Rethinking Primate Origins

The characteristic primate traits cannot be explained simply as adaptations to arboreal life.

Matt Cartmill

If you asked a student of human evolution to explain why human beings, unlike other mammals, walk around on only two legs, you would be baffled and unhappy if he answered, "Because in man's ancestral lineage, individuals who could not run away from predators left fewer offspring." You would be justified in retorting that the same remarks apply equally to thousands of other species of mammals, yet none of these have developed upright bipedal locomotion. The purported explanation, you would properly conclude, may be a true proposition, but is worthless as an explanation.

An explanation is a hypothesis of a complex sort. Ordinarily, to explain one fact in terms of another requires that there be an a posteriori rule which allows us to deduce the first from the second, and which warrants testable expectations other than the one in question (*1*). We reject the foregoing "explanation" of human bipedality because we sense that its explanatory force depends on the lawlike generalization, "Natural selection favors bipedal locomotion in any mammal species that has predators," and that this generalization is false. Yet some evolutionary biologists and philosophers of science (*2*) have argued that evolutionary explanations do not involve any such generalizations, and hence are not subject to refutation by counterexamples. In this view, we have no grounds for dismissing the "explanation" with which I began; the objection that the same remarks apply to species which have remained quadrupedal is beside the point.

I have suggested elsewhere (*3*) that this and similar objections are very much to the point; that, when valid, they demonstrate the inadequacy of the explanation in question; and that such objections must be raised systematically if we wish to arrive at adequate explanations of historical processes. These assumptions underlie the following reassessment of what has been called the arboreal theory of primate evolution.

The Arboreal Theory and Its Background

The Linnean concept of the order Primates, which included the bats and colugos, was still current as late as 1870 (*4*). In 1873, Darwin's antagonist Mivart proposed ordinal boundaries which excluded these animals, but which (unlike the taxonomies then advocated by Milne-Edwards, Grandidier, and Gervais) included the prosimians as a suborder of Primates (*5*). Mivart also proposed a list of traits that distinguished prosimians and anthropoids from other placental mammals. These traits included a complete bony ring around the eye, a well-developed occipital lobe of the cerebral cortex, and a grasping hind foot with an opposable, clawless first toe.

In the second decade of the 20th century, G. E. Smith and his pupil, F. W. Jones, put forth the first systematic attempts at explaining these and other characteristic primate traits in terms of natural selection. Smith, a comparative neuroanatomist, was principally concerned with explaining the distinctive features of primate brains. He proposed (*6*) that the remote ancestors of the primates were shrewlike terrestrial creatures that entered upon an arboreal way of life. In the complex networks of tree branches through which these early primates moved and foraged, the olfactory and tactile receptors in the snout did not provide adequate guidance; snuffling blindly along in hopes of scenting something edible, as most living insectivores do, was no longer a viable foraging pattern. Accordingly, vision gradually replaced olfaction as the dominant sense. In correlation with this, the hand assumed the tactile and grasping functions primitively served by the mouth and lips; eye-hand coordination replaced nose-mouth coordination. Arboreal life also required more precise and rapid motor responses. Thus, Smith was able to account for the primates' reduced olfactory centers and elaborated visual, tactile, motor, and association cortex in terms of the selection pressures exerted by the arboreal environment.

Jones's reinterpretation of these ideas (*7*) reflects his professional interest in the anatomy of the hand and foot. Jones proposed that the arboreal habit led to a functional differentiation of the limbs. While the foot remained a relatively passive organ of support and propulsion, the hand, used by the primate ancestors for reaching out and grasping new supports when climbing about in trees, became specialized for prehension—and therefore preadapted to take over the mouth's functions of manipulation and food-gathering. As the snout lost importance as a sensory and manipulative organ, it dwindled in size; and the eyes were perforce drawn together toward the middle of the flattening face. The progressive specialization of the hind limb for support and propulsion led to a more upright posture, with correlated changes in the axial skeleton, gut, and reproductive organs. For Jones, most of the things that distinguish human beings from typical quadrupedal mammals were originally adaptations to living in trees.

The arboreal theory was open to the obvious objection that most arboreal mammals—opossums, tree shrews, palm civets, squirrels, and so on—lack the short face, close-set eyes, reduced olfactory apparatus, and large brains that arboreal life supposedly favored. Jones tried to account for these counterexamples. Accepting Matthew's thesis (*8*) that primitive mammals had been arboreal creatures with opposable thumbs and first toes, Jones proposed that the absence of primate-like traits in other arboreal lineages resulted from a period of adaptation in each lineage to terrestrial locomotion. During this period, the thumb and first toe became reduced, the primitive reptilian flexibility of the forelimb was lost, and the primitive flat nails were replaced by claws. These changes blocked the spe-

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cialization of the forelimbs for prehension. Accordingly, in nonprimate mammals that had reentered the trees, the primate evolutionary trends did not materialize.

Stated thus baldly, Jones's thesis is obviously inconsistent. His treatment of the evolution of the brain, which he borrows from Smith, presupposes that primitive mammals were small-eyed terrestrial beasts that nosed their way through the world, guided by specialized olfactory and tactile receptors in the snout; but when the evolution of the limbs is in question, he assumes that arboreality is primitive and that early mammals were neither terrestrial nor typically quadrupedal.

