How did rodents and lagomorphs (Mammalia) originate?[1]

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Abstract:

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

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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 main purpose of the present paper is to reconstruct, to the extent possible, the adaptive and morphological changes involved in the origin of each order. For this it is necessary to review in detail the evidence for Glires, which I do from a perspective different from those perspectives which underly recent studies. The Appendix 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, with 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.

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The present paper was accepted, after review, for the Bulletin of the American Museum of Natural History, but proved to be too long for the volume it was intended for. A shorter variant, incorporating some of the material here, will be published in that journal, but the present paper is the definitive one.

Lagomorpha

The situation for the lagomorphs is more straightforward than that for the rodents despite a controversy with respect to homology of the elements of the upper molars. In 1964 I suggested, as a secondary possibility, that the large central cusp is the protocone, shifted labially by the strong lingual hypsodonty characteristic of lagomorph ancestors, in which the homology of the central cusp is obvious. McKenna (1982) and others have advocated this view. Such an association occurs in other groups, such as the Taeniodonta and the periptychid Condylarthra. The main alternative interpretation is that of Averianov (1998), who regarded it as the metacone, on the basis of occlusal analysis. Meng and Wyss (2001) agree with Averianov because his interpretation makes the protoloph of unquestioned lagomorphs homologous to that of the related families Mimotonidae and Eurymylidae rather than to their small precingulum. If the protoloph homologization is taken as primary, then the rather large metaconule of *Mimotona* would be available to become the central cusp. That would, however, require the protocone to return to its original lingual position, a possible byproduct of the transition from lingual hypsodonty to full hypsodonty. Discovery of a morphological intermediate will probably be necessary to fully resolve the question, although the mimotonid protoloph had been strengthened from its own ancestry and the precingulum reduced. I thus provisionally prefer the metaconule as the homolog, which would make the mesiolingual cusp the protocone rather than a pericone and involve a reversal in its position.

What should be taken as the beginning of the Lagomorpha is somewhat arbitrary, as such a choice involves an artificial imposition of a sharp discontinuity on what was actually a continuum. In accordance with the principle that supraspecific taxa are adaptively unified segments of phylogenies (Van Valen, 1978a), the boundary should reflect a rather significant (if perhaps gradual) adaptive change. There is more than one of these in the ambiguous interval of the phylogeny, but I take the origin of evergrowing incisors (with their enamel now mostly restricted to the labial surface, and followed by a long diastema) and the positioning of the third upper incisor, dI^3, nearly or quite behind the evergrowing dI^2 as perhaps most important. The latter arrangement lets the enamel of dI_2 be self-sharpened, dI^2 having already evolved to be sharpened by its occlusion with dI_2 during gnawing. This positioning is associated with the formation of stiffening Hunter-Schreger bands in the inner part of the enamel of the evergrowing incisors. From this perspective the Mimotonidae are seen as the basal family of lagomorphs rather than as the family immediately ancestral to the order. I regard the family as now consisting of *Mimotona*, *Mimolagus*, *Anatolimys*, and *Gomphos*.

Mimotona itself is then the earliest known lagomorph, first known from about the middle Paleocene of China. It does not seem to have any known apomorphies not also characteristic of the main lagomorph radiation, except for a slightly greater degree of hypsodonty, and therefore (as a genus) it can provisionally be regarded as ancestral or nearly so to more derived families.

As I proposed some time ago (Van Valen, 1964), the lagomorphs appear to be derived from the Anagalidae (including Pseudictopidae), a group contemporary and sympatric with early as

