Volume 325, number 1,2, 152–159 FEBS 12394 June 1993

Minireview

Towards a molecular resolution of the ordinal phylogeny of the eutherian mammals

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Received 4 March 1993; revised version received 19 March 1993

Reconstructing the evolutionary relationships among the orders of eutherian mammals entails the identification of a single true phylogenetic tree out of approximately 10^{19} possible ones. The morphological and paleontological legacy to the field consists of numerous contradictory trees that are mostly devoid of binary resolution. With the introduction of molecular methodologies, several superordinal relationships have been identified, and in several instances a complete taxonomic revision was indicated. In this review, I present a summary of the phylogenetic affinities of the eutherian orders as revealed by molecular studies, and outline the differences between the molecular phylogenetic schemes and the phylogenetic trees produced through the use of morphological data. Questions of monophyly or paraphyly of the eutherian orders are also discussed. It is estimated that all but 10^9 of the 10^{19} possible phylogenetic trees have been ruled out by molecular analysis, and that DNA and protein sequences with their potential to supply millions of phylogenetically useful characters will resolve the phylogeny of the orders of mammals into a consistently bifurcating tree in the not-so-distant future.

Molecular phylogeny; Eutheria

1. INTRODUCTION

The higher-level classification of eutherians (placental mammals) constitutes a complex phylogenetic problem that is concerned with two issues: (1) the reconstruction of the phylogenetic relationships at the ordinal level, and (2) the testing of the internal monophyly of each order. Eutherians represent the great majority of extant mammals, and an interest in their higher-level classification has existed among biologists since the beginning of the nineteenth century. Because of a lack of progress, for much of the twentieth century, the interest in higher-level classification waned, and systematists have mainly dealt with phylogenetic relationships at the familial, generic or species levels. Recently, the higher-level classification of eutherians has again started to attract a great deal of attention. There are essentially three factors that have contributed to this surge in interest. First, molecular data have proved extremely powerful in resolving phylogenetic quandaries that could not be resolved by the traditional methods of evolutionary inquiry. Second, the phylogeny of species used as models in the laboratory and their relatedness to humans has been shown to be of practical importance in reaching rational inferences in medical and pharmacological research. And third, it has been realized that inferences concerning evolutionary mechanisms at the molecular level, such as the rate of substitution, the pattern of gene duplication, and horizontal gene transfer, depend on phylogenetic knowledge of the organisms under study. In this article I review the progress that has been made in the higher-level classification of eutherians since the introduction of molecular methodologies, and compare the emerging molecular picture with the phylogenetic framework provided by morphology and paleontology.

2. THE PHYLOGENETIC PROBLEM

A phylogenetic tree, or cladogram, is a graph composed of nodes and branches that represents the evolutionary relationships among taxonomic units. The evolutionary process of speciation is binary, and therefore, the nodes of a phylogenetic tree should be bifurcated, i.e. from each node only two immediate branches should descend. A multifurcation means that a binary resolution could not be obtained. The sequence of speciation events that has led to the formation of any group of taxa is historically unique, i.e. only one tree represents accurately the true evolutionary history of the group [1]. The aim of phylogenetic reconstructions is to identify this tree from among all possible ones. In the absence of a complete resolution of the phylogenetic relationships among the taxa under study, the purpose of the phylogenetic reconstruction is to identify constituent monophyletic clades, i.e. subgroups of taxa whose

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Published by Elsevier Science Publishers B.V.

common ancestor is not shared by any taxon outside the subgroup. A taxonomic entity that is not monophyletic is called a paraphyletic group, and from an evolutionary viewpoint, it is invalid.

Subclass Eutheria is one of three divisions of class Mammalia, the others being Prototheria (monotremates) and Metatheria (marsupials). Eutheria consists of about 4,000 species, and is currently divided by most authorities into 18 extant orders (Table I). Reconstructing the phylogenetic relationships among these orders requires the building of a cladogram consisting of 34 branches and the inference of 17 ancestral taxa. The number of different binary cladograms that can be built is 6,332,659,870,762,850,625 [2]. If some of the more speciose orders turn out to be paraphyletic internally, then the number of possible phylogenetic trees may increase by several orders of magnitude. A complete solution of the ordinal phylogeny of eutherians entails the identification of a single cladogram out of these approximately 10^{19} possible phylogenetic trees. Finding the proverbial needle in the haystack seems like a trivial problem in comparison with the task of solving the ordinal phylogeny of eutherians.