The late W. E. Le Gros Clark's reformulation of the arboreal theory, which more skilfully conceals this inconsistency, has been almost universally accepted by other students of primate evolution. Much of Le Gros Clark's primatological work centered around the now-discredited (*9*) proposition that the tree shrews (Tupaiidae) are persistently primitive lemuroids that have somehow failed to develop the perfected adaptations to arboreal life seen in the other extant primates. Le Gros Clark believed that primitive Insectivora were tree-climbing beasts

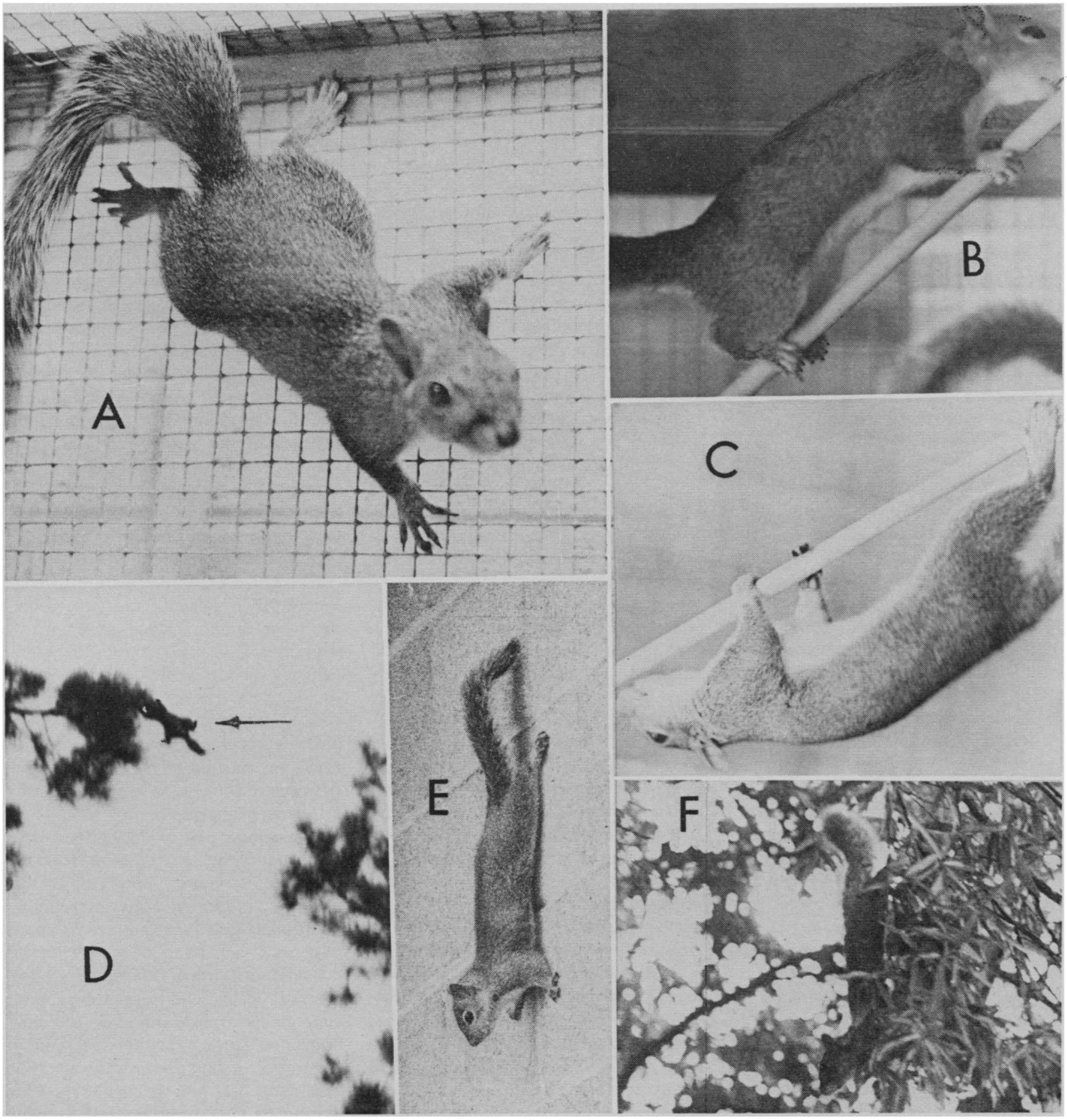

Fig. 1. The Carolina gray squirrel, *Sciurus carolinensis,* (A) hanging from wire grid, showing nonopposable first digits; (B) climbing thin sloping support; (C) descending underneath thin sloping support; (D) (squirrel shown by arrow) leaping across gap in the canopy, about 20 m above the ground; (E) clinging to vertical cinder block wall; and (F) foraging in terminal branches of a willow oak (*Quercus phellos*), hanging bipedally.

with clawed, nonprehensile hands and feet, small eyes and brains, and elaborate olfactory apparatus. The unspecialized, squirrel-like climbing habit of tree shrews (and ancestral primates) is invoked by Le Gros Clark to explain their incipiently primate-like morphology; tree shrews have a complete bony ring around the orbit, a relatively extensive visual cortex, a highly differentiated retina, some simplification of the olfactory apparatus, and a few minor grasping adaptations of the joints and muscles of the hind foot. More perfect arboreal adaptations, of the sort seen in lemurs, involve the replacement of sharp claws by flattened nails overlying enlarged friction pads, the divergence and enlargement of the first toe and thumb to produce effective grasping organs, and the approximation of the two eyes toward the center of the face. This last change, in Le Gros Clark's view, had a positive selective advantage for acrobatic arboreal mammals; it produced a wide overlap of the two visual fields, allowing stereoscopic estimation of distance in jumping from branch to branch (*10*).

