CHAPTER FOURTEEN

Ancestral Locomotor Modes, Placental Mammals, and the Origin of Euprimates: Lessons from History

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INTRODUCTION

The title of this chapter has a double entendre embedded in it. It is a truism that biological history, in addition to ongoing adaptive demands, is decisive in shaping properties of lineages. But it is also uncontestable that precedent notions, influential contributors, or specific papers, right or wrong, channel and continue to profoundly influence thinking on many issues in science. There is a difference, however, in these two processes of canalization. In the evolutionary dynamic, there is no right or wrong, and the inherited attributes are the initial and boundary conditions that define the avenues open for subsequent phylogenetic/adaptive change. These paths do not only constrain but facilitate as well. At any rate, whales are not fish, so history fundamentally

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matters in all biological science. Genotype encoded factors which sum up history, beyond the maternal contribution in the egg, guide the change, adaptive or not, which is phylogeny.

Such largely adaptive phylogeny is an ongoing probabilistic outcome of environmental demands, which determine the frequency of individuals that make it through the survival and reproductive bottlenecks of each generation. The necessity to consider this theoretical foundation should be, therefore, neither surprising nor burdensome for natural historians who study morphological attributes or behaviors. Sundry disciplines, in particular research from behavioral ecology, provide fundamentally important plausibility hypotheses for paleobiologists, who seek such questions as this conference set out to do. The task, however, to reconstruct adaptive phylogeny is within the realm of paleontologists and morphologists who must tie the fossil record, through a variety of procedures referred to as modeling (see Szalay and Sargis, 2001), to information and ideas from neontology. This is done by testing specific historical-narrative explanations (i.e., phylogeny or taxon hypotheses; see Figure 1 in Szalay, 2000) against various areas of information. Historical narratives of science are tested against evidence of all sorts (Bock, 1981)—an activity not indulged in by Kipling. So contrary to Popperian thinking, much of science consists of historical-narrative explanations offered within the confines of law-like explanations, in juxtaposition to Cartmill's (1990) opinion that only the law-like statements are scientific. Law-like statements must be part of the context within which the various topics of becoming are explained (Bock, 1981; Szalay and Bock, 1991). But nomological-deductive explanations (law-like statements) alone, obviously, do not suffice in any science where history played a role. It is all those specific and contextual historical "mistakes" in the law-like workings of chemistry that result in consequences for replication, transcription, and translation of nucleic acids where the science of evolutionary change begins and couples with the vicissitudes of the environment.

The aim of this chapter is relatively straightforward, but because of space constraints, it is more of a review of some literature debates and an outline of some issues related to the origin of both the Plesiadapiformes and Euprimates (perhaps best considered as sister orders at present) rather than detailed documentation. To achieve these goals I will (1) examine, in a historical framework, selected examples of hypotheses in which conceptual methods, as well as empirical emphasis or de-emphasis, have had a significant role in the construction of these hypotheses, as well as their consequences, for analyzing the phylogeny of adaptations for plesiadapiforms and euprimates; (2) present my views on modeling in paleobiology and the testing of homology hypotheses; (3) remark on the evidence related to locomotor strategies of Cretaceous and some recent therians that are relevant to the assessment of the ancestral pattern in the Eutheria, and of a clade within that group, the Placentalia; and (4) reassert the importance of the "morphotype locomotor mode" concept as a critical connection between phylogeny estimation and adaptational (functional, in a broad sense) assessment. As an example, I point to some evidence from hard anatomy for the ancestral euprimate locomotor mode. The latter was first referred to as "grasp-leaping" in Szalay and Delson (1979) and subsequently more fully developed in Szalay and Dagosto (1980, 1988). R. H. Crompton (1995) appears to strongly second this view.

The Placentalia, diagnosed elsewhere based on tarsal attributes and four premolars, is the taxon that stems from (back in the Cretaceous) the last common ancestor of the Cenozoic and surviving eutherians. This is not just the living crown group because it includes now extinct orders as well. The corresponding stem group of the Eutheria from which the Placentalia arose is the paraphyletic Eoeutheria that diverged from Metatheria at least 125 MYA.

GLIMPSES OF HISTORY OF RESEARCHES REGARDING ARCHONTAN, PLESIADAPIFORM, AND EUPRIMATE MORPHOTYPE LOCOMOTOR STRATEGIES, AND THEIR INFLUENCE

The customary empirical efforts to study extant forms and fossils often break down into two approaches, the functional (in a broad sense) and the phylogenetic (see Szalay, 2000, for review). As a consequence, the conceptual methods that should guide the analysis of the various facets of a problem become simplified either into functional undertakings or synapomorphy sorting through parsimony analysis, or other phyletic approaches. In addition, it is not unusual at all for many scientists leaning in one or another direction regarding morphological analysis to completely barricade themselves into either of these two, often walled-off, compartments, stating they are not really interested in the "other" questions. This is not an exaggerated rendering of the state of affairs, particularly either for functional anatomy or parsimony cladistics-based studies, with the subsequent distortion of the questions and a loss of the evolutionary explanation that one is interested in.

There have been valiant undertakings to somehow combine function and taxonomic position in one fell swoop, although some of these quantitative efforts have, unfortunately, resulted in such empirical conflation of data that all that followed were strikingly visual “species stamps,” rather than any illumination of the role of heritage in the evolution of functional complexes (e.g., Oxnard et al., 1990). While the aim of these studies was laudable, the setting aside of the complex but feasible and complementary interrelationship of functional-adaptive and phylogenetic methods for the analysis of evolutionary origins (problems of transformation from one stage to another in the history of lineages) suffered, or simply was not part of the analysis.

As attested to by this conference and many others before it, primates generate great interest among an inordinately large number of natural historians of all sorts, morphologists among them. This is understandable but it makes for an enormous literature, and extremes of conceptual approaches to problems of adaptation of ancestral conditions and disagreements about the specifics of an ancestral lineage. At this conference (and before), for example, I or Dagosto viewed the ancestral euprimate as the phyletic antecedent of the reasonably well-known Eocene strepsirhines and haplorhines, whereas others considered a cheirogaleid such as *Microcebus* as a stand-in for this ancestor. In spite of such a difference in perception, which is almost never explicitly stated, what is less understandable is how several past contributions on the deep adaptive history of primates were based sometimes on a lack of expertise in evolutionary morphology, on highly selected literature contributions, or on a neglect of the specifics of extant species. Some of these publications were often by primatologists, who have written about bones and fossils with little experience either in the theoretical issues surrounding evolutionary analysis of morphology or the fossil record. This state of affairs, however, has considerably improved recently due to competitive pressures resulting from an upwelling of young talent specializing in these complex and intertwined fields of analysis. But the past has shown its powerful constraint on the collective minds of a whole subfield. Some textbooks and reviews have helped to perpetuate uncorroborated ideas about locomotor inferences regarding protoplacentalians, plesiadapiforms, and the stem euprimates. In the review given in later section, I will comment briefly on some such examples.

