Chapter 8

Adaptation and the Origin of Rodents

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ABSTRACT

To the extent now possible, I trace out what appear to be the adaptive changes involved in the origin of rodents. This requires, as a preliminary, a critical analysis of the existing evidence that bears on their phylogenetic relationship to other groups. Part of the paper provides such an analysis, from an unusual perspective. The evidence for a phylogenetic association of rodents and lagomorphs is weaker than is usually claimed but may nevertheless reflect reality. In particular, the precursors of rodents are not yet adequately identified. The initial adaptations of rodents were for the most part quite different from those of lagomorphs, despite their similar gnawing. There is evidence that the Myomorpha constitute the earliest diverging branch of extant rodents. *Conapomorphy* and *spermativore* are new terms.

INTRODUCTION

The main purpose of the present paper is to reconstruct, to the extent possible, the adaptive and morphological changes involved in the origin of rodents. For this, it is necessary to review in detail the evidence for association of lagomorphs with rodents into a group called Glires. I do so from a perspective different from those perspectives that underlie recent studies. Appendix 8.1 summarizes aspects of this perspective.

There doesn't seem to be a term for shared derived character states in a descriptive sense. ''Synapomorphy'' is often used but, as with Hennig (1950, 1966), it implies that the different occurrences of the state are historically homologous. The resulting ambiguity is sometimes confusing. Frequently, prior to phylogenetic analysis (or even after, given inadequate support), one can be adequately confident of the polarity of a character but not of whether different occurrences of a derived state are homologous or homoplastic.

I therefore propose *conapomorphy* (despite its barbarity to the philologically sensitive; *con-*, ''together'' or ''with'') as an inferentially neutral and merely descriptive term for a shared derived character state. A conapomorphy is also a synapomorphy when it is homologous among the taxa under consideration.

The present paper is dedicated to Malcolm McKenna, from whom I learned more than he probably realizes. It is also what some Japanese call a noodle paper, omitting much because of restrictions unrelated to the paper's content. The complete version will appear as Van Valen (in press); most of the evidence is given in that paper, as are discussions of the Lagomorpha and Anagalida. Figure 8.1 summarizes my phylogenetic and taxonomic conclusions.

EURYMYLIDAE

The Eurymylidae are a family of gliriform mammals that are currently regarded as close relatives of rodents. They resemble the Mimotonidae, the basal family of lagomorphs, and perhaps should not be separated from them at the family level. However, they have lost dI3 rather than modifying its function, and their inclusion in the Lagomorpha would therefore be somewhat anomalous despite their ever-growing dI2 and di2 and related synapomorphies. I therefore retain them as a separate family, one of two in the order Anagalida.
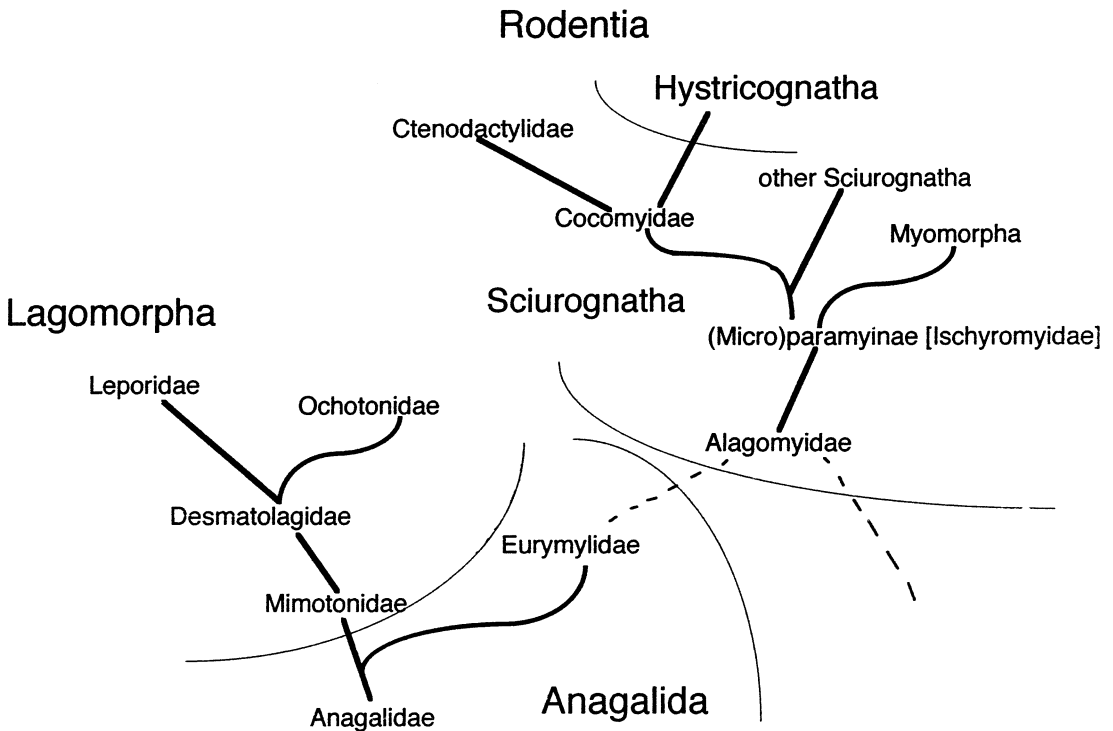
Fig. 8.1.   Inferred phylogeny of Anagalida, Lagomorpha, and Rodentia.