The Comparative Evidence

If progressive adaptation to living in trees transformed a treeshrew-like ancestor into a higher primate, then primate-like traits must be better adaptations to arboreal locomotion and foraging than are their antecedents. This expectation is not borne out by studies of arboreal nonprimates. The diurnal tree squirrels (Sciurinae) provide the most striking counterexample. The eyes of squirrels face laterally, the two visual fields having only about a 60° arc of overlap (*11*); the olfactory apparatus is not reduced by comparison with terrestrial rodents (*12*); all the digits (except the diminutive thumb) bear claws, which are sharper and more recurved than those of terrestrial sciurids (*13*); and the marginal digits of the hand and foot are not opposable or even very divergent (Fig. 1). Yet squirrels are highly successful arboreal mammals, and seem to have little difficulty in accomplishing the arboreal activities in which primates might be expected to excel. Despite their laterally directed eyes (and presumed lack of stereoscopy), squirrels of several genera may leap from 13 to 17 body lengths from tree to tree (Fig. 1D) (*14*), which compares favorably with the 20 body lengths reported for the saltatory lemuroid *Propithecus verrauxi* (*15*). Although squirrel hands and feet are not adapted for grasping, squirrels easily walk atop or underneath narrow, sloping supports, and can forage for long periods in slender terminal branches hanging by their clawed hind feet (Fig. 1, A to C, F). Clearly, successful arboreal existence is possible without primate-like adaptations.

A partisan of Le Gros Clark's form of the arboreal theory might still postulate that tree squirrels are under selection pressure which favors their developing primate-like morphology, but have not undergone a long enough period of adaptation to arboreal life for them to have converged markedly with primates. Accepting this, we would still expect that arboreal squirrels would differ in primate-like ways from terrestrial sciurids, at least to a slight extent. We would have similar expectations about arboreal members of other nonprimate families.

The facts do not bear out these expectations. Virtually the only features of the hands and feet which systematically distinguish arboreal from terrestrial squirrels are the longer fourth digits and generally larger carpal pads of the former; the arboreal genera show no tendency toward enlargement of the thumb, reduction of claws, or development of a wide or deep cleft between the first and second digits (*16*). Orbital convergence in all sciurids is slight, and is actually greater in the more terrestrial species (Fig. 2E), although the optic axes of ground squirrels' eyes are not more convergent than those of tree squirrels'.

Since small mammals have relatively large eyes, orbital-margin convergence in most mammals varies inversely with size, other things being equal (*3*). For a given skull length, this convergence is somewhat greater in higher primates than in lemurs (*17*). When convergence is plotted against skull length for several families of arboreal mammals and the lemuriform and haplorhine regressions are traced on the plot (Fig. 2), it is evident that arboreality (or saltatory arboreal locomotion, in wholly arboreal taxa) does not correlate with proximity to the primate regressions. The slow-moving lorises have, for their size, more convergent orbits than the saltatory galagos (Fig. 2A). Among feloid carnivores (Fig. 2B), the terrestrial *Felis bengalensis* approaches the primate regressions most closely. Both arboreal and terrestrial procyonids (Fig. 2D) fit a regression parallel to those of the primates, from which the semiarboreal coatimundi is widely displaced away from the primate lines.

Certain primate-like specializations of the visual pathways of the brain may perhaps represent adaptations to arboreal life per se. Diamond and his coworkers (*18, 19*) have found that the common tree shrew and the Carolina gray squirrel resemble *Galago senegalensis* in having little or no overlap between the projection from the retina to the occipital visual cortex (relayed via the lateral geniculate) and a significant visual projection to the temporal cortex from the superior colliculus (via the pulvinar). This is not the case in the cat, in which these areas overlap widely and the temporal cortex is given over to projections from the medial geniculate. Since arboreality is about the only thing that tree shrews, squirrels, and galagos have in common, the suggestion that this represents a specifically arboreal adaptation (*18*) may be correct. However, its adaptive significance is obscure. The expectation that "*any* mammalian line that relies heavily on visual cues" will develop a visual temporal lobe (*19*) is clearly unwarranted; cats rely heavily on visual cues, and in fact show several primate-like features of the visual system that are absent or unknown in squirrels and tree shrews—for example, parallel optic axes, substantial ipsilateral radiations of each optic nerve, and the presence of "binocular depth cells" in the striate cortex (*20, 21*). These features are all functionally related to stereoscopic depth perception. Since most of the projection from the retina to the lateral geniculate body seems to correspond to the binocular portion of the visual field (*11, 22*), the relative de-emphasis of the older tectopulvinar system in cats can even be described, from a different perspective (*20*), as a special similarity to higher primates.

The comparative evidence, then, does not support the idea that the selection pressures of arboreal life favor the replacement of tree shrew-like morphology by primate-like morphology. In many respects, the first sort of morphology is actually of superior adaptive value. Clawed fingers and toes are superior adaptations for locomotion on nonhorizontal surfaces with large radii of curvature—including vertical walls (Fig. 1E) as well as tree trunks (*23*). Like marmosets (*24*), squirrels tend to avoid very thin branches in normal arboreal locomotion, but can walk on them easily enough, relying on the largely passive grip of the proximal volar pads when the support is horizontal and (unlike marmosets) gripping with opposed hands and opposed feet when the support is sloping (Fig. 1B). Primate-like approximation of the orbits increases visual field overlap, but decreases parallax, reducing the distance over which visual field disparities can provide distance cues. In a leaping arboreal animal, selection should act against the extreme orbital approximation seen in tarsiers and higher primates. This expectation is borne out by a comparison of lorises with galagos; the slow-moving *Loris* and *Nycticebus* have more convergent and closely approximated orbits than the saltatory galagos (*25*), whose wider interorbital space allows stereoscopic ranging over greater distances.

