

CHAPTER 3A SHORT HISTORY OF THE TAXONOMY OF
THE BATHYERGIDAE

Although it is not the intention of this work to attempt solving phylogenetic problems and other aspects on supergeneric rank of the bathyergids, it should serve a useful purpose to give the reader a short review of the history of classification of the bathyergids.

Wood (1955, 165) states that the current classification of the rodents is inadequate and that there are two general philosophies underlying the current classification:

- (i) A theoretical ideal, in which the classification should reflect interrelationships of the animals involved and this implies the use of various criteria which are not agreed upon by all authorities on the animals concerned. Consequently, forms of uncertain relationship are either grouped together and assigned to a position in a classification in a more or less arbitrary manner, or they are indicated as incertae sedis. The latter point of view has been advocated by Simpson (1945).
- (ii) The other alternative is a classification involving the use of key characters resulting in a system based on different criteria into which all the different forms can fit. This approach has been used extensively by Ellerman (1940). According

to/...

to Wood (op.cit.) this solves the problem as to where to place all the various families of rodents, but leaves many of them in positions that do not seem to be correct from a phylogenetic point of view.

An obvious deficiency concerning the evolution of rodents in general is the dearth of paleontological data, especially with a sharp break in rodent history at the Eocene-Oligocene boundary. Wood maintains (quite rightly) that this situation still holds, particularly for African rodents where the fossil history of rodents is poorly known (see de Graaff, 1961, 191). As a result of his detailed paleontological work, Wood stresses the fact that parallelism in rodents extends to the structure of the infraorbital region as well as to the teeth and these results indicate that the whole basis of rodent classification must be derived and that no classification based on key characters "is likely to agree with one based on the phylogeny of the order" (p.166). It is his opinion that one is not to rely on morphological criteria alone until it has been demonstrated by phylogenetic studies to be valid. In Wood's proposed classification he stresses the occurrence and development of similar physical features independently in diverse and geographically isolated groups of rodents. In a later paper (1958), Wood even poses the question "are there rodent suborders?" and this question has also been discussed by various other authorities, e.g. Kretzoi (1943). The latter author divides the rodents in but two suborders while at the other extreme the order is divided into seven suborders (Wood, 1955) which could perhaps/...

perhaps be increased to as many as eleven, according to a suggestion by Lavocat (1956, 52-53).

If this is the current overall position of the supergeneric ranks of the rodents (for further details the reader is referred to some of the papers quoted above), it is clear that the correct systematic position of the bathyergids is also still far from finalized.

A brief discussion on the history of classification concerning the bathyergids can be found in Landry (1957, 65). These aspects are elaborated upon to a certain extent in the present work.

The mole-rats were listed as a subfamily under the Muridae (Myomorpha) in 1838 by Waterhouse (Landry, op.cit.) while in 1855 Brandt first proposed the subdivision of the simplicidentate rodents into the three classical suborders ("waste-paper baskets", Ellerman, 1940, 8). This subdivision into Sciuromorpha, Myomorpha and Hystricomorpha was based on the structure of the masseter muscle. This system has also been called the "classical" arrangement by Simpson (1945). Brandt names the bathyergids Spalaces subhystriciformes (Landry, 1957, 66) and as Waterhouse has done in 1838, Brandt also placed them under the myomorphs.

Alston (1876) largely followed this classification of Brandt but merged the bathyergids with the spalacids in a single family, also under the Myomorpha.

In 1887 (and also 1924) Winge placed the mole-rats as a subfamily (tribe) Bathyergini under the Hystricidae (Hystricomorpha) (Landry, 1957, 66).

Ellerman (1940, 21) feels that Winge's classification of the Hystricidae is unnatural "... with the inclusion of the Bathyergidae". As a basis for his classification, Winge used the structure of the paroccipital process, which to Ellerman seems to be a very variable character "even within a genus". Winge also appreciated the virtual impossibility of dividing the rodents into three or four groups "with any likelihood of the arrangement being correct" (Wood, 1955, 168), and so split them into nine groups (Ellerman, op.cit.) attempting to avoid the difficulties of the classical approach (Wood, op.cit.).

Thomas (1896) again placed the bathyergids under the myomorphs (as Waterhouse, Brandt and Alston have done previously) "but divorced them from the spalacids" (Landry, 1957, 66), where they were provisionally placed by Alston. Landry also states that although Waterhouse, Brandt and Alston recognised the hystricognathid jaws of the bathyergids, they were more impressed "by habitus resemblances of these forms to other burrowing rodents and also by the fact that the tibia and fibula of the bathyergids are fused distally as in the myomorphs" (p. 66). These facts presumably also prompted Thomas to place them under the myomorphs. According to Ellerman (1940, 7), "this classification is admittedly nothing more than a rearrangement of an earlier classification of Alston".

