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Rodent taxonomy at the end of the 20th century

Delectatur musica

by Marco CORTI

Why rodent taxonomy? Rodents are so numerous and diverse so that they have been able to colonise most of habitats on the Earth. They are widespread in all continents and in the past they even reached areas of the world which were previously unoccupied. Rodents therefore represent one of the most suitable animal groups for the study of biological mechanisms promoting biodiversity and for biodiversity management, a primary task today.

Furthermore, alterations of natural habitats which occurred during Neolithic agriculture have determined a close association between many rodents and humans as can be seen in the extraordinary success of *Mus musculus* (BROTHWELL, 1981). Others, such as the rat, have caused plagues that repeatedly heavily reduced human populations in Europe and Asia in historical times. During 165 BC, at the time of Antoninus Pius, the plague was widespread all over the Mediterranean basin causing the death of millions of people. The Black Death in the 14th century determined an enormous number of deaths reaching two-thirds or three-fourths of entire populations in the first epidemic in some parts of Europe. Other species of rodents today cause severe damage in developing countries where agricultural practices need to expand due to an increase in the human populations and their needs, so that different programmes have started concerned with the management of rodent populations and a new science, called "rodent pest control", has developed (BUCKLE & SMITH, 1994).

How many rodent species have been identified? The total number of mammals has grown from the original 210 found in the tenth edition of Systema Naturae (LINNAEUS, 1758), to