Evidently, the close-set eyes and grasping extremities typical of extant primates are adaptations to some activity other than simply running about in the trees; arboreal life per se cannot be expected to transform a primitive tree shrew-like primate into a lemur. Le Gros Clark's version of the arboreal theory is not adequate.

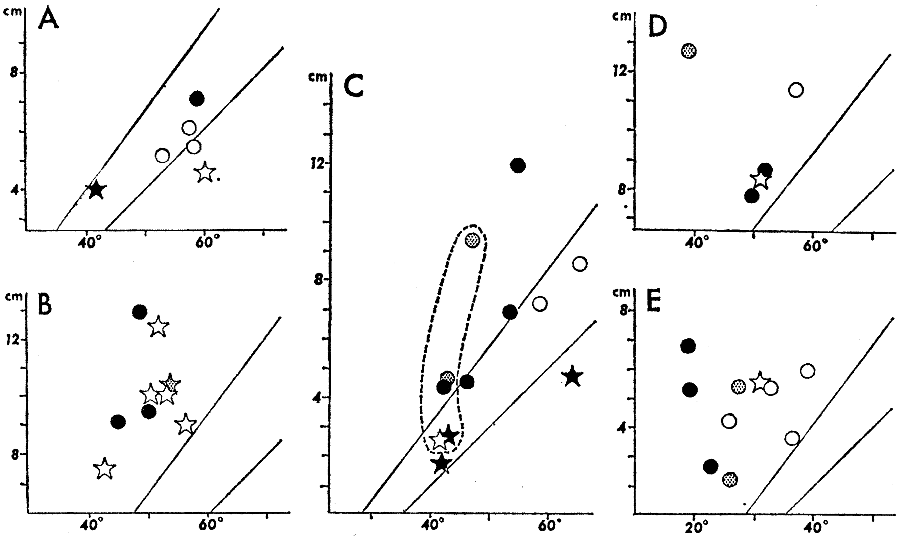

Fig. 2. Five bivariate plots of species mean values of skull lengths (prosthion to inion, centimeters) and orbital convergence (dihedral angle between orbital and midsagittal planes, degrees): (A) lorisiform prosimians, (B) feloid carnivores, (C) didelphids (dashed line) and diprotodont marsupials, (D) procyonid carnivores and (E) sciurids. White symbols represent terrestrial animals (such as *Monodelphis*) or slow-moving arboreal forms (such as *Phalanger*); stippled symbols represent semiarboreal animals (such as *Didelphis*); stars represent predominantly carnivorous animals (such as *Monodelphis*). In each plot, the diagonal lines represent the least-squares regression of convergence on skull length for Madagascar lemurs (upper line) and haplorhine primates (tarsiers and anthropoids: lower line). [Data from (*17*)]

Were Primitive Mammals Arboreal?

Jones's version of the arboreal theory holds, not that the primate characteristics will be selected for in any arboreal mammal lineage, but that they all result from the primates' unique preservation of the grasping hands and mobile forelimbs supposedly found in the arboreal ancestors of the Mammalia. This conception of what early mammals were like can be traced to several sources. Huxley (*26*) and Dollo (*27*) proposed that the last common ancestor of the living marsupials had a grasping hind foot, but they thought this represented an arboreal specialization and that early mammals were terrestrial. Matthew (*8*), following Cope (*28*), reinterpreted this trait as a primitive retention, and suggested that Eocene and Paleocene placental mammals (and early ungulates in particular) also showed features indicating derivation from an arboreal ancestor.

Most of the supposedly arboreal features identified or inferred for the ancestral mammals by Matthew and his inheritors (*8, 29, 30*) can be shown (*17, 31*) to be either chimerical or irrelevant to arboreality. Others represent specializations fixed at various points along the reptilian lineage leading to mammals (such as the loss of all but two phalanges in the thumb and first toe, the "anomalous" arrangement of the thumb's extrinsic muscles, and the appearance of a tuber calcanei). Some are mere amphibian retentions (for example, persistence of the clavicle) that were lost in later mammalian lineages that developed cursorial specializations. Most of those who have believed that primitive mammals were lemur-like arboreal animals have also thought that terrestrial habits select for cursorial locomotion and thus for simplification and stabilization of the limbs; that "the final stage of this process is exemplified in the horse" (*7*); and that primates could therefore not be descended from ancestors that had long been terrestrial. However, the fact that placental ancestors could not have been very much like horses does not imply that they were very much like lemurs. The same suite of primitive retentions seen in the primates is also seen in many terrestrial Insectivora. Most extant insectivores manifest no ungulate-like trends toward simplifying the limb skeleton—apart from a general but not universal tendency toward distal tibiofibular fusion, which can also occur in arboreal primates (*Tarsius*) and marsupials (*Marmosa*) (*32*). Cursorial specializations are adaptations for rapid visually directed pursuit of prey or rapid and prolonged flight from predators, and are best developed in large mammals inhabiting open country. They would have had little or no selective advantage for the small, shrewlike mammals of the Mesozoic, and their absence does not imply arboreality.

