

lower carbon number *n*-alkanes in migrated mixtures is probably due to their lower tendency to be absorbed or adsorbed by the matrix of the host sediment relative to higher carbon number *n*-alkanes and the other solvent soluble components present<sup>17,18</sup>. If this absorption-adsorption process is not easily reversed then the preferential retention of certain components could alone explain all of the effects reported above. If, however, desorption readily occurs, then the distributions must be the consequence of chromatographic effects, with, for

example, the higher molecular weight species moving more slowly. The increased viscosities resulting from the temperature drop associated with either the introduction of permafrost<sup>19</sup> or uplift the sequence in the late Tertiary<sup>20</sup> may have slowed the migration sufficiently so as to help preserve any chromatographic separations.

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## New Palaeogene primate basicrania and the definition of the order Primates

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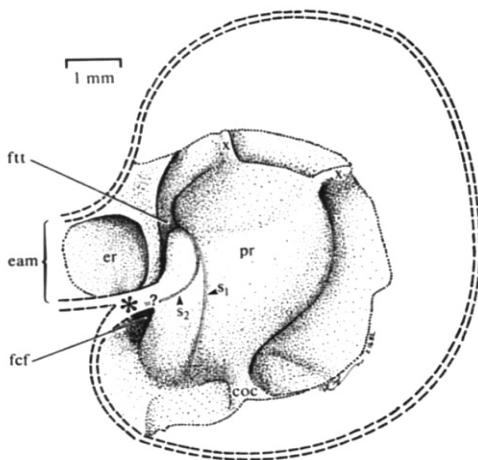
The anatomy of the posterior basicranium has been repeatedly invoked in systematic definitions of Primates. One widely cited definition<sup>1,2</sup> of the order claims that 'all undoubted primates'<sup>3</sup> are distinguished from other mammals by two basicranial specializations: (1) absence of a major vascular foramen on the medial side of the auditory region, and (2) development of the auditory bulla from the petrosal bone. As we show here, specialization (1) does not apply to the paromomyid *Ignacius*, and is of uncertain incidence in other unquestioned members of suborder Plesiadapiformes (archaic primates from the early Cenozoic of Europe and North America). Specialization (2) cannot be demonstrated without ontogenetic evidence, and all relevant plesiadapiform fossils are adult. In fact, the only plesiadapiform with an arterial pattern remotely resembling that of early primates of modern aspect (or 'euprimates'<sup>4</sup>) is the microsopid *Cynodontomys*, but it is often regarded as non-primate because it lacks a petrosal bulla. Although plesiadapiforms resemble euprimates in traits of the cheek teeth and postcranium<sup>5–7</sup>, some other (presumably non-primate) groups possess these traits as well. Since the order Primates is not clearly definable by unique specializations, the best grounds for regarding plesiadapiforms as euprimate antecedents are stratigraphic and phenetic. This fact may be best expressed by systematic arrangements that emphasize adaptive grades rather than unsubstantiated clades.

Euprimates resemble insectivores and microchiropteran bats, but differ from most other placental and all non-placental mammals, in having a promontory artery<sup>8</sup>. This vessel, the homologue of the intracranial part of the human internal carotid artery, characteristically runs in a groove or canal across part of the cochlear promontory. Among Microsopidae, *Cynodontomys* exhibits a deep promontory sulcus<sup>9,10</sup> that matches in calibre and position the carotid canals of the earliest euprimates (members of the families Adapidae and Omomyidae). Other plesiadapiform families lack this feature. In known

Plesiadapidae, promontory grooves (Fig. 1) are tiny and highly variable in orientation within and between species<sup>11,12</sup>. These grooves are more likely to have contained divisions of the tympanic nervous plexus than the promontory artery (which, even if present, would have been vestigial). In known Paromomyidae there are no identifiable promontorial grooves, but there is a longitudinal ridge that runs the length of the middle-ear cavity. In *Phenacolemur* this structure has been tentatively identified as a promontory canal<sup>13</sup>, but as the 'canal' is imperforate in both *Phenacolemur* and the related genus *Ignacius*, the paromomyid forebrain must have been supplied by a vessel other than the promontory artery.