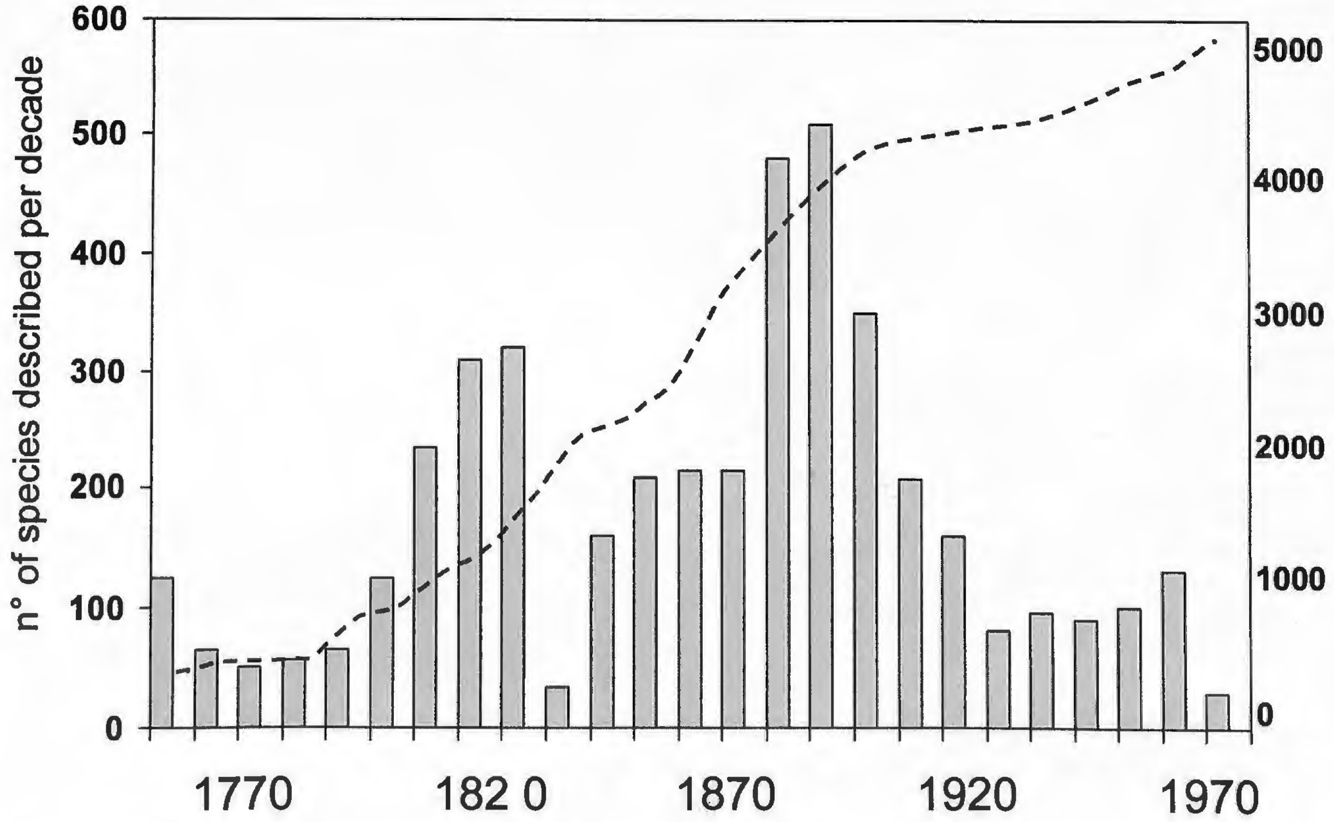

Fig. 1. – The increase in the number of mammal species from the tenth edition of Systema Naturae up to 1993. Bars represent the number of species of mammals described for each decade and the line represents the cumulative number of species up to 1993 (redrawn from WILSON & REEDER, 1993).

4629 (WILSON & REEDER, 1993), 2021 of which are rodents. This constitutes nearly 50% of the entire class, including monotrems and marsupials (Fig. 1). How was it possible to arrive at such a figure? What kind of taxonomy has been used to depict this outstanding scenario? This review presents current developments in rodent taxonomy at the turn of the millennium by revising the major scientific events that have contributed to current researcher attitude. Most of the advances in rodent taxonomy have occurred during the second half of the 20th century, many of which during the last two decades. This development is still in progress in many laboratories world-wide and much of this review reflects a personal attitude towards the present, near past and future of this discipline. To fulfil the task, the following topics will be considered:

1. The Rodents' *Systema Naturae.* How has the knowledge on the rodent fauna evolved to the present day, and how was the current classification system developed? The question also concerns the base unit of classification - the species – and the different philosophies of hierarchical grouping, from the species level up to the order.
2. The origin and development of biometry, morphometrics and the new geometric morphometrics.
3. The impact of Numerical Taxonomy, as the explicit definition of the different taxonomic philosophies which determined classification.
4. Rodent cytotaxonomy and speciation.
5. Biochemical systematics.

Taxonomy is not a trivial question, as different lines of thought can produce very different results. For example, hierarchies can be constructed on the basis of similarities, certain aspects of the phenotype or by ancestor - descent relationships.

Systematics, taxonomy and classification are often used as interchangeable terms, and it was SIMPSON (1961) who defined their meaning definitively, in order to avoid confusion. However, they are always connected in our day to day work. According to SIMPSON (1961), systematics is *"the scientific study of the kinds and diversity of organisms and of any and all relationships among them".* Classification is defined as *"the ordering of organisms into groups (or sets) on the basis of their relationships".* Taxonomy is *"the theoretical study of classification, including its bases, principles, procedures and rules".*

The term "relationships" could obviously cause some confusion because it may imply or not an ancestor - descendant relation exclusively. Taxonomy must therefore follow precise rules and aims.

Since SIMPSON's time, there has been an evolution and tuning in classification. It took time to agree on the fact that biological species exist (according to the Modern Synthesis definition) and that taxa must be defined on the basis of their ancestor – descendant relation (see MAYR & ASHLOK, 1991, for a general review).