In support of Matthew's hypothesis, Lewis (*33*) points out that in reptiles the peroneal muscles arising from the fibula insert on the fifth metatarsal, but in mammals part of this musculature forms a peroneus longus muscle, whose tendon runs across the sole to insert on the first metatarsal. Lewis suggests that peroneus longus originally acted to adduct a divergent first toe in arboreal grasping. However, in extant mammals with rudimentary first toes, the peroneus longus typically persists, shifting its attachment one toe over to the base of the second metatarsal. This demonstrates that it has some important function unrelated to adduction of the first toe. An alternative explanation of its original adaptive value is that it acted to evert the foot against resistance. If the earliest mammals walked with their feet pointing somewhat sideways, as echidnas do (*34*), eversion would have added propulsive thrust at the end of the stance phase, and would have worked more efficiently if part of the everting musculature exerted its force through an attachment at the anterior (preaxial) edge of the foot. Intermediate stages in the shift of this attach-

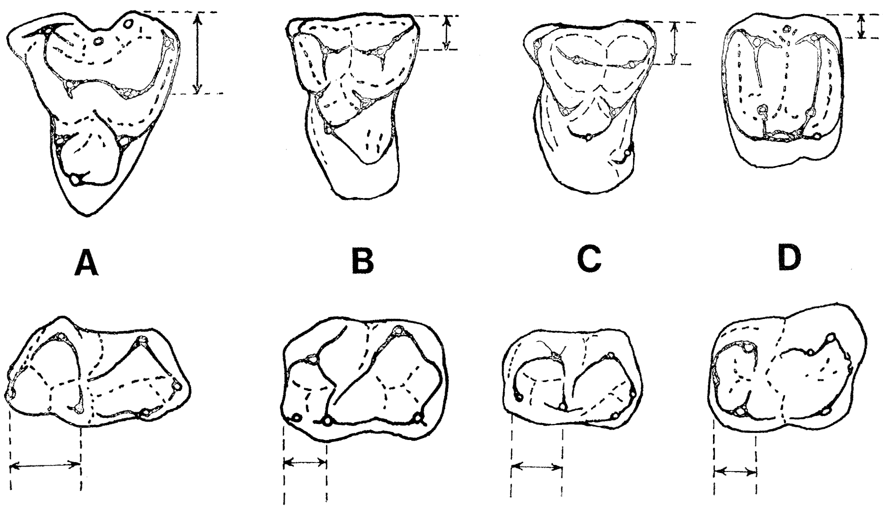

Fig. 3. Upper left (above) and lower right (below) molar teeth of (A) the Cretaceous opossum *Alphadon wilsoni*, (B) the mid-Paleocene plesiadapoid *Palenochtha* minor, (C) the Late Cretaceous ungulate *Protungulatum donnae*, and (D) the early rodent *Paramys copei*. In the latter three, the stylar shelf (vertical arrows, above) and trigonid (horizontal arrows, below) are reduced by comparison with the more primitive condition seen in *Alphadon*.

ment across the sole would yield progressively more efficient eversion, whereas, if its original function had been to adduct the first toe, selectively advantageous intermediate stages would not be possible.

In short, there is no reason to believe that the Triassic ancestors of the Mammalia had clawless, grasping extremities, as Jones's version of the arboreal theory requires. The point may be settled by forthcoming studies of the virtually complete skeleton of the Triassic mammal *Megazostrodon* (*35*). There is in any event ample evidence to show that late cynodont reptiles and their mammalian descendants progressively developed a more elaborate olfactory apparatus than is found in other reptilian lineages (*36*), and that the earliest mammals had relatively small and degenerate eyes, in which the sauropsidan mechanisms of accommodation and nictitation had been lost (*37*). These facts suggest that the earliest mammals were shrewlike terrestrial creatures, guided largely by olfactory and tactile stimuli. This does not mean that early mammals were incapable of climbing branches that presented themselves as supports or obstacles; as Jenkins (*38*) points out, any small mammal needs this ability in a forest community.

The Visual Predation Hypothesis

If primate traits cannot be interpreted either as the products of a primitive arboreality retained only in primates, or as specializations necessarily selected for in any lineage of arboreal mammals, then neither form of the arboreal theory can explain why primates differ from squirrels or opossums, and an alternative set of explanations is needed. One recently proposed alternative (*3, 23*) has been induced from a survey of the distribution of primatelike traits in other taxa.

Grasping hind feet with a divergent first toe are characteristic of marsupials, chameleons, and certain arboreal mice and rats. Their adaptive significance varies. In at least some climbing mice, the grasping hallux is an adaptation to locomotion on the large siliceous stems of bamboos (*39*), on which claw grip is useless. In chameleons, grasping extremities represent a predatory adaptation, permitting prolonged and stealthy locomotion on slender terminal branches in pursuit of insects, which these specialized lizards stalk in the dense marginal undergrowth and lower canopy of tropical forests (*40*).