3. THE LEGACY OF MORPHOLOGY AND PALEONTOLOGY

For reasons of intrinsic limitations, morphology has failed to resolve the higher-level classification of mammals, and despite continuing progress, is unlikely to resolve the mammalian phylogenetic tree in the future. In fact, for almost half a century, the field of mammalian phylogeny has been dominated by Simpson's pessimistic view, according to which the great burst of mammalian radiations in the Cenozoic has rendered the ordinal phylogeny of mammals insolvable [3,4]. The alternative view, i.e. that resolution is possible given additional data, was unpopular with morphologists and paleontologists, probably because its acceptance would essentially mean the end of the road for morphology.

Morphological phylogenies are characterized by two features: (1) the various trees disagree with one another in almost all respects despite the fact that many of them are based on essentially identical sets of data [3,5–12], and (2) all morphological cladograms exhibit considerable 'bushiness', i.e. they contain numerous unresolved multifurcations. Morphological studies have essentially left us not with a unique tree, but with many phylogenetic bushes devoid of binary resolution. Moreover, most of the superordinal relationships identified by morphology (Table II), e.g. the close relationship of rodents and lagomorphs within Glires, the clustering of chiropterans and dermopterans, and the close affinity of edentates and pholidotans, are crumbling under molecular scrutiny.

4. MOLECULAR DATA IN PHYLOGENETIC STUDIES

In the last few years, the morphological pessimism concerning eutherian ordinal phylogeny has started to dissipate as several superordinal relationships were identified through the use of molecular data, i.e. DNA and protein sequences. Molecular methodologies have already yielded significant insights and changes in our understanding of mammalian phylogeny, so that the phylogeny of the orders of eutherian mammals may be

Table I

The traditional classification of the extant orders of eutherian mammals

Order	Number of			Representative members
	Families	Genera	Species	
Artiodactyla	9	81	211	pigs, hippopotamuses, camels, deer, cows, giraffes
Carnivora	10	100	274	cats, dogs, seals, walruses, bears
Cetacea	13	41	79	whales, dolphins, porpoises
Chiroptera	18	186	986	bats
Dermoptera	1	1	2	flying-lemurs
Edentata	4	13	30	sloths, anteaters, armadillos
Hyracoidea	1	3	7	hyraxes
Insectivora	7	65	390	hedgehogs, shrews, moles
Lagomorpha	2	13	69	hares, rabbits, pikas
Macroscelidea	1	4	15	elephant-shrews
Perissodactyla	3	6	17	horses, asses, zebras, rhinoceroses, tapirs
Pholidota	1	1	7	pangolins
Primates	13	71	233	lorises, lemurs, tarsiers, marmosets, monkeys, apes
Proboscidea	1	2	2	elephants
Rodentia	29	426	1814	rats, mice, mole-rats, squirrels, porcupines, guinea-pigs
Scandentia	1	5	16	tree-shrews
Sirenia	2	2	4	sea-cows, manatees
Tubulidentata	1	1	1	aardvarks

Data from Nowak [38].

resolved into a consistently bifurcating tree in the near future.

Because they are inherited in a straightforward genetic fashion and can be defined unambiguously, molecular characters are extremely useful in a phylogenetic context. Molecular homology can be ascertained unambiguously, the probability with which a molecular character-state changes into another is roughly calculable, and the characters are phylogenetically robust, i.e. they do not lose too rapidly their phylogenetic usefulness the more distant the taxa are from one another. Moreover, the rate of nucleotide substitution in the majority of nuclearly-encoded protein-coding genes and the rate of transversion in mitochondrial DNA are particularly suitable for resolving the phylogenetic relationships among the mammalian orders, which have presumably diverged from one another 25–120 million years ago [1]. Finally, DNA and protein sequences can supply millions of phylogenetically useful characters. In contrast, while the 'morphological arsenal' may not yet be depleted [9], it is reasonable to assume that the number of morphological characters that can be added to a taxonomic analysis of eutherian orders is quite small. These features allow for the development of objective methods of tree reconstruction, in which the assumptions can be stated explicitly, and of exact protocols that can be repeated and tested. Thus, taxonomy ceases to be an 'art' [3] and becomes science.