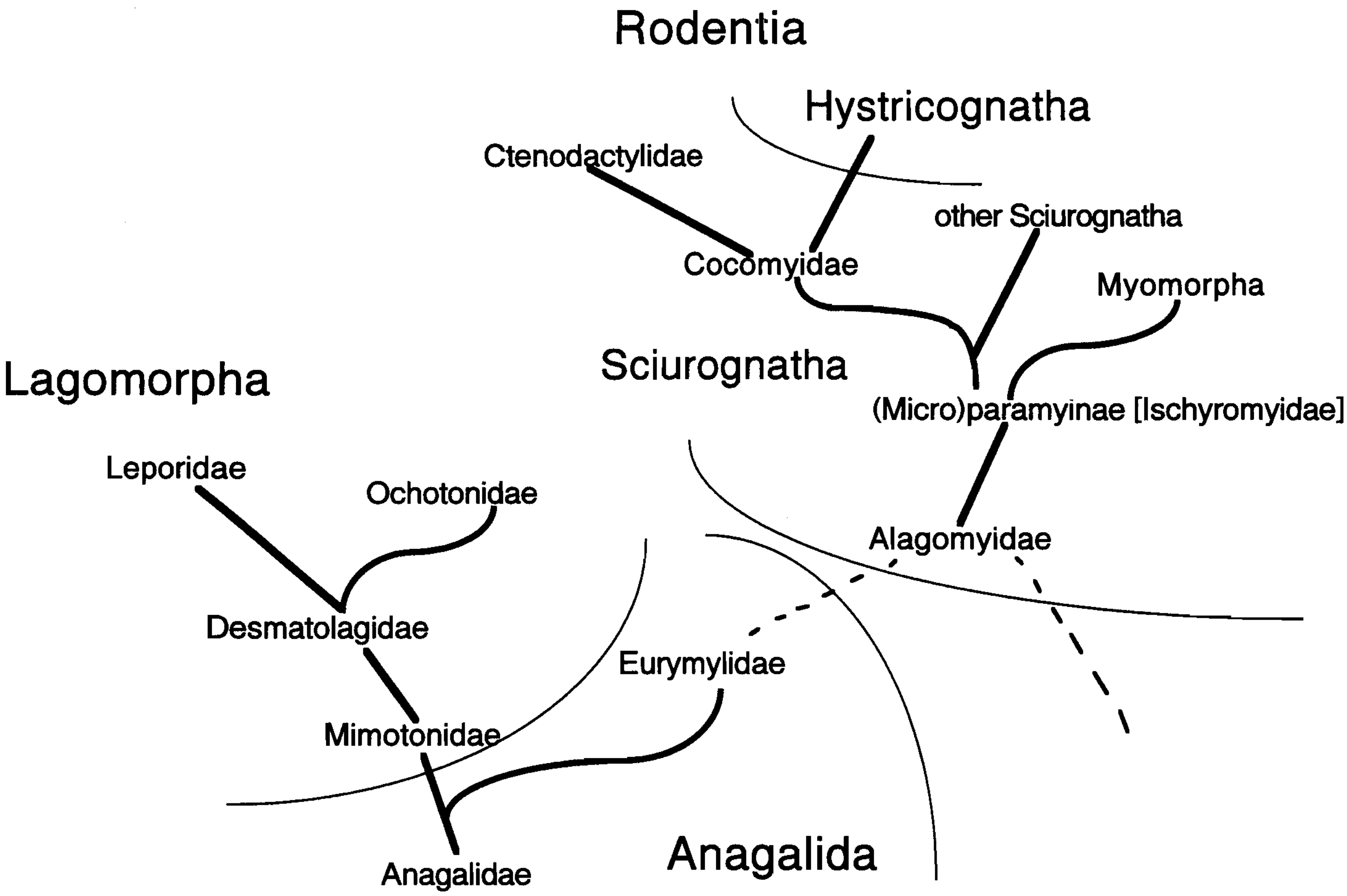

Figure 1. Inferred phylogeny of Anagalida, Lagomorpha, and Rodentia.

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well as late Mimotonidae. Thus the time of lagomorph origination has the middle Paleocene for an upper bound. Its lower bound is less well defined, but the continuing absence of anagalids from deposits of Cretaceous age suggests that they hadn't yet originated then. This would make the origin of lagomorphs a part of the great and rapid radiation of therian mammals in the first half of the Paleocene. Figure 1 shows my interpretation of the phylogeny of the relevant groups.

The origin of the anagalids themselves remains sufficiently unclear that adequate consideration of earlier adaptive changes must await future discoveries. Thus, e.g., the placement of the Macroscelidea as their sister group or even closer to the Lagomorpha (cf. McKenna and Bell, 1997; Meng and Wyss, 2001) may conceivably be correct, but there is what appears to me better evidence that the Macroscelidea were derived from louisinine hyopsodontid condylarths (Hartenberger, 1986; Simons et al., 1991; Tabuce et al., 2001 [I disagree with the dismemberment of the Louisininae by the latter authors]).

A unique deletion of nine nucleotides in the gene BRCA1 (Madsen et al., 2001) strongly indicates a phyletic relationship of the Macroscelidea to the African ungulates, including the Tubulidentata, plus the Tenrecidae and Chrysochloridae, to form a group called the Afrotheria. (I discuss such evidence in a later section. It is stronger than the contrary morphological evidence [especially Asher, 1999] in the present case, and agrees with weaker molecular evidence from sequence analysis.) Such a relationship is consistent with a hyopsodontid origin for the Macroscelidea as currently circumscribed, which would then apparently be the basal afrotherians, although the Embrithopoda (with their apparently ancestral family Phenacolophidae) would then seem to become anomalous. (The Anthracobunidae would appear as a basal side branch of an expanded Tethytheria and possibly not even specially related to the Proboscidea.) The Macroscelidea themselves may conceivably then be regarded as surviving (if now insectivorous) condylarths, as *Plesiorycteropus* (on which see MacPhee,1994, for data), from the Madagascan Pleistocene, more clearly is, although such a position for the Macroscelidea will probably prove implausible. The anagalids give no indication of condylarth ancestry, so they would then lack special affinity to macroscelideans.

The Zalambdalestidae are another candidate (Van Valen, 1964; McKenna and Bell, 1997; Archibald et al., 2001), but their affinity, if there is a special one at all (which I now doubt), is sufficiently distant and divergent that their information on ancestral features would be dubious. For instance, the enlarged and rootless lower incisor is (d)I_1 (Fostowicz-Frelik and Kielan-Jaworowska, 2002) and so is nonhomologous with the rootless dI_2 (as now identified: Luckett, 1985) of lagomorphs.

Nevertheless, anagalids share a number of synapomorphies with lagomorphs, and these may provisionally be regarded as characterizing anagalid origin. With the discovery of the largely primitive anagalid *Eosigale* (Hu, 1993), there do not appear to be any known anagalid synapomorphies not also shared with lagomorphs.

In this provisional context, the following changes seem to have occurred during or somewhat before the origin of the Anagalidae. The list, and others, is based mostly on Meng and Wyss (2001), Dashzeveg et al. (1998), and Shoshani and McKenna (1998 and appendices on the Web site http://www.academicpress.com/www/journal/fy/paris/shoshani.zip), supplemented by much other literature and many personal observations and interpretations. Characters have sometimes been polarized incorrectly in the relevant literature, in part because of inappropriate use of outgroups, but I agree with all the polarities which Meng and Wyss use although not with other aspects, such as much of their cookbook treatment of multistate characters. In all comparisons I know of no disconfirming characters except those which I explicitly mention, and most of the changes are also found elsewhere in mammalian evolution.