Landry (1957, 66) states that Tullberg (1899) was the first to amass considerable evidence in favour of placing the bathyergids with the hystricomorphs. Apart from Winge's interpretation (1887) it is clear that this is definitely the case.

Tullberg/...

Tullberg also felt that the classical threefold arrangement of the rodent order was not correct and he classified the rodents on a different basis to that of Alston or Thomas. He split the rodents into two major groups, the Sciurognathi and Hystricognathi based on the inflection or lack of inflection of the angle of the lower jaw and these subdivisions were again divided into the Sciuiromorphi and Myomorphi on the one hand and the Hystricomorphi and Bathyergomorphi on the other. According to Wood (1955, 167), this division of Tullberg was based on the structure of the infraorbital foramen and the masseter muscle.

The Bathyergomorphi thus formed a sub-tribe of the tribe Hystricognathi. It is Ellerman's (1940) opinion that this is perhaps the best classification of the order that has hitherto been done. Landry, (op.cit. p. 66) mentions the fact that Tullberg was the first person to provide sound evidence for placing the bathyergids with the hystricomorphs, for it "was he who pointed out that these forms possess in common such important features as the fused malleus and incus, the sacculus urethralis, the extention of the internal pterygoid muscles through the pterygoid fossa into the orbit, as well as the hystricognath jaw."

The next classification to be taken into consideration was the one proposed by Weber (1904 and also 1928). In this case, the bathyergids are listed as a separate group, the "tribus" Bathyergoidea. Ellerman (1940, 13) finds that as far as the superfamily grouping is concerned, this classification is quite acceptable. However, Weber indicates no closer/...

closer affinities or possible relationships of the bathyergids with any other rodents.

Weber's classification was followed by the scheme proposed by Miller and Gidley (1918) who again abandoned the classical triple subdivision and divided the rodent order into five superfamilies, based on the zygo-masseteric structure. The mole-rats are credited with superfamily rank, the Bathyergoidae, equal in rank to the other four superfamilies (i.e. Sciuroidae, Muroidae, Dipodoidae and Hystricoidae). Ellerman (p. 17) states that this classification attends much more to detail characters than either those of Winge or Weber. As was the case in Weber's classification, these authors also refrained from indicating possible affinities for the bathyergids.

In his well known Checklist of African mammals, Allen (1939) treated the bathyergids as a separate family.

Ellerman (1940) attempted to combine as far as possible various morphological criteria which appeared (to him) to be correct in the classifications of Thomas, Tullberg, Weber, Miller and Gidley and finally Winge, although he followed Tullberg in his major groupings. In this way, the bathyergids are interpreted as a major subdivision (Bathyergomorph series) of the Hystricognathi coordinate with the Hystricomorph series (p. 23).

Simpson (1945) again classified the rodents according to the Brandtian three-fold scheme and he placed the bathyergids incertae sedis within the hystricomorphs (p. 99). This authority states that although these animals are fairly abundant and quite well/...

well known, there are few more doubtful points of classification than the affinities of the bathyergids. However, he also says (p. 213) the following: "Everyone agrees that they are extraordinarily isolated among rodents, and those who commit themselves further agree that if they have any special, though distant, affinity it is with the hystricomorphs". (For further remarks on the supposed 'isolation' of these animals, see Chapter 5 in the present work).

Romer (1933, second edition 1945, Seventh Impression 1958, 501) is one of the few authors who place the bathyergids under the Sciuromorpha, and this is evidently based on the possible cylindrodontid nature of the Oligocene Mongolian fossils, Tsaganomys and Cyclomytus. (See Chapter 2 in the present work). (It is interesting to note that in the work done by Landry (1957, 66) he states, that as far as he was aware, no one has grouped the bathyergids with the sciuromorphs.) Romer included them under the sciurids "for want of any better place to put them" (Romer, 1958, 501), but that they "are sometimes associated, rather dubiously, with the hystricomorphs because they show an out-turned angular region of the lower jaw seen in characteristic members of that suborder". Romer states however that there are no other features suggesting such relationships and "... the diagnostic masseteric structures are of the primitive type seen only in the early sciuromorphs." This statement is however not borne out by the work done on these forms by both Tullberg (1899) and Landry (1957). Romer furthermore mentions the fact that these bathyergids are/...

are not closely related to any other group and they are placed as a superfamily Bathyergoidea within the suborder Sciuromorpha (Romer, 1958, 625).