Eurymylids are unknown before about the beginning of the Eocene, when a moderate diversity of them appears. Their weak divergence from mimotonids could therefore have occurred over as long a time as most of the Paleocene.

The adductor muscles of the jaw are characteristically modified in lagomorphs and rodents. Qualitative comparisons on most aspects can be made from adequately preserved fossils, but quantitative comparisons require soft tissue. My comparisons here are based especially on Lopez Martinez (1985) and Turnbull (1970).

Rodents, like other primary herbivores (including lagomorphs), have reduced their temporalis muscle and enlarged their masseter. In rodents the mass of the temporalis is about 15 to 30% of the total adductor mass, although in lagomorphs it is only about 12 to 15%. The masseter is about 60% in both groups, averaging a little higher in rodents. Its high mechanical advantage gives it an even greater proportion of the power available for grinding (Turnbull, 1970). The external pterygoid is somewhat enlarged, to about 4 to 7% in both groups. The internal pterygoid, on the other hand, is not noticeably enlarged in rodents, at about 6 to 11%, but lagomorphs and ungulates enlarge it to 20% or more.

The muscular differences between rodents and lagomorphs reflect somewhat different jaw mechanics. The rodent temporalis is normal, if rather small and functioning mostly as a retractor in anteroposterior chewing. The temporalis of lagomorphs, on the other hand, is horizontal near its origin, becomes tendinous and loops over the postorbital bar present in that group, and descends vertically to its insertion on the remnant of the coronoid process. It is unclear why the temporalis took this form in lagomorphs; perhaps it was to stabilize the jaw joint. The medial (deep) masseter of rodents differentiates anteriorly as a partial opponent of the temporalis, but that of lagomorphs differentiates posteriorly, originating from a long process that extends posteriorly from the zygomatic arch.

The late Paleocene eurymylid *Heomys* has teeth that resemble those of *Cocomys* (Li et al., 1989) enough that Flynn (1994) even included *Heomys* in the Cocomyidae. With the discovery of the Alagomyidae, however, it should be clear that the special resemblance is convergent, a conclusion reached by several workers even before alagomyids were known (e.g., Hartenberger, 1980). The cheek teeth of alagomyids are much more like those of other early placentals than are those of either of these genera; a cocomyid relationship for *Heomys* would require a complex and functionally implausible reversion by alagomyids.

GLIRES?

From morphological evidence, it is now widely accepted (e.g., Meng and Wyss, 2001) that rodents and lagomorphs are phyletically closer to each other than either group is to any other extant mammal, although molecular evidence is usually regarded as ambivalent. The existence of such a clade (called Glires) appears quite possible, although it presents difficulties. The discovery of the late Paleocene alagomyid genus *Tribosphenomys*, on which see especially Meng and Wyss (2001) but also Meng et al. (1994), has greatly improved our knowledge of basal rodents while, paradoxically, not similarly improving our knowledge of their ancestry. Such a conclusion needs careful justification; it conflicts with all other recent work on rodent origins.

Tribosphenomys is indeed a remarkably primitive rodent. In fact, I have been unable to identify any clear autapomorphies for it relative to other rodents. I therefore regard it as perhaps indistinguishable from a late common ancestor of all other rodents, and possibly as even being such an ancestor.