It is relevant to note that *Linnania*, a quite derived anagalid (Hu, 1993), is known from the early part of the Paleocene. Unless anagalids did indeed radiate, somewhere, in the Maestrichtian, evolution within the Anagalidae as well as from it to the Mimotonidae was unusually rapid. Such rapid evolution also occurred, with much better documentation, in other groups in North America (Van Valen, 1978b, 1990; Alroy, 1999).

1. Previously brachyodont cheek teeth become unilaterally hypsodont (lingually on upper teeth, labially on lower teeth), adapting to a diet that included abrasive plant material such as opal phytoliths and probably the grit of a semiarid region.
2. The mandibular condyle becomes raised somewhat above the level

of the toothrow, giving a leverage advantage to the masseter and pterygoid musculature over the temporalis, as is perhaps universally the case for herbivores.

3. A protoloph forms in the upper molars by the accentuation of the paracingulum as a continuation of the preprotocrista, with a concomitant reduction of the paraconule to become part of the modified crest. This improves shear of tough food.
4. In a related adaptation, the protocristae of the upper molars become strong and meet at an acute angle, forming a V-shaped protocone.
5. The upper molars change from a roughly triangular shape, in occlusal view, to a roughly rectangular shape, by evolution of a hypocone and enlargement of the protocone. This increases the occlusal surface.
6. The metaconule becomes indistinct and incorporated into a metaloph formed by coalescence of the postprotocrista and metacingulum. This is again an adaptation for horizontal shear.
7. The lower cheek teeth increase in size distally, giving greater surface area for horizontal occlusion.
8. The trigonid of each lower molar forms a single, well-defined wear surface with the talonid of the tooth immediately mesial to it, beginning in early wear. This perhaps unique adaptation provides a large surface for occlusion with the corresponding upper molar and encourages transverse grinding. The retention of a vertical postvallid provides a staircase-like effect that limits posterior occlusal movement of the mandible while providing both vertical and transverse shear.
9. As an aspect of the above adaptation, the protocristid of the lower molars becomes strong.
10. Another aspect is that the wear on the upper molars is predominantly as a single surface, beginning at the tall protoloph and extending basodistally, encompassing the protofossa and protocone but not the paracone and metacone.
11. The hypoconulid of M_3 becomes expanded into a broad third lobe of the tooth, functioning in the place of the trigonid of a nonexistent fourth molar to expand distally the wear surface of the M_3 talonid.
12. The trigonid of the lower molars becomes somewhat compressed mesiodistally.
13. P_3 and P_4 each develops an incipient (P_3) or expanded (P_4) trigonid and broadens its talonid, thereby increasing its surface occlusion at the expense of its puncturing ability.
14. The anterior part of the nasals is somewhat expanded.
15. The jugal extends to the front of the orbit.
16. An ossified auditory bulla forms by medial expansion of the ectotympanic, both protecting the middle ear and giving it a sound chamber.

With the exception of the last three items, all the above features are aspects of the single adaptation for effective chewing of abrasive plant food. Other mammalian groups with the same adaptation, including but not quite restricted to all those with hypsodont teeth, manifest it in morphologies which differ in various aspects from those of anagalids and lagomorphs, as well as differing among themselves. It is therefore unclear how many effectively independent characters are involved and therefore just how strong the actual support is for an origin of lagomorphs from anagalids. [This is because two associated characters constitute together effectively (2 - r^2) independent ones (Van Valen, 1974.)] The spatiotemporal congruence of early and basal members of both groups does add some additional and imprecise support.

An auditory bulla evolves homoplastically in almost all placental groups, every suitably situated bone and cartilage being used in at least one group. A bulla formed solely from an expanded ectotympanic is the most common kind in this significantly heterogeneous distribution of origins; therefore its presence in both anagalids and lagomorphs supports their relationship but does so less strongly than would a bulla formed in a less common way.

In the transition from anagalids to lagomorphs there are additional changes, mostly (insofar as known) being further improvements in the mastication of relatively coarse vegetation. The later genus *Gomphos*, from about the beginning of the Eocene (McKenna and Meng, 2001), is probably a mimotonid but lacks some lagomorph synapomorphies; some others are not preserved.

The origin of lagomorphs can then be characterized as follows.

1. dI_2 and dI^2 become evergrowing, with the former extending at least as far as M_3. They are therefore unreplaced, and the first incisors are also lost. A long diastema is produced in each jaw by the loss of all teeth between the incisors and the third premolars, except for the retention of P^2, which has become reduced and conical. The enamel on dI_2 and dI^2 becomes mostly restricted to the labial surface.
2. P^3 (unknown for *Gomphos*) changes from triangular to oval in occlusal view, and (d)I_3 is reduced and procumbent. Averianov (1994) said that P^3 is much reduced in the Mimotonidae, but this is untrue for at least *Mimotona*, as shown by a cast of the type of *M. wana*, IVPP V4324.
3. dI^3 shifts posterior to dI^2, as a stop for dI_2 in the cropping mode of incisor occlusion in which dI_2 shears against the back of dI^2. The incisor region is unknown for *Gomphos*. In *Mimotona*, where it is best known among early genera (Li et al., 1987), dI^3 is indeed posterior to dI^2, but it is nevertheless still in its primitive position at the jaw margin because the snout is relatively narrow. The fully lagomorph condition was apparently achieved by the position of dI^3 becoming developmentally associated with that of dI^2 rather than with the margin of the jaw; its new function would select for such a developmental shift.
4. Hunter-Schreger bands form in the incisor enamel, producing a distinct inner layer that strengthens it. Such bands often evolve in mammalian enamel subjected to large absolute stress (von Koenigswald et al., 1987; von Koenigswald, 1988; Rensberger, 1995).
5. The paracone of P^4 becomes surrounded by strong crests, helping horizontal occlusion.
6. The protoloph of the upper molars is similarly enlarged, with near or complete loss of the precingulum.
7. Concomitantly, the paraconid of the lower molars has been lost and the trigonid further compressed mesiodistally.
8. The centrocrista of the upper molars becomes incomplete or absent.
9. The incisive foramen is much elongated posteriorly.
10. The orbit shifts anteriorly relative to the dentition, with the posterior edge of the anterior zygomatic root being above M^2. Possibly the concomitant reduction of the snout comes from the placement of the large dI^2. The mandible shortens appropriately.