The notion that ancestral marsupials had a grasping hallux remains generally accepted. In the smaller South American opossums like *Marmosa robinsoni*, this trait correlates with a chameleonlike way of life involving visually directed predation on insects "in the intricate interlacing of vine and branch that characterizes the second growth which abounds around the edges of clearings" (*41*). Insects, which these small didelphids require for adequate nutrition (*42*), are seized either in the hands or the mouth, bitten, and eaten held in one or both hands (*41, 43, 44*). The occasional use of the hands by didelphids in seizing prey becomes the most frequent pattern in small bush-frequenting Australian marsupials, including diprotodonts like *Cercartetus* as well as polyprotodonts like *Antechinus* (*43, 45*). *Cercartetus* and related small insect-eating diprotodonts like *Burramys* differ from other arboreal marsupials and resemble primates in having much-reduced claws (*46*). When allowance is made for allometry, insectivorous diprotodonts also have more convergent orbits than other marsupials (see Fig. 2C).

These comparisons suggest that the close-set eyes, grasping extremities, and reduced claws characteristic of most post-Paleocene primates may originally have been adaptations to a way of life like that of *Cercartetus* or *Burramys*, which forage for fruit and insects in the shrub layer of Australian forests and heaths. By this interpretation, visual convergence and correlated neurological specializations are predatory adaptations, comparable to the similar specializations seen in cats and owls, and allowing the predator in each case to gauge its victim's distance accurately without having to move its head. The grasping feet characteristic of primates allow insectivorous prosimians like the smaller cheirogaleines and lorisiforms to move cautiously up to insect prey and hold securely onto narrow supports when using both hands to catch the prey. Although claws are advantageous in most arboreal locomotor situations, they are actually a hindrance for a bush-dwelling animal that grasps slender twigs by opposition of preaxial and postaxial digits, and has little occasion to climb on larger supports (*23*).

Olfactory regression has not been characteristic of most arboreal mammals. The slight simplification of the olfactory apparatus seen in strepsirhine prosimians, and the marked regression found in haplorhines (tarsiers and higher primates), are necessary results of the approximation of the medial walls of the two orbits; since the optic nerve leaves the base of the skull and the orbital openings lie in the dermal bones of the skull roof, the olfactory connections between braincase and snout must necessarily be constricted if the orbital cones draw closer together. This effect is evident in a comparison of small felids with canids: in the former, the interorbital space is generally narrower, and the olfactory bulbs are correspondingly smaller and have constricted connections with the olfactory fossa (*47*). In *Tarsius*, the close approximation of the huge eyeballs reduces the interorbital volume (filled, in typical mammals, by olfactory scrolls of the ethmoid) to a single plate of compact bone, the interorbital septum, over the top of which a few olfactory fibers arch to reach a much-reduced nasal fossa (*3, 48, 49*). Small ceboids and cercopithecoids resemble *Tarsius* in these respects. Other lineages of visually directed predators have achieved comparable degrees of visual field overlap without pronounced olfactory constriction; in marsupials (cover photograph), optic convergence is produced by the coexistence of a low frontal region with a broad and high zygomatic arch (*3*), while in lorises the eyeballs come together around and outside the olfactory connections, which reach the nasal fossa between the optic nerves (*3, 49*). The unique arrangement seen in the smaller extant haplorhine primates probably reflects derivation from a big-eyed Eocene prosimian like *Pseudoloris* (which appears to have had a *Tarsius*-like interorbital septum); it does not represent perfected adaptation to arboreal life. Marsupial lineages which have evidently been arboreal since the Cretaceous have undergone no olfactory regression; arboreal life per se does not encourage loss of olfactory acuity.

Most of the distinctive primate characteristics can thus be explained as convergences with chameleons and small bush-dwelling marsupials (in the hands and feet) or with cats (in the visual apparatus). This implies that the last common ancestor of the extant primates, like many extant prosimians (for example, *Tarsius, Microcebus, Loris, Arctocebus*, and the smaller galagines), subsisted to an important extent on insects and other prey, which were visually located and manually captured in the insect-rich canopy and undergrowth of tropical forests.

The Fossil Record

Like any other evolutionary explanation, the visual-predation theory must be tested against the relevant paleontological data. Here it encounters difficulties. However we choose to define the order Primates, its early representatives differ from the earliest placentals in several features of the molar teeth, including reduction of the stylar shelf and associated cristae and decrease in the size and height of the trigonid. Since similar changes are seen in the earliest rodents and ungulates (Fig. 3), Szalay (*50, 51*) has proposed that the differentiation of the Primates from the Insectivora involved an adaptive shift from an insectivorous diet to a predominantly herbivorous one. If true, this vitiates the visual-predation hypothesis.

Szalay's thesis has recently been challenged by Simons (*52*), who suggests that, in at least four of the six families of early Tertiary mammals usually assigned to the order Primates, the earliest representatives have molars functionally similar to those of the carnivorous prosimian *Tarsius*. Although it has been said that the carnivorous diet of *Tarsius* could not be inferred from the morphology of its dentition (*51*), my colleague R. F. Kay has recently developed a multivariate biometric statistic which is over 90 percent accurate in "predicting" the dietary habits of the extant primates, including *Tarsius*. Despite the reduction of the stylar shelf in extant prosimians, at least some of them have recognizable dental adaptations for masticating prey; other shearing mechanisms have replaced the primitive shear of trigonid against paracrista and metacrista (*53*). The application of Kay's procedure to early primate dentitions will permit us to test certain aspects of the visual-predation theory.