5. COMPREHENSIVE MOLECULAR PHYLOGENIES

Molecular phylogenetic reconstructions of eutherian orders fall into two categories: comprehensive and partial. Comprehensive reconstructions attempt to identify the evolutionary relationships among all or at least the vast majority of orders. Partial reconstructions concern themselves with only a few orders at a time. The first comprehensive molecular phylogeny was proposed by Miyamoto and Goodman [13]. More recently, an updated phylogenetic reconstruction based on a maximum of eight polypeptide sequences from 107 species has been published [14].

Wyss et al. [15] have claimed that the degree of confidence that can be placed on comprehensive molecular phylogenies is rather low. This claim was based on comparisons of consistency indices between molecular and morphological cladograms. (The consistency index is a measure of the relative proportion of unique changes in character-states out of the total number of changes required by a given cladogram. The closer the value of the consistency index is to 1, the more reliable the tree is considered.) Wyss et al. found that consistency indices of both morphological and molecular cladograms vary from 0.48 to 0.82, with no evidence for any significant advantage of one method over the other, and concluded that "morphology remains the most powerful tool available for identifying eutherian orders and their mutual affinities".

There are, however, two problems with this conclusion. The first concerns the measure itself. It is implicitly assumed that the probability of reversals, convergences and parallelisms (homoplasies) is the same for molecular and morphological characters. For instance, it is assumed that the probability of a nucleotide to change and then change back, say from A to G and then to A again, is the same as the probability of a morphological reversal, say the disappearance of the supraorbital foramen and its reappearance later. This assumption is unwarranted since a reversal in a complex morphological trait presumably entails many changes at the DNA level. Therefore, a molecular tree is more reliable than a morphological tree with the same consistency index. The second problem concerns the validity of the comparison between morphological trees and molecular ones. Wyss et al. do not take into consideration that in many cases comprehensive molecular phylogenies are based on a single or a few sequences, whereas morphological phylogenies are based on numerous characters. The fact that molecular phylogenies based on meager data emerge as reliable as morphological phylogenies based on an abundance of data merely strengthens the opinion that only molecular characters have the potential to untangle the eutherian phylogenetic tree.

Until sufficient molecular data are available, however, the range of orders for which phylogenetic relationships are sought should be severely restricted by the amount of available data. In other words, at present one should seek to resolve only parts of the mammalian tree. Researchers who attempt to reconstruct a phylogenetic tree for all the recognized eutherian orders on the basis of the currently available data are making too big a meal out of too small a bite.

6. PARTIAL MOLECULAR PHYLOGENIES

Partial phylogenetic solutions of the eutherian higher-level classification problem are those studies in which only a few orders are considered at a time. We note, however, that the combination of several partial trees does not result in a unique inferred tree. For example, let us consider the hypothetical example in FIg. 1. Let us assume that based on one set of data, the phylogenetic tree of lagomorphs, primates, artiodactyls and rodents has been determined unambiguously, i.e. one tree out of the 15 possible ones has been shown to be the true tree. Let us assume additionally that based on a second set of data, the phylogenetic tree of sirenians, primates and hyracoids has also been determined unambiguously, i.e. one tree out of the three possible ones has been shown to be the true tree. By combining these two resolved trees, we obviously cannot identify the true tree for the six orders; however, we can rule out approx-

