

PROBLEMS OF CLASSIFICATION AS APPLIED TO THE RODENTIA

by

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ABSTRACT

A classification should be both usable and useful, not too complex either in the amount of splitting or in the number of hierarchies involved, and not so simple as to give a false assurance of knowledge of relationships. Classifications are only possible because we do not have complete knowledge of the evolution of the organisms concerned, because gaps in the record are necessary to allow the separation of the various taxa. Rodent classification is complicated by the large number of organisms involved and by the great amount of parallelism that has taken place in the evolution of any and all features. If several independent features are characteristic of a certain taxon, should an effort be made to define the group on the basis of all the features, or should only one be selected as *the* determinant? Unless the evolution of the several features was closely linked, the former solution will sooner or later lead to insurmountable problems.

A classification is a formal arrangement that expresses the author's opinion of the relationships of the organisms concerned. It should be an attempt to approximate the actual genetic relationships existing, or that formerly existed, among the pertinent organisms. During the course of organizing a classification of the mammalian Order Rodentia, I encountered a number of problems of a general nature, some of which are discussed below.

Usually, there are extensive gaps in our knowledge of organisms, particularly of fossil ones. These are useful in classification, because we use the gaps to delimit the various units being classified. As our knowledge increases, many gaps become smaller and smaller, producing problems of how to draw the boundaries in our classification. If we knew all the organisms that ever lived, no one would be able to draw any « natural » boundaries between taxa of any size. We are a long way from having such extensive

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knowledge, but occasionally we approach such a state in limited areas, and these occurrences result in marked disagreements as to how to classify the organisms concerned.

With complete knowledge, the only way to separate taxa of organisms would be by placing all those that were buried before a certain instant of time in one taxon, and those buried later in another. This not only might result in separating parents from offspring, or siblings from each other, but might even separate growth stages of the various parts of a single individual. However, this is still only a theoretical and not a practical problem.

There is no way, so far as I am aware, to prepare a meaningful classification that does not include a very large subjective element — the feeling as to the weight to be given various characters and as to the relationships of the organisms on the part of the person who is preparing the classification. How close these subjective results come to expressing the actual genetic relationship that once occurred among the organisms concerned depends, among other things, on the ability, knowledge and general awareness of the person preparing the classification, as well as on the state of knowledge of the organisms, both fossil and Recent, of their morphology, ontogeny, physiology, ecology, *et al.*, that is available at the time of the preparation of the classification.

There have been attempts to reduce the amount of this subjectivity by mathematical means, but, since there is no non-subjective method of defining a unit character, these methods offer only a pseudo-accuracy that does not really exist. A mathematical approach would increase the reliability of the classification only if we knew which genes were producing each and every recognizable character, and if the organisms were then classified on the basis of the sum total of their genes. Whether such a classification would be more or less useful than one based on the Linnaean method is unknown.

Two important aspects of a classification are (or should be) that it is both usable and useful. A classification should include all the levels of the hierarchy that are meaningful in the frame of reference of the proposed classification, but there is no reason to include intermediate levels that serve no useful purpose. There is a current fad to establish a new taxonomic level at every point in the history of life where a split occurred (*e.g.*, McKenna, 1975). From the point of view of pure logic, this *may* make sense. From the point of view of preparing a useful classification, it most certainly does not. If we had a complete set of historical data, I think that we might well find that there had been many thousand such splits, *seriatim*, in the history of any modern taxon of rodents. Even the recognition of such a situation, let alone its formalization in taxonomic terms, becomes thoroughly confusing.

For example, *if* it should turn out that the classification of the rodents is best expressed as several large groups, subdivided into Suborders, Infraorders, Superfamilies and Families, but with a number of other, less successful and diversified but nevertheless long-lasting groups, that do not require categories at the superfamilial or infraordinal level, it does not seem advisable, to me, to create such terms for these groups, merely to have a complete classification (*cf.* Thaler, 1966, table 1). As an example, I

believe that the Family Pedetidae, currently restricted to Africa and known from a single living genus with a single living species, has had a long independent history. The family is also represented by two Miocene genera, each with but a single described species. Although the Pedetidae fit into the Suborder Sciurognathi, none of the known genera shows any evidence of relationship to any other sciurognaths at the suprafamilial or infraordinal level, so that their union with any other sciurognaths is unwarranted. However, at the present time, the establishment of a Superfamily Pedetoidea and an Infraorder Pedetomorpha, to demonstrate such a separation, would not add to our understanding of the evolution and relationships of the pedetids, and would not provide taxa that would have any conceivable utility except that of providing a complete set of taxonomic terms, useful or otherwise, for every taxon. Creating such terms, of course, does provide a measure of immortality for the perpetrator of the names. I therefore leave the Pedetidae as a sciurognath family, *incertae sedis*, which is the best description of our present knowledge of its evolutionary position.

