(1980) J. Appl. Ecol. 21, 623–634
14 Clò, M.E., Onfing, J.K., Brzuela, M.A. and Whisker, A.D. (1999) Oecologia 80, 268–276
16 Clò, M.S., Onfing, J.K., Whisker, A.D. and Brzuela, M.A. (1990) Ecology 71, 543–551
17 Stevenson, C.E., Marland, H.F., Roxenau, R.G. and Adas, K.H. (1989) J. Range Manag. 42, 123–127
18 Hammesz, H.N. (1988) Phytochemistry 27, 2349–2378
19 Bester, S., Watson, S.D., Edwards, P.J. and Niemann, H.M. (1991) Ann. Appl. Biol. 118, 239–250
20 Niemann, H.M. et al. (1989) Phytochemistry 28, 145–149
11 Thackray, D.I., Wratten, S.D., Edwards, P.J. and Niemann, H.M. (1990) Ann. Appl. Biol. 116, 573–582
15 Lyytop, G.G., Ageppanna, V.H., Niemann, H.M. and Centeuro, L.J. (1991) Phytochemistry 30, 3649–3651
23 Bentais, B.A., Cooper-Driver, G. and Bilgener, M. (1989) Adv. Ecol. Res. 19, 263–302
24 Schultz, J.C. (1988) in Chemical Mediation of Coevolution (Spencer, K.C., ed.), pp. 39–68, Academic Press
25 Schultz, J.C. and Keating, I.T. (1991) in Phytochemical Induction by Herbivores (Tallamy, D.W. and Raupp, M.J., eds), pp. 201–228, John Wiley & Sons
26 Denno, R.F. and McClure, M.S. (1983) Variable Plants and Herbivores in Natural and Managed Systems, Academic Press
27 Fritz, R.S. and Simms, E.L., eds (1992) Plant Resistance to Herbivores and Pathogens: Ecology, Evolution, and Genetics, University of Chicago Press
28 Coley, P.D. (1983) Ecol. Monogr. 53, 209–233
29 Stinmann, N.M. et al. (1989) Phytochemistry 28, 145–149
30 Thackray, D.I. Wratten, S.D., Edwards, P.J. and Niemann, H.M. (1990) Ann. Appl. Biol. 116, 573–582
31 Woodhead, S. and Bernays, E.A. (1978) Entomol. Exp. Appl. 24, 123–144
35 Cooper, S.M. and Owen-Smith, N. (1985) Oecologia 67, 142–146
36 Bryant, J.P. et al. (1991) in Secondary-Plant Metabolism (Insect Herbivore Interactions) pp. 79–95
39 Dawson, A.J. and Wilson, I.B. (1995) J. Exp. Biol. 41, 89–95
16 Garthwaites, J. (1983) Rev. Cyt. 102, 127–203
17 Haines, D.C., Barrera, R.P., Simmons, A.B. (1985) J. Theor. Biol. 113, 205–215
18 Wakmman, D.C., Barrera, R.F., Simmons, A.B. (1985) J. Theor. Biol. 113, 205–215
20 Salas, M.L. and Carrasco, L. (1990) J. Chem. Ecol. 16, 301–315

34 Amason, J.T. et al. (1992) J. Stored Prod. Res. 28, 119–136
37 Capinera, J.L., Renaud, A.R. and Roehrig, N.E. (1983) J. Chem. Ecol. 9, 1425–1437
38 Owens, W.R., Wiesman, R.K., Tukahara, D.L. and Hill, N.S. (1993) J. Agric. Entomol. 6, 47–60
19 Den Otter, C.J. (1992) Entomol. Exp. Appl. 62, 143–147
30 Rudlak, R.A. (1983) in Integrated Pest Management on Rangeland: A Shortgrass Prairie Perspective (Capinera, J.L., ed.), pp. 38–55, Westview Press
31 Dreyer, D.L., Reese, J.C. and Jones, K.C. (1981) J. Chem. Ecol. 7, 273–284
33 Woodhead, S. and Bernays, E.A. (1978) Entomol. Exp. Appl. 24, 123–144
35 Cooper, N.J. and McCormick, S.J. (1985) Oecologia 65, 289–296
13 Dowd, P.F. (1988) Entomol. Exp. Appl. 47, 69–72
16 Garthwaites, J. (1983) Rev. Cyt. 102, 127–203
18 Wakman, D.C., Barrera, R.F., Simmons, A.B. (1985) J. Theor. Biol. 113, 205–215
37 Amason, J.T., Philogène, B.J.R., Morand, P. et al. (1989) Insecticides of Plant Origin (ACS Symp. Ser. 387), American Chemical Society
38 Isman, M.B., Proksch, P. and Wratten, S.D. (1985) Pestic. Sci. 16, 165–174
39 Singh, N.K. and Schandl, G.G. (1991) in