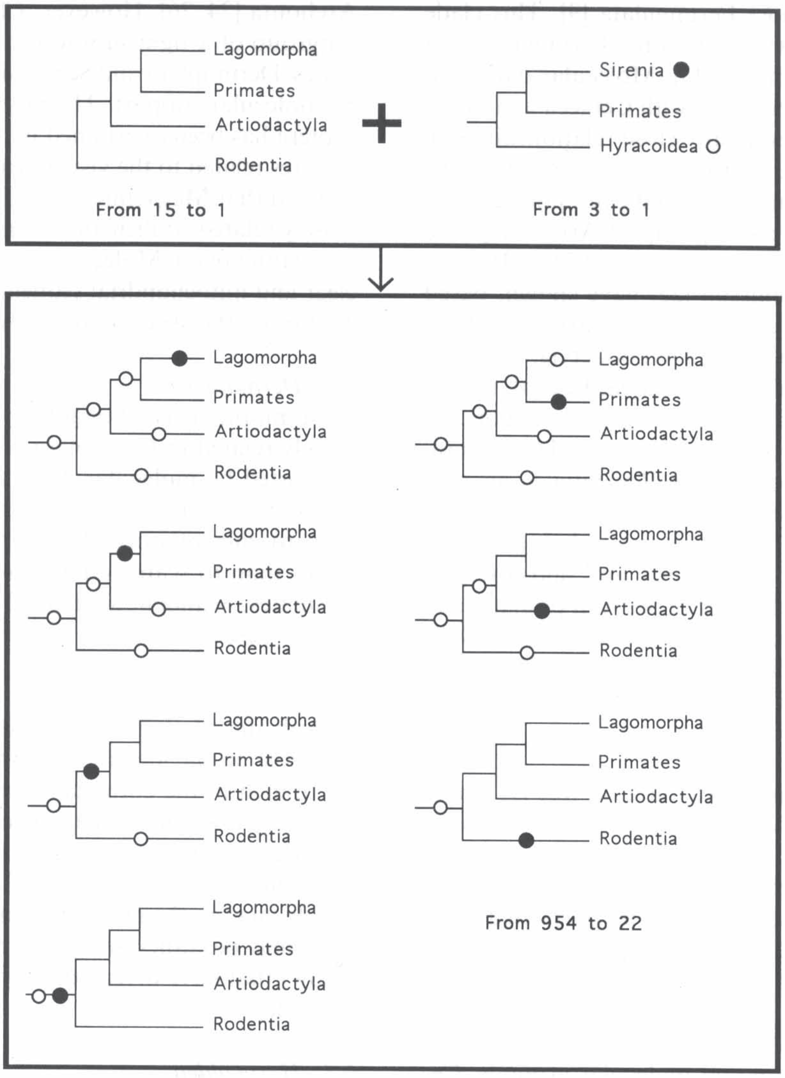

Fig. 1. The combination of two partial cladograms (upper box) does not result in the inference of a unique tree. In this hypothetical example, Sirenia (black circles) can occupy seven different phylogenetic positions. The possible branching points for Hyracoidea (empty circles) are determined by the phylogenetic position of Sirenia. The seven trees in the lower box represent 22 phylogenetic schemes (out of 954 possible ones) for the 6 taxa under study that are compatible with the trees in the upper box.

imately 98% of the 954 possible trees, and that constitutes significant progress towards the binary resolution of the tree.

There are essentially two types of partial phylogenetic studies. The first type includes those studies in which the phylogeny is inferred from a single gene, a single gene family or a single molecular trait. With the advent of the polymerase chain reaction technology, the number of single gene phylogenies in the literature has been growing exponentially. The degree of confidence that one can place on any superordinal clustering resulting from such a study depends on the strength of the support for the particular clustering as opposed to the support for the alternatives. For example, if the difference between the number of synapomorphies supporting a particular clade and that supporting alternatives clades is very large, or the clade is supported by a rarely occurring molecular synapomorphy, such as an inversion, a large insertion or a gene duplication, then it is possible to be confident in the inferred clustering. The second type of phylogenetic studies involves the comparison of many homologous genes. This type of study is much rarer since it involves the sequencing of many genes from a large number of taxa. The degree of confidence one can have in such phylogenetic trees is usually much higher than that of single-gene phylogenies.

In the following, I present a summary of the phylogenetic affinities of the eutherian orders as revealed by molecular studies and discuss the differences between the molecular phylogenetic schemes and the phylogenetic trees produces through the use of morphological data.

6.1. *Artiodactyla*

Morphologically, Artiodactyla is placed within Novacek's unresolved cohort Ferungulata [9]. This clade is essentially identical with Simpson's Ferungulata but it does not contain Carnivora [3]. Molecular data confirm the affinity of Artiodactyla with Cetacea and Perissodactyla, but do not reveal any close relationship with tubulidentates, hyracoids, proboscids or sirenians [16–19]. In addition, molecular data indicate quite conclusively that Cetacea is a sister group of Artiodactyla to the exclusion of Perissodactyla [13,14,20,21]. More recently, Arnason and Johnsson [22] have shown, based on the entire sequence of the mitochondria, that Carnivora is a sister group of the (Artiodactyla, Cetacea) clade to the exclusion of Perissodactyla. Li et al.'s analysis of 14 nuclear genes [23] also provided support for a close relationship between Artiodactyla and Carnivora. This analysis also indicates that Rodentia is an outgroup of Primates, Artiodactyla and Carnivora, in contradistinction to most morphological phylogenies in which artiodactyls and carnivores are said to have branched off before the divergence between primates and rodents. A recent molecular analysis (D.G. and D.G. Higgins, submitted) indicates that the order Artiodactyla should be redefined to include Cetacea (see below).