Taxonomy concepts changed through time after the modern origin of the rodent Systema Naturae established by Carolus LINNAEUS. In the *Editio Decima* (1758), LINNAEUS was able to determine 36 species in the Glires, although he also included lagomorphs and the rhino in the group. He classified the six genera forming the order providing detailed descriptions of the fore and front limbs, tail, pelage, ears, dentition, all characters which are still widely accepted in creating a reliable classification system, at least at the family level. LINNAEUS also indicated a series of behavioural characters in his key, with a premonitory sense for a classification that should also include traits that are not directly measurable from the morphology of the organism, an attitude that has been neglected for a long time. For the description of *Mus musculus* he wrote: "M. cauda elongata subnuda, palmis tetradactylis, plantis pentadactylys. Mus cauda nudiuscula, corpore cinereo-fusco, abdomine subalbescente. ...*Habitat in domibus. Unguis pelliciaris palmarum nullus, quo a Ratto differ. Delectatur musica*[1], *non facile incarceratur, polyphagus".*

After LINNAEUS, the nineteenth century was characterised by an effort to produce catalogues of regional faunas, a series of works which reached maturity during the second half of the 19th century 'and the beginning of the 20th century.

The most comprehensive and modern systematic catalogue for Western Europe (excluding Russia), was published in 1912 by MILLER, one of the major figures amongst the founders of modern rodent taxonomy. MILLER personally examined 11500 specimens from the British Museum, the United States National Museum, and from private collections. The catalogue comprises 26 genera and 88 species of rodents, making up a total of 139 taxa including subspecies. After identification keys, MILLER provided tables of individual skull measurements, such as condylobasal length, zygomatic breadth, interorbital constriction, and others intended for use in taxon diagnosis. This represents one of the first attempts in providing a reference to study character variation between and within species. However, the data was set out poorly in a flat table with no analysis and poor geographic sampling. This lack has in part been covered by developments during the last 50 years, but much has still to be done.

At the turn of the 20th century a modern attitude for the studies on rodents has been established, Oldfield THOMAS becoming one of the prominent figures. Among his papers, there is an article of just six pages published in 1905 in which he presents the precise description and nomenclature for the main linear measurements to be collected on the rodent skull for taxonomic purposes (Fig. 2). The need for such a definitive description arose from the increasing amount of species description at that time (Fig. 1). Many of the comparisons were made from skull measurements, such as MILLER's (1912), and there was an obvious need for an unequivocal description of characters to be measured.

The outstanding work of MILLER, THOMAS and other scholars brought the original 36 species of Glires of LINNAEUS to 2021. This was the number counted by WILSON & REEDER in

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[1] It loves music.