Arboreality as a Novel Strategy for the Stem of Archonta

Over and beyond the obvious specifics of arboreal heritage in the morphology of living primates, in the 1960s, the debate over this heritage has entered a new phase with an admittedly confusing framework for considering primates with or without the archaic primarily Paleocene radiation of the Plesiadapiformes. While the evidence now is overwhelming regarding the arboreality of plesiadapiforms (and their close phyletic ties to euprimates without the interference of dermopterans; see Bloch and Boyer, 2001; Bloch et al., 2000, 2001a,b,c 2002; Boyer and Bloch, 2000; Boyer et al., 2001), the history of the literature regarding archontans, tupaiids, and plesiadapiforms is highly instructive.

The initial and widely read impetus (if one was to start somewhere in a quasi-historical assessment such as this) that euprimates owe their particular morphological (and functional in a broad sense) divergence from their ancestry due to a particular locomotor behavior that involved leaping, was the contribution of Napier and Walker (1967)—a study that advocated vertical clinging and leaping as the initial stage of euprimate locomotor evolution. This restatement of previous views on leaping but with greater force and examples were significant because they went beyond the customarily evoked arboreality as an explanation for euprimate attributes. Much of the development of the insight regarding leaping in euprimate ancestry was largely due to the seminal studies of Walker (1967) on the subfossil and extant osteology of the Malagasy strepsirhines. The extended debate about vertical clinging and leaping that ensued is interesting history, but not directly relevant here. The theoretical underpinnings of the ecomorphological assessment of the vertical clinging Malagasy lemurs, galagos, and tarsiers were obviously sound. Much of the following debate focused, correctly, on the applicability of those conclusions to the fossil postcranial morphology, the area of anatomy that should have been logically the most significant for locomotor assessment of the fossil record. But that is not what happened.

Visual Predation as the Strategy for the Stem Lineage of Euprimates

Cartmill (1972) has presented the ambitious "visual-predation hypothesis" based on cranial attributes and grasping hands that was to explain the whole diagnostic structural make up of the protoeuprimate, and, at the same time, came to de-emphasize not arboreal locomotion as such, but the importance of grasping related leaping that shaped this ancestor. The whole argument was an attack on the straw man of "arboreality," without any consideration given to the multitude of ways that adaptations may be required to fulfill various kinds of positional regimes, arboreal or otherwise. The fact that clawed hands work very well in all predatory mammals, from opossums to cats as a tool for prey capture, however detected, was coupled with the need to climb cautiously and grasp tightly on small branches. With an emphasis on grasping hands and the loss of the claws coordinated with stereoscopy and appropriate neurology, Cartmill has relegated the powerful and larger grasping hindfeet (compared to the hands) as a means to allow "...to move cautiously up to insect prey and hold securely onto narrow supports when using both hands to catch the prey" (p. 440). What was largely missing from this overarching hypothesis is the accounting for the skeletal evidence known by then for a number of early euprimate lineages. Cartmill (1975) further developed his views along similar lines. It should be emphasized here that Cartmill's (1972, 1974) views (or those of Hamrick, 1998) regarding the reduction of claws are not supported by the targeted selective loss of the falcula on the hallux in didelphids and descendants. The correlation in extant marsupials appears to be with the powerful grasp of the pes and a postulated selective disadvantage of the sharp falcula on the hallux on smaller branches.

What also complicates matters of historical reconstruction regarding the evolution of various published perspectives on primate morphotype locomotion, and the implicit assumptions that these views rest on, is the apparent inconsistency of some published views. Issues of phylogeny, latent in any adaptive hypothesis, but almost always implicit when they should be explicit, point to some critical inconsistencies in the presentation of the visual predation hypothesis of Cartmill. For example, Cartmill (1974: 74) has given confusing testimony about the historical context of his views on claw "loss" (part of a transformation series of the homologues called digital ungulae) in the protoeuprimate. In fact, Cartmill (1974) and later Hershkovitz (1977) have strongly supported the transformation of falculae (claws) into the tegulae of platyrrhines independently from other euprimates, with Cartmill, in particular, arguing for "greatest parsimony." This is particularly puzzling because Cartmill's "visual-predation" hypothesis launched in 1972, and expanded in 1975 was critically dependent on the assumption of a nailed condition in the euprimate stem. Regarding the loss of claws in euprimate ancestry Cartmill (1974: 74) says that: "The comparative anatomical evidence indicates that the hands and feet of the last common ancestor of the extant primates [i.e., Euprimates] must have resembled those of the opossum; claws have been lost independently in four or five parallel lineages of primates." On the same page further down Cartmill explicitly supports the notion that claw loss can be the result of a "...trend toward increased size in animals inhabiting the higher strata of tropical forest, or from the restriction to the lower strata of a relatively treeless heath or scrub floral community." It is also relevant here that Lewis (1989, based on a series of articles published in 1980) explicitly supported an arboreal ancestry for the last common ancestor of the fossil and living placentalian mammals—a view that Martin (1990) has continued to champion. This appears to be decidedly untrue for the Placentalia, and probably also for the stem of the Early Cretaceous Eutheria as well.

To put it bluntly, contrary to pronouncements, the comparative anatomical evidence never "indicates" anything; one explicitly tests and interprets homology hypotheses, which Cartmill did in an unacceptable way (see detailed discussion of this in Szalay, 1981b: 40–44). But the most striking feature at that time, given the "visual-predation" hypothesis (which one might have thought was based on a homology-based phylogenetic position, i.e., "claw-loss" and postorbital bars) was the concept of parallelisms in Cartmill's theoretical and historical-narrative explanations (i.e., the recurrence of parallel trends in the evolution of euprimates).

Added to this, I believe, was a connection to the "Plesitarsioidea" versus "Anthrolemuroidea" view of primate phylogeny, an interesting historical curiosity (Gingerich, 1974; 1975a,b; see also Krishtalka and Schwartz, 1978; and Schwartz et al., 1978) which is relevant here. This view of primate phylogeny, which posited an unacceptable wedding (then or now) of the plesiadapiforms and one of the early euprimate groups (the Tarsiiformes) as a clade, represented at that time a significant manifestation of primate evolutionary studies in contrast to the strepsirhine–haplorhine dichotomy advocated by others. The disregard for the very accessible postcranial evidence of fossils (Szalay et al., 1975) and the extant postcranial osteology by both the proponents of the "visual-predation" hypothesis and the taxonomic notion of the "Plesitarsiiformes" (this latter derived from, and synonymous with, the "Plesitarsioidea") points out that postcranial attributes (at the level perceived by these authors) were considered (if examined at all) as rife with "parallelisms," hence not very reliable.