6.2. *Carnivora*

Novacek's most recent morphological tree [9] places Carnivora in an unresolved superorder, called Epitheria [7,10]. Molecular data, on the other hand, place Carnivora quite conclusively as an outgroup of the (Artiodactyla, Cetacea) clade [22,23]. The purported close affinity of Carnivora to Pholidota [13,14] cannot be ruled out at the present time.

6.3. *Cetacea*

On both morphological and molecular grounds, Cetacea is thought to be closely related to Artiodactyla [9,13,14,20–22]. The morphological affinity, however, is deemed ambiguous [9]. On the basis of amino acid and nucleotide sequences, Cetacea was shown not only to be intimately related to Artiodactyla, but to be deeply nested within the artiodactyl tree (D.G. and D.G. Higgins, submitted). That is, Cetacea is a sister group of one suborder of artiodactyls, Ruminantia (deer, giraffes, cows, goats, and sheep) to the exclusion of the other two suborders, Suiformes (pigs, peccaries and hippopotamuses) and Tylopoda (camels and llamas). Therefore, Cetacea should be deprived of its ordinal status and be submerged within the order Artiodactyla.

6.4. *Chiroptera*

Modern morphological studies place Chiroptera as a sister taxon of Dermoptera, and both taxa are aligned closely with the (Primates, Scandentia) clade [9]. This clustering is identical with Gregory's superorder Archonta [6], but is not reflected in Simpson's cohort Unguiculata [3,4]. Analyses of both mitochondrial and nuclear DNA sequences confirm the monophyly of Archonta [24–26]. However, Chiroptera emerges as an outgroup of a tight unresolved clade that includes Primates, Dermoptera and Scandentia. Unguiculata receives no molecular support. The monophyletic status of Chiroptera has been questioned by Pettigrew on the basis of features related to the visual neural pathways [27,28]. He claimed that Megachiroptera (fruit-eating bats) is more closely related to Primates than to Microchiroptera (insect-eating bats). Molecular analyses involving both nuclear and mitochondrial sequences have overwhelmingly confirmed the strict monophyly of Chiroptera [24–26].

6.5. *Dermoptera*

Dermoptera is thought by morphologists to be closely related to Chiroptera [9]. This contention is not supported by molecular data, which indicate that they are more closely related to primates and scandentians than to chiropterans. Whether they are closer to primates than to scandentians [24] or an outgroup of the (Primates, Scandentia) clade [25] cannot be determined at the present time.

6.6. *Edentata*

Both morphological and molecular results seem to converge on the idea that Edentata represents the earliest branch in the eutherian tree [9,13,14]. Morphological data, however, cluster the edentates with Pholidota [9], whereas molecular data indicate no such affinity [14]. The molecular data is unfortunately too meager to decide on even the purported antiquity of Edentata, and there may be eutherian orders (e.g. Hystricomorpha, see below) that have diverged prior to the edentates (D.G., unpublished results).

6.7. *Hyracoidea*

Simpson [3] and Shoshani [29] put Hyracoidea within the superorder Paenungulata, although their definitions of the superorder are somewhat different (Table II). In turn, Paenungulata is said to belong to cohort Ferungulata [3]. Novacek places Hyracoidea within the Paenungulata (*sensu* Simpson) as an outgroup of the (Proboscidea, Sirenia) clade [9]. There are also claims in the morphological literature that Hyracoidea may be related to Perissodactyla [30]. Molecular data are quite scarce, however, they confirm the monophyly of the Paenungulata *sensu* Shoshani [13,14,29]. The molecular possibility that Hyracoidea is a sister group of Macroscelid will be discussed below. Neither cohort Ferungulata nor the affinity of hyracoids and perissodactyls receive any molecular support. On the basis of the available molecular data, the internal branchings within the Paenungulata cannot as yet be resolved.