Situations may arise where two or more radiating lines, that have already diverged in features that are, *e.g.*, of specific value, are in the initial stages of giving rise to two or more higher-level divergent descendant lines. But, if these ancestral forms are sufficiently closely related so that a contemporary taxonomist would have united them at the generic level, should we not do so, even though their descendants diverged? This problem faced me many years ago in studying the evolution of the Heteromyidae, when I suggested (Wood, 1939, p. 560) that different species of the Oligocene genus *Heliscomys* should be referred to the various Miocene to Recent subfamilies to which I thought the species to be ancestral. This action has generally been ignored, although Simpson (1945, p. 81, footnote) described it as « an arrangement less fantastic than it appears at first sight, but still quite unacceptable. » It is worth stressing that, assuming the correctness of my belief that three species of *Heliscomys* were ancestral to three modern subfamilies, there is no way of preparing a classification that does not draw arbitrary lines between closely related forms, either ancestors and descendants or closely related species. There is clearly no justification for placing the three species of *Heliscomys* in separate genera. Placing three species of a single genus in three subfamilies at least calls attention to the fact that this is an unusual situation, requiring an unusual solution.

In the case just described, the three species of *Heliscomys* were placed in the descendant subfamilies because the subfamilial features were already being developed. A similar problem arose to plague me in connection with the evolution of the Eocene rodents that I (Wood, 1962) included in the Family Paramyidae. In that paper, I recognized that some members of this group, the Subfamily Reithroparamyinae, were incipiently hystricognathous (Wood, 1962, pp. 117, 122, figs 41E, 46B, 48D). This hystricognathy is undoubtedly present, even though clearly only incipiently so (Dawson, 1977, p. 197, footnote). If, as I now believe, these animals were structurally (and possibly even genetically) ancestral to some or all of the Oligocene to Recent Hystrico-

gnathi, should the Subfamily Reithroparamyinae be included in the Suborder Hystricognathi ? When I recognized the importance and unity of the North American Eocene hystricognaths by erecting an Infraorder Franimorpha, I suggested (Wood, 1975, p. 78) that there was justification for separating the Reithroparamyinae from the other paramyids at the subordinal and infraordinal levels, but not at the family level, and I therefore divided the Family Paramyidae between two suborders. This seemed (and still seems) eminently reasonable to me ; the Reithroparamyinae had developed features that later became further emphasized to become diagnostic at the subordinal level in their descendants, but they had not yet differentiated enough from the other paramyids (*sensu* Wood, 1962) so that a contemporary taxonomist would have considered them a distinct family. I have been persuaded that such an arrangement, whether or not it is reasonable, would be unacceptable to other taxonomists, and hence I am, elsewhere, reluctantly recognizing a Family Reithroparamyidae, although I am still uncertain as to what might be its *familial* characteristics.

These two examples are illustrations of an important, but unsolved, problem that is usually merely ignored. This is : does a higher taxonomic level arise before, after, or at the same time as a lower one ? Is one situation as likely to occur as another ? For example, does all evolution involve the differentiation of species, genera, families, superfamilies, infraorders and suborders in that sequence, or can the individual categories originate in any sequence that happens to occur ? Modern evolutionary theory would have it that speciation is the initial stage in evolutionary divergence. But is there any reason to believe that the specific characters that separate one population from another are more likely to be those that later are considered to be of generic importance, rather than those later given subordinal weight ? The answer, of course, is « yes », merely because the evolution of new genera is much more frequent than the evolution of new suborders. In any individual instance, however, one can only say that the situation that has developed, did develop.

The problems involved in the classification of rodents are more complex than those in any other order of mammals. At the present time, perhaps half the species of living mammals are rodents. The order has been abundant and highly successful for much of the Cenozoic. Because of the initial evolutionary developments that established them as rodents (the evolution of elongate, ever-growing incisors with the enamel restricted to the anterior face ; the development of a glenoid cavity and associated jaw muscles that permitted the anteroposterior motion of the lower jaw and the use either of the cheek teeth or of the incisors, but not of both at once ; and the shortening of the effective tooth row by the reduction of the tooth formula to a maximum of I1/1 P2/1 M3/3), the subsequent evolution of members of the order was limited to those changes that took place in directions predetermined by these initial changes. Because the rodents became very successful and numerous and invaded a variety of physical habitats in all parts of the world, there were many different species evolving in the same general directions and being acted upon by rather similar selective pressures. Be-

cause, in addition, there was a considerable amount of common genetic background, the rodents have developed an amount of parallelism that is without comparison among the mammals, a fact not fully understood by specialists on other groups.