So what group gave rise to *Tribosphenomys*? This question is more difficult to answer than it would first appear. There are indeed a number of conapomorphies that it and more derived rodents share with the Eurymylidae, and these have, reasonably, persuaded most workers of a close relationship (see Van Valen, in press.) If they are also synapomorphies with the Rodentia, then rodents would be an exgroup from the eury-

mylid-lagomorph cluster. In addition, basal rodents share with at least the eurymylid *Rhombomylus* a posterior process on the distal end of the tibia, on which the distal facet for the astragalus is located. Such a process also occurs in at least leptictids and the mimotonid *Mimolagus*; it is absent from at least more derived lagomorphs. Rose (1999) found it variably developed in several placental groups.

Landry (1999) has emphasized an infolding of the lips in both orders, which separates the incisors from the cheek teeth. *Daubentonia* and the Procaviidae have similar but less developed infoldings; it may be relevant here, and elsewhere, that rodents and lagomorphs are the only mammals to have had ever-growing incisors for most of the Cenozoic, thereby giving them more time to elaborate structures functionally related to these.

Landry also takes as a synapomorphy a set of gut characters. There is a large, spiral caecum in which bacteria and protozoans ferment otherwise indigestible cellulose and produce vitamins. The product is packaged into special fecal pellets, which pass out of the large intestine, the diameter of which is said to be actually less than that of the small intestine. The animal then eats the pellets, which are readily digestible.

Some other proposed synapomorphies, such as a relatively high extension of the orbitosphenoid in the orbit, have unclear polarity for rodents or else unclear distribution among placentals. The scapular notch of paramyines is normal for mammals, so its deepening in most other rodents and in lagomorphs is probably convergent.

The optic foramen, or at least a perhaps sometimes conjoined foramen (the interorbital foramen of Wahlert, 1985) is relatively large and extends through the cranium, which is quite narrow here, to the foramen in the other orbit, thereby transmitting a vein. This condition, however, may be plesiomorphic and changed only by enlargement of the brain; alternatively or complementarily, it could be a byproduct of unusually large eyes. Paramyines seem to lack conjoined foramina (Wahlert, 1974), although in *Cocomys* there is quite a large hole (Li et al., 1989).

Ade (1999) has discussed the rhinarium in some detail and proposes that its appreciable reduction (perhaps related to the gnawing incisors) can be taken as a synapomorphy. She also proposes that its similar subdivision in the two orders be so regarded, but 1 or 7 of the 13 rodent families listed seem to lack this; the number is unclear from her table. Moreover, the plesiomorphic state for rodents is unknown.

Shoshani and McKenna (1998) give several other conapomorphies for rodents and lagomorphs, most of the possibly useful ones being for foramina: buccinator, masticatory (both unusual), mastoid, and medial-angular-process foramina (unusual) present, and the inferior ramus of the stapedial artery being intracranial only. Members of both orders also have a lacrimal tubercle and, unusually, the tegmen tympani is expanded to cover the epitympanic recess. Such characters are often evolutionarily labile, but do have real value; none are yet known for the Alagomyidae.

The other conapomorphies of rodents and lagomorphs, for which a function is apparent, all seem to be related, directly or somewhat indirectly, to the acquisition of ever-growing incisors for gnawing. The same may be true for most of those in the preceding paragraph. Although other possibilities aren't excluded in principle, the first and second incisor positions are the only ones where placentals are known to have evolved gnawing incisors. Among those for which the existence of replacement has been determined, I know of no case where a gnawing incisor has a developmental precursor or where different positions are used in the lower and upper jaws. The lack of replacement is actually to be expected functionally if gnawing begins early in postnatal life. From these considerations the probability that a convergent evolution of gnawing incisors will be of dI2 and di2, given another taxon with this homology, can be roughly estimated as about 0.4. Thus such an occurrence doesn't seem implausible, even if one were to estimate a rather lower probability.

Apparently more important conapomorphies come from fetal membranes (Luckett, 1985):

1. The placenta is hemochorial to hemoendothelial, and therefore it is invasive and deciduous.
2. The trophic villi from the chorion are initially restricted to a discoidal region, the trophoblast.
3. At implantation the trophoblast is located opposite the area where, on the outside of the uterus, the mesometrial support of the uterus occurs. The embryonic knot (or disc, or mass) itself is thus on the side of the placenta closest to the mesometrium.
4. The allantoic vesicle is moderately reduced.