In *Ignacius* the cerebral blood supply appears to have been channelled along the medial side of the auditory region, rather than through it as in a primitive euprimate. This inference is based on the bilateral presence of smooth-walled apertures situated between the sphenoid and bulla in a recently discovered partial cranium of *Ignacius graybullianus* (collected with associated dentition by B. Holly Smith from University of Michigan locality SC-6 in the Clark's Fork Basin, Wyoming; Fig. 2a). These apertures, although distorted *post mortem*, are strikingly similar to the middle lacerate foramina of lorisid and cheirogaleid primates, muroid rodents, dogs and various other placentals<sup>14–18</sup>. In these groups the middle lacerate foramen transmits arteries that contribute to cerebral circulation: a medially positioned internal carotid, or a branch of the ascending pharyngeal artery, or both<sup>15,16,19</sup>. The medially positioned internal carotid is thought by some to be a homologue of the promontory artery<sup>20,21</sup>, but it is more widely regarded as a distinct vessel, the 'medial entocarotid'<sup>9,13,22</sup>. Szalay<sup>23</sup> considers that both the medial entocarotid and a separate promontory artery were present in early eutherians, but that the first-named vessel was lost in the line leading to primates. Accordingly, he has defined the loss of the medial entocarotid (and its foramen) as a feature marking the boundary between primates and non-primates. If *Ignacius* retained the medial entocarotid, then according to this criterion the genus cannot be primate. If, instead, the medial vessel was an enlarged ascending pharyngeal which supplied the endocranium, *Ignacius*' basicranial vasculature might have been superficially loris-like (Fig. 2b). However, because the arterial arrangement characteristic of modern lorisiforms is almost certainly derived from the more primitive pattern found in early Eocene Adapidae, any special resemblances between lorises and *Ignacius* must represent convergences, of no value in inferring phylogenetic relationships. Neither *Ignacius* nor any other plesiadapiform shares significant vascular homologies with early euprimates.

The medial bullar wall is a lamina continuous with the petrosal bone in all euprimates and adequately known

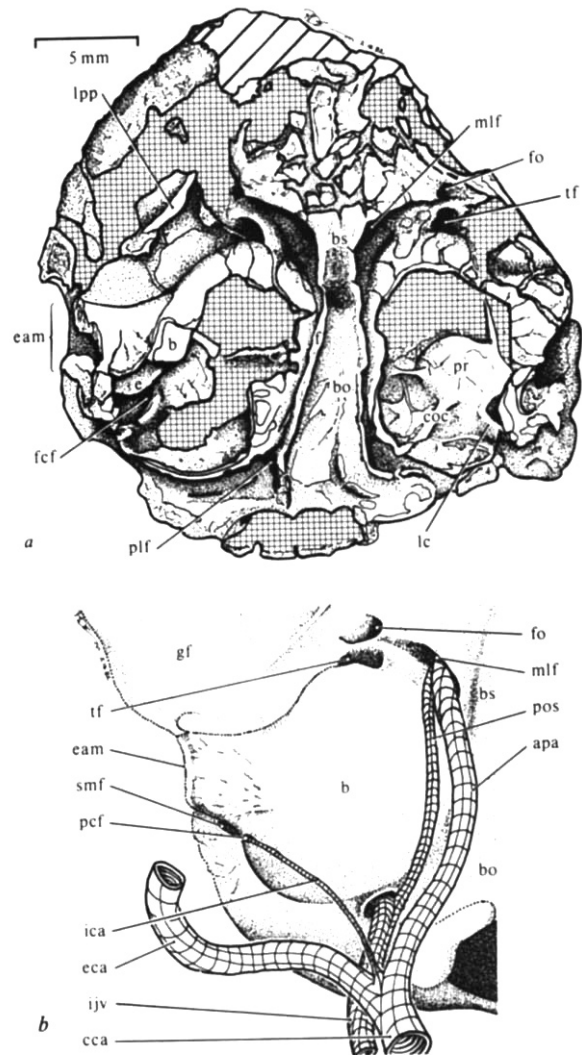


**Fig. 1** Variability of promontorial grooves in plesiadapiforms. Semi-schematic ventral view of right petrosal of the plesiadapid *Nannodectes*, based on two incomplete specimens (*N. intermedius*, United States National Museum no. 309902, and *N. gidleyi*, American Museum of Natural History no. 17388). In USNM 309902, there is an apparent vascular sulcus ( $s_1$ ) originating near the roof of the middle ear cavity; the sulcus does not lead to an external aperture, and we suspect that it carried a nerve (tympanic nerve?) during life. In AMNH 17388 sulcus  $s_1$  does not exist, but there is another ( $s_2$ ) which is not represented in USNM 309902. Sulcus  $s_2$  grooves, but does not seem to perforate (?), the bridge of bone (\*) uniting the promontory and the posterior bullar wall. In specimens of the related genus *Plesiadapis*, the equivalent of  $s_2$  often leads to an aperture which has been identified as the homologue of the posterior internal carotid foramen of lemurs. The variable presence and size of  $s_2$  and its foramen suggests that the internal carotid (even if present) would have been of no functional importance. Middle-ear septa (x), sometimes thought to represent canal-like continuations of these sulci, are imperforate and do not, in any event, connect with the sulci (which seem to end within the fossa for m. tensor tympani). For key to abbreviations, see Fig. 2.