11. The masseter lateralis now originates from a fossa on the lateral surface of the zygomatic arch.
12. A short, broad process of the maxilla extends ventrally from the zygoma, serving as the origin of the masseter superficialis.
13. A long process of the premaxilla extends backward to contact the frontal.
14. The horizontal ramus of the mandible has become relatively deep and short, with the symphysis tapering anteriorly.
15. The mandibular condyle has risen appreciably above the toothrow, the coronoid process has nearly been lost, and the angular process is expanded. These modifications reflect the masseter and pterygoid musculature having become predominant over the temporalis, as is true for almost all herbivores although not all in the same way (cf. Turnbull, 1970).
16. The glenoid fossa is now longitudinally oriented but short, and the postglenoid process is lost. This permits the extensive anteroposterior movement of the mandible for gnawing and cropping. The glenoid fossa also becomes more dorsal than the auditory canal, as has happened for a number of herbivores and as is retained in the formerly herbivorous Macroscelididae. The glenoid fossa of all putatively primitive placentals is relatively low.
17. The nasals are about as wide as the palate.
18. The sustentacular facet of the calcaneum has become directly median to the astragalar facet; the sulcus separating them has been lost.
19. The upper ankle joint, above the astragalus, is constrained to anteroposterior movement by the deep astragalar trochlea.
20. The lower ankle joint, below the calcaneum and astragalus, is highly flexible anterioposteriorly (Szalay, 1985), suggesting that even mimotonids had acquired the additional (tarsal) segment of the hind leg enjoyed by extant lagomorphs.

In addition to the above notations on incomplete knowledge, the states of characters 9, 10, 11, 12, 13, 17, 18, 19, and 20 are unknown for *Gomphos*, and those of 15 and 16 for any mimotonid.

Lagomorphs more derived than *Gomphos* have lost the ectocingulum of the upper molars and have extended the masseteric fossa of the mandible anteriorly below M_3. *Gomphos* itself lacks known autapomorphies other than an almost completely molariform P_4, if that tooth is correctly identified; Text-figure 23c of Dashzeveg and Russell (1988) suggests, however, that it may instead be a dP_4, with somewhat greater wear than the adjacent M_1.

The various lagomorph synapomorphies, like those for anagalids and almost every other group of organisms, don't permit an accurate assessment of the number of independent changes. For instance, all lagomorph synapomorphies except for the modification of the ankle seem to be aspects of improved adaptation to tough plant food.

The Lagomorpha contains three families more derived than the Mimotonidae: the extant Ochotonidae and Leporidae, and their immediate ancestral group the Desmatolagidae. The desmatolagids further refine the general adaptation of the Mimotonidae, and become more divergent. They go beyond the mimotonids in the following ways, which are retained in later lagomorphs:

1. The cheek teeth become quite hypsodont.
2. P_3 is much enlarged, with an occlusal surface initially of enamel folds.
3. P^3 becomes molariform and P^2 has an enamel fold.
4. M^3 and M_3 are appreciably reduced, as part of a forward shift in

mastication; the hypoconulid of M_3 becomes incorporated into the postcristid, as is foreshadowed in *Gomphos*.
5. P^4 evolves a transverse hypocone and P_4 a correspondingly fully crested talonid.
6. On the upper molars, the metaconule has become the predominant cusp and is in a central to somewhat labial position; the paracone and metacone are fully labial, reduced, and variably merged with each other; and a large protocone and hypocone are adjacent to each other and dominate the lingual part of the tooth. The vertical cleft between the latter two cusps (the hypostria) greatly widens later to provide enamel in the center of the tooth.
7. dI_2 extends only to M_1, and has a vertical groove on the enamel in front.
8. $(d)I_3$ is lost and dI^3 moves in from the jaw margin (as the snout becomes relatively broader) to be immediately behind dI^2; dI^3 is reduced in size but not in function.
9. In extant lagomorphs and adequately known extinct genera, the lower tooth rows are closer together than are the uppers, an apparently unique apomorphy. Cheek-tooth occlusion then occurs for only one side at a time, and occlusal force and wear are greater labially on the lower teeth and lingually on the uppers. Mimotonids (and eurymylids) apparently lack this feature, and the transformation of unilateral hypsodonty into full hypsodonty was probably necessary for its appearance.
9. The palate is shortened.
10. The facial exposure of the maxilla becomes highly fenestrated, perhaps as part of the moderate kineticism of the skull characteristic of, and apparently unique to, at least extant lagomorphs.
11. A narrow anterior process of the frontal extends between the maxilla and the extension of the premaxilla.
12. The fibula regains its contact with the calcaneum as the latter elongates.
13. The elbow is modified to preclude rotary motion of the forearm.
14. A canal runs obliquely through the calcaneum, transmitting vascular element(s) displaced by the closer fitting of bones in the ankle (Bleefeld and Bock, 2002). The canal is apparently absent in at least *Mimolagus*, *Anagalopsis*, and *Pseudictops* (Bohlin, 1951; Szalay, 1985; Bleefeld and McKenna, 1985; Sulimski, 1969). At least *Pseudictops* and *Mimolagus* have an interosseous canal between the calcaneum and astragalus (Sulimski, 1969) that may have contained the same vascularization.