Microbial Diversity of Leaves (Andrew, J.H. and Hirano, S.S., eds), pp. 108–121, Springer-Verlag
16 Day, E. (1991) in Microbial Ecology of Leaves (Andrew, J.H. and Hirano, S.S., eds), pp. 331–344, Springer-Verlag
16 Day, K. (1991) in Microbial Mediation of Plant–Herbivore Interactions (Barbosa, P., Krischik, V.A. and Jones, C.G., eds), pp. 199–226, Wiley
20 Berenbaum, M.R. (1988) in Chemical Mediation of Coevolution (Spencer, K.C., ed.), pp. 99–141, Academic Press
35 Howard, M.D., Heuchtberg, E.D., Bickery, R.W., Mitchell, J.C. and Lowry, S.R. (1989)
2 Astor, 265, 15, 221–237
44 Clay, K. (1990) Ecology 71, 558–570
45 Siegel, M.R., Latch, G.C.M. and Johnson, M.C. (1987) Annu. Rev. Phytopathol. 25, 293–315
46 Hardman, M., Schuen, R.W., Morgan, R., Lewis, R., Staffer, J.M., Cole, R.J., Clark, C.W., Dahlman, D.L., Varney, D.R. and Elmore, M.R. (1984) New Zeal. J. Agric. Res. 27, 309–316
45 Howard, M.D., Huettbertig, E.D., Bickery, R.W., Mitchell, C.G. and Lowry, S.R. (1992) J. Anim. Sci. 70, 1221–1237
44 Clay, K. (1990) Ecology 71, 558–570
45 Siegel, M.R., Latch, G.C.M. and Johnson, M.C. (1987) Annu. Rev. Phytopathol. 25, 293–315
4 Hietanen, A.L. and Summermatter, K. (1993) Microbiol. Biotechnol. 8, 381–409
7 Latch, G.C.M. (1993) Agric. Ecosyst. Environ. 44, 143–156
48 Siegel, M.R. (1990) in Microbial and Chemical Pollution of Forest Ecosystems (Agrawal, S.B. and Agrawal, M., eds), Yale University Press

Molecular Phylogeny and the Higher Classification of Eutherian Mammals

Dan Graur

Reconstructing the evolutionary relationships among the orders of eutherian mammals constitutes a formidable phylogenetic task. It entails the identification of a single true phylogenetic tree out of 10^{34}–10^{39} possible ones. For almost half a century, the field of mammalian phylogeny has been dominated by a pessimistic view, according to which the great burst of mammalian radiation more than 65 million years ago has rendered the ordinal phylogeny of mammals insoluble. In the last few years, this secession has started to dissipate as several supraordinal relationships were identified through the use of molecular data. DNA and protein sequences of complete mitochondrial and nuclear genomes may now be resolved into a consistently bifurcating tree in the not-too-distant future.

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The higher classification of eutherian mammals is concerned with the reconstruction of phylogenetic relationships among taxa at or above the ordinal level. Such studies deal, for instance, with the evolutionary relationships among carnivores, primates, rodents and artiodactyls, as

well as with questions pertaining to the monophyly or paraphyly of the eutherian orders. The articulation of molecular methodologies is expected not only to resolve the higher classification of mammals, but has already yielded significant insights and changes in our understanding of mammalian evolution.

Let us first define the magnitude of the phylogenetic problem at hand. Class Mammalia consists of about 1000 extant species, and is divided into three subclasses: Prototheria (monotremes), Metatheria (marsupials) and Eutheria (placentals). The Eutheria is probably monophyletic and divided into 15–25 orders[1,2]. Some of the orders, such as Rodentia and Artiodactyla, are extremely speciose; others, such as Tubulidentata and Lagomorpha, contain a single or a few species. Reconstructing the phylogenetic relationships among the eutherian orders requires the building of a cladogram consisting of at least 28 branches and the relation of at

least 14 ancestral taxa. (For a brief introduction of the nomenclature used in connection with phylogenetic trees, see Box 1.) If we assume that there are 15 orders of placental mammals, then the number of different phylogenetic trees that can be built is approximately 10^{34}. If the number of orders is 25, then the number of possible trees becomes approximately 1×10^{39}. Since the evolutionary process is unique, only one of these phylogenetic trees represents faithfully the true evolutionary relationships among the eutherian orders: the rest are 'false'. To put it in another way, the random probability of finding the true tree may be as low as 10^{-34}. The problem of classifying the orders of mammals in a phylogenetically meaningful manner can be restated quite simply as a problem of finding a very minuscule and lonely needle in a haystack of gigantic dimensions. Improving our chances of finding the true tree... the random probability