A peculiar inversion of the proximal part of the omphalopleure (a membrane of two layers: yolk-sac wall with expanded endoderm plus expanded chorionic trophoblast) occurs in both orders, in relation to a sinking (descriptively) of the embryo into the yolk sac. This is sometimes used as a striking synapomorphy, but it doesn't occur in ''sciurids, aplodontids, pedetids, and anomalurids'' (Luckett, 1985: 255, apparently implicitly contra Luckett, 1993: 520). The conapomorphy is thus (cf. appendix 8.1) presumably homoplastic. It is probably parallel rather than convergent, because the omphalopleure itself is nonvascularized and the inversion may help to increase exchange of material.

Since this conapomorphy is probably homoplastic, it is plausible that the other four, which are less striking, are also homoplastic. However, only the first, second, and fourth conapomorphies are common among placentals; the third is shared with only the Macroscelididae.

There is therefore some positive evidence, if less than now commonly claimed, for a derivation of rodents from the vicinity of eurymylids and thus lagomorphs, and this positive evidence seems to be greater than that for the relationship of rodents to any other known group. There are, however, two apparently serious difficulties with such an origin. One is that all known eurymylids, mimotonids, and anagalids have cheek teeth that are distinctly unilaterally hypsodont (cf. Hartenberger, 1980). (Brachyodont genera, such as *Astigale*, which have been referred to the Anagalida, appear to belong to other groups: cf. McKenna and Bell, 1997. Teeth of some eurymylids have sometimes been called brachyodont, but this is incorrect except in a

relative sense.) On the other hand, basal rodents such as *Tribosphenomys* and *Paramys* have quite brachyodont cheek teeth. I know of no case where even slightly hypsodont teeth have reverted to brachyodonty, and even no case of reduction in the degree of hypsodonty. It isn't just the eurymylids, the putative stem for rodents if the Glires hypothesis is correct, that have presumably homologous hypsodonty of their cheek teeth, but also their own ancestors, the anagalids. It is indeed possible that there was a brachyodont lineage, as yet entirely unknown, that gave rise seriatim in the early Paleocene to the several hypsodont groups and also to rodents. Perhaps it has escaped discovery because of small body size, like that of the Alagomyidae. However, the currently known distribution of conapomorphies doesn't appear to me to give adequate evidence that this was actually the case. The characteristic anagalid-lagomorph two-tooth wear surface of the lower molars (Van Valen, 1964), which persists in the eurymylids, provides corroborating evidence similar to that of the related hypsodonty. It too would have to be evolved iteratively in the same groups as hypsodonty, but it is a feature unknown outside the anagalid-lagomorph sequence and therefore would have been unlikely to have repeatedly evolved there.

It is thus untrue, contra Meng and Wyss (2001: 2) and others, that "dismissing the derived resemblances of these groups to convergence requires identification of some third taxon sharing a unique common ancestry with one of the two groups, but lacking the derived similarities common to both." The presence of effectively irreversible changes throughout an identified ancestral group can give an alternative argument; there may be others.

MOLECULAR EVIDENCE

The other possible difficulty, or set of difficulties, comes from molecular data. These are often taken (by molecular chauvinists) to be inherently superior to morphological (and other nonmolecular) evidence, but what advantage they have in the usual kind of analyses is just in a large number of characters (nucleotides or amino acids.) How useful a single character of any kind can be depends on its degree of independence (functional as well as developmental and structural) from others, its rate of change, and its probability of homoplasy if it does change. By the latter criterion, phenotypic characters usually fare better, especially in comparison to nucleotides, because they can usually vary in more ways.

Rate of change has also usually given a poorer result for molecular characters in practice. For any character or set of characters, there is in principle a fuzzily bounded window of time that may give informative results. Too short a time makes it likely that no change will have occurred. Too long a time, on the other hand, saturates the character with multiple changes, making it uninformative in a different way, now producing the noise of nonsense rather than nothing. Although there is no interval that entirely escapes both these effects, a useful intermediate interval usually exists, and there can even be more than one such interval if well-defined classes such as transitions and transversions have appreciably different characteristic rates.

Thus I look with some skepticism at sequence-based inferences from molecular data. Nonetheless, such inferences usually do seem to have more than zero information, although it is often impossible to disentangle this signal of information from the pervasive noise and biases. Each of the problems above is recognized by at least some practitioners, and there are now methods to ameliorate some of them. Some of these methods are more or less mutually exclusive but, to the extent that they give similar results, such results are strengthened. As Levins (1966) put it in an analogous context, "Truth is the intersection of independent lies."