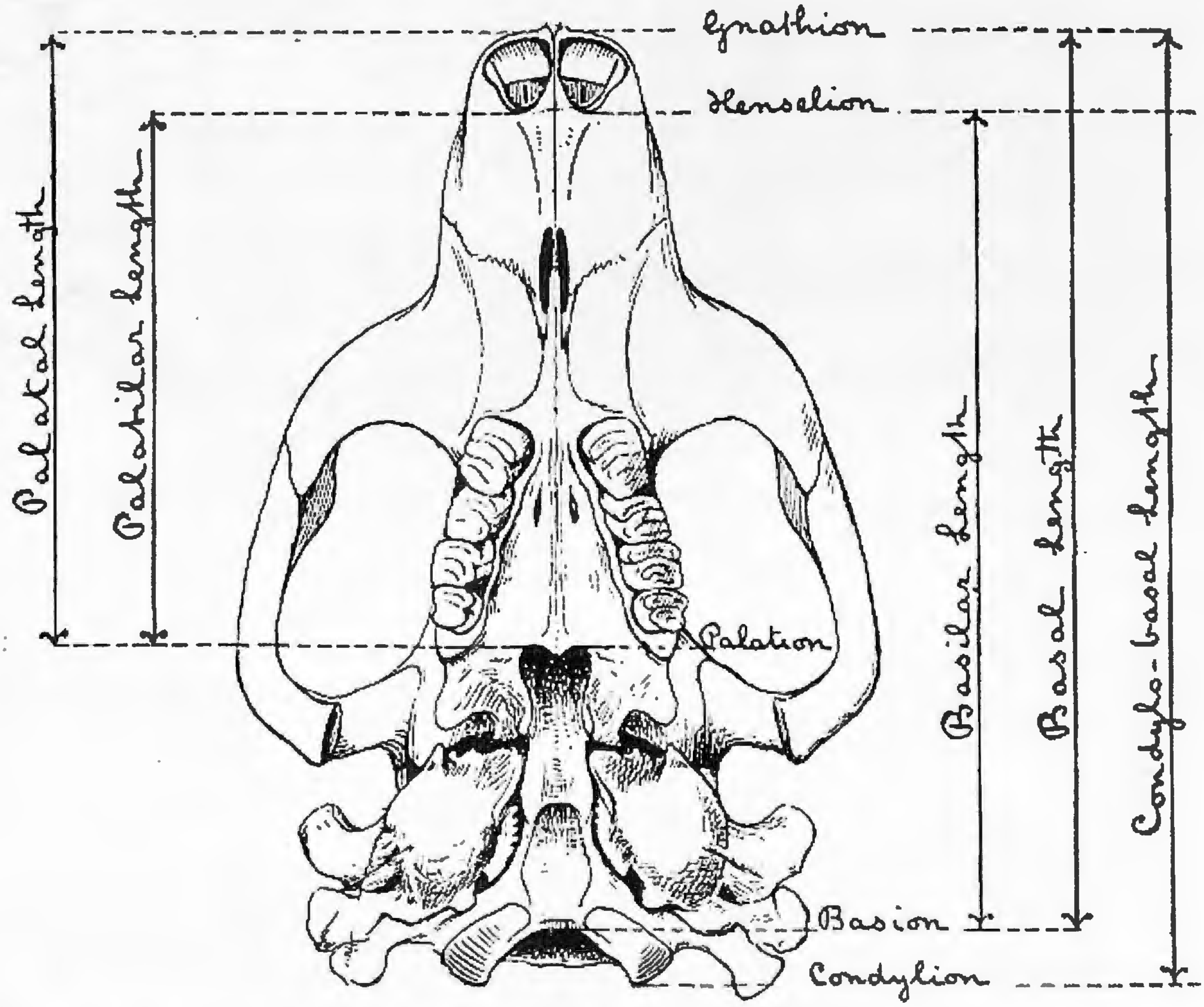

Fig. 2. – The precise definition made by THOMAS (1905) for the main measurements of the rodent skull.

their 1993 second edition of Mammal Species of the World (Fig. 1). There has been a 4.2% increase in the number of species during the 11 years between the first edition in 1982 by HONAKI *et al.* and the second in 1993 by WILSON & REEDER. Much of this increase can be explained by a better tuning of taxonomists, i.e. taxa finally accepted as good species, rather than by new discoveries.

Nonetheless, revisions through the decades have been characterised by alternate attitudes of lumping and splitting. This attitude accepted the fact that rodents include groups that are characterised by a particularly high number of cryptic or sibling species, i.e. distinguished by a high rate of speciation, which however are difficult to identify. Taxonomy and systematics therefore need a continuous revision due to continuous new findings which suggests that many species are in fact species complexes.

As an example, one may cite the African *Arvicanthis* LESSON 1842, which through the years reached the conspicuous number of 44 species, later reduced by HONAKI *et al.* (1982) to the single species A. *niloticus,* and then incremented to five species by CORBET & HILL (1991) and MUSSER & CARLETON (1993), but with some contradictions between the two classifications. Further studies on this genus carried out during the last ten years (VOLOBOUEV *et al.*, 1988; AFEWORK BEKELE *et al.*, 1993; CORTI *et al.*, 1995; CORTI & FADDA, 1996; CAPULA *et al.*, 1997; DUCROZ *et al.*, 1997; FADDA & CORTI, 1998) have shown that there is even a higher number of species occurring in the complex, and that science has to wait for the definitive taxonomy of the genus as well as for others.

Higher level systematics

Rodent taxonomy it is not just a matter of species identification and classification. Higher rank systematics is a current matter under discussion which has not yet completely been solved.