The plesiadapoids of the Paleocene (Plesiadapidae, Paromomyidae, Carpolestidae) are assigned by paleontologists to the order Primates, although they show none of the diagnostic primate traits listed by Mivart (*5*). Where known, plesiadapoid orbits are small

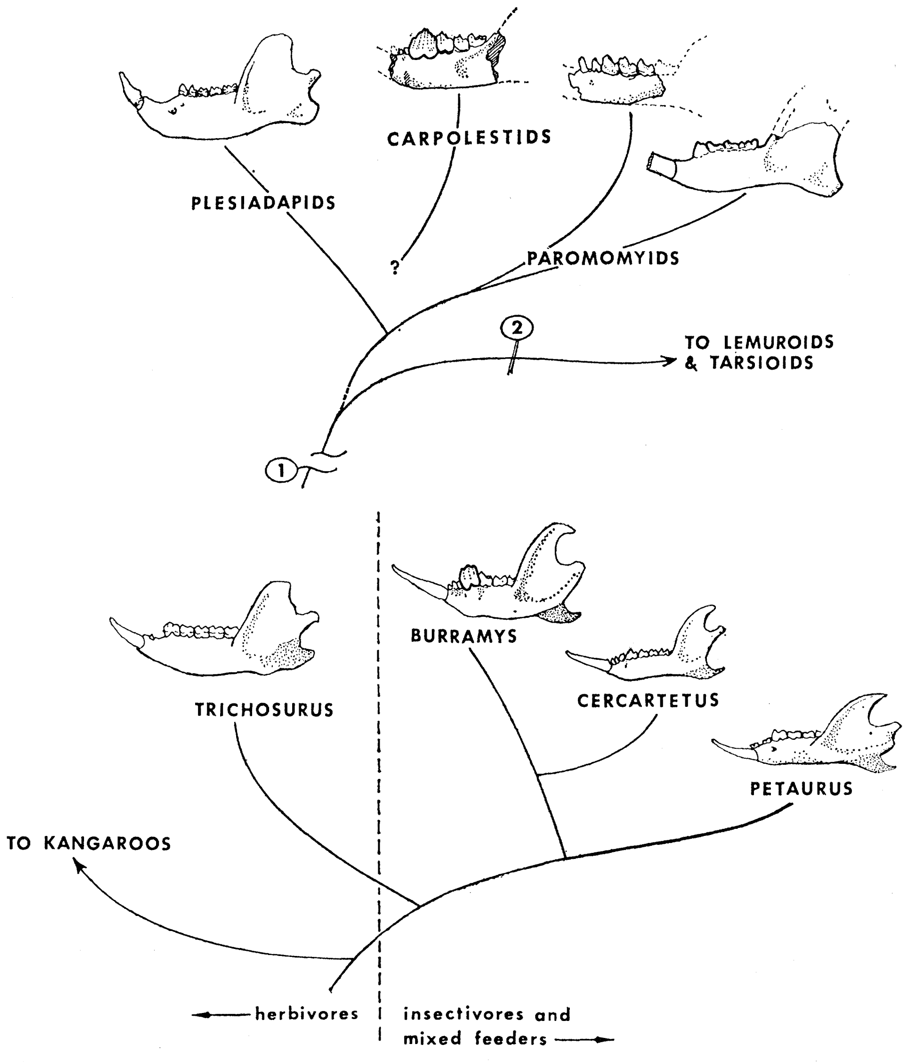

Fig. 4. (Above) Representatives of the plesiadapoid radiation (left to right: *Plesiadapis tricuspidens, Carpodaptes aulacodon, Palaechthon alticuspis, Phenacolemur jepseni*). (Below) Possibly comparable extant representatives of the phalangeroid marsupial radiation: phylogenetic relationships after Kirsch (*58*). The morphological shift at ①, which established the dental traits shown in Fig. 3B, is usually taken as the boundary of the order Primates. The inferred shift at ②, here considered to be a shift toward visually directed predation, could (if monophyletic) serve as the boundary of a more coherent primate order.

and widely set, there is no postorbital bar, the braincase is small relative to the facial skeleton, and there is no apparent reduction of the olfactory apparatus; *Plesiadapis*, at least, also had clawed digits resembling those of a squirrel or dermopteran (*50, 54*). The plesiadapoids are assigned to the primates on the basis of minutely detailed resemblances between their molars and those of later undoubted primates; where known, the ear region of plesiadapoids also shows certain diagnostic primate features (*50, 55*).

There is little doubt that the plesiadapoids are close collateral relatives of the Eocene prosimians. There is also little doubt that the known plesiadapoids are not directly ancestral to the Eocene prosimian families, since at least one genus in two of the three Eocene families (Adapidae, Anaptomorphidae, and Tarsiidae) retained teeth that had been lost in known plesiadapoids (*56*). Plesiadapoid lineages that can be traced through time did not converge with the early lemurs and tarsiers of the Eocene, but developed progressively more specialized dentitions displaying loss of canines and anterior premolars, hypertrophy of the fourth lower premolar, enlargement and complication of the anterior incisors, and other peculiarities. The fossil evidence suggests that the (unknown) lineages leading to the Eocene "primates of modern aspect" (*57*) must have branched off from the plesiadapoid lineages at least by the Torrejonian (mid-Paleocene).