Recently Murphy et al. (2001a, 2001b) have claimed good support for a sister-group relation (among extant mammals) between the Rodentia and Lagomorpha, unlike the almost uninterpretable noise of numerous earlier and even contemporary attempts. Their analysis does seem to be the best to date that is based on processing of molecular sequences, cf. Whelan et al. (2001). However, it is still susceptible to most of the problems given above and to some others; although their

cladogram is plausible I would prefer other evidence.

In particular, I would prefer the discovery of effectively irreversible and unrepeatable markers in the DNA of extant mammals. It was such a discovery (Shimamura et al., 1997) that convinced me that whales are quite probably an exgroup (the standard term for a group derived from another one) from artiodactyls, and another (Madsen et al., 2001) has been validly used to support holophyly of the Afrotheria. Relevant markers aren't changes in base pairs, even rather large numbers of which have a distressing tendency to give ambiguous conclusions, but larger-scale phenomena. An example, of the sort used in the whale-artiodactyl analysis, is the kind of repetitive sequence called small interspersed elements (SINEs). These are retroposons, reverse-transcribed from RNA, which insert themselves into DNA throughout the genome. There is no known preference for sites of insertion, which therefore appear to be random. There is also no known mechanism that precisely removes them, although they can evolve in concert. They are therefore, on current knowledge, as close to perfect apomorphies as one can hope for. The presence of the same SINE, especially at the same location, in two different groups is strong evidence that the groups form a clade separate from all groups that lack the SINE (there), unless the whole region of DNA is deleted in a comparison group. Multiple co-occurring insertions of course strengthen the argument further. And insertion of SINEs isn't the only marker that behaves like this. A wider class of examples comes from chromosomal rearrangements such as translocations, deletions, and inversions. There is indeed some variation among sites in their propensity to break, but the requirement of two or more breaks, as in the above classes, makes the reversal or separate occurrence of such rearrangements exceedingly unlikely.

Such markers have in fact been used three times in the study of rodent phylogeny. BC1 is a functional retroposon that codes for a kind of RNA that is expressed only in some neurons. It is probably present in all rodents; the only directly relevant family not sampled is the Ctenodactylidae (Martignetti and Brosius, 1993). Moreover, BC1 is absent from all nonrodents sampled, including the Lagomorpha. It is therefore good evidence of rodent holophyly. Remarkably, during the curious controversy on rodent holophyly, it seems to have been quite forgotten; the entire controversy was otherwise based on sequences and morphology.

Serdobova and Kramerov (1993) found a SINE, which had earlier been named B2, in the Muridae (sensu lato), Spalacidae, Dipodidae, and Zapodidae. It was absent from the Caviidae, Sciuridae, Gliridae, and nonrodents. Kramerov et al. (1999) extended their analysis, finding a new SINE (B1-dID) in the Caviidae, Hystricidae, Castoridae, Sciuridae, and Gliridae but not in the families above that have B2. B1-dID evolved somewhat within the Rodentia, and it is more similar between the Sciuridae and Gliridae than between the Gliridae and the three other families. The latter were not compared among themselves. Thus these five families appear to form a clade among those tested. Whether the sciurid/glirid variant is derived, as they assume, is unclear but plausible.

Their evidence rather strongly supports a basal derivation of the Myomorpha, as sister to a clade consisting of the other Sciurognatha plus the Hystricognatha. Such a divergence is congruent with the otherwise anomalously early genus *Apatosciuravus*, on which see Korth (1984) (although Ivy, 1990, disputed conspecificity of relevant specimens). This is because it seems likely that *Apatosciuravus* at least approximately gave rise to the Myomorpha (cf. Wang and Dawson, 1994).

CONCLUSION

It is likely that both rodents and lagomorphs are early branches on the placental tree. Whether they have a common stem separate from the trunk is still unclear despite the great recent increase in evidence. So what would effectively decide this question? I can see two main possibilities, although further accumulation of evidence like what is now available may alternatively decide the matter in due course.