The 32 extant families of rodents (HARTENBERGER, 1985) show a considerable amount of shared morphological characters, including (and above all) those relative to the mastica-

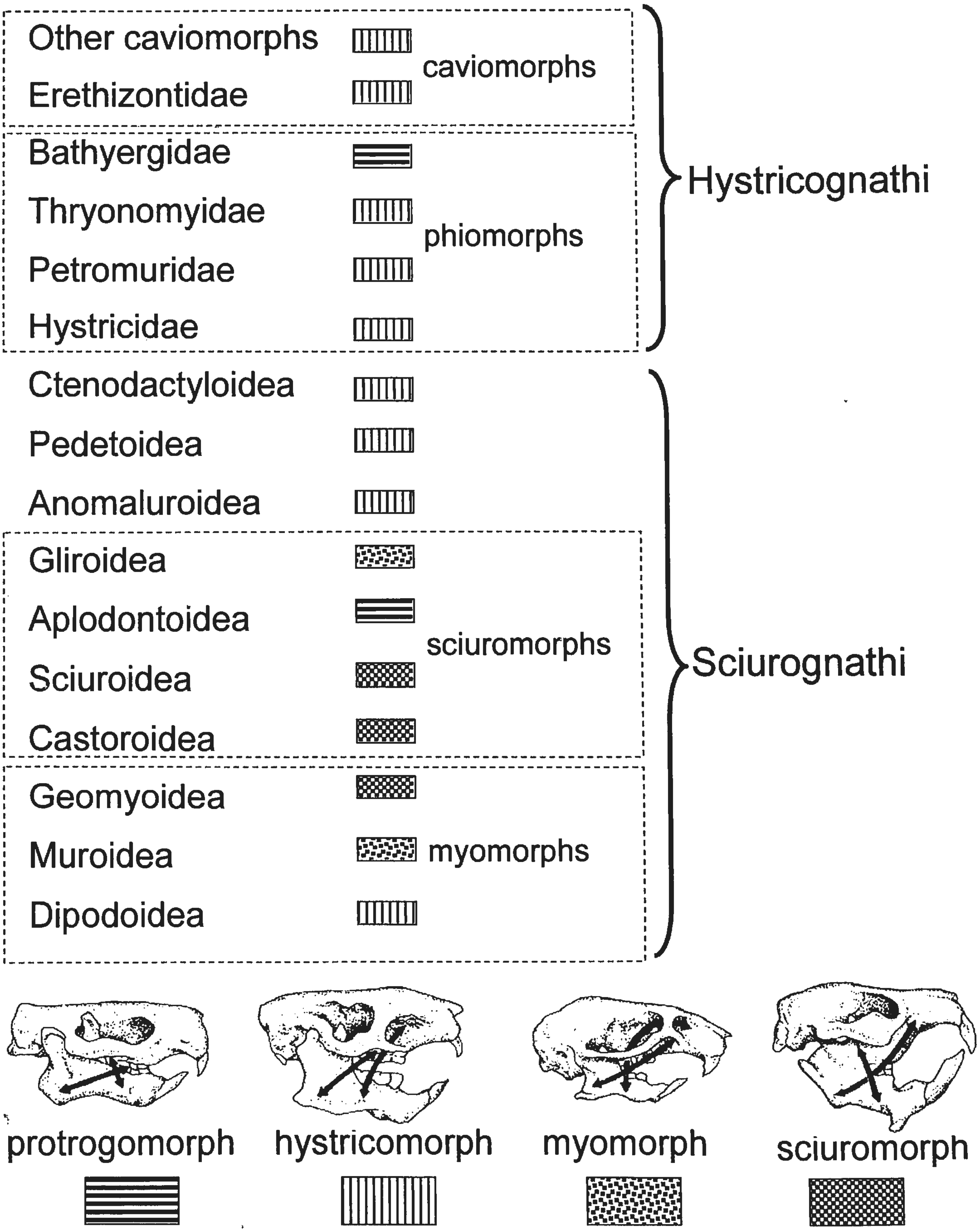

Fig. 3. – The division of Rodents into the two suborders Hystricognathi and Sciurognathi, and the further subdivision of the families into the four groups of Caviomorphs, Phiomorphs, Sciuromorphs and Myomorphs. Boxes represent the four zygomasseteric conditions (shown at the bottom). Note that Anomaluridae, Ctenodactylidae and Pedetidae have an intermediate condition of both sciurognathy and hystricomorphy.

tory apparatus, which strongly support a monophyletic hypothesis for the order.