Box 1. Phylogenetic trees

A phylogenetic tree or a cladogram is a graph composed of nodes and branches. Only one branch connects any two adjacent nodes. The purpose of a phylogenetic tree is to illustrate the evolutionary relationships among a group of organisms. The nodes represent the taxonomic units and the branches define the relationships among the units. The branching pattern of the tree is termed the topology. There are two types of nodes, external and internal. External nodes represent the taxonomic units under study, also called the operational taxonomic units; internal nodes represent inferred ancestors, sometimes referred to as hypothetical taxonomic units. The taxonomic units can be individuals, populations, species or higher taxa.

The evolutionary relationships of a group of organisms can be summarized through a binary tree, and the trees can be bifurcated, i.e. from each node only two immediate branches should descend. A multifurcation at a tree resolution could not be obtained. Only rarely is a multifurcation in a tree assumed to represent a true multifurcation event. The sequence of speciation events that has led to the formation of any group of taxa is historically unique; thus, the phylogenetic tree that represents the true evolutionary history of the group. The phylogenetic tree reflecting this historical sequence is called the true tree. A tree inferred by using a particular set of data and a certain methodology of tree reconstruction is called an inferred tree. Obviously, the aim of phylogenetic reconstructions is to obtain an inferred tree that is identical to the true tree. However, since the true tree is not known (otherwise we would not bother to reconstruct it), the merits of an inferred tree are usually assessed by using statistical methods.

One of the main purposes of grouping taxonomic units is the construction of phylogenetic groups. A clade is defined as the group of all taxa that share a specific common ancestor; this ancestor is not shared by any taxa outside the clade. A taxonomic entity that is not monophyletic is called a paraphyletic group, and from an evolutionary point of view, it lacks taxonomic validity. The reptiles, for instance, are a paraphyletic taxon, since the common ancestor of all reptiles was also the ancestor of the birds and the mammals, which are not included within the reptiles. The mammals, on the other hand, do constitute a monophyletic status in recent years. Prokaryota, Animalia, Plantae, Fungi, Protista, Invertebrata, Pisces, Reptilia, Linguula and Rodentia are but a few of the well-known taxa that are known or suspected to be paraphyletic.

The inferred tree may differ from the unknown true tree. It is, therefore, customary to regard the inferred tree as a statistical or hypothesis for which a measure of probability or reliability is calculated. If the probability is smaller than an arbitrary value determined by the researcher, the null tree is judged to be improbable enough to warrant rejection. One such reliability measure is the consistency index, which is a measure of the relative proportion of parallel changes and reversals in character-states out of the total number of changes required for a given cladogram. The value of this index ranges from 0 to 1, for which a value of 0 indicates that a character has undergone many changes and a value of 1 indicates the consistency index is 1. The closer the value of the consistency index to 1, the more reliable the tree is considered.

For details of tree building methods, see Ref. 30.

Moreover, all the morphological cladograms are characterized by considerable 'fuzziness'. For example, the most recently published morphological cladogram is completely dominated by a pentafurcation encompassing 16 out of the 18 eutherian orders in the study. Multifurcations, which constitute the characteristic earmarks of 'fuzzy' phylogenetic trees, can essentially be interpreted in two ways. Either they represent the true sequence of events at the end of the speciation process, or they represent the incapability of the particular method to resolve the phylogeny. In the first interpretation, mammalian orders diverged from one another essentially simultaneously; or they may simply signify that the data are not sufficient to resolve the tree into a consistently bifurcating one.