But subsequent to Cartmill (1972), Szalay and Decker (1974), and Szalay et al. (1975) have assessed the then known skeletal collections of *Plesiadapis* (the former study emphasizing the tarsus the latter the remainder of the skeleton) and concluded that the only reasonable explanation of the evidence was unquestionable arboreality for the archaic plesiadapiforms. Szalay and Decker (1974), Decker and Szalay (1974), and Szalay et al. (1975) emphasized in particular both the similarities to but also the differences in arboreal adaptations in the tarsus between plesiadapiforms and euprimates in contrast to latest Cretaceous eutherians. These conclusions were dismissed as doubtful by Cartmill (1975: 32), without any indication that he considered the evidence. But then, it appears, that Cartmill was wedded to the notion that arboreality was primitive for the ancestry of living placentalian mammals, and therefore, his attacks on the arboreal theory of primate origins, as he called it, were justified only on the grounds that attributes related to other than some specific arboreal locomotion were necessary to explain the origin of both the Plesiadapiformes and the Euprimates. Martin (1990), in his text also insisted that the plesiadapiforms simply retained arboreal modifications already present in a remote placental ancestor. This unfortunate disregard for the fossil evidence (dubbed as "special problems of the fossil record" by Martin, 1986: 4) was also evident earlier. [Martin's statement (1986: 23) about *Plesiadapis* that its hallux "might have been totally lacking," is particularly revealing in light of the fact that in the same volume Gingerich illustrates and makes a note about the preserved big toe, suggesting a lack of familiarity with the record. Yet, this unfamiliarity with the specifics of fossil evidence did not prevent that author to present high profile discourse about fossil primates elsewhere as well (see for example Martin, 1993)].

There can be little doubt that there was a nearly complete disconnect between phylogenetic thinking and adaptive assessment by Cartmill (1975: 32–33) when one reads that "[if] the characteristic primate traits are the result of progressive adaptation for arboreal visual predation in one line of descent from an early plesiadapoid... thrusting the plesiadapoids...back into the ancestral order Insectivora would make the order Primates more coherent, However, we must not forget...[that]...If, for instance, it turns out that anaptomorphids arose from very early paromomyids, while adapids evolved separately out of the earliest plesiadapids, it might still prove true that the lines leading to the Eocene families went through an adaptive shift to visual predation, in parallel in two different lineages...". It is difficult to see how the more complex areas of the skeleton, particularly the carpus and tarsus, failed to convince these authors both about the unequivocal arboreality in the plesiadapiform ancestry and the unquestioned monophyly of the Euprimates, except if one considers the overwhelming "scenario" bias by Cartmill and a then prevalent dental mindset by Gingerich and associates. After the widely available postcranial evidence had been repeatedly pointed out in the literature in the 1970s and 1980s (Szalay, 1972) the polyphyletic notion of the euprimates was finally abandoned.

It should be added here that parsimony (a useful notion if properly applied to not only relevant "facts" but to all the complex interpretations necessary in the construction of tested hypotheses regarding properties) was much used then as it is now. Such procedures, however, rapidly (and properly) turn into a series of Bayesian considerations. This is an approach not much appreciated by Popperian systematists in primatology who became advocates of a falsificationist approach to cladogeny based on algorithm research, as opposed to an incremental research program leading to phylogeny estimation (e.g., Szalay, 2000). The unfortunate reality has been, however, that either erudite and literary rhetoric about scenarios or unexamined character lists require more than "parsimonious thinking" or scholastic Aristotelian logic (algorithmic or not) for nonmonotonic testing procedures in evolutionary morphology and the testing of historical-narrative explanations. The arguments about plesiadapiform and euprimate relationships and adaptations, and the methods of assessment, continued in the literature.

Kay and Cartmill (1977: 19) in their restudy of a crushed skull of the Torrejonian Paleocene *Palaechthon* concluded that while euprimates were derived from plesiadapiforms, the cranial adaptations of the latter (exemplifying primitive plesiadapiforms) reflect a "...predominantly terrestrial insect-eater, guided largely by tactile, auditory, and olfactory sensation in its pursuit of prey." Even more interestingly (and in stark contradiction to Cartmill's views on ancestral placental arboreality), they noted that "Adaptations to living in trees and feeding on plants probably developed in parallel in more than one lineage descended from the ancestral plesiadapoids." It was pointed out subsequently in a critique by Szalay (1981a: 157) that Kay and Cartmill in their analysis of the cranial evidence based their conclusions regarding plesiadapiform adaptations on: (a) nonphylogenetic and static assumptions, (b) misinterpretation of the form and mechanics of the attributes analyzed, and (c) employment of irrelevant characters for the establishment of substrate preference (e.g., infraorbital foramen size). Szalay criticized the general outlines for adaptational analysis espoused by Kay and Cartmill, and the positions taken by these contending parties on the type of character choices and functional interpretations are still the general positions that endure in many debates today. Namely, in dealing with fossils, how should one approach the difficult issue of adaptational assessment (see Szalay, 2000, contra the arguments offered by Anthony and Kay, 1993: 374)?

My arguments in 1981 were in juxtaposition to the practice of indiscriminate use of ancestral characters that could be correlated with some habitat in living animals (e.g., the relative size of the infraorbital foramen in archaic primates used by Kay and Cartmill, 1977, to argue for terrestriality in paromomyid plesiadapiforms). While the persistence of functional correlates of even primitive traits can be useful in framing an adaptational analysis, primitive traits are often revealing of ancestrally acquired adaptations within a different context. The human thorax, shoulder complex, and elbow joint are good examples. These heritage traits, a group's synapomorphies, set the limits for various trajectories of the more derived features. For example, the contact of the fibula with the femur, and also via the parafibula (the fibular fabella), correlates only with some aspect of therian primitiveness in the knee complex, but no ecologically meaningful differentiating function can be associated with it in marsupials that show different habits today. Both the most arboreal and terrestrial marsupials have this as part of the knee complex, although instructively, with different conformation of the proximal fibula. The extreme narrowing of the proximal fibula (and attendant muscular and mechanical correlates) occurs only in highly terrestrial metatherians (see later section). Similarly, the repeated narrowing of the lateral femoral condyle in terrestrial didelphids, bandicoots, basal, and all other kangaroos, as well as in the ancestral placentalian, also closely predicts terrestriality (Szalay and Sargis, 2001). But the narrowing of the proximal fibula that also occurred in protoplacentalians does not rewiden again in Cenozoic and recent arboreal eutherians, nor does the medial femoral condyle changes its proportions. The extant eutherian lineages (and their fossil relatives which postdate the stem of these) are likely all derived from the terrestrially modified eutherian that was the stem of the Placentalia.

The Role of Leaping in the Ancestral Euprimate

By 1979, Szalay and Delson noted that the likely breakthrough *from* an arboreal plesiadapiform ancestry (unequivocally suggested as such by Szalay and Decker, 1974, and corroborated beyond any reasonable expectation by the efforts of Bloch and Boyer) involved "...the establishment of *grasp-leaping* arboreal adaptations ...necessitated by a particular feeding regime" (p. 99) for the stem of the strepsirhines, considered by them to be the best approximation of the euprimate stem. Szalay and Dagosto (1980) in their extended discussion of what they defined as *morphotype locomotor modes* (a concept which incorporated a phylogenetic context into the assessments of locomotor behavior/anatomy) have discussed *claw-climbing* as reflected in the protoplesiadapiform condition. They also emphasized in some detail that the interpretation of skeletal features strongly supports grasp-leaping as a *monophyletic acquisition* of the protoeuprimate. They essentially agreed with Le Gros Clark (1959) that arboreal locomotion (but a particular type) was likely part of the causal nexus of the cranial features one observes in the Eocene primates—a foundation on which modern diversity is based. They disagreed with Cartmill's hypothesis, and stated that "The greater importance and more severe selectional consequences of judging distances by quadrumanous *fast* grasp-leapers would clearly put a greater premium on stereoscopy than just running and walking along branches in an arboreal environment. There is no evidence for uniquely associating quadrumanous primate grasp-leaping with arboreal insectivory-omnivory. The first euprimate grasp-leaper may or may not have been primarily phytophagous, zoophagous, or ominivorous." (p. 35).