Parallelism is rampant in all aspects of rodent morphology (Wood, 1936 c), as, for example, in the development of hystricomorphy (Wood, 1974, p. 44 and table II ; 1975, pp. 75-77, fig. 1), but it most clearly seen in the evolution of cheek-tooth structures. There are, essentially, no features of rodent cheek-tooth morphology that have not developed independently two or more times. This is an easy fact to forget, and it is easy to conclude that similar cheek-tooth patterns are proof of relationship, rather than merely examples of parallelism. Most particularly, the five-crested cheek-tooth pattern has been interpreted as indicative of relationship wherever it occurs among the rodents, by paleontologists who were not only extremely competent, but also well acquainted with the order (Schlosser, 1884, pp. 98-108 ; Stehlin and Schaub, 1951, *e.g.*, p. 3 ; Schaub, 1953, pp. 389-400 ; 1958, pp. 684-694 ; Lavocat, 1976, pp. 84-86). Nevertheless, the evidence is extraordinarily strong that these authorities were wrong, and that the development of five-crested cheek teeth, with essentially identical end results, was an almost necessary result of selection for increased length of tooth-row (*i.e.*, increase in occlusal surface) in populations with a reduced dentition faced with abrasive food supplies. If this is correct, as I believe it to be, the presence of five-crested cheek teeth is *per se* no indication of relationship below the ordinal level. Certainly, the pentalo-phodont cheek teeth of the Cricetidae, Dipodoidea, Castoridae, Theridomyoidea and Hystricomorpha *must* have evolved independently of each other. It is probable that the same structures, when they appear in the Eomyidae and Anomaluridae, have also evolved independently. And, since the cheek-tooth pattern of the most primitive caviomorphs, Lavocat (1976) to the contrary notwithstanding, is *not* identical to that of the earliest phiomyids, it indicates to me that the similarities in tooth structure between the caviomorphs and phiomyids are no more than what might be expected from two lines derived independently from Eocene members of the Framimorpha.

Parallelism also appears in the development of separate evolutionary lines within closely related groups of rodents. Studies by Rensberger (1971, 1973 a, 1973 b) have shown that there were a number of distinct lines during the Miocene within what Wood (1936 a, p. 4-5) called the entoptychine geomyids. Rensberger has now raised these to subfamilial level. The rodents described by Wood (1936 b) as florentiamyine heteromyids may belong here as well (Rensberger, 1971, p. 151). These lines share heteromyid and geomyids features and, as a result, in the Miocene, the separation between the heteromyids and geomyids is blurred, and some authors (*e.g.*, Shotwell, 1967, p. 10) have suggested that the two families should therefore be united. However, the distinction between the modern forms is quite clear, and I believe that no useful purpose would be served by uniting the two families merely because the common ancestral stock and its immediate derivatives are difficult to allocate to one or the other of the modern families (Munthe, 1977, pp. 5-7). Nor are these intermediate groups of sufficient importance to

warrant their being elevated to family status. If the principle were adopted that the two families should be united merely because it is impossible to establish a clear distinction between them at the time they were originating, the advance of knowledge would ultimately require that all animals be placed in a single family. I therefore continue to separate the Heteromyidae and Geomyidae with some uncertainty as to the familial position of a few groups. I also feel that elevating all the lines discussed by Rensberger (1973 b) to subfamily status is unjustifiably inflating the taxonomy, and I therefore continue to divide the Geomyidae into the Geomyinae and the Entoptychinae, placing in the latter a series of tribes, including the Entoptychini, Pleurolicini, and probably the Florentiamyini.

The same question of how far to unite (or separate) taxa arises in the Muroidea. It seems highly probable that the Cricetidae, *sensu stricto*, gave rise, perhaps in the early Miocene, to the Muridae. This has not yet been demonstrated, but is the most reasonable interpretation of limited data (Jacobs, 1977, pp. 8-9). It is clear that, at a later date, another line split from the cricetid stock to become the microtines. This being the case, should all three groups be considered families, as is sometimes done; should they be allocated to the Families Cricetidae and Muridae (as I do); or should only one family be recognized (as is also sometimes done)? Assuming the accuracy of the evolutionary picture as I have just outlined it, any one of the three solutions would be logical. I believe, however, that uniting all these rodents in a single family would produce such a topheavy unit as to be unwieldy. Since the cricetid origin of the murids has not as yet been unequivocally demonstrated, I feel that this is a reasonable justification for me to continue to recognize two families as a combination of caution, conservatism and convenience. The acceptance of three families would, it seems to me, be a more useful procedure than their union into a single one.