For almost half a century, morphologists and paleontologists have followed Simpson, who believed that the eutherian orders emerged in a great burst of speciation around 65–80 million years ago. As a consequence, the prevailing opinion was that the fundamental features of eutherian evolution will never be obtained by molecular means due to the phylogenetic reasons. The

alternative view (i.e. that more data are needed) was unpopular with morphologists, probably because its acceptance would essentially mean a dead-end for morphology. With few exceptions, few discriminate morphological characters are unlikely to be discovered – certainly not in great numbers, and therefore, the resolution of the multifurcations and topological ambiguities of the eutherian tree by means of morphological analysis alone is an unachievable prospect.

Molecular data is phylogenetic studies

Molecular phylogenetic studies use comparisons of DNA and protein sequences. Such sequences are customarily deposited in computerized databases as soon as they are produced. The use of these databases has been growing explosively since the 1970s (Refs 12,13), and the rapid accumulation of DNA sequence data has already had a great impact on molecular phylogeny in general[14] and on mammalian higher classifications in particular.

In the following, I enumerate some of the conditions that must be met if a character is to be useful in a phylogenetic context, and show why molecular characters are suitable for purposes of determining phylogenetic topologies. The first and most important condition is that the character should be inherited in a simple/clear genetic fashion, as opposed to many morphological characters, for whom the genetic basis of this criterion is in memory.

The second condition is that the character state and changes in the state can be defined unambiguously. Molecular data, such as the nucleotide comprising a certain position in a gene, can always be defined with precision – an A, a C, a G, or a T. Similarly, a change in a molecular character state can also be described unambiguously, e.g. a transversion from G to T, a deletion of an A in the fifth position.

The third condition is that homologous characters should be ascertained unambiguously. The problem of homology in molecular analyses can be solved by a genealogy problematic: parts of two paralogous genes, and the sequence of

large number of unlinked sequences to decrease the relative weight of each mistaken homology. No such simple protocol exists for morphological characters.

The fourth condition is that the probability with which a character state changes into another should be calculable, at least roughly. The existing quantitative knowledge on the dynamics of change of a genetic character enables us to deduce how frequently such a change is likely to occur during a given period, and, hence, we can estimate the probability for convergent or backward changes to occur. In contrast, detailed knowledge on the dynamics of change of morphological characters is mostly lacking.

The fifth condition is that the characters should be phylogenetically robust – their phylogenetic usefulness should not be lost too rapidly the more distant the taxa are from each other. Morphological characters are not very robust. Therefore, as far as distant phylogenetic relationships are concerned, there are almost no morphological characters that can be used. In contrast, all organisms possess in common ribosomal RNAs, and a large but of equivocal and structural proteins. By choosing suitable DNA segments, one can tackle higher order phylogenies almost as easily as tackling phylogenetic relationships among closely related organisms[*]. Segments that evolve fast may be used for resolving recent divergence events, whereas slowly evolving segments are useful for resolving distant relationships. Different DNA segments have different 'toolkit times'[*], i.e. a segment of DNA can be used to infer speciation events that are neither more recent nor more ancient than the 'window of opportunity' afforded by its characteristic rate of evolution. Interestingly, most nuclear protein-coding genes evolve at rates that are particularly suitable for resolving the phylogenetic relationships among mammalian orders, which have presumably diverged from one another from 120 million years ago to about 25 million years ago. As far as mitochondrial sequences are concerned, their transmission occur at a low orders at a time.

Finally, one should be able to increase the number of characters in the sample size to achieve the desired topological resolution. DNA sequences does meet this requirement because they can potentially supply millions of phylogenetically useful characters. While it may be correct that the 'morphological arsenal' has not yet been depleted[*], 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. One should note that even the 'best' molecular phylogenetic trees today rely on a mere 0.00002% of the potential data.

Molecular phylogenies of mammalian orders – comprehensive window?

The use of molecular traits in phylogenetic reconstructions began as far back as the early part of the century with a study by Nuttall[*], who used serological cross-reactions to demonstrate that man's closest relatives were the African apes, followed in order of relatedness by the Old World monkeys, the New World monkeys, and the prosimians. Molecular phylogenetic reconstructions of eutherian orders fall into two categories: comprehensive and partial. Comprehensive phylogenetic studies attempt to reconstruct the evolutionary relationships among all or at least the vast majority of orders. Partial studies concern themselves with only a few orders at a time.