In 1992, Cartmill reviewed, with candor, the differences between the grasp-leaping and the visual predation hypothesis as contributing causal factors in the development of the protoeuprimate cranioskeletal complex, although he continued to think of "arboreality" as some monolithic causal agent. He correctly cites my often-stated view (following those of, e.g., Darwin, Gregory, Matthew, and Simpson, and others'), namely that evolutionary transformations are constrained by history in a highly contingent way, and that the new adaptive solutions mirror that heritage, often to a considerable degree. This view, in light of the prevalence of mosaic evolution (bolstered by an understanding of modularity by students of EvoDevo), demands character level, rather than a taxic, analysis of homologies (the former dubbed as null-group comparison; Szalay, 1994; Szalay and Bock, 1991). In order to arrive at reasonable phylogenetic estimates of character complexes (and subsequently taxon phylogeny hypotheses), the development, functional biology, and adaptation of taxonomic properties need to be considered, in contrast to the declared primacy of algorithm-based rooting with taxic outgroups.

Nevertheless, following our debates of the extant and fossil evidence regarding the ancestral stage of euprimate locomotion, Cartmill has come to consider the issue of phyletics of characters and even the notion of (Darwinian, i.e., evolutionary) homology somewhat moot points (see Cartmill, 1994, on the issue of homology hypotheses; and Cartmill, 1990, for his rejection of historical-narrative explanations as science). In arguing against the grasp-leaping euprimate locomotor mode, Cartmill (1992: 107) noted that "...particular evolutionary events cannot in principle be explained except as instances of some more general regularity," and also stated that "...adaptation to a grasp-leaping habit unique to euprimates, explains nothing." He has professed this belief in a variety of ways, in fact arguing against the very practice of historical-narrative explanations in science. I (and others) completely reject such ahistorical theoretical assumptions about the nature of science.

Cartmill (1992: 107) was correct in stating that other arboreal mammals "...do not look much like euprimates." Of course, few other arboreal mammals (with their independent heritage) do the acrobatic antics of those grasp-leaping lemuriforms whose general skeletal anatomy shows the same derived suite of features that can be reasonably attributed to the protoeuprimates as well. And those skeletal attributes appear to be diagnostic of the order based on the Eocene evidence (i.e., they represent a derived suit of features of the stem). But Cartmill's (1992) discussion of the issue of the euprimate morphotype locomotor mode, including his evaluation of the proposals of Sussman (1995) and Rasmussen (1990) were, in my view, deeply flawed. This was so not only on the theoretical grounds regarding his perspective on how one employs living model species to evaluate fossil animals (e.g., Szalay, 1981a,b; Szalay and Sargis, 2001; and later section). But perhaps more importantly than anything else, Cartmill continued to make only casual, if any, use of the highly specific and functionally well-understood aspects of postcranial morphology for interpreting the fossil postcranial evidence when discussing locomotion in the euprimate stem. This is odd enough by itself, but the postulate that (rapid and frequent) leaping and precise landing by grasping small branches has obvious consequences for both the nervous system and vision should not have been ignored. Habitual great leaping ability in the three-dimensional arboreal environment would certainly suggest a causal relationship to enhanced vision and attendant neurology. And to consider the reduction of the snout, olfaction is far less important for the execution of a leap than visually judging distance and points of landing among variable-sized branches for animals, whose size we cannot be certain of. Nevertheless, the issue remains a particular type of arboreal locomotion (grasp-leaping), not just "arboreality," and testing of that issue resides primarily in the mechanics of the joints of the skeleton of an inferred common ancestor and their near-fossil relatives.

The general area of modeling ecological morphology and its use for fossil species (see later section) is a lot more complex but also far more applicable than Cartmill's (1992: 107) statement that only parallelisms can be explained adaptively. For example, Szalay (1981a) argued against the thesis presented by Kay and Cartmill (1977) that large infraorbital foramina of the plesiadapiform *Palaechthon* pointed to a terrestrial, hedgehog-like habitus. I pointed out the difficulties of judging habitus (real-time adaptation in a species) based on primitive features because primitive features, while perfectly functional (obviously), do not reflect the most recent shifts in a lineage, unlike their derived attributes. Convergences of complex derived attributes of recognized mechanical consequences, however, are powerful "postdictors" of the habitus of fossil species, and are the most potent tests of historical-narrative explanations. I showed that relatively very large infraorbital foramina persist in some very arboreal species. Therefore, such features simply cannot be very useful in interpreting fossils, "parallelism" aside. Rather instructively, the size of various foramina continues to have a rather checkered history in predicting anything, including scenarios pertaining to the hominid realm.

It is exactly the rejection of the analyzed, ordered, and polarized use of character states of homologous features that is missing from the notion of "parallelism" dictated by Cartmill's views on homology. Is one's assessment of parallelism the result of parsimony analysis? Are we considering some convergent aspects of features, given distinct phylogenetic/taxonomic contexts? For establishing convergence (a tested, and failed homology hypothesis, without the somewhat obfuscating discussion and mixing of levels of organization by Lockwood and Fleagle, 1999), however, one should have some criteria other than the leftover traits expressed as a consequence of "CI" indices of parsimony-derived taxograms. The notion of convergence that Cartmill subscribes to in his pledge to taxic analysis as the arbiter of the nature of similarities is, *ipso facto*—a residue of a "losing batch of synapomorphies" that one now calls "convergent" (see Szalay, 2000). *But beyond how homology is established with some probability, there is the key issue of what particular convergent/parallel properties one is going to employ to explain a particular facet of adaptational history or a fossil species.*

R. H. Crompton (1995) has presented a detailed analysis of the literature (albeit with some studied omissions) regarding the origin of feeding and locomotor strategies of the euprimate ancestor. He has paid laudable attention to the connection that must exist between feeding and locomotor strategies. His conflation of the arboreal and scansorial strategy that was suggested for the plesiadapiforms by Szalay (1972) is taken by him as that for the protoeuprimate, one that is a minor *lapsus* by a primatologist with little practice in systematics or acquaintance with the fossils. What is, however, a recurring pattern in his critique of Cartmill (as well as in Cartmill's own previous contribution) is the consistent lack of attention paid to the details of the fossil dental and postcranial evidence. The circular "chop" diagrams of "total adaptive strategies" of various extant primate species published by Oxnard et al. (1990) are hardly a substitute for the independent assessment of the relevant fossil or even extant evidence. Unfortunately, a remark by Crompton (1995: 19) that a general arboreal form of locomotion "...is typical of many small, primitive mammals...," has less meaning than no statement at all. Within the even conventionally accepted concept of Mammalia, different groups undoubtedly had different primitive locomotor patterns (i.e., morphotype locomotor modes) with their attendant morphological properties that are amenable to specific model-based analysis (see later section).

