PERSPECTIVES: PALEONTOLOGY

Primate Origins Nailed

Eric J. Sargis

The origin of euprimates (primates of modern aspect, including living primates) has been debated for 30 years. Several adaptive scenarios have been proposed to explain this important event, but the fossil evidence needed to test these scenarios has been lacking. On page 1606 of this issue, Bloch and Boyer (*1*) describe a remarkably well-preserved 56-million-year-old skeleton of *Carpolestes simpsoni* (see the first figure) from the Clarks Fork Basin, Wyoming. The fossil allows, for the first time, a test of the proposed events leading to the evolution of euprimates.

Carpolestes belongs to Carpolestidae, one of several families in Plesiadapiformes. Traditionally considered to be an archaic group of primates, plesiadapiforms have alternatively been included in the order Dermoptera (*2*). Recent phylogenetic analyses have shown, however, that plesiadapiforms are probably the closest relatives of euprimates and should thus be retained in the order Primates (*1*, *3*). Flying lemurs (Dermoptera), tree shrews (Scandentia), and primates form a supraordinal grouping called Euarchonta (*4*); the Archonta also includes bats (Chiroptera) (see the second figure) (*5*).

The carpolestid skeleton was prepared out of a freshwater limestone block. From similar blocks, Bloch and Boyer also recovered several other important small-mammal skeletons (*6*), including paromomyids and micromomyids (other families of plesiadapiforms), insectivores, marsupials, and rodents. The paromomyid and micromomyid skeletons are particularly important because they will help to resolve whether these mammals were capable of gliding (*7*)—a hypothesis that has been rejected repeatedly (*8*–*10*).

Field crews from the University of Michigan have collected more than 100 limestone blocks from over 30 localities in the Clarks Fork Basin. Bloch and Boyer are also expanding their research into the Bighorn Basin, Wyoming, and the Crazy Mountain Basin, Montana. The fossil mammals prepared from these limestones are reminiscent of the Eocene (55- to 34-million-year-old) fossils from Messel in Germany, and the Cretaceous (145- to 65-million-year-old) fossils from the Yixian Formation in China, in that the skeletons are nearly complete and almost fully articulated (although impressions of fur are not found in the limestones).

An important difference between the fossils from Wyoming and those from Germany and China is that the Wyoming specimens are not flat and can be examined in three dimensions. Of equal importance is the development by Bloch and Boyer of a technique to document associations of skeletal elements with dental specimens (*6*) because most fossil mammals are known from only their teeth.

Early grasping. Reconstruction of *Carpolestes simpsoni*, a plesiadapiform primate, foraging for fruit in the terminal (slender) branches of a Cornelian Cherry tree (dogwood species, *Cornus mas*). *Carpolestes* is known from the late Paleocene epoch (65 to 55 million years ago) of Wyoming, where such trees are also found. *Carpolestes* has a grasping foot that shares several features with that of modern primates (euprimates), including an opposable big toe with a nail rather than a claw. It could probably grasp with its hands as well. These features allowed *Carpolestes* to move in the terminal branches of trees where food resources like this fruit are found.

The *Carpolestes* specimen has major implications for hypotheses of euprimate origins. Euprimates are characterized by grasping hands and feet with opposable thumbs and big toes. They have nails on their digits (instead of claws), convergent eye sockets (that is, forward-facing eyes and orbits) with postorbital bars (bony rings around the orbits), and large brains. The earliest euprimates (adapids and omomyids) also exhibited several adaptations for leaping (*11*).

There are four main hypotheses for how these characteristics may have evolved. According to Cartmill, orbital convergence, grasping extremities, and nails on the digits evolved together for visually directed predation of insects on terminal (slender) branches (*12*). Sussman has proposed that grasping extremities and nails on the digits evolved for eating fruit on terminal branches of angiosperms (*13*). In Szalay and Dagosto's scenario, euprimate features—including grasping extremities, nails on the digits, and leaping adaptations—evolved together for grasp-leaping locomotion (grasping during climbing and during landing after leaps) (*11*). Finally, Rasmussen has proposed that grasping evolved first to exploit angiosperm food products in the terminal branches, and orbital convergence evolved later for visually directed predation of insects (*14*).

As Cartmill stated, it would "help if we knew something about the order in which the various primate peculiarities were acquired" (*12*, p. 111). The *Carpolestes* skeleton is important in this regard because it exhibits a mosaic of primitive plesiadapiform features and derived, euprimate-like characters that allows a consideration of the steps leading up to the origin of euprimates. For instance, *Carpolestes* lacks euprimate visual specializations such as orbital convergence and postorbital bars. A functional analysis of its skeletal morphology shows that it was also not adapted for leaping (*1*).

It did, however, have a euprimate-like grasping foot with an opposable big toe (hallux). It also had a nail on its big toe, but claws on its other digits. These features would have allowed *Carpolestes* to move in the terminal branches of trees in addition to moving on larger arboreal supports. It seems, therefore, that powerful, euprimate-like grasping evolved in primates before the evolution of orbital convergence and leaping. This sequence of acquisitions is consistent with the scenarios of Sussman and Rasmussen (*13*, *14*).

That *Carpolestes* had a grasping foot is not surprising. *Plesiadapis*, another plesiadapiform, was probably also capable of grasping (*11*, *15*, *16*). The articulation of the big toe in *Plesiadapis* is similar to that of the arboreal tree shrew *Ptilocercus*, which is capable of a primitive form of grasping (*11*, *15*, *16*). *Plesiadapis* did not, however, have an opposable big toe like that of *Carpolestes*. The articulation of the big toe in *Carpolestes* is more like that of euprimates, forming a saddle-shaped joint capable of a greater degree of divergence.