These characters are variably known for the several genera of desmatolagids, and the derived states mentioned appear at different stages well into the Eocene (Li, 1965; McKenna, 1982).

Eurymylidae

The Eurymylidae resemble the Mimotonidae and perhaps should not be separated from them at the family level. However, they have lost dI^3 rather than modifying its function, and their inclusion in the Lagomorpha would therefore be somewhat anomalous despite their evergrowing dI^2 and dI_2 and related synapomorphies. (Of the above list of lagomorph synapomorphies, the Eurymylidae share 1, 8, 10, 13, and 14, giving evidence of a common origin.Their state for some others is unknown.) I therefore retain them as a separate family, one of two in the order Anagalida.

Synapomorphies of eurymylids not entirely shared with the lagomorphs include the following:

1. The diastema is extended by loss of dI^3 and dI_3, P^2 also being lost after the divergence or transformation of the primitive genus *Sinomylus*.
2. The coronoid process is somewhat reduced, a common conapomorphy for herbivores which lagomorphs take further. Li et al. (1987) said, however, that the eurymylid *Heomys* has a large coronoid process, although it is unclear what they are comparing it to. *Heomys* has been inadequately described in the literature I know and needs study.
3. The glenoid fossa is elongate and somewhat concave.
4. The incisive foramen is posterior and moderately elongate. The elongation is an early stage of the greater elongation characteristic of lagomorphs but the restriction to a posterior position is not. I don't know the functional significance of such changes.
5. P^4 acquires a metacone, only incipient in *Sinomylus*.
6. The protoloph of the upper molars becomes strong, forming a shearing edge and incorporating the paraconule. Again *Sinomylus* is intermediate.
7. In relation to this, the protocone of the upper molars becomes ridged and remains V-shaped.
8. The upper molars acquire a large stylar shelf.
9. The masseter lateralis originates from the lateral surface of the zygomatic arch, but not from a fossa there as it does in lagomorphs.
10. The masseter superficialis originates from the lateral surface of the zygoma, rather than more ventrally as in lagomorphs.
11. The orbits are even more anterior, relative to the toothrow, than in lagomorphs.
12. The glenoid fossa is elongated; this may be a lagomorph symplesiomorphy also.
13. The auditory bulla includes a contribution from the mastoid (known only in *Rhombomylus* [Ting and Li, 1984] and possibly an autapomorphy for it. In this genus, at least, the mastoid is greatly expanded otherwise also.)

Eurymylids are unknown before about the beginning of the Eocene, when a moderate diversity of them appears. Their weak divergence fron 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).

Both lagomorphs and rodents, like other primary herbivores, have reduced their temporalis muscle and enlarged their masseter. In lagomorphs the mass of the temporalis is only about 12 to 15 percent of the total adductor mass, and in rodents it is about 15 to 30 percent. The masseter is about 60 percent 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 percent in both groups. The internal pterygoid, on the other hand, is not noticeably enlarged in rodents, at about 6 to 11 percent, but lagomorphs, like ungulates, enlarge it to 20 percent or more.

The muscular differences between the two orders reflect somewhat different jaw mechanics. The rodent temporalis is normal, if rather small and functioning mostly as a retractor in anteroposterior chewing, but that of lagomorphs is horizontal near its origin, becomes tendinous and loops over the postorbital bar they have, and descends vertically to its insertion on the remnant of the coronoid process. I don't understand why lagomorphs did this; perhaps it stabilizes the jaw joint. The medial (deep) masseter of rodents differentiates anteriorly as a partial opponent of the temporalis, but that of lagomorphs differentiates posteriorly. It originates from a long process extending posteriorly from the zygometic arch. The zygomatic arch of lagomorphs extends farther laterally than does that of most rodents, and contraction of the medial masseter pulls the mandible out and back, pressing on the inclined occlusal surface. The internal pterygoid, on the other hand, has an anterior and somewhat medial vector and may function in lagomorphs mostly in gnawing, in conjunction with the lateral masseter.

When these characteristic muscular patterns originated is partly unclear. *Rhombomylus*, at least, seems to have had an only moderately reduced temporalis. The zygomatic arch of *Mimotona* had not yet bowed laterally, and the posterior half of the zygomatic arch has not been described for any eurymylid or mimotonid. *Mimotona* did, though, have lagomorph-like origins for more anterior parts of the masseter; however, Li and Ting (1985) reconstruct an apparently rodent-like anterior development of the deep masseter for *Rhombomylus*. The angular process is infrequently preserved in such early mammals, but even in *Eurymylus* (Sych, 1971) and *Rhombomylus* (Li and Ting, 1985) it is large and turned inward, suggesting an expanded internal pterygoid.

The late Paleocene eurymylid *Heomys* has teeth which 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.

Rodentia

The discovery of the late Paleocene 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 whatever, relative to other rodents. I therefore regard it as perhaps indistinguishable from a late common ancestor of all other rodents, and possibly even being such an ancestor. Meng and Wyss (2001) did propose two synapomorphies for the two known Asian members of the Alagomyidae (*Alagomys* and *Tribosphenomys*), overall the two most primitive known members of the family, and three autapomorphies for *Tribosphenomys* itself. Quite possibly the European Ailuravinae should also be included in the Alagomyidae, as Hartenberger (1995) and Escarguel (1999) have proposed; in that case the name of the family would have to become Ailuravidae, the earlier name.