One possibility is the discovery of ancestors or near-ancestors to *Tribosphenomys* that provide a sufficiently dense chain to an an-

cestral group, or at least to an unambiguous phyletic position. It seems reasonable, if hardly predictable, that such a chain will be discovered in the Asian Paleocene. This is where both *Tribosphenomys* and primitive members of both the sciurognaths and hystricognaths occur. *Alagomys*, *Acritosciuravus*, and *Paramys atavus* are indeed all found in North America, but there is a much better record of Paleocene mammals here than in Asia. This isn't to say that the North American record is adequate, or nearly so, to exclude ancestors, but the current status of the Asian record is like that of the opening up of the American West in the nineteenth century. For adaptive reasons (see below) I would expect at least most of an ancestral chain to occur in more mesic environments than can be inferred for most existing Asian deposits. Some or all may be unusually small mammals, as is *Tribosphenomys*.

The other possibility is the discovery of a SINE or other suitable chromosomal variant, as discussed above, that uniquely characterizes rodents and some other order.

Rodents were not initially adapted for grazing. The minute size of *Tribosphenomys* and *Alagomys*, together with their very brachyodont, little worn, and cuspidate teeth (features that persisted in the paramyines, which were larger) suggests a diet of small seeds and the like. Landry (1999), however, noted that the large caecum and coprophagy characteristic of most rodents suggests an ancestral diet like that of lagomorphs. These two conflicting inferences cannot be easily resolved by invoking a brachyodont ghost lineage, because brachyodonty is maladaptive for a diet of coarse vegetation, and the invocation of massive parallel evolution to grazing would be unparsimonious. A resolution could be provided by a reversal of unilateral hypsodonty to brachyodonty, and concomitant loss of the two-tooth wear surfaces of the Anagalida. This, though, would be both unprecedented and developmentally awkward. Thus I cannot resolve the conflict. However, since the basal rodents were clearly not even close to being grazers, the *spermativore* (seed-eater, new term) hypothesis may be provisionally accepted.

If so, they were presumably derived from an insectivorous ancestry via supplementa-

tion of the diet with seeds. Rodents are unknown before the late part of the late Paleocene, so there would have been adequate time for an only moderately fast divergence after dinosaur extinction. Other presumptive spermativores, notably in the Multituberculata, plesiadapiform Primates (Van Valen, 1994), and Condylarthra, as well as birds, insects, and fungi, already existed and may well have delayed the expansion of the rodents. However, there is as yet no evidence that this actually happened, and the origin of rodents may alternatively have been quite rapid. Their initial radiation from their origin was indeed rapid, probably close to exponential in species number until some time in the early Eocene and comparably fast in morphology and adaptation. They were thereby likely to have been important in the gradual extinction of their presumptive mammalian competitors (Van Valen and Sloan, 1966). It isn't possible, however, to specify just why they were so successful. A group advantageous in one respect is often disadvantaged in other ways, and it isn't possible even to infer much of early rodent biology. It's easy and tempting to make quite reasonable hypotheses, in this case and others; unfortunately one can't usually investigate to what extent they may be unrelated to the actual processes of replacement.

The minute size of the two known alagomyid genera is itself significant. Three somewhat more derived genera, *Decipomys*, *Orogomys*, and *Ivantonia*, are of similar size and may possibly have retained their size from their alagomyid ancestry. The same may even be true for the early myomorphs, into the middle Eocene (*Hydentomys*; Tong, 1997). Such small mammals would have had difficulty thermoregulating when necessary. Perhaps they spent much of their time in burrows. Even central Asia would have been more equable in the Paleocene and Eocene than it is today, partly because of a warmer Earth and partly because the Himalayas and Tibet hadn't yet started to rise. Like shrews today, they may have used torpor to become facultatively heterothermic. The high metabolic rate of at least temperate shrews, even higher than expected for their body size (McNab, 1983), may be for such thermoregulation. A higher metabolic rate requires a

greater intake of food to support it, and ala-gomyids, like many recent rodents, may well not have given up occasional or even regular consumption of insects and the like.

Spermativores are indeed found in semi-arid regions today, but seeds, like other life stages and components of plants, are more abundant in mesic habitats. A transition from insectivory to spermativory would presumably be helped by an abundance of seeds. It therefore seems likely that, if the spermativore hypothesis is correct, alagomyid ancestors lived mostly in mesic or even moister areas. It is relevant that most specimens of alagomyids and basal paramyines have come from apparently wooded or wet habitats: Big Multi Quarry and Bear Creek in North America, and Wutu in China (Dawson and Beard, 1996). And *Tribosphenomys* has been recovered only from carnivore coprolites (Meng and Wyss, 2001) and therefore may have lived in a more mesic habitat than where it was preserved. Only the apparently three specimens (Tong and Dawson, 1995) of *Alagomys inopinatus*, from the early Eocene of Tsagan Khushu in Mongolia, seem actually to have some positive evidence of having lived in a relatively dry habitat.