6.8. *Insectivora*

On morphological grounds, Insectivora has been variably claimed to be (1) a sister taxon of the scandentians, (2) a sister taxon of the Macroscelidea, (3) a member of the superorder Archonta, (4) a member of the now-defunct superordinal taxon Ungulata, or (5) a descendant of a remote branching at the base of the eutherian tree [11]. The very scant molecular data pertaining to Insectivora [14] provide limited support for an affinity with the Archonta, but its position cannot otherwise be determined with any degree of confidence.

6.9. *Lagomorpha*

The Lagomorpha started its phylogenetic career as a suborder of Rodentia, but was subsequently awarded an independent ordinal status. However, the close affinity between the two taxa was maintained by the vast majority of morphological studies from 1910 and onwards [3,6–11], with Rodentia and Lagomorpha being placed in the monophyletic cohort Glires. The minority verdict by McKenna [7] places Lagomorpha and Macroscelidea within the grandorder Anagalidia. Molecular results starkly contradict both morphological verdicts. For example, on the basis of several isozymes of carbonic anhydrase and the pattern of duplications in the class I alcohol dehydrogenase locus, Lagomorpha was shown to be more closely related to perissodactyls, artiodactyls and primates than to rodents [16–19]. On the basis of several nuclear sequences, Lagomorpha was placed closer to Primates, Scandentia, Dermoptera, Chiroptera and Artiodactyla, than to Rodentia [23,25,31]. Thus, the molecular evidence against the validity of Glires is overwhelming. However, the molecular data have failed to provide strong positive evidence for the superordinal affinities of Lagomorpha, and the molecular studies that have dealt with this order reached different conclusions. In the studies by Goodman's group [13,14,25], Lagomorpha emerges as a sister taxon of Scandentia, to the exclusion of Primates, Dermoptera, and Chiroptera, i.e. it should be included within the Archonta. In contrast, in Li et al.'s study [23], Lagomorpha emerges as an outgroup of Artiodactyla, Carnivora and Primates. With the rapid accumulation of molecular data, the elucidation of the phylogenetic position of Lagomorpha is just a matter of time, and judging from present trends, this order is bound to shake the foundations of the traditional mammalian tree.

6.10. *Macroscelidea*

Most morphological phylogenies place Macroscelidea as an outgroup of cohort Glires [7,9]. Since Glires is most certainly invalid, the position of Macroscelidea should be assessed molecularly. The αA crystallin of the elephant shrew *Elephantulus rufescens* turned out to contain three synapomorphies with the paenungulates and to be identical in sequence with the homologous protein form hyrax, *Procavia capensis* [32]. Tentatively, therefore, Macroscelidea should be considered a sister group of Hyracoidea.

6.11. *Perissodactyla*

The most recent morphological review places Perissodactyla as an outgroup of Hyracoidea, Proboscidea and Sirenia [9]. Molecular data, on the other hand, place Perissodactyla as an outgroup to Artiodactyla (inclusive of Cetacea) and Carnivora [17–21].

6.12. *Pholidota*

Novacek places Pholidota as a sister group of the Edentata, and the ancestor of these two taxa is claimed to represent the oldest internal branching within Eutheria [9]. Molecular data support neither the clustering of pholidotans and edentates nor the antiquity of the pholidotan lineage. Rather, pholidotans tentatively emerge as a sister group of the carnivores [13,14].

6.13. *Primates*

By virtue of the fact that the vast majority of researchers belong to this taxon, Primates is the most thoroughly studied order within subclass Eutheria. Both morphological and molecular studies place Primates within the Archonta [9,16–18,24,25]. Morphological studies, however, place Primates and Scandentia in one clade and Chiroptera and Dermoptera in another [9], whereas molecular studies place Primates, Scandentia, and Dermoptera closer to one another than to Chiroptera [24,25].