One proposed alagomyid synapomorphy is that "the paracone and metacone are well separated by a broad, transversely oriented trigon valley. The cusp surfaces facing the valley are steep." This description does indeed apply correctly to both Asian alagomyid genera and to none of their known close relatives outside the family. However, the synapomorphy has two components, the broad valley itself and the steepness of the cusp surfaces which mostly bound its mesial and distal surfaces. The valley itself occurs also in early paramyines, although not in *Cocomys*, the most primitive known member (Dashzeveg and Meng, 1998) of the ctenodactyloid-hystricognath clade. It is associated in each case with a very enlarged hypoconid, which moves transversely along it in occlusion. It may indeed be that *Cocomys* retains the ancestral condition for rodents in this case, but it may alternatively represent a partial reversal in conjunction with crest development. The relatively steep surfaces are merely the result of the enlarged valley having occurred in genera with the primitive state of relatively tall cusps,

The other synapomorphy proposed for the Alagomyidae is that the M_3 has its previously enlarged third lobe (hypoconulid) reduced and "distinct but narrow." The description is indeed correct; however, because the more derived rodents have an even more reduced cusp, it being incorporated into the postcristid, the alagomyid condition is presumably merely a stage in this reduction and therefore plesiomorphic for rodents.

The three autapomorphies proposed for *Tribosphenomys* would all be reversals. The incisor enamel is regarded as losing the layer of Hunter-Schreger bands that had originated at some earlier time which is undefined but which would not have been later than the origin of the supposedly related family Eurymylidae. Such a loss may have occurred, although the eurymylid *Eomylus* also lacks the Hunter-Schreger layer and would also have had to lose it. The taxonomic distribution of this layer is quite inadequately known, although it is clear that it has originated many times among mammals. I have not found an adequately documented case of its loss, although the leporid lagomorphs did lose the outer layer of enamel, consisting of radial prisms (Martin, 1999, who clarified a previously murky subject.) It seems likely that both *Tribosphenomys* and *Eomylus* merely retained the ancestral bandless condition. In addition, the eurymylid *Decipomys* has what is called tangential enamel as an inner layer (Dashzeveg et al., 1998); this is an alternative way of strengthening the enamel, derived from the primitive fully radial condition, and apparently neither it nor Hunter-Schreger bands can be derived from the other.

The two other supposed reversals are even less likely. *Tribosphenomys*, like most early therians, has an ectocingulum on the upper molars. This is a remnant of the primitive stylar shelf, which narrowed concomitantly with the origination and enlargement of the protocone (Patterson, 1956). The ectocingulum itself is commonly incomplete or entirely lost, again a condition achieved in multiple lineages with further labial movement of the paracone and metacone. I know of no case of its reappearance after having been lost, although it is occasionally widened when still present. It also occurs on the molars of at least the eurymylid *Amar* and the mimotonid *Gomphos*, and on the DP^4 of the basal ctenodactyloid rodent *Cocomys*.

Tribosphenomys also has a paraconid on the lower molars, and one also occurs on the single molariform tooth known (probably dP_4) of the eurymylid *Zagmys* and, vestigially, on at least M_1 of the eurymylid *Eomylus*. The presence of a paraconid is primitive for therians; it is often lost, as the origin of a hypocone on the upper molars causes it to interfere with occlusion. The other eurymylids, and basal rodents, have a moderate to large hypocone and no paraconid, in those for which both conditions are known. Occasionally, even in some later rodents, a cusp (then called an anteroconid) reappears close to the position of the lost paraconid, but this functions in a more derived grinding occlusion in a single plane.

However, unlike *Alagomys*, *Tribosphenomys* has a small hypocone on its upper molars. More derived rodents, and also eurymylids and other Anagalida, also have a hypocone or hypocone shelf. This cusp is much more often gained than lost and aids in the transition from vertical shear to chewing. *Alagomys* is more derived than *Tribosphenomys* in several respects, one of which is the loss of the paraconid of the lower molars and the even greater mesiodistal compression of the molar trigonid, almost to a single moderate crest. The paraconid is commonly lost, or much reduced, after the origin of a hypocone, as these cusps tend to interfere with each other in chewing. The lingual part of the upper molars of *Alagomys* is as long (mesiodistally) as the labial part, and no embrasure shear is retained. Thus *Alagomys* may well have been derived from a form with both a hypocone and somewhat less compressed trigonid, like *Tribosphenomys*.

Thus we can take *Tribosphenomys*, at least provisionally, as the basal rodent. Its temporal position relative to the few other Paleocene rodents known is unclear, and the very rapid evolution of early rodents makes this uncertainty rather more important than it would otherwise be, but any temporal incongruence relative to the actual initiator of the rodent clade would be small and peripheral to the present discussion.

Landry (1999) has placed considerable emphasis on the position of the nasolacrimal duct relative to the base of dI^2. In hystricognaths and their ctenodactyloid relatives, it passes inside dI^2 (entodacric), while it is outside (ectodacric) in the remaining rodents. A developmental shift from one condition to the other would be difficult, and I agree with Landry's emphasis. The condition in *Mimatuta* and *Rhombomylus*, and that for alagomyids, can't be determined from available illustrations, but the lacrimal foramen of *Cocomys* is lateral and Landry regards it as ectodacric. From the figure of Li et al. (1989), however, it is unclear whether the highly curved dI^2 extends quite so far back. If it doesn't, that would provide a straightforward means for a transition. Possibly the same is true for *Pedetes*, an extant sciurognath with some entodacric conapomorphies and an enormous preorbital fossa that may constrain the anterior border of the orbit.