The late Eocene to earliest Oligocene rodent *Simimys* provides an example of another type of problem. As demonstrated by Wilson (1949, pp. 22-24) and Lillegraven and Wilson (1975, pp. 871-873), *Simimys* combines features of the hystricomorphous Zapodidae and of the myomorphous Cricetidae. The cheek teeth of *Simimys*, however, are much too specialized to have given rise to those of the earliest known members of either the cricetids or the zapodids and dipodids (Wilson, 1949; Lillegraven and Wilson, 1975). Lindsay thought *Simimys*, which seems to have had a large, dipodoid-like infra-orbital foramen (*i.e.*, it was hystricomorphous) to have been ancestral to the myomorphous cricetids, apparently by way of such a form as *Cricetops* (Lindsay, 1977, pp. 604-607). It is possible that myomorphy arose from hystricomorphy, but it seems to me more probable that the presence of a hystricomorphous *Masseter medialis* would have prevented the forward growth of the *Masseter lateralis* to produce myomorphy, and I would strongly suspect that myomorphy arose by the *simultaneous* forward migration of the origins of both muscles. Whatever the actual relationships, *Simimys* could only have been ancestral to the Oligocene cricetids or to the Miocene dipodoids if there had been a pronounced secondary reversion of the cheek-tooth pattern to a more pri-

mitive appearing condition — an event of whose occurrence I am profoundly dubious. The best solution to the problem, it seems to me, is to recognize that *Simimys* is neither a cricetid nor a dipodoid, but, most probably, a precociously advanced member of whatever Eocene population gave rise to one or both of these other groups.

In preparing a classification, one selects certain features of the organisms concerned for emphasis. But should one use a single feature at each level of the classification, or try to combine all the features that characterize the group of organisms concerned? The former is the simpler system; the latter enables one to describe the organisms being classified with greater completeness. For example, as indicated above, rodents are characterized by possessing ever-growing incisors with the enamel limited to the anterior face, a dental formula reduced at least to I1/1 P2/1 M3/3, and a glenoid fossa that permits either the incisors or the cheek teeth to function, but not both at once. These are generally considered to be a related group of features, but did they originate at one time? I strongly suspect that they did not, and that one of them preceded and led to the acquisition of the others. The reduction of the dental formula is almost certainly secondary to the other two features, and evolved to improve the either-or gnawing-chewing mechanism. Increase in height of crown of the incisors surely preceded the modification of the glenoid fossa. But there is no way of determining, at present, whether restriction of the enamel to the anterior face of the incisor and the development of ever-growing incisors preceded, followed, or accompanied the glenoid modifications. If the three features developed at three different times, in the ultimate definition of the Rodentia, only one of these features should be used. For the present, this problem is not important, because the earliest known rodents already possessed all of these features, and no possible ancestors are known that possessed any one of them, to the exclusion of the others.

Within the Rodentia, however, this problem of the multiplicity of diagnostic features becomes vitally important. Lavocat (1973, pp. 167-172) and Wood (1975, p. 76), following Tullberg (1899), divided all rodents into two Suborders, the Sciurognathi and the Hystricognathi. Among other features, the modern members of the Hystricognathi have a hystricognathous angle (excepting the Caviidae and Hydrochoeridae); a hystricomorphous snout resulting from the forward movement of the origin of the *Masseter medialis* through (and enlarging) the infraorbital foramen, to arise from the premaxilla and maxilla; a pterygoid fossa that opens into the braincase; a postcondyloid process of the mandible for the insertion of the *Masseter lateralis profundus, pars posterior* (deep) (Woods, 1972, p. 127); fusion (in most forms) of the malleus and incus; multi-serial incisor enamel; and propalinal chewing (Wood, 1975, fig. 1; Landry, 1957).