[One would, in general, hope for the recognition by students of living primate ecology that feeding and locomotor strategies are primarily reflected in the morphologies of the relevant regions of the hard anatomy. Furthermore, it is appropriate to state here that feeding and locomotion can be decoupled not only in terms of morphological mosaic evolution, but also in terms of various solutions for the feeding/locomotion dilemma faced by all lineages. Nothing better exemplifies the mosaic nature of adaptive solutions than the variety of strategies seen within the lorisiforms—a group cited repeatedly by R. H. Crompton.]

Contrary to Crompton's statement (1995: 21), which is relevant here, there is no morphological evidence of any sort that would suggest dwarfism in the ancestry of the living tarsiers, only perhaps if one assumes a large-bodied haplorhine ancestry. As I noted earlier, we cannot be certain of the size of either euprimate, strepsirhine, or haplorhine ancestries, even though great antiquity does tend to preserve some aspects of morphology that indicate general functional features. Tarsiers are well within the size range of the group—which they are a relict of—the fossil Tarsiiformes of the Eocene. Their enormous eyes are probably a reflection of the compensation required by secondary nocturnality in a probably diurnal lineage that has shed the tapetum lucidum in its ancestry. But in his conclusions, Crompton (1995) seems to agree with the locomotor mode designation that was proposed by Szalay and Dagosto (1980, 1988) as grasp-leaping, and which was specifically tied to ancestral euprimate postcranial morphology and its inferred biological role (Crompton did not use that term, nor did he cite the 1980 article). Crompton's conclusions certainly corroborate those of Szalay and Dagosto (1980, 1988). Crompton, in spite of his strong disagreement with Cartmill, however, goes on to endorse the dietetic component of Cartmill's visual predation hypothesis. Unfortunately, there is no evidence from the dentition of the earliest euprimates, or from the best estimates of the adaptations of the morphotype of euprimates, that insectivory and predation were the preponderant ancestral dietary strategy. The postcranium and inferred leaping is neutral on that important question. The variety of dental pattern is great, however, so inference as to diet is at best a variety of fruit, flower, nectar, gum, and insect feeding, with no clear-cut emphasis in any reconstructed common ancestor.

It must be stressed that early dietary strategies in the protoeuprimate are not as yet understood, in spite of the often-cited deductive argument of Kay (1984) based on the body weight and diet of living primates, asserting that size is a predictor of diet. Body size is also often inferred from fossil teeth themselves, often a poor measure. According to that view, small fossil primates were, *ipso facto*, primarily insectivores—a gross oversimplification even on general grounds restricted to living primates as models. Assertions that because some small living lipotyphlans or primates are primarily insectivorous, all small fossil primates had to be as well, are divorced from morphological analysis. Many small fossil primates (as well as marsupials) with the appropriate dental and cranial attributes were probably oblivious to "Kay's rule" (contra Kay and Covert 1984) when it came to their dietary regimes. Similarly, the extant *Hapalemur* and *Lepilemu*r, or even cheirogaleids, do not adhere to such a rule. Morphological and functional patterns, in light of the appropriate models (but not size alone) supply convincing paleobiological explanations. As argued before (Sussman, 1995; Szalay, 1968, 1969, 1972), the dental evidence leaves little doubt that among early plesiadapiforms and euprimates, a mixed feeding strategy, evidenced by relatively low crowned and quasi-bunodont cheek teeth was likely to be both the ancestral and one of the more widespread conditions. One has to look no further than the variety of small rodents who find ample energy and nourishment primarily from seed consumption, ignoring this general "rule." Small fossil primates were not necessarily obligate insectivores unless their morphology corroborates such assessment.

It is also of some importance to note here the relevant point that contrary to Martin (1993), the radiation of a mammalian group is not usually that of an algorithm-based inverted pyramid, and therefore, the living radiation of primates is a poor foundation to model the early story that was driven by ecological context and biogeography, in spite of the putative elegance of such iconography. Given the enormously more extensive favorable habitats for primates in the Paleogene of Holarctica (and probably Africa as well), experimentation of many early lineages among the euprimates probably resulted in a far greater diversity of small omnivorous primates than there is today. An understanding of the fossil record helps in this regard. Massive extinctions with the changing of habitats have resulted in a pattern nearly the opposite of the computer-generated diagram of Martin (1993).

Sussman (1995) and I are in broad agreement on the importance of frugivory early in primate evolution. Regarding the close relationship of habitat and primate strategies, it is perhaps important to note that primates did not "invent the rainforest," although they certainly carry on the roles started by other clades. At least in South America, where primates did not arrive until relatively late in the Tertiary (and certainly never in Australia and New Guinea until humans ventured there), the radiation of arboreal marsupials was well under way since the Latest Cretaceous or Earliest Paleocene in tropical rainforest environments of South America, and sometime later in the antipodes. And even prior to that, a variety of atribosphenic mammals undoubtedly interacted in a number of ways with the tropical forests and angiosperms of that continent. It should be emphasized that the derived suit of postcranial traits of the stem euprimate certainly does not preclude a reliance on fruits, flowers, gums, or seeds, together with insects as the main items of its dietary regime, although such a diet can be attained by a whole variety of ways other than grasp-leaping. The most corroborated explanation for the morphotype skeletal evidence, however, is a regular practice of bounding leaps and landing with a hindfoot/forefoot grasp ("grasp-leaping"). But such interpretation, of course, does not mean that an animal with such morphology cannot slowly climb, walk, shamble, or in any other way get to its food, or stalk insects. But leaping does make a particular combination of *energetic and* *competitive* sense when particulate and discontinuously distributed clumps of food are sought after by many parties, both intra- and interspecific.

It is gratifying indeed that the general idea of grasp-leaping as the euprimate morphotype locomotor mode is so thoroughly circumscribed and argued for and advocated in all but name (i.e., without reference to the article by Szalay and Dagosto, 1980, where the hypothesis was first explicitly outlined and supported) by R. H. Crompton (1995).

MODELS AND THE LOCOMOTOR STRATEGIES OF EXTINCT TAXA

Central to paleobiological research that aims to explain both aspects of behavioral ecology of extinct forms and patterns of historical factors (these efforts are usually limited to dietary and locomotor strategies) is the analysis of skeletal remains. Living species models with their rigorously analyzed form-function attributes and their ecological causality lay the foundation for not only character analysis in systematics (as opposed to taxic analysis), but also for analyzing, through the use of convergence and matching, the form-function of the fossils as well (Szalay, 2000). Biomechanical generalities, such as occlusal mechanics of teeth or the loading of joints are paramount, but because, due to the uniqueness of lineages, there are no living species that match exactly the habitus of fossil entities.