Table II

A selection of superordinal eutherian taxa

Taxon	Constitutent orders
Ferungulata *sensu* Simpson	Cetacea, Tubulidentata, Perissodactyla, Hyracoidea, Proboscidea, Sirenia, Carnivora
Ferungulata *sensu* Novacek	Cetacea, Tubulidentata, Perissodactyla, Hyracoidea, Proboscidea, Sirenia
Epitheria	All orders with the exception of Edentata and Pholidota
Archonta	Chiroptera, Dermoptera, Primates, Scandentia
Unguiculata	Chiroptera, Dermoptera, Primates, Scandentia, Insectivora, Edentata, Pholidota
Paenungulata *sensu* Simpson	Hyracoidea, Proboscidea, Sirenia
Paenungulata *sensu* Shoshani	Hyracoidea, Proboscidea, Sirenia, Tubulidentata
Glires	Rodentia, Lagomorpha
Anagalidia	Lagomorpha, Macroscelidea
Tethyteria	Proboscidea, Sirenia

6.14. *Proboscidea and Sirenia*

It is agreed by both morphological and molecular studies [9,25,29] that Proboscidea and Sirenia are the two members of the monophyletic taxon Tethyteria. Together with Hyracoidea and Tubulidentata, the Tethyteria is placed within the superorder Paenungulata *sensu* Shoshani.

6.15. *Rodentia*

On morphological grounds, Rodentia and Lagomorpha are placed within cohort Glires, and the divergence between these two orders is deemed to be the most recent such event within Eutheria [9]. In marked contrast, all molecular studies indicate quite strongly that Rodentia diverged very early in the evolution of placental mammals. In fact, Rodentia has been shown to be an outgroup of many eutherian orders, such as Perissodactyla, Artiodactyla, Lagomorpha, Cetacea, Proboscidea, Primates, Carnivora, Chiroptera, Dermoptera, and Scandentia [16–24,26,31]. Moreover, the very monophyly of Rodentia came under molecular fire. Based on comparisons of protein and mitochondrial DNA sequences [33–37], it has been shown that one suborder of rodents, Hystricomorpha (guinea-pigs, porcupines), is related evolutionarily to neither of the two other suborders, Myomorpha (rats, mice) and Sciuromorpha (squirrels). Rather, myomorphs and sciuromorphs are more closely related to Primates and Artiodactyla than they are to hystricomorphs. The hystricomorphs probably represent one of the most ancient branches in eutherian evolutionary history. Therefore, the Hystricomorpha (or Hystricognathi) should be awarded an independent ordinal status within subclass Eutheria. Similarly, Sciurognathi (Myomorpha and Sciuromorpha) should be elevated to the rank of order. A similar, albeit more tentative, conclusion has been reached for the family Ctenodactylidae (gundis), a group of several North African rodents with no known extinct or extant affinities [36]. The disassembly of Rodentia into paraphyletic taxa renders it an empty taxonomic entity, a *nomen nudum*.

6.16. *Scandentia*

Scandentia is placed within the Archonta on both morphological and molecular grounds. On the basis of the mitochondrial cytochrome oxidase II gene sequence, Adkins and Honeycutt [24] place Scandentia, Dermoptera and Primates in a natural clade to the exclusion of Chiroptera. Whether Scandentia is closer to Primates, or to Dermoptera, or constitutes an outgroup to the (Primates, Dermoptera) clade cannot as yet be decided. On the basis of a study of nuclear DNA sequences [25], Scandentia tentatively emerges closer to Primates than to Dermoptera. Unfortunately, in this study the (Scandentia, Primates) clade is split by Lagomorpha, resulting in a ((Scandentia, Lagomorpha), Primates) clustering. Therefore, the possibility that Scandentia is a sister group of Lagomorpha [13,14] cannot as yet be refuted.

6.17. *Tubulidentata*

The position of Tubulidentata in morphological trees varies widely among the different studies. For example, Novacek [9] classifies it as an independent lineage in a trifurcated clade, the others being (Cetacea, Artiodactyla) and (((Sirenia, Proboscidea), Hyracoidea), Perissodactyla). In contrast, Shoshani [12] places Tubulidentata as an outgroup of the (Artiodactyla, Perissodactyla) clade. The only molecular study that includes the Tubulidentata places it quite firmly within the Paenungulata *sensu* Shoshani [14]. Its exact position within Paenungulata, however, remains undecided.