What is surprising is that *Carpolestes* had a nail on its hallux, but claws on its other dig-

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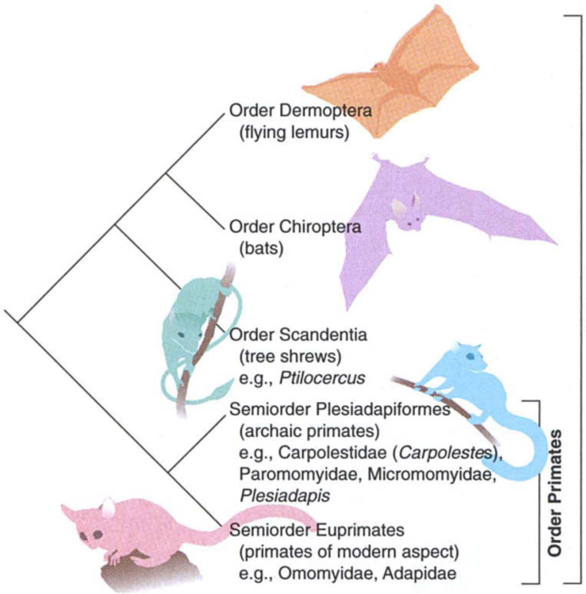

Archontan relations. Cladogram of archontan mammals, including the taxa discussed in the text.

its. Other plesiadapiforms have claws on all digits, whereas euprimates have nails on all digits (primitively). *Carpolestes* thus appears to exhibit an intermediate condition, providing the first evidence for the transition from claws to nails in primates.

The evolutionary history of grasping among archontan mammals is complex. The ancestral archontan or euarchontan likely lived in trees (*15*, *17*) and probably evolved a primitive form of grasping foot like that of *Ptilocercus* (*11*, *15*, *16*), with claws on all digits and without an opposable big toe. A more powerful, euprimate-like grasping foot with an opposable big toe, a nail on the big toe, and claws on the other digits then evolved in plesiadapiforms such as *Carpolestes*. Finally, orbital convergence and leaping evolved in euprimates.

As Cartmill explained, we "can only hope that new fossil finds will help us to tease apart the various strands of the primate story, giving us clearer insights into the evolutionary causes behind the origin of the primate order to which we belong" (*12*, p. 111). This is certainly true of the *Carpolestes* skeleton because we now have a much better idea of the sequence of acquisitions in the primate lineage. Fortunately, the limestones of Wyoming should continue to produce fossils that will enlighten us about primate and mammalian evolution for years to come.

References and Notes

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18. I thank J. I. Bloch and D. M. Boyer for useful discussions and L. Swedell for helpful comments. I also thank D. M. Boyer for preparing the first figure and P. Morrighan for preparing the second figure.

PERSPECTIVES: LINGUISTICS

Noam's Ark

Thomas Bever and Mario Montalbetti

Language is naturally viewed as a unique feature of being human. Accordingly, the study of what language is—linguistics—has been very influential, primarily in the social and behavioral sciences. On page 1569 of this issue, Hauser, Chomsky and Fitch (*1*) expand the scope of language study with their demonstration that complex behaviors in animals and nonlinguistic behaviors in humans can inform our understanding of language evolution.

The origin of human language has been an evanescent topic in the history of ideas for many centuries. It pops up in philosophical debates as a conceptual exercise on the nature of humanity and then, just as capriciously, disappears from the intellectual scene. Two principal ideas have been presented in these forays that emphasize the functional basis of language or alternatively its expression of humanity. For example, Rousseau (*2*) famously argued that language flows from emotions; shortly thereafter, Herder (*3*), a bit less famously, suggested that language is a special expression of human rationality. Of course, available theories of language and evolution vastly underdetermined empirical answers. In desperation, the 19th century Linguistic Society of Paris banned the inconclusive topic of the origin of language.

Darwin inaugurated a new era by creating an empirical basis for what had been a purely conceptual debate. He suggested that language emerges from more primitive emotional communication abilities in animals. The notion that language is a gradually selected capability timidly appeared, accompanied by new methods for studying morphological evolution that embraced comparative analyses of fossils and genetics. However, the best part of the 20th century contributed little to the subject because—as Hauser, Chomsky and Fitch point out—"linguistic behavior does not fossilize." Understanding the relation between genetics and behavior is still in its infancy, and has been complicated by the absence of a clear model that delineates what language itself *is*. Chomsky's linguistic theory—which redefined language as a cognitive computational faculty—afforded hope for a conceptually and empirically illuminating discussion of the evolution of language. In their review in this issue, Hauser *et al.* (*1*) sketch a broad programmatic outline of how to understand human language better by comparing its computational component to the computational capacities of our contemporary earthly coinhabitants, the ones that survived the flood.

A brief dip into recent linguistic history will help us to understand the importance of the authors' approach. Chomsky's first great impact on behavioral science was his notion that sentence structure can be studied independently of meaning. His notorious demonstration of this is the sentence "Colorless green ideas sleep furiously" (*4*). Although it is nonsense, it is nonetheless recognizable as a well-formed English sentence (compared, for example, with "Ideas green sleep furiously colorless"). The first step in the new linguistic science of sentence structure was to become more abstract, leaving behind meaning to study the pure laws of syntax.

This led to the formulation that even the simplest sentences have an inner "abstract" syntactic form. The problem for linguistic research became redefined: how the inner form is mapped onto the outer forms that

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