plesiadapiforms (other than microsypids, in which bulla-petrosal continuity was absent<sup>9,10</sup>). Among living primates, this continuity reflects the fact that the bulla originates in the fetus as an outgrowth of the ossifying petrosal. This ontogenetic pattern, in its details, distinguishes modern primates from all other extant mammals<sup>14,24</sup>. However, such patterns can only be properly established by studies of prenatal development. It is not possible to infer anything about bullar composition from an absence of bullar sutures in adults; a number of extant mammals (for example, some rodents<sup>25</sup>) develop a non-petrosal bulla which fuses seamlessly with the petrosal in postnatal life. Postnatal fusion may or may not have occurred in archaic primates; but while there are no fossils of fetal plesiadapiform ear regions, the question is (and is likely to remain) open.

The available fossil evidence does not support the conclusion that the earliest primates were distinguished from their nearest relatives by a 'tube-enclosed carotid circulation within the petrosal-derived bulla'<sup>2</sup>. The carotid part of this definition excludes known non-microsypid Plesiadapiformes, and the bulla part is not demonstrable for any fossil primate. It is parsimonious to assume that the ancestral euprimate, like its living descendants, had a petrosal bulla; but the last common ancestor of euprimates and microsypids did not, and so bullar composition in other archaic primates is not inferable from parsimony considerations. Other attempts<sup>26-28</sup> to find unique features for the plesiadapiform-euprimate clade have similarly ended in failure<sup>29,30</sup>, and the position of the lower taxonomic boundary of primates remains controversial<sup>31</sup>.

The search for exclusive features diagnostic for primates might be better replaced by attempts to formulate and account for the significant grade boundaries found within the order.