The radiation of the phalangeroid diprotodont marsupials in Australia provides suggestive parallels with the plesiadapoid radiation. Plesiadapoid-like dental specializations, including reduction of the stylar shelf and hypertrophy of the lower central incisors, must have characterized the last common ancestor of the diprotodonts. Of the three extant diprotodont superfamilies (*58*), the phalangeroids have been the most successful. The ancestral phalangeroids were probably small arboreal mixed feeders; from these are derived not only the kangaroos, but also a complex radiation of arboreal marsupials. These include many forms with plesiadapoid counterparts (Fig. 4). The larger and more herbivorous phalangeroids like *Trichosurus* and *Pseudocheirus* have strong claws and a postincisor diastema, and are roughly comparable to the plesiadapids. Smaller phalangeroids have retained varying amounts of insect prey in their diets, and generally more complete dental formulas; they can be compared to the early paromomyids. From such an ancestry there have arisen the gliding omnivore *Petaurus*, likened by Gingerich (*59*) to the specialized paromomyid *Phenacolemur*, and the mountain pygmy possum *Burramys*, whose enlarged, serrated third lower premolars, used in cutting open seeds and hard insect cuticles (*60*), find a parallel in the carpolestid plesiadapoids. Unspecialized paromomyids like *Palaechthon* (Fig. 4) may prove to be plesiadapoid counterparts of *Cercartetus*.

As shown above, the adaptations of *Cercartetus* for visually directed predation among fine branches represent plausible structural antecedents for the traits that distinguish the extant primates. However, *Cercartetus* is considerably more primitive in these respects than superficially similar prosimians like *Microcebus murinus*. This is equally true of *Palaechthon*, which resembles *Plesiadapis* and differs from typical Eocene prosimians in having widely separated orbits, an unossified postorbital ligament, and a relatively small braincase (*54*).

Since early plesiadapoids had not acquired the traits (considered here to be adaptations to visually directed predation in forest undergrowth) that distinguish primate families from the Eocene on, and since later plesiadapoids did not converge with the true prosimians of the Eocene, it has been suggested (*3*) that the order Primates would be more coherent if the plesiadapoids were relegated to the Insectivora, and the postorbital bar and clawless, divergent hallux were taken as diagnostic primate traits, as Mivart considered them 100 years ago. It has been objected that "this diagnostic simplification certainly would not justify the resulting loss of phylogenetic information" (*61*). Similar objections could be made to the exclusion of the therapsid reptiles from the Mammalia, or of the rhipidistian fishes from the Amphibia. Taxonomic boundaries must reflect more than mere phylogenetic affinity; they must also mark important adaptive shifts that underlie the evolutionary trends characteristic of a radiating higher taxon.

Summary

Clawed digits, nonopposable thumbs and first toes, and wide-set eyes are primitive mammalian traits. For an arboreal mammal, the adaptive value of these traits is equal or superior to that of primate-like grasping extremities and closely apposed eyes. The loss of the primitive traits in the order Primates therefore cannot be explained by merely invoking the putative selection pressures imposed by arboreal locomotion per se. Visually directed predation on insects in the lower canopy and marginal growth of tropical forests is characteristic of many living prosimians, and also of small marsupials and chameleons. Primate-like specializations of the visual apparatus and extremities occur in all these groups. This suggests that grasping extremities were evolved because they facilitate cautious well-controlled movements in pursuit of prey on slender supports; and that optic convergence and stereoscopy in primates originally had the same adaptive significance they have in cats. The arboreal theory of primate differentiation, proposed in two incompatible forms by G. E. Smith and F. W. Jones, can be shown to be inadequate by counterexamples drawn from other lineages of arboreal mammals. Although some evolutionary biologists and philosophers regard such counterexamples as irrelevant, their relevance must be admitted if we want to work toward genuinely explanatory accounts of historical processes.

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NEWS AND COMMENT

Energy Reorganization: Progress in the Offing

In his periodic energy messages, President Nixon has drummed a persistent theme during the past 2 years that a dilatory Congress was holding up some of the Administration's major legislative initiatives, chief among them proposals to reorganize the government's tangled energy bureaucracy. The President's complaints were not without justification, although there are indications that the White House neglected to push its own proposals very hard before last summer.

There was, in any case, movement on two fronts last week that promises by early this summer to lob the reorganization initiative back into the White House court.

On 10 April the Senate reorganization subcommittee managed to resolve a months-long impasse and report out to the full committee a key Administration bill that would split the Atomic Energy Commission into two agencies—an Energy Research and Development Administration (ERDA) and a new regulatory body, the Nuclear Energy Commission (NEC). An AEC spokesman said that the bill seemed to contain no fundamental conflicts with a similar measure passed by the House in December. The spokesman predicted unofficially that the reorganization bill could be on the President's desk by early June. Allowing for built-in statutory delays, the AEC's metamorphosis could take place this fall.

Two days later, by coincidence, a study group commissioned by the White House last June released its analysis of organizational problems afflicting the federal regulation of energy resources, prices, and technology. William O. Doub, the AEC commissioner who headed the study, told a news conference that a major streamlining of the regulatory machinery could be undertaken by the White House within the next 12 to 18 months, largely without asking Congress for special legislation.

No major reorganizations are proposed, beyond those already before Congress, and no new regulatory powers are requested. Instead, Doub and his group offer up four ideas for coordinating and refereeing the activities of some 40 federal entities with a hand in energy regulation. They recommend:

- A National Energy Council, "to provide general policy guidance" where none now exists.
- A licensing coordination office to shepherd applications for energy projects through the wilderness of agencies.
- A permanent Energy Data Office to serve as a central source of supply-and-demand information.
- "New structural mechanisms," only vaguely defined, to improve relations between federal, state, and local governments in planning energy projects.

Doub's study is not the first to explore this particular regulatory jungle