One of the first comprehensive molecular phylogenies was proposed by Miyamoto and Goodman[*]. More recently, Goodman and his colleagues published an update[*] (Fig. 2). Their phylogenetic reconstruction was based on a maximum of eight polypeptide sequences: α-, β- and embryonic α-haemoglobin chains, myoglobin, α-crystallin A chain, cytochrome c, pancreatic ribonuclease and fibrinopeptides A or B, and their taxonomic sampling consisted of 107 species. Their tree contains a hexafurcation and a trifurcation; five binary clades were identified: Pholidota + Carnivora, Eulipotyphla + Lagomorpha, Cetacea + Artiodactyla, Hyracoidea + Proboscidea and Cetacea/Artiodactyla + Perissodactyla. In addition, four major superordinal
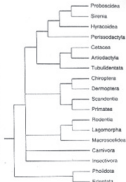

Fig. 1. Phylogenetic relationships among 18 eutherian orders based on morphological data as proposed by Novacek[*]. Note that the tree is binary, containing essentially two major supraordinal clusters, a small one consisting of the Carnivora and the Pholidota, and a large one consisting of all the other eutherian orders.

Lineages are recognized: Glires/ Theriodictae (Rodentia, Lagomorpha, Primates, Dermoptera, Scandentia), Ungulata (Artiodactyla, Cetacea and Perissodactyla), Paenungulata (Hyracoidea, Proboscidea, Sirenia and Tubulidentata) and Edentata
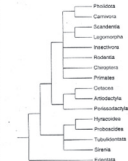

Fig. 2. A comprehensive molecular phylogenetic tree depicting the relationships among 18 eutherian orders, after Czelusniak et al.[*]. Note that the tree is not binary, and it contains a hexafurcation and a trifurcation.

(consisting of a single order). As opposed to their previous study[9], ... Theridoidea could not be distinguished from each other. None also that the morphological tree and the molecular one (Fig. 1, 3) have little in common.

How much confidence should we have in these conclusions about molecular phylogenies? Wyss et al.[9] claimed that the degree of confidence that can be placed on such taxonomies is rather low. They found very low consistency indices for both morphological and molecular cladograms, with no evidence for any significant advantage of one method over the other.

Despite several methodological problems, Wyss et al.'s conclusion is essentially correct. Comprehensive molecular phylogenies of mammalian orders are at the present time notoriously unreliable. The main reason for this state of affairs is that not enough homologous genes are available from a sufficient number of euthenian species to resolve the phylogenetic relationships among all the euthenian orders. To date, all attempts to reconstruct the evolutionary affinities among all euthenian orders contain not even one gene that has been sequenced in all the orders, and many interordinal comparisons

are based on a single polypeptide. Researchers who attempt to reconstruct a phylogenetic tree for all the recognized euthenian orders on the basis of currently available molecular data are making too big a meal out of too small a bite.

Therefore, until sufficient molecular data are available, the range of orders for which phylogenetic relationships are usually should be severely restricted. In other words, one should only deal with a few orders at a time, and seek to resolve only parts of the mammalian tree.

Molecular phylogenies of mammalian orders – partial solutions

Partial phylogenetic solution for the mammalian higher 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 into a single phylogeny is not always possible. For example, let us assume that, based on a set of data, we have come to the conclusion that rodents are closer to primates than they are to artiodactyls, and that based on a second set of data, we concluded that rodents are closer to chiropterans than they are to carnivores. From these two studies we cannot say whether rodents are more closely related to primates or to chiropterans. We can, however, conclude that it is unlikely that the rodents are an outgroup for primates, chiropterans, carnivores and artiodactyls.

There are essentially two types of partial phylogenetic studies in mammals. 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, it has become very easy to sequence homologous genes from many species, and the number of single gene phylogenies in the literature is growing exponentially. The degree of confidence that one can place on any supraordinal 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 tree and that supporting the
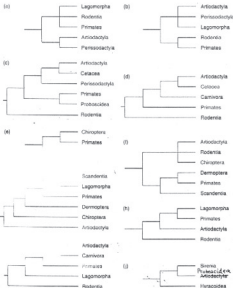
Fig. 1. Partial molecular cladograms of eutherian orders. [Adapted from (a) Hewett-Emmett et al.[38], (b) Nauratzov et al.[?], (c) Irwin et al.[44] and Arnason et al.[45], (d) Arnason and Johnsson[?], (e) Miyamoto et al.[?], (f) Adkins and Honeycutt[?], (g) Bailey et al.[?], (h) Czelusniak[?], (i) Li et al.[?], and (j) Shoshani[?].]
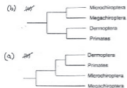
Fig. 4. Phylogenetic relationships among Megachiroptera, Microchiroptera, Dermoptera, and Primates according to (a) Archonta [a,b] [morphological data] and (b) Miodetti et al. [c] and Adkins and Honeycutt [d] [mitochondrial DNA data and Bailey et al. [e] nuclear DNA data.
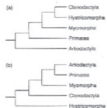

Fig. 5. Phylogenetic relationships among primates, artiodactyls and rodents. (a) Classical taxonomy regards the Rodentia as a monophyletic taxon. (b) Molecular data indicate that the order Rodentia is paraphyletic. Adapted from Graur et al. [f].

and Macroscelidea are still awaiting investigation at the molecular level.