Alternatively, it is possible (if somewhat difficult) to adopt Landry's proposal to transfer *Cocomys* to the Paramyinae. [In the present paper I use 'Paramyinae' in the sense of the Paramyidae of Wood (1962), without further implication.] Doing so would raise the possibility that there were two origins for the rootless condition of rodent incisors, one each for Landry's suborders Entodacrya and Sciurognathi (or clades similar to these if some modification is necessary.) If so, it may prove desirable to regard rodents as diphyletic after all, depending on the nature of the transitions, and thus constituting two orders, although they would still form a more inclusive clade. Alagomyids presumably would fall within one of the clades, although their known morphology is fully primitive for both and thus, under this hypothesis, rootlessness would probably have originated only shortly before. However, the conapomorphies of entodacryans and sciurognaths (relative to alagomyids) would then become homoplastic, a result which I accept as seriously disconfirming.

Glires?

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. Most of these I have already given as synapomorphies for the Lagomorpha (1, 8, 10, 13, 14, 15, and 17) and Eurymylidae (1, 2, 3, and 4.) If they are also synapomorphies with the Rodentia, then rodents would be an exgroup from the eurymylid-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) emphasizes 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 evergrowing 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 lagomorphs and rodents, 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.

The other conapomorphies of lagomorphs and rodents, for which a function is apparent, all seem to be related, directly or somewhat indirectly, to the acquisition of evergrowing incisors for gnawing. 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 dI_2 and dI^2, 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) 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.

This conapomorphy being 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 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 unless 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, which 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, p.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 rate of change and its probability of homoplasy if it does change. By the latter criterion, phenotypic characters are usually better, especially in comparison to nucleotides.

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 which 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 which 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.

This rate effect is well known but is too often forgotten. Most of the genes which have been used in inferences on the higher-level phylogeny of mammals change at too fast a rate to give more than suggestions. McNiff and Allard (1998) have recently pointed out the problem for 12s ribosomal RNA in mitochondria, but it is more widespread. The problem is complicated for nucleotides by the ordinarily more rapid rate of substitution in the third (usually silent) position of codons than in the first two, and by similar effects. Here is a deliberately incomplete list of other difficulties largely or entirely restricted to molecular evidence: alignment of sequences, treatment of very short insertions or deletions (indels), heterogeneity of rate among genes and within genes, several related problems with transversions and transitions, treatment of introns and other noncoding but perhaps functional sequences, relative codon use, variation in base composition among genes (usually by isochores) and especially among species, long-branch attraction, paralogous and multiple-copy genes, and pseudogenes not recognized as such. Some important and often overlooked difficulties shared with phenotypic characters are the position of the root, independence of characters (most obvious for molecular data in double-stranded parts of transfer and ribosomal RNAs but occurring elsewhere also) and heterogeneity in rate among clades, within clades, and over time. Most of these difficulties are accentuated rather than reduced by incorporation of more data; they produce bias rather than just inaccuracy.

A further problem comes with inferred cladograms. Ordinarily there isn't a unique cladogram which is, somehow, obviously the only one consistent with the data, whether or not we regard the data as a sample from a much larger set of potential data. Like most of the problems above, this one is often just ignored, although it gets at least lip service more often than it used to. Use of statistics like bootstrap and, more rarely, "Bremer" support is at least now seen as good practice. Unfortunately, even if such statistics had an unambiguous relation to how much confidence a rational person should place in a tree given the data and method used (and they don't, even for a non-Bayesian), they still would be compromised by the various problems inherent in the data and methods of analysis themselves. Discussion of these problems is unfortunately beyond the scope of the present paper. It is, however, important to note that the focus of papers is almost always on the "best" cladogram, or set of *n* equally well "supported" cladograms, rather than on the entire set of cladograms (or more general phylogenies) that are consistent with the data, as it should be.

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,b) 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 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 which 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 which 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 kind of marker which 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 which 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).

Alternatives

If rodents actually are only convergent on lagomorphs, the nature of their separate ancestry would need consideration. Unfortunately, there is little that can be said about this yet. The cranial synapomorphies of rodents are mostly related to the gnawing incisors, so these wouldn't be expected in a non-gnawing ancestor. I have found no group with a set of conapomorphies with rodents that is at all convincing as synapomorphies. However, such a lack doesn't mean that there are no reasonable candidates. For instance, the Adapisoricidae (*sensu lato*), Leptictidae, Pentacodontidae, and even Purgatoriidae have rather similar cheek teeth except for obvious apomorphies of *Tribosphenomys* and a few of their own, and leptictids do have some development of the posterior distal process of the tibia (Rose, 1999). The pentacodontids are still known from only teeth and jaws.

The Adapisoricidae, on the other hand, are better known and gave rise to at least the extant Erinaceidae. *Placentidens*, a basal Eocene genus from Europe perhaps correctly allocated here (McKenna and Bell, 1997), converges on alagomyids in the transverse valley on the upper molars, although it is narrower in *Placentidens*. The particular advantage of adapisoricids, though, is that we can look at their descendants. And in fact they do share a moderate number of relatively infrequent nondental conapomorphies with rodents:

1. There is a lacrimal tubercle.
2. An alisphenoid canal is present.
3. The transverse canal in the basisphenoid is present.
4. There is a mastoid foramen.
5. There is a baculum.
6. A third trochanter of the femur is present and is located about midway down the shaft.
7. The astragalar trochlea is deep.

