigonid by a deep valley is a feature shared among *Tarsius*, *Afrotarsius* and *Pseudoloris*, although the more lingual placement of a relatively large paraconid in *Afrotarsius* is more reminiscent of the condition in *Tarsius* than of that in *Pseudoloris*. Also shared is the distinctive posterolabial inflection of the M_3 entocristid, an

unusual feature that seems to link *Afrotarsius* and *Tarsius* to the exclusion of other primate species. The presence of a tall, wall-like entocristid with an indistinct talonid notch, the direct opposition of the M_1 metaconid and protoconid, and the development of tall hypoconids (not relatively short as in *Pseudoloris*) are additional features linking *Afrotarsius* more closely to *Tarsius* than to *Pseudoloris*. Thus, the combination of these and the other diagnostic features demonstrate that *Afrotarsius* is closer in its dental morphology to *Tarsius* than to the Omomyidae, but within that family, *Afrotarsius* most closely resembles *Pseudoloris*.

Unfortunately, canines and incisors, which most clearly distinguish microchoerines and *Tarsius*, are unknown for *Afrotarsius*. Microchoerines, like other omomyids, tend to have a relatively large front tooth in the lower jaw. Of the two teeth immediately posterior to the front tooth, at least one is also relatively large. The anterior three teeth in the lower jaw of *Tarsius*, on the other hand, consist of a very large tooth flanked both anteriorly and posteriorly by much smaller teeth. The divergent structure and placement of the paraconid serve to distinguish the molars of representatives of the omomyid sub-families Omomyinae, Anaptomorphinae and Microchoerinae[1,13–15]. We believe that the paraconid condition in *Afrotarsius* is most similar to that of *Tarsius* and that in both it is different from that of omomyids. Because only one (if any) of the four basic types of paraconid development can be primitive for primates of modern aspect, we feel that the paraconid condition in *Afrotarsius* is probably the most useful morphological guide to its relative kinship to other primates.

Concerning the palaeobiogeography of Tarsiiformes, relatively little more can be adduced from the discovery of a tarsier-like primate in Egypt. Given the Oligocene palaeogeography of Africa, Europe or Asia are the obvious contenders for the geographical origin of *Afrotarsius* and/or its ancestors. Either solution implies the presence on one of these continents of an unknown stock of *Tarsius*-like Prosimii. Of these two possibilities, an Asian origin is perhaps the more likely, though supported only by circumstantial evidence: (1) there are no known suitable morphological candidates for the ancestry of *Afrotarsius* in the relatively well-sampled fossil record of the Euramerican Eocene Omomyidae; (2) the dentition of *Afrotarsius* is structurally most similar to that of living South-East Asian *Tarsius*; and (3) at least some floral[16] and faunal[17] elements of the Egyptian Oligocene might have been more closely linked to those of various parts of Eocene and present-day South-East Asia than they are to floras and faunas of the early Tertiary of Europe. If *Afrotarsius* or its ancestors immigrated to Africa from either Europe or Asia, this dispersal is most likely to have taken place during the late Eocene–early Oligocene Tethyan regression, an event that facilitated the entry of marsupials into Africa from Europe[18]. A last possibility is that *Afrotarsius* originated in Africa from an otherwise unknown (possibly omomyid) prosimian stock. By this viewpoint, *Tarsius*-like primates were deployed from Africa to Asia some time in the Tertiary. However, it is impossible at present to distinguish between these possibilities.

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A variant of the mammalian somatotopic map in a bat

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Two ordered representations of the body surface, S-I and S-II, have been described on the cortical surface of the brains of a variety of mammals; additional separate topographical maps have been found in the somatosensory cortex of the cat and monkey[1–5]. Except for minor variations in the placement of the body parts, the basic somatotopy of the maps is remarkably consistent across species[5]. As the reasons for this consistency and the minor variations are unclear, we examined the somatotopy of the bat, whose body plan has been modified extensively so that the forelimb can be used for flight[6]. We report here that in both S-I and S-II of the grey-headed flying fox, not only is the representation of the distal forelimb displaced from its usual position on the map, but the digits are directed caudally instead of rostrally as they are in all other mammals studied. The variant somatotopy appears to reflect the postural differences between flying and walking mammals, supporting the notion that topographical maps may have functional significance apart from their point-to-point connections with the sensory periphery.

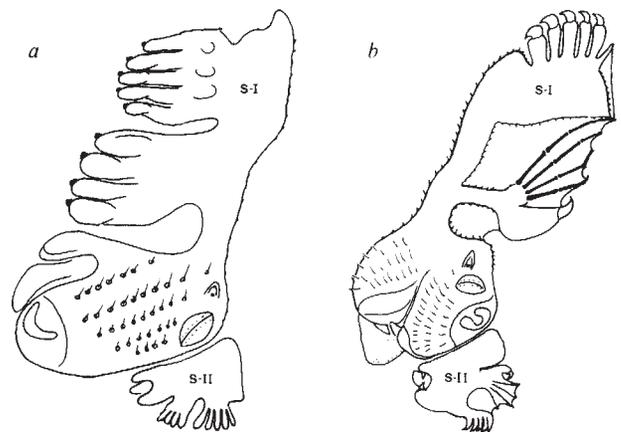Standard microelectrode mapping techniques (see, for example, ref. 4) were used to study the organization of

Fig. 1 Schematic representations of the body surface ('homunculi') on the somatosensory cortex of the rat (*a*, redrawn from ref. 5) and the flying fox (*b*, drawn, with artistic licence, from data on 785 recording sites and summarized more accurately in Fig. 2*d*). The rat, like opossum, squirrel, galago, cat, tree shrew and various New World and Old World monkeys (see ref. 5) has a somatotopic representation in which the forelimb digits are directed rostrally in both S-I and S-II. In contrast, the bat has a representation in which the forelimb digits are directed caudally, reflecting the altered position of these digits for use in the wing.