7. THE MONOPHYLY OF THE TRADITIONAL EUTHERIAN ORDERS

The higher-level classification of mammals concerns itself not only with interordinal relationships but also with questions pertaining to the monophyly or paraphyly of the traditional eutherian orders. In most cases, molecular studies have confirmed the monophyletic status of the eutherian orders, as indeed the monophylies of class Mammalia and subclass Eutheria [14,15]. For instance, the monophylies of Lagomorpha, Perissodactyla, Primates, and Chiroptera have been confirmed by molecular data [14,15,38]. Questions of monophyly do not arise as far as orders containing a single or a few species, e.g., Tubulidentata, are concerned. The monophyly of the order Artiodactyla can be maintained if we demote Cetacea to the rank of suborder and include it within Artiodactyla. Rodentia, on the other hand, has been shown to be paraphyletic, and therefore devoid of taxonomic validity. In the future, the monophyly of other highly diversified orders, e.g. Edentata and Insectivora, should be tested molecularly. The most promising candidate for disassembly is Carnivora, which is already divided by several morphological taxonomists into two paraphyletic suborders: Pinnipeda (marine carnivores) and Fissipedia (terrestrial carnivores).

8. PROGRESS?

In Fig. 2, I present a summary of our present knowledge regarding eutherian ordinal phylogeny. Note that the tree contains only 15 of the 18 traditional orders; the position of the other three being so uncertain as to preclude their inclusion within the tree. One order, Cetacea, is included within another, Artiodactyla, and a second order, Rodentia, is split tentatively into three independent taxa. The position of two orders, Lagomorpha and Ctenodactylidae is highly uncertain, and the tree contains three multifurcations. In addition, many of the

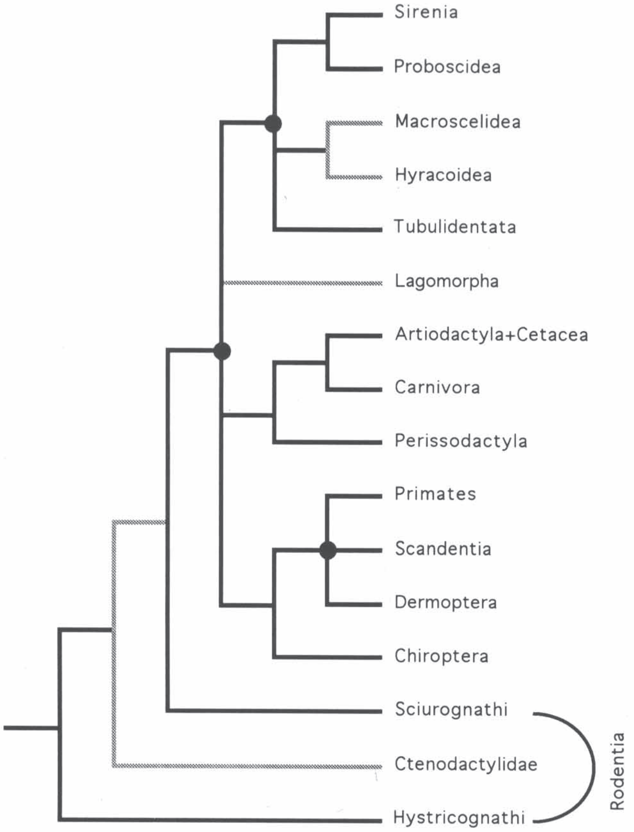

Fig. 2. Schematic representation of the phylogenetic relationships among eutherian orders on the basis of molecular data. The gray lines represent ambiguous branches. Note that the tree contains several multifurcations (filled circles) and that three orders of mammals whose phylogenetic position could not be determined even roughly are not included.

'resolved' internal branches are statistically insignificant, and much more data are needed to increase our confidence in them to acceptable values. However, out of the approximately 10^{19} initial trees, we are probably left with only about 10^9 phylogenetic trees that deserve further consideration. Of course, it is disappointing to realize that we cannot yet identify the true tree for the eutherian orders, and that the task facing us is still of momentous magnitude. Nevertheless, we must admit that tremendous progress has been made in a relatively short time. 'The final verdict' is indeed 'not yet in' [14], but there is no doubt in my mind that the eutherian tree will ultimately be solved and that mammologists are in for some big 'molecular' surprises.

Acknowledgements: I dedicate this paper to Prof. David Wool on the occasion of his sixtieth birthday. This study has been supported by a grant from the US–Israel Binational Science Foundation.

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