In summary, I concur with Czelusniak et al.[a] that the final verdict is not yet in, but there is no doubt that mammalogists are in for some big surprises in far as the higher classification of mammals is concerned.

Questions of monophyly

As mentioned at the beginning of this article, the higher 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 the class Mammalia and of the subclass Eutheria[a]. For instance, the monophylies of Lagomorpha, Perissodactyla, Primates, Chiroptera and Cetacea have been confirmed by molecular data[a,b]. In reviewing case, molecular studies have involves Cetacea. Its monophyletic status has been

questioned on the basis of morphological features related to the visual nasal pathways[a,b]. It has been claimed that the Megachiroptera (fruit-eating bats) are more closely related to primates than to the Microchiroptera (insect-eating bats) and, therefore, that flying emerged twice during the evolution of mammals. Molecular analyses involving both nuclear and mitochondrial sequences, on the other hand, have overwhelmingly confirmed the strict monophyly of this order[a,b] (Fig. 4).

There are, however, cases in which the monophyly of a mammalian order came under molecular fire. In one such instance, the possibility that the order Rodentia is paraphyletic has been raised[a,b]. Based on comparisons of protein sequences, Graur et al. found that the guinea pig (Cavia porcellus), which is a hystricomorph exhibiting numerous anatomical and biochemical peculiarities[c], is not related evolutionarily to the myomorph rodents. Rather, mice and rats (myomorphs) are more closely related to humans and monkeys (primates), and to pigs, camels and cows (artiodactyls), than they are to the guinea pig (Fig. 5). In fact, the guinea pig probably represents one of the most ancient branches in the evolutionary history of eutherian mammals. Therefore, the lineage represented by the guinea pig and their Old World relatives, the porcupines (Hystricomorpha), should be posited an independent ordinal status within the class Mammalia. A later analysis of 125 ribosomal RNA sequences from the mitochondria added support for the disassembly of the Rodentia[d]. The bootstrap probability for the maximum parsimony tree in which the Rodentia are paraphyletic is 0.5% (Ref. d), whereas three maximum likelihood analyses failed to distinguish between the alternative phylogenetic trees. A similar, albeit more tentative, conclusion has been reached for the guinea (Chonolophine point, an enigmatic North African rodent that has no known extinct or extant relatives[e]. The Rodentia seem, therefore, destined to join the burgeoning ranks of the classical taxa that have been recently deprived of their validity (see Box 1).

- In a second instance, the redefi-

nition of the order Artiodactyla has been suggested by the molecular evidence (Graur and Higgins, unpublished). On the basis of amino acid and nucleotide sequences, it has been shown that the Cetacea are deeply nested within the artiodactyl tree. That is, the Cetacea seem to be a sister group of one suborder of artiodactyls, the Ruminantia (e.g. elk, deer, giraffes, cows, goats, sheep and chevrotains) 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 Artiodactyla. Complementarily, the definition of the Artiodactyla should be modified to include the Cetacea.

The future: as assessment of a proposal
Will molecular traits replace morphology in the main tool of taxonomy and phylogeny in the future? They may, but such an event would have undesirable consequences. A more fruitful venue would be to utilize both morphological and molecular data in a phylogenetically meaningful manner, so that we may gain insights into the process of evolution at both levels. One of the major advantages of morphological data in an evolutionary context is the apparance of their dynamics of change. We do not know how often a certain character arises in evolution, and hence we have no way of judging whether the extent of homoplasy in an inferred tree is reasonable or not. Therefore, I suggest that whenever possible, phylogenetic cladograms derived from molecular data be used as ad hoc true trees (in which morphological characters could be imposed). By so doing, we will be able to deduce whether many morphological characters are derived in primitive, the frequency with which a character state changes along a given evolutionary lineage, and the degree of homoplasy that is expected for a given trait.