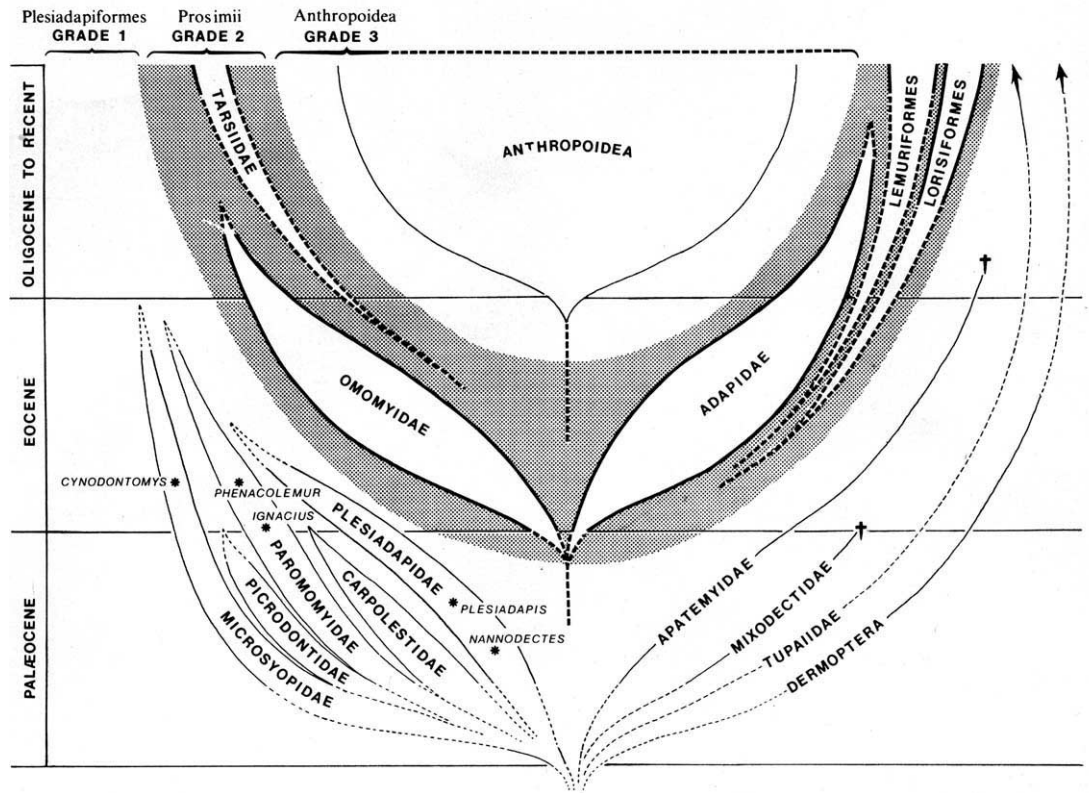


**Fig. 2** Ventral view of *Ignacius graybullianus*, University of Michigan Museum of Paleontology no. 68006 (a) and reconstruction of fossil's right auditory region and major vascular channels (b). Key: apa, ascending pharyngeal artery; b, bulla; bo, basioccipital; bs, basisphenoid; cca, common carotid artery; coc, cochlear canalculus; e, medial rim of ectotympanic; eam, external acoustic meatus; eca, external carotid artery; er, epitympanic recess; f, flange on basioccipital; fcf, fossula of the cochlear fenestra; ftt, fossa for tensor tympani muscle; gf, glenoid fossa; ica, internal carotid artery; iju, internal jugular vein; lc, longitudinal ridge; lpp, lateral pterygoid plate; mlf, middle lacerate foramen; pcf, posterior carotid foramen; plf, posterior lacerate foramen; pos, petro-occipital sinus; pr, promontory; smf, stylomastoid foramen; tf, foramen for auditory tube. In a, matrix-filled areas on the crushed and somewhat distorted skull are identified by cross-hatching. In b, vessel reconstruction is based on pattern found in modern lorises and cheirogaleid lemurs; precise calibre of vascular channels and their furcation points are, of course, not known. The fossil does not exhibit a recognizable pcf, and the ica may therefore have been completely absent.

Only two major grade transitions, delimiting the upper and lower boundaries of Prosimii, can be defined at present. The antecedent plesiadapiform grade cannot be precisely defined, and it may even be polyphyletic. Polyphyletic origin of a grade damages its taxonomic status but enhances its evolutionary significance, because a grade boundary crossed by several parallel lineages is correspondingly more likely to reflect adaptation under pervasive selection pressures rather than historical accident. The five plesiadapiform families (Fig. 3, bottom left of diagram) share euprimate-like features of molar morphology that give them particular significance for understanding



**Fig. 3** Major primate taxa and possible primate relatives, organized in the form of grades. Temporal distributions of major primate taxa (including plesiadapiform genera mentioned in text) are shown in outline, and unresolved phylogenetic relationships (for example, origin of Anthropeida, origin of prosimian groups) are purposely left ambiguous. Resemblances of Plesiadapiformes to Omomyidae, formerly regarded by P.D.G. as indications of direct relationship, are now thought to represent convergences<sup>32</sup>. In cladistic terms, only grade 3 is strictly monophyletic; we acknowledge that grade 2 is paraphyletic, and that grade 1 is polyphyletic (and would probably remain so even if restricted to the families on the bottom left). However, uncertainties of cladistic reconstruction have not so far been, and need not be regarded as, barriers to analysis of the morphological novelties indisputably associated with each grade boundary.



primate origins, even if it is not possible to resolve their precise relationships to one another, to euprimates, and to the slightly less 'plesiadapiform' families noted on the right of Fig. 3.

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## Chemolithoautotrophic metabolism of anaerobic extremely thermophilic archaeobacteria

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Several types of extremely thermophilic archaeobacteria have recently been isolated from sulfataric water holes, hot springs and hot sea floors<sup>1-6</sup>. It has been shown that some of them can live using sulphur respiration of reduced carbon substrates as a source of energy, a type of metabolism previously described for the eubacterium *Desulfuromonas*<sup>7</sup>. We report here that several extremely thermophilic archaeobacteria can live with carbon dioxide as their sole carbon source, obtaining energy from the oxidation of hydrogen by sulphur, producing hydrogen sulphide. They are thus capable of a new type of anaerobic, purely chemolithoautotrophic metabolism, a possible primaevial mode of life.

The conservation of energy from the oxidation of molecular hydrogen with elemental sulphur by *Spirillum* 5175 (ref. 8), and the formation of H<sub>2</sub>S from hydrogen and sulphur by suspensions of *Campylobacter* sp. (ref. 9) are evidence that H<sub>2</sub>S formation can be the basis of a chemolithotrophic existence, though acetate is required as a carbon source in the first instance, and no coupling to growth has been demonstrated in the latter.

The archaeobacterium *Thermoproteus tenax* Kral (DSM 2078) is able to grow with carbon monoxide as sole carbon source, provided that elemental sulphur is available as terminal electron acceptor<sup>1,10</sup>. Equivalent amounts of H<sub>2</sub>S and CO<sub>2</sub> are produced.

Many isolates of *Thermoproteus* from Icelandic and North American solfataras, among them *T. tenax* and *Thermoproteus neutrophilus* (F. F., K.O.S. and W.Z., unpublished), and the yet unnamed isolate H3 (Fig. 1a), can even grow in the presence