8. The internal carotid is transpromontorial.
9. The placenta is deciduous and discoidal.

I don't mean to promote a special relationship of rodents to adapisoricids, but merely to indicate that the Anagalida isn't the only more or less reasonable candidate for rodent ancestry.

Primitive retentions

An additional matter of interest is the presence in at least some lagomorphs, rodents, or both, of some surprisingly primitive character states. These of course provide no information on the possible existence of a rodent-lagomorph clade, but they do give evidence on the relative divergence times of these orders from others whose morphotypes share conapomorphies for the relevant characters. The Xenarthra is now usually, following McKenna (1975) [but see Gaudin et al., 1996], placed as the earliest-diverging extant order of placentals for this reason, as is indeed true for the Monotremata among extant mammals. Most of the following discussion is based on Shoshani and McKenna (1998).

As in xenarthrans, a precoracoid bone is present in both orders and a separate coracoid in at least lagomorphs.

Epidermal scales, apparently homologous to those of reptiles (Shoshani and McKenna, 1998, *contra* the usual view), are present in rodents, as they are in the Xenarthra, Pholidota, and Lipotyphla.

If lagomorphs diverged before rodents, the lack of a baculum in lagomorphs may be primitive. It is also absent from ungulates (including Tubulidentata), except for the Cetacea, and from the Xenarthra and Pholidota. Whether its occurrence in whales is a retention or reappearance is unclear, as is the reason for its loss by ungulates. At least some tenrecids have a baculum (Olson, 1999). The bone is apparently absent from the other Afrotheria, including the related Chrysochloridae, and whether it is a neomorph in tenrecs is unknown.

The uterus in both the Lagomorpha and Rodentia is duplex, the two horns opening separately, with separate cervices, into the single vagina. No other placental order retains this primitive state. Moreover, both orders retain a cloaca, as well as a urogenital sinus in females. Of other orders, only the Xenarthra and Lipotyphla retain a cloaca.

Conclusion

It is thus 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 be decisive in due course.

One possibility is the discovery of ancestors or near-ancestors to *Tribosphenomys* that provide a sufficiently dense chain to an ancestral 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 great clades of rodents occur. *Alagomys* and *Paramys atavus* are indeed both 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 so-far-discovered Asian deposits. Some or all may be unusually small mammals, as *Tribosphenomys* is.

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.

The sequence from anagalids to mimotonids to more derived lagomorphs seems well supported. The main adaptation throughout this sequence appears to be for acquisition and processing of relatively tough vegetation of low nutritional quality, such as grasses. The initial transition to a grazing adaptive zone occurred rather or quite rapidly, although consolidation in the zone (after *Mimatuta*) was at a more sedate pace. Unfortunately there isn't enough evidence yet for quantitative estimates of the relevant rates. Some intermediate stages (*Anagale*, *Mimolagus*) were able to persist throughout the Paleocene and Eocene in the company of their more derived cousins. No member of this assemblage is known to have become either large or particularly small.

Rodents, on the other hand, were not initially adapted for grazing. The minute size of *Tribosphenomys* and *Alagomys*, together with their squirrel-like and very brachyodont, little worn, and cuspidate teeth (features which 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 can't be easily resolved by invoking a brachyodont ghost lineage, because brachyodonty is maladaptive for a diet of coarse vegetation and 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 can't resolve the conflict. However, since the basalmost known rodents were clearly not even close to being grazers, the *spermativore*[1] hypothesis may be provisionally accepted.

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

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[1] *Spermativore*, new term: an animal that eats seeds. *Sperma*, Greek, seed, as in *Spermophilus* or Angiospermae.

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, however, possible to specify just why they were so successful. A group advantageous in one respect is often disadvantaged in other ways, and it isn't even possible 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 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 alagomyids, 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 semiarid 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, and is still an *(o)scuro* to their *chiaro*.

Appendix: Summary of some perspectives relevant to this paper

Although I reject cladistic classification, for reasons given elsewhere (Van Valen, 1978a, 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 which 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 which 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. Multistate characters are often treated as multiple binary characters. 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. Unfortunately information is usually inadequate to quantify the interdependence for even a single species, whence the practice of ignoring it. But even swept under the rug it still fouls the machinery.

Moreover, lack of independence has an even more serious manifestation. Here the relevant consideration isn't how characters are interrelated within species, but rather whether a change in one character affects the probability of subsequent or coeval change in another character. Similarly for different states in a multistate character. Such interdependencies can be asymmetrical and even differ in different lineages. This general interdependence is ubiquitous, even for molecular data, and affects probably all cladograms inferred by any canned program. Unfortunately it probably can't be quantified even in principle.

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. Criteria of optimality such as parsimony and maximum likelihood depend strongly on knowledge we don't have. That doesn't mean that they, and cladograms inferred by using them, are useless or have no information content. What it does mean is that in present practice there is no way, even in principle, to decide what tree or set of trees actually gives the best fit to the data. It also means that measures of relative fit such as bootstrap value or "Bremer support" fail in their attempt to quantify the unquantifiable.

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." And the drunk still looks under the streetlight.

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.[2]

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[2] If one drops the restriction that the time plane of reference be the present, as has been suggested, then any clade can become a crown group by a suitable arbitrary choice of time plane. Such a ploy isn't an improvement. And that some people ignore extinct organisms in their classifications is a reflection on them rather than something to be encouraged. No time plane is intrinsically more important than any other to the organisms themselves, and it is the organisms themselves that we try to classify.

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