Do these features represent a single functional complex that evolved together? Although we have no absolute proof on this point, I feel that the chances are exceedingly slim that, e.g., the fusion of the malleus and incus had anything functional to do with the forward expansion of the origin of the *Masseter medialis*. The lateral shift of

the angular process to produce hystricognathy is most probably to be interpreted as a method of increasing the length of the *Pterygoideus internus* (Woods, 1972, p. 131), which would increase the strength of the forward movement of the lower incisor in gnawing. The deepening of the pterygoid fossa helps to produce the same end result, acting on the origin of the muscle. Were these two changes taking place at the same time? We do not know, but the evidence suggests that they may not have been, and that the initial lateral shift of the angular process preceded the deepening of the pterygoid fossa (cf. the condition in the Eocene to Oligocene Cylindrodontidae, where hystricognathy of the angular process had been initiated, but there was no apparent deepening of the pterygoid fossa). Certainly hystricognathy and hystricomorphy are not temporally associated in their origins, as witness the numerous hystricomorphous sciurognaths and the protogomorphous but hystricognathous Bathyergomorphs.

Apparently hystricognathy arose before any of the other features that characterize the modern Hystricognathi. However, it did not spring into existence, as it occurs in modern hystricognaths, like *Athena*, full blown, but it first appeared as a very slight lateral shift of the angular process, which I have elsewhere (Wood, 1962, p. 122) referred to as being «incipiently hystricognath». This is a nuance that is visible, but so slight as to have led Dawson (1977, p. 197, footnote) to describe it as «a sciurognathous jaw, "incipient" only *a posteriori*.» She was correct; if full hystricognathy were not known, the slight hystricognathy of *Reithroparamys* would not be worthy of note. This condition of incipient hystricognathy characterizes most of the North American Eocene Infraorder Franimorpha, although some of the southern forms have become more hystricognathous. All of the described skulls of Eocene franimorphs are badly damaged in the region of the pterygoid and temporal fossae, which suggests the possibility of a weakness in this area that may have resulted from a deepening of the pterygoid fossa.

If the late Paleocene to Eocene franimorphs are hystricognaths, as I believe, it becomes evident that none of the other characteristics of modern hystricognaths listed above, except *possibly* the deepening of the pterygoid fossa, was initially associated with *hystricognathy*. We therefore are given one morphological feature, the lengthening of the *Pterygoideus internus*, as *the* diagnostic feature of the Hystricognathi, although this is expressed, osteologically, as the lateral shift of the angular process and, perhaps simultaneously, as the deepening of the pterygoid fossa.

The other features of the modern Hystricognathi, then, arose later, either in later members of the Franimorpha or as parallel trends within the other infraorders. For example, multiserial incisor enamel occurs in all caviomorphs, hystricomorphs and bathyergomorphs, as well as in the sciurognathous ctenodactylids and pedetids (Wahlert, 1968, pp. 16-17), but has not as yet been reported in any franimorph.

The development of hystricomorphy began within the Franimorpha. The late Eocene genus *Protoptychus* was clearly hystricomorphous (Wahlert, 1973, p. 7). Other Eocene genera had enlarged infraorbital foramina, whether or not the *Masseter medialis*

passed through them (cf. *Prolapsus* — Wood, 1977, p. 104). The earliest (early Oligocene) members of the African Phiomysidae and of the South American Caviomorpha were hystricomorphous although the infraorbital foramen of *Platypittamys* from Patagonia is very much smaller than that of other genera. Lavocat (1973, p. 168) considered that the universal enlargement of the foramen is one evidence of descent of the Caviomorpha from the Phiomysidae, but the equally notable presence of hystricomorphy in such sciurognaths as the Dipodoidea, Theridomyoidea, Anomaluridae, Ctenodactylidae and Pedetidae, which clearly had no special relationships to the Hystricognathi, and probably none to each other, should make it obvious that there is no reason why hystricomorphy may not have arisen independently several times in the hystricognaths as well as in the sciurognaths.

In summary, it seems clear to me that there has been a great deal of parallelism in rodent evolution, and that there are great portions of rodent history of which we are still profoundly ignorant. Furthermore, I believe that progress in unraveling the details of rodent history will be made more rapidly by making minimal assumptions as to potential long-range evolutionary trends, and concentrating on provable or nearly provable conclusions. As one example of what I am arguing against, Lavocat (1973, 1976) has proposed that the African phiomysids were ancestral to the South American caviomorphs. Whatever may have been true of the unknown Eocene ancestors of the phiomysids (which may or may not have lived in Africa), the known phiomysids could not have given rise to the caviomorphs. As another example, one author postulated that certain small rodents in a restricted area of southern California evolved from being members of the protrogomorphous Family Sciuravidae to being members of the sciuro-morphous Family Eomyidae, and then to the hystricomorphous *Simimys*, all during a short part of the late Eocene, and all this on the basis of isolated cheek teeth ! (Lindsay, 1968, p. 12).

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