It is not unusual that a living analog is used to find similarity (a concept fundamentally context- and paradigm-driven) for some sort of fossil morphology without functional, and therefore, causal reasons. The lack of a causal analysis (i.e., ecological, real-time) in the process of modeling does not allow one to conclude that selected matching morphologies indicate adaptive (ecological) similarities between the model and the fossil. Nevertheless, this approach can supply some meaning for paleobiological assessment if a whole skeleton is available for the fossil. Without complete specimens, however, the modularity-based and well-corroborated patterns of mosaic evolution render such assessments problematic for functional units of the skeleton. Such a general similarity evaluation lacks, as its basis, the necessary character analysis that functional-adaptive approaches provide and which test the nature of similarities before these are used either for paleobiological assessment or phylogenetics.

Modeling relies heavily on theoretical perspectives, as well as the experiences of the modelers with the subjects that they are focused on. A far more desirable procedure than mere similarity matching is the construction of mechanically and adaptively meaningful relationships in character complexes in a number of distantly related species that display attributes which are more likely convergent than homologous (e.g., Szalay, 1981a). One may call this a convergence-based "modular-function" approach. It is important to have some strong ecologically compelling evidence that certain recurrent attributes are (given a similar level of basic mechanical organization of the skeletal biology) under strong selectional imperatives for their recurrent development. An understanding of functional-adaptive significance (and consequently the probability of convergence versus homology of properties) is decisive in establishing a list of tested taxonomic properties. This approach has both an inductive component in using the recurrent correlations between morphology and mechanics and the ecological context, as well as a deductive one in applying the correlations to the fossil taxa. *Uncovering consistently convergent, biomechanically significant, features that have strong functional associations with either feeding or locomotor strategies in the skeleton of extant mammals does supply us with powerfully modeled "postdictors" for adaptations in the fossil record.*

Furthermore, if the probability is high that one or more aspects of properties in two or more taxa examined are the result of phyletically independent adaptive responses (rather than ancestral constraints), then, such convergent attributes (not to be considered taxonomic properties at a level higher than species) become excellent indicators of ecologically meaningful aspects of the fossils under study. Once the initial and boundary conditions (both phyletic and adaptive in a morphotype) are established for extant model species, and the fossils can be placed in a particular ecologically meaningful framework, then further analysis of the attributes of these fossil taxa becomes properly constrained for phylogenetically useful character analysis.

Models are particularly significant as they represent results of judiciously chosen surrogate evolutionary processes for a particular set of adaptive transformations. These selected extant models are chosen based on form-functional considerations with the heritage attributes *often necessarily de-emphasized!* These tested models (i.e., whose causal correlations with their various biological roles are well understood), as noted above, like all models, can never be a complete match for extinct organisms, or their aspects, that are subjected to analysis. Nevertheless, when size is controlled for, and functional (mechanical) attributes are correlated with some well-understood adaptations in the living models, many behaviors can be inferred for those fossils that share these features (for detailed examples see Court, 1994, for assessing *Numidotherium*, or Cifelli and Villarroel, 1997, for an interpretation of *Megadolodus*). Such procedures provide a corroborated level of character explanation (to varying degrees), both functional (nomothetic, nomological in essence) and phylogenetic (evolutionary, i.e., unique, idiographic, historical). Szalay and Sargis (2001) have demonstrated this to be the case in their use of selected osteological attributes of four extant model species of metatherians (boosted by numerous other examples examined there in less detail) for interpreting adaptive strategies in fossil marsupials.

In light of the foregoing I should comment here on the use of *Caluromys*, and various concepts of the didelphid ancestry, as models for interpreting the origins of the euprimates or their relatives, the plesiadapiforms. Morphology is the only point of reference that fossils can offer for analysis, and similarly, the assessed morphotype locomotor mode of a group is grounded in osteology. This should be connected with functionally well understood similar, or instructively contrasting, morphology in proper models that represent aspects of extant species, whose biological roles have been well investigated. Explaining fossil morphology should not consist of picking a living species based on some *behavioral criterion*, and stating categorically that its behavioral or physiological state (or another attribute) was probably similar to that in a postulated fossil taxon or an inferred common ancestor. Unfortunately, sometimes this has been done in primatology (not frequently, fortunately) even when the morphology of the designated extant “model” is singularly dissimilar to the inferred fossil condition. This dissimilarity is not only phyletic (as expected) but functional as well. The use of some marsupials is a case in point. For example, Rasmussen (1990) chose the didelphid *Caluromys* as a “model” for the protoeuprimate. Some of the factors he recognized, regarding arboreal adaptations of the euprimates, were no doubt correct, but these are not diagnostic of the stem of that clade. The type of arboreality displayed by arboreal didelphids, however, is a very good approximation of what the emerging evidence suggests for plesiadapiforms. *Caluromys*, therefore, may be a very good model for the origins of arboreality for the archontan or plesiadapiform stem.

Rasmussen (1990) posited that the relatively large brain and eyes, small litters, slow development (meaning postparturition because preparturition development is nearly uniform in all didelphids and fundamentally different from the universally “accelerated” condition of eutherians when these are compared to metatherians), and agile locomotion (compared to clumsier similar-sized arboreal didelphids such as the not infrequently terrestrial and scansorial species of *Didelphis*) represent a suite of attributes that is convergent to the euprimate ancestor. He stated (p. 263) that these "analogous...selection pressures, represent an independent test of the arboreal hypothesis,...the visual predation hypothesis,...and the angiosperm exploitation hypothesis of primate origins." Regrettably, the prehensile-tailed *Caluromys* does not have special similarity in its osteological properties to the diagnostic conditions of early euprimates, and therefore, cannot support the consensus of views envisaged by Rasmussen. Nevertheless, this was a useful analysis in that it resignaled the importance of marsupials for the study of archaic primates. However, among its numerous critical attributes the protoeuprimate, unlike the clawed *Caluromys* (which occasionally indulges in small leaps), had nails (for details see later section) and had a hindleg superbly adapted for leaping. No extant and arboreal marsupial comes close to the level of biomechanical attributes displayed by the Eocene euprimates. There are no osteological attributes of *Caluromys* that parallel euprimate osteological features, and therefore, this genus (or any didelphid) is an inappropriate model for interpreting euprimate ancestry. But a strong case can be made that, osteologically, *Caluromys* probably approximates a good model for the arboreal protodidelphid (but not for the didelphidan or sudameridelphian ancestry)—one that significantly differed in its advanced arboreal abilities from the postcranially more primitive sudameridelphians of the Paleocene (Szalay, 1994; Szalay and Sargis, 2001) whose stem, in a departure from Cretaceous metatherians, may have been more terrestrial. The well-known agility of *Caluromys* (and other didelphids as well) compared to *Didelphis*, which is quite scansorial and is at home on terrestrial substrates, does not provide evidence for the argument that the agile arboreality of *Caluromys* is a derived condition within the Didelphidae. Many smaller species of didelphids are also quite agile and quick in an arboreal environment (see discussion of the Didelphidae in Szalay, 1994). Although a proposed model species like *Caluromys* tells us little about the origins of euprimate skeletal morphology (and therefore the inferred habits from that), it does, however, as noted, may be very useful for comparisons with archontans and plesiadapiforms. The stem euprimate lineage was likely transformed, via a still poorly understood arboreal archontan stage, from an essentially terrestrial placentalian heritage into an ancestor with a relatively well-understood primitive euprimate postcranial state whose obligate leaping behaviors were not unlikely (Dagosto, 1988; Dagosto et al., 1999; Szalay et al., 1987).