Lavocat (1951) reverts back to the dual classification proposed by Tullberg and in his classification he especially emphasises the structure of the mandible. Although "... he presents only a partial classification of the order, it is definitely an advance in separating the "Hystricognathes" into "Orthohystricognathes: Rongeurs sud-américains" and "Parahystricognathes: Formes palae-arctiques et africains" (Wood, 1955, 168). The bathyergids are consequently placed under the latter group.

Roberts (1951) suggests separate suborder rank for the bathyergids, the Bathyergomorpha, equivalent to the Hystricomorpha, Sciuromorpha, Dipidomorpha and Myomorpha in rank. (According to Wood (1955, 194) Roberts gives no indication whether this term may have been used previously by some one else.)

Schaub (1953) also discussed the classification of rodents with special emphasis on the hystricomorphs. He does not agree with the other authorities using such characters as the infra-orbital foramen and masseter muscle as the basic criteria for classification. It may be concluded that he feels that dental characters may also be used (without danger of aspects due to dental parallelisms) which may indicate relationships, although according to Wood (1955, 169) Schaub may not accept parallelisms in other structures.

Schaub proposed the erection of a new suborder, the Pentalophodonta to include all forms
with/...

with teeth having a five-crested ancestry. This suborder is divided into two infra-orders, the Palaeotrogomorpha and Nototrogomorpha. The latter infra-order contains the South American hystricomorphs (= suborder Caviomorpha (suggested by Simpson in 1950) and erected by Wood and Patterson (1959) in a review of the South American rodents.) The former infra-suborder, Palaeotrogomorpha contains the superfamilies Theridomyoidea, Hystricoidea and Castoroidea, together with a series of families, incertae sedis, including among others, the Bathyergidae, Spalacidae and Rhizomyidae (Wood, 1955, 169).

One of the more recent classifications of rodents has been attempted by Wood (1955). In this case, Wood retains the classical suborders of Brandt, i.e. the Sciuromorpha, Myomorpha and Hystricomorpha and adds the Theridomyomorpha and Caviomorpha as new suborders. The bathyergids are retained as a separate suborder, the Bathyergomorpha, as was suggested (possibly for the first time) by Roberts (1951).

Landry (1957) has provided some of the latest data concerning the possible classification of the bathyergids. He clearly treats them as hystricomorph rodents and he also accepts the splitting of the rodents into sciurognath and hystricognath lineages as was proposed by Tullberg (1899). Summarizing the Old World Hystricomorpha, he credits the mole-rats with superfamily rank (Bathyergoidea) containing a single family (Bathyergidae) and two subfamilies, the Bathyerginae (including Bathyergus, Cyclomytus and Tsaganomys as genera) and the Heterocephalinae (with Cryptomys, Georychus/...

Georychus, Heliophobius and Heterocephalus as genera). The other superfamilies which he considers and which are equal in rank to the Bathyergoidea, are the Ctenodactyloidea, Petromyoidea, Thryonomyoidea and Hystricoidea (Landry, 1957, 80, 97).

In connection with the facts given above concerning the classification of the mole-rats it is clear that three main tendencies emerged since 1838, i.e. to isolate them and to treat them as an isolated group, or, alternatively to place them either with the myomorphs, or with the hystricomorphs or, in one isolated instance, with the sciurormorphs. These facts may be summarised as follows:-

CONSIDERING THE BATHYERGIDS AS			
(a) An isolated group	(b) Sciuro-morpha	(c) Myo-morpha	(d) Hystrico-morpha
		Waterhouse (1838)	
		Brandt (1855)	
		Alston (1876)	
			Winge (1887)
		Thomas (1896)	
			Tullberg (1899)
Weber (1904)			
Miller and Gidley (1918)			Winge (1924)
Weber (1928)			
Allen (1939)			Ellerman (1940)
			Simpson (1945)
			<u>inc. sedis.</u>
	Romer (1945, 1958)		
			Lavocat (1951)
Roberts (1951)			Ellerman <u>et. al.</u> (1953)
			Schaub (1953)
			<u>inc. sedis.</u>
Wood (1955)			
			Landry (1957)

It/...

It is clear that with few exceptions the earliest taxonomists regarded them as myomorphs. During the 20th century (especially since 1940 onwards) the weight of evidence tends to place the bathyergids with the hystricomorphs. On the other hand, during the course of the 20th century, a number of authorities accepted them provisionally as an isolated group. Furthermore, it is clear that even in the more recent literature there is still no general overall agreement where the mole-rats are to be placed taxonomically. It is not unreasonable to assume their stronger hystricomorph affinities and for the purposes of the present work, they are considered as such (see below for a brief discussion of anatomical features pointing to their hystricomorph relationship). However, Simpson (1945) expressed the following warning which should also be borne in mind: "While awaiting better evidence, it is considered inadvisable to base a major division of rodents on these few aberrant genera".