The tiny size of alagomyids may possibly have been significant in another way also. It is a frequent but far from universal occurrence that important evolutionary transitions occur at a small body size. By gaining adaptations to small size, pre-existing adaptations to larger size and perhaps many other things are lost or decreased in importance. This makes it easier for new adaptations to originate and pass through their initial stage.

The diversity of problems remaining with respect to the origin of rodents contrasts with the apparently straightforward path we can now glimpse in the origin of lagomorphs (Van Valen, in press), and is still an *(o)scuro* to the latter's *chiaro*.

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APPENDIX 8.1

SUMMARY OF SOME PERSPECTIVES RELEVANT TO THIS PAPER

Although I reject cladistic classification, for reasons given elsewhere (Van Valen, 1978, 1989) and partly amplified in a paper in preparation, I agree with the basic principle (Hennig's) underlying the cladistic approach to phyletic inference (e.g., Van Valen, 1965, 1979). I see canned programs such as PAUP* as having a limited role to play, by establishing an initial hypothesis in complex analyses. As a geneticist, I also regard an individual or group as having just as close a relationship to its sibs as to its offspring. Justification of such heresies is outside the scope of the present paper but is something that I have in progress.

When using canned programs it is always easier, and usually necessary, to use only discrete character states. Unfortunately, many real characters and character complexes lack naturally discrete boundaries, and the possibility of intraspecific variation is also made unwieldy. Such problems exemplify a remarkable and more or less ubiquitous feature of canned programs and also of surveys: rather than permitting their own modification to accommodate what is in the real world, they expect the world to modify itself for their benefit. Distortion thereby results and can't be corrected later.

PAUP* treats inapplicable characters, such as differences in a structure that itself may sometimes be entirely absent, in the same way that it treats lack of information. However, they differ in their effects.

A more serious problem, and one that can affect the topology appreciably, is the choice of characters. This problem is widely known but nevertheless is widely ignored. Part of it comes from functional and developmental interrelations among putative characters. Both function and the pattern of developmental integration are evolutionarily labile, so separate change of characters in one group doesn't imply even partial independence elsewhere. Partly interdependent characters can each be weighted as less than a full character in all or part of the tree, however. For two such characters the effective number of independent characters is $1 + (1—r^2)$, or $2—r^2$. I have given a multivariate generalization of this expression elsewhere (Van Valen, 1974) and have a more elegant version in progress.

A closely related problem is that of the directionality of character change. There aren't many characters for which change is clearly irreversible, but it is common for one direction to be more likely than another. Rather than confining oneself to the extremes of equidirectionality and irreversibility, it would be better to use intermediate relative transition probabilities or weightings.

Fuzzy boundaries reflect reality; reality never requires discreteness.

Lack of serious attention to such problems gives false precision, a much greater appearance of precision than is justified by the data used. As Tukey (1962) put it, "Far better an approximate answer to the *right* question, which is often vague, than an exact answer to the *wrong* question, which can always be made precise."

I agree with Shoshani and McKenna (1998) in taking an order to have its morphotype characterized by the primitive state for a character if such a plesiomorphy occurs in the order. I go beyond them in applying the same procedure to any clade, unless there is reason to suspect that a particular application of it may be incorrect. Such a practice eliminates many biologically implausible reversals imposed by the blind acceptance of output from general-purpose canned programs.

It has become fashionable to disparage what are then called scenarios, inferred sequences of adaptive changes, such as the subject of the present paper. However, such adaptive sequences represent the selective causes of the observed phenotypic changes and are thus important to understand as well as possible. Sometimes, if adequately based, they can even give information relevant to the path of phenotypic change itself. As Frazzetta (1975: 20) noted, "The evolutionary process is, in a real sense, the gradual improvement of a machine while it is running!" Adaptive plausibility is often a useful criterion in evaluating proposed phylogenies, but it obviously must be used cautiously—here too our inferences are fallible.

Even if I were a cladist in classification, I would reject crown groups. Their most important defect is that they privilege one slice of time over all others, which are equally relevant to the organisms themselves. Thus an important part of what they classify is *our relation* to the organisms.