In attempting to explain arboreal attributes of the inferred common ancestry of euprimates, Lewis (1989, and references to his previous articles therein) has derived the various primate attributes from an essentially didelphid condition—the latter standing in as a surrogate for a "marsupial stage" prior to eutherian arboreality. Neither the phylogenetically troubling details that primates are eutherians with their own highly taxon specific constraining heritage that circumscribes their morphology, nor the fact that didelphids appear to be a particularly derived arboreal clade among South American Metatheria, have constrained Lewis' explanation. His transformational analysis lacked the necessary and appropriate phylogenetic context. Furthermore, many of the problems with his proposed transformations were also due to a lack of ecomorphologically meaningful assessment of details. The general notion that some aspects of marsupials are probably primitive (e.g., their reproductive or developmental patterns) compared to their eutherian homologues does not mean that there is a functional similarity between eutherian skeletal attributes and those of didelphid marsupials (Szalay, 1984, 1994). Hence, the same applies even more emphatically to any attempt to understand euprimate origins based on didelphids.

Another inappropriate use of various modeled conditions of metatherian and eutherian skeletal adaptations was made by Martin (1990). He provided narratives, based on the contributions of Lewis (summarized in 1989), that were supposed to connect (historically!) metatherian morphology to the Paleocene plesiadapiform evidence, certainly well understood by that time in *Plesiadapis.* The explanations advanced by Martin heavily relied on implicit assumptions about the relevance of didelphid attributes for evaluating fossil eutherians. Martin confused the application of modeled properties in his text. He presented a lengthy, literature-based analysis of selected osteological attributes of euprimates and their possible closest relatives, specifically the plesiadapiforms, colugos, and tupaiids. In writing about the evolution of mammalian locomotion, primate arboreality, and the specifics of the osteological evidence retrieved from the literature, a number of issues that relate to modeling and phylogenetic analysis of the metatherian-eutherian dichotomy framed his account. His views on the alleged homology of arboreality in marsupials and protoplacentalians, on the supposed "primitiveness" of the cheirogaleid primates within the euprimates, and the use of the various didelphid attributes for an arboreal habitat preference have provided confusing examples of modeling. Additionally, gross mistakes were committed when critical morphological details were misperceived or mistakenly reinterpreted from the literature.

It needs to be emphasized how important unexamined assumptions can be in any search for causal explanations of euprimate origins. Martin interpreted morphology in light of his assumption that ancestral placentalians were arboreal—a view which framed his ideas on the origin of the euprimate radiation. Interestingly, one who believed that the stem placentalian was arboreal (and who categorically continued to dismiss the relevance of the Plesiadapiformes) could accept the Archonta in spite of the fact that the modern rebirth of that concept (Szalay and Decker, 1974) was largely based on diagnostic arboreal adaptations (albeit taxon specific ones). Martin's published illustrations do not represent the actual morphology that he used to support his views. He overlooked, and missed the significance of the fact that, unlike the relatively free upper ankle joint adjustments in such primitive living marsupials as didelphids (with their meniscus mediated fibular contact that puts little restraint on the upper ankle joint laterally), the protoplacentalian condition has evolved considerable tibial and fibular restraint for the upper ankle as reflected by the astragalus.

Similar, but taxon specific and independently evolved ankle restriction patterns can be found in obligate terrestrial marsupials like peramelids and macropodids. Martin and others failed to recognize (even though this has been painstakingly detailed in the literature) that the extensive lower ankle joint adjustments of plesiadapiforms, euprimates, and all other obligate arboreal placentalians became constrained by the protoplacentalian adaptation, and that the most extensive adjustments to pedal inversion have invariably occurred in these taxa in the lower ankle joint. As a result, evolution of a morphological complex in the lower ankle joint that facilitates inversion is invariably a derived condition among early placentalians that show such morphotypic attributes, albeit convergently, such as archontans, some lipotyphlans, creodonts, carnivorans, and rodents.

HOMOLOGY IN EVOLUTIONARY MORPHOLOGY

The issue of homology testing cannot be divorced from any discussion of adaptation and phylogeny. So these remarks are very relevant here. It was only in the 1980s that many primatologists and other students of fossil mammals increasingly accepted the notion that the determination of levels of relatedness between lineages was not tied to any one kind of evidence, such as teeth or skulls only, but that the whole skeleton (along with other attributes, of course) was at least as important. What matters in phylogenetic estimation is the nature of complexity of properties that are being utilized, as well as the relevance of these to adaptive solutions. The latter assessments aid in the recognition of heritage features, and the particular stage of evolution designated of a character complex (its polarity), not necessarily in that order.

But what renders discourse sometimes nearly impossible, however, is the assumptions (both implicit and explicit) of some workers about homology. Some have stated recently that phylogenetic or Darwinian homology (as opposed to Owen's views) is "logically" flawed. Such remarks overlook the fact that a theoretical definition of homology requires specific hypothetical statements regarding properties in different species, and that these hypotheses are to be operationally and independently tested against specific criteria relevant to the proposition. Much more cannot be asked of any other science (contra Cartmill, 1990).

So, impediments to the practice of testing phylogenetic homology are views that relate to the credo of parsimony cladists, whose assumptions were explicitly espoused by Cartmill (1994). The roots of such a change are difficult to trace in anyone's contributions, but the issue of morphological homology was undoubtedly troubling for Cartmill. In spite of the long and erudite introduction and his selective use of the literature that led up to his changed views, what remains is Cartmill's acceptance of algorithmic analysis as the ultimate arbiter of homology testing. The tone of the bottom line has the customary declarative "truth component" of theorizing by parsimony cladists. "The concept can be made intelligible in an evolutionary context only by giving it a cladistic interpretation that makes homology judgments dependent on the outcome of a phylogenetic analysis. It follows that such judgments cannot play a role in evaluating conflicting phylogenetic hypotheses" (p. 115). Clearly, for Cartmill, they cannot, but they certainly did and continue to do so for the assessment of a large and growing body of phylogenetic hypotheses, even if many feel the necessity for an algorithmic, *a posteriori* cloak to legitimize their efforts within a Kuhnian community.