In essence, I suggest using molecular data as the basis for the characterization of the dynamics of morphological changes in evolution. As a consequence, several morphological attributes may mean the conditions necessary for a charac-

ter to be of use in phylogenetic reconstructions. In the distant molecular future, the extreme paradox may arise in which molecular phylogeny may turn out to be the only means through which morphology may retain its scientific value in taxonomy.

References

1 Penascek, M.J., Wyss, A.R. and Novacek, M.J. (1988) in The Phylogeny and Classification of the Tetrapods (Benton, M.J., ed.), pp. 1–31, Clarendon
2 Simpson, G.C. (1945) Bull. Am. Mus. Nat. Hist. 85, 1–350
3 Needham, J. (1986) Mol. Biol. Evol. 3, 225–342
4 Li, W-H. and Graur, S. (1991) Fundamentals of Molecular Evolution, Sinauer
5 Gregory, W.K. (1910) Bull. Am. Mus. Nat. Hist. 27, 1–524
6 McKenna, M.C. (1975) in Phylogeny of the Primates: A Multidisciplinary Approach (Luckett, W.P. and Szalay, F.S., eds), pp. 21–46, Plenum
7 Novacek, M.J. (1982) in Macromolecular Sequences in Systematic and Evolutionary Biology (Goodman, M., ed.), pp. 3–41, Plenum
8 Novacek, M.J. and Wyss, A.R. (1986) Cladistics 2, 257–287

10 Novacek, M.J. (1992) Nature 356, 121–125
11 Simpson, G.C. (1978) Proc. Am. Philos. Soc. 112, 318–328
12 Raetsch, A. and Boeckmann, S. (1992) Nucleic Acids Res. 20, 2019–2022
13 Higgins, D.G., Fuchs, R., Soppitz, P.J. and Cameron, G.N. (1991) Nucleic Acids Res. 19, 6023–6024
14 Smith, A.B. (1992) Trends Ecol. Evol. 7, 224–229
15 Sytsma, M.J. (1990) Trends Ecol. Evol. 5, 104–110
16 Gojo, M.W., Ladengen, R., Albert, V. and Zurkoff, D. (1989) Proc. Natl Acad. Sci. USA 86, 6201–6205
17 Wiener, C.R. (1987) Mol. Biol. Evol. 4, 105–122
18 Ortolani, R.E. (1987) Off JNRN and OKFL: incorrectly Science Books
19 Rudolph, G.D-T. (1984) Blood Immunity and Phylogenetic Relationships of Mammals, Princeton
20 Miyamoto, M.M. and Cracraft, J. (1990) eds Phylogenetic Analysis of DNA Sequences, Oxford
21 Penascek, J.P. (1989) Blood Diseases and Phylogeny, University Park Press
22 Cartmill, J. et al. (1986) Curr. Anthropol. 27, 199–237
23 Hennig, W. (1966) Phylogenetic Systematics, University of Illinois Press
24 Teglas, R.L., Hewett-Emmett, D., Strouss, W.T. and Templeton, A.R. (1991) in Kinship and Behavior in Primates (Else, J. and Lee, P.C., eds), pp. 19–32, Cambridge University Press
25 Felsenstein, J. (1985) Evolution 39, 783–791
26 Teglas, R.L., Rawlins, R.G., Hewett-Emmett, D. and Sarich, V. (1991) in Biochemical and Physiology of Certain Disorder (Bauer, C., Case, G. and Slenzka, H., eds), pp. 169–176, Springer-Verlag
27 Simpson, G.C. (1959) Am. J. Hum. Genet. 11, 144–157
28 Inawi, E., Edjker, T.D. and Williams, D.L.

(1991) J. Mol. Evol. 33, 126–144
29 Armason, U., Gullberg, A. and Widegren, B. (1991) Mol. Biol. Evol. 8, 556–568
39 Arnason, U. and Johnsson, S. (1992) J. Mol. Evol. 34, 493–505
31 Westell, D.P., Dick, C.W. and Baker, R.J. (1991) Proc. Natl Acad. Sci. USA 88, 10522–10526
32 Adkins, R.M. and Honeycutt, R.L. (1991) Proc. Natl Acad. Sci. USA 88, 10317–10321
33 Ruvro, W.J., Stevenson, J.L. and Goodman, M. (1991) Science 21, 124–129
34 Sanwal, S. (1992) Cancer Lett. 33, 396–99
35 Preola, G., Silvas, E., Mignano, P. and Saccone, C. (1991) J. Mol. Evol. 33, 142–143
36 Saccone, C., Lanave, G., Pesole, G. and Preold, G. (1990) Methods Enzymol. 183, 570–583
37 Shoshani, J. (1991) Am. J. Zool. 36, 335–344
38 De Jong, W.W. (1985) Mol. Biol. Evol. 2, 484–493
39 Pettigrew, J.D. (1986) Science 231, 1304–1306
40 Pettigrew, J.D. (1991) Syst. Zool. 40, 199–216
41 Graur, D., Hide, W.A. and Li, W-H. (1991) Nature 351, 649–652
42 Graur, D., Hide, W.A., Zharkikh, A. and Li, W-H. (1992) Comp. Biochem. Physiol. 101B, 495–496
43 Li, W-H., Hide, W.A., Zharkikh, A., Ma, D-P. and Graur, D. (1992) J. Hered. 83, 174–181
44 Li, W-H., Hide, W.A. and Graur, D. (1992) Nature 359, 277–278
45 Walton, J.A. (1992) Nature 359, 277–278
46 Winkler, L.E. (1984) Comp. Biochem. Physiol. 79B, 271–274
47 Bennett, S.L. and Honeycutt, R.L. (1990) Mol. Phylogenet. Evol. and Kingsdon, J. (1984) Ann. NY Acad. Sci. 403, 41–95
48 Swofford, D.L. and Olsen, G.J. (1990) in Molecular Systematics (Hillis, D.M. and Moritz, C., eds), pp. 411–501, Sinauer
49 De Jong, W.W. (1982) Trends Biochem. Sci. 7, 185–188
50 Baker, R.J., Honeycutt, R.L. and Van Den Bussche, R.A. (1992) Bull. Am. Mus. Nat. Hist. (in press)

Plant Senescence in Fire-prone Perennials

In his review on plant senescence, Watkinson[1] wondered how common it was for fire-sensitive species to have high levels of fruit production confined to their first few flowering seasons. This pattern is only convincingly documented for some legumes with long-lived (hard) seeds[2,3]. The seeds are released at maturity, but may survive beyond the next fire (although usually stimulated to germinate by that fire) and even beyond the normal lifespan for that species. Where fire intervals are fitful, it makes adaptive sense for fire-sensitive, hard-seeded species to flower and fruit precociously in the early years, taking advantage of the enforced levels of nutrients, water and light in the few years after fire.

In contrast, escalating seed production over time occurs in many other fire-killed trees and shrubs[4,5]. This pattern occurs in species whose seeds are

seeds are shorter lived than the evolutionarily significant fire intervals, with the seeds released at maturity or held in the canopy until (near) release is stimulated by fire[?]. On the other hand, many fire-tolerant resprouters, usually muricoid, also flower and fruit best immediately after burn[?]. These have short- or long-lived seeds. Since there is both reproductive and vegetative invigoration after fire, the post-reproductive phase is one of reduced fecundity which should decline to dormancy (until the next fire). Since most resprouters rarely from fire. Some resprouters remedy senescence[?] while others do so as the (second) senescence many years after fire.[4] As Watkinson notes, senescence is indeed a confusing word

References

1 Watkinson, A. (1992) Trends Ecol. Evol. 7, 417–420
2 Moore, D., Pate, J.S. and Loneragan, W.A. (1991) Aust. J. Bot. 39, 89–102
3 Auld, T.P. and Myerscough, P.J. (1986) Aust. J. Ecol. 11, 219–234
4 Hansen, A., Pate, J.S. and Hansen, A.P. (1991) Oecologia 87, 194–200
5 Lamont, B.B. (1985) Acta Oecol. 6, 341–345
6 Lamont, B.B. and Barker, M.J. (1988) Bot. Gaz. 149, 370–375
7 Bradstock, R.A. and Myerscough, P.J. (1981) Aust. J. Bot. 29, 521–531
8 Lamont, B.B. (1976) Biol. Rev. 51, 385–395
9 Lamont, B.B., Le Maitre, D.C., Cowling, R.M. and Enright, N.J. (1991) Bot. Rev. 57, 277–317
10 Lamont, B. and Downes, S. (1979) Nature 279, 527–529
11 Lamont, B.B. (1985) Aust. J. Bot. 33, 199–217

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