Similarly, Lieberman's (1999) generally peculiar stance on the "relative goodness" of homology hypotheses, but particularly Lieberman's (2000: 152) opinion, misses the theoretical versus operational empirics of homology evaluations. In his deceptively authoritative sounding essay on homology, he overlooks the fundamental requirement for any (Darwinian, hence phylogenetic) homology hypothesis, namely, its phylogenetic (and level specific) context and a rigorous delineation of either the phenotypic or genotypic condition about which a hypothesis is proposed (gene trees, character transformations, taxograms, and phylogenetic trees express different things). Generally the same may be stated regarding the confusion of levels for the equivocating perspective of Lockwood and Fleagle (1999), who analyzed the meaning of homoplasy. Hypothesis and operational testing are (or rather should be) independent from one another. Lieberman (2000: 152), when he states that he agrees that phylogenetic homology concepts are fine "...but it remains true that the concept is *logically* problematic in the absence of *a priori* knowledge of the phylogeny in question" (italics supplied), adds an unwanted level of confusion to the already enormous literature. I note here that Lieberman, like Cartmill, obviously does not believe in the independence of homology testing, and therefore, neither can they *logically* consider testing phylogenies against independently tested and corroborated homologies. So for both Lieberman- and Cartmill-proposed phylogeny hypotheses of taxa should remain just that, vacuous proposals, as they cannot test these against independently corroborated homologies. Lieberman, or anyone else, who holds forth in detail about homology (or homoplasy) without some experience in the procedures of phylogenetic estimations in systematics, and who vaguely cites EvoDevo studies and equivocates on the level-specific meaning of these concepts to somehow support their taxic perspective has a serious problem. These workers have to grapple with the fact that the key conceptual contribution of evolutionary developmental genetics (that character complexes are modular in spite of the phenomenon of epistasis) obviously means that phylogeny estimation of these modules are likely to be independent from those of others in the same species, and therefore, in higher taxa as well. Mosaic evolution is back under the cloak of modularity (contra the opinion expressed by Tattersall, 2000, that it is a "hoary old concept"), showing us that the logical positivism of cladism is incapable of setting the ontological foundations for the theory of descent. Consequently both the choices of characters for analysis and the taxic approach to phylogenetic estimation may have to be seriously reconsidered in the near future.

TRANSITIONS LEADING UP TO THE ARCHONTAN AND EUPRIMATE LOCOMOTOR STRATEGIES AND SUBSTRATE PREFERENCE

I will not belabor the platitude that the postcranial record of Mesozoic eutherian (or other) mammals is still relatively poor, and that such a state of affairs makes for very tentative conclusions regarding locomotor adaptations in the stems of various higher taxa within the Eutheria, Metatheria, and Theria (the latter restricted here to the concept of monophyletically tribosphenic mammals). There is certainly overwhelming evidence that the extant Metatheria had a specifically arboreal ancestry, except perhaps for the Caenolestidae, the stem of the Sudameridelphia (Szalay, 1994; Szalay and Sargis, 2001), and for some early lineages like *Asiatherium* (Szalay and Trofimov, 1996). Similarly, there is little doubt at present that the last common ancestor of extant eutherians (all placentalians), various extinct Cenozoic groups, and lineages related to these extending back to the Cretaceous, were derived of a terrestrially committed stock, the stem of the Placentalia (Szalay, 1984, 1985, 1994; Szalay and Decker, 1974; Szalay and Drawhorn, 1980; Szalay and Lucas, 1993, 1996; Szalay and Schrenk, 1998). Prior to the recent description of some postcranial remains of Cretaceous mammals the same may have been said of the then known Eutheria (Szalay, 1977).

But beginning with the increased recovery of a variety of cladistically unquestioned eutherians from the Cretaceous in the last three decades, it became apparent that the eutherian branch of the Theria probably had a great variety of postcranial properties that cast serious doubt on the wholesale categorization of the stem Eutheria based on the extant forms and Cenozoic fossils. Szalay and Trofimov (1996, Figure 26) made the suggestion that the early, basal, radiation of the Eutheria probably retained a reproductive strategy that could be characterized as "marsupial" in a general way, and from such an undoubtedly many-branched paraphyletic entity (dubbed above as Eoeutheria) arose the last common ancestor of, what I call here, the Placentalia. All of that implies that there is no simple way to characterize the postcranially unknown lineages of 60–70 MY of evolution prior to the Cenozoic. For example Kielan-Jaworowska (1975) reported the presence of epipubics in a clade of early eutherians, and more recently Horovitz (2000) described the tarsus of the asioryctithere *Ukhaatherium*, also from the Cretaceous of Mongolia. The palmate and broad proximal fibula of *Ukhaatherium*, among other features, suggests grasping (as inferred from a well developed peroneus longus that is probably indicated by that type of proximal fibula; Argot, personal communication), and its highly mobile calcaneocuboid joint suggests a marsupial-like mobility of the foot. An ongoing study (Szalay, Sargis, Archibald, and Averianov, in preparation) of mammal postcranials from the Santonian Cretaceous of Uzbekistan (see Archibald et al., 1998) will also help the ongoing assessment of problems regarding early locomotor strategies in the Eutheria. To complicate matters even for the archimetatherian (early) marsupial radiation, the skeleton of *Asiatherium*, from the semiarid environments of the Late Cretaceous of Mongolia suggests a terrestrial locomotor strategy, very tentatively.

LOCOMOTION AND THE ORIGINS OF EUPRIMATES

I believe that all the known placentalian arboreal adaptations are secondarily derived from a terrestrial stem—a point that has been amply documented before. The previously elaborated explanations that pointed to the derived nature of pedal mobility in the lower ankle joint (Szalay, 1984, 1994) in placentalians are also corroborated from other areas of the skeleton in the known Early Tertiary representative of eutherian orders.

While the issue of Archonta will continue to be debated as new fossils are described, the morphotypic skeletal adaptations unique to the euprimate stem are relatively well established (Dagosto, 1985, 1986, 1988; Decker and Szalay, 1974). Among other attributes, the early euprimates had a flattened ilium to accommodate a musculature hypertrophied for leaping. They had fast, deep, and highly stabilized knee joints superbly constructed for powerful leaping in conjunction with a foot that had an equally speed-adapted upper ankle joint capable of rapid flexion, combined with a highly helical lower ankle joint articulation, totally unlike we see in arboreal didelphids. Although the general condition of the upper ankle joint is a eutherian one, the euprimate condition is highly derived in its astragalar construction for extensive flexion-extension (with its great angular distance of the tibial articular surface) and the attendant speed. While the euprimate feature for obligate inversion was held over in the lower ankle joint from its archontan ancestry (and further evolved for specific regime of locomotion on arboreal substrates), this happened within the highly constrained cruropedal contact that characterizes eutherians (Szalay and Decker, 1974).

Neither merely obligate arboreality, as such, nor visual predation accounts for the postcranial heritage of the euprimates acquired from their last common ancestor. The transformation of claws into nails, and the evolution of hypertrophied feet (compared to smaller hands) and powerful pedal grasping coupled with mechanical solutions of the entire pelvic limb do, however, account for a particular kind of arboreality. These features are related to explosive long jumps, combined with the precise ability to grasp small branches when landing usually with the feet first. Grasp-leaping appears to have been the morphotypic locomotor mode for the stem lineage of the Euprimates.

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