The original classification (BRANDT, 1855) recognised three major suborders, i.e. Sciuromorpha, Myomorpha, and Hystricomorpha, prevalently, on the basis of the insertion of massetere muscles in relation to the infraorbital foramen, the rostrum and the zygomatic bar (Fig. 3). The generally accepted classification by TULLBERG (1899) recognises two major suborders: Sciurognathi and Hystricognathi, following the insertion of massetere muscles (Fig. 3).

However, there is a high degree of convergence and parallelism between families of these suborders, suggesting that they may not represent natural groups (HARTENBERGER, 1985; JAEJER, 1988). From a palaeontological viewpoint, sciurognathy in the lower jaw, and the protrogomorphous condition relative to the zygomatic bar is a primitive condition (JAEJER, 1988). Nonetheless, it is present in the Bathyergidae and Aplodontidae, although perhaps this is a secondary condition. Families in the Hystricognathi show both hystricomorphous and hystricognathous features; and the Sciurognathi are protogomorphous, sciuromorphous, hystricomorphous and myomorphous, although all sciurognathous (Fig. 3). This resulted in several different suborder classifications (MILLER & GIDLEY, 1918; ELLERMAN, 1940; SIMPSON, 1945; WOOD, 1955, 1965, 1985; CHALINE & MEIN, 1979).

It was therefore to be expected that paraphily of the Sciurognathi (HARTENBERG, 1985) has been investigated. There is a series of other characters, which do not produce a consistent scenario of natural groups. Among the others, the same incisor enamel microstructure is shared by Hystricognathi and the families Pedetoidea and Ctenodactyloidea but not by Anomaluroidea and Dipodoidea (MARTIN, 1993). The growth of cytogenetics followed by DNA/DNA hybridisation and DNA sequencing has brought further insight and clarification in this complex matter (see below).

The impact of Numerical Taxonomy

It should be mentioned that the attitude to rodent taxonomy and systematics during the course of last 30 years has changed - like for students of many other animal and plant groups - considerably since the development of Numerical Taxonomy. The idea of treating taxa numerically (Operational Taxonomic Units, OTUs, in the original formulation) was presented by two scientists, Philip SNEATH and Robert SOKAL, in a paper published in Nature in 1962; and followed later by two books: *Principles of Numerical Taxonomy, in* 1963, and *Numerical Taxonomy. The principles and practice of numerical classification,* in 1973.

Many of the ordination and clustering techniques to identify homogeneous groups or patterns of variation that we still use today derive or have their roots in those original texts. It is peculiar, however, that those ideas are generally regarded as "phonetics", where the taxonomic rules are the general and unweighted similarity between OTUs. There is a good part reported by SNEATH & SOKAL that defined rigorous bases for phylogenetic reconstruction through the identification of primitive and derived states in characters. They also, without doubt, introduced the scientific world to the ideas of phylogenetic systematics or cladistics which, after their original formulation by HENNIG (1966), had remained ignored for a few years before being rediscovered and generally accepted (see HULL, 1990, for an historical discussion).

Much of the development in rodent taxonomy we will see hereafter has its roots in SOKAL & SNEATH's original work.

Morphometrics and multivariate morphometrics

Metric (continuous and qualitative) characters have, for considerable time, been the only characters used to study within- and between-species variation since MILLER's (1912) and colleagues' times. Morphometrics and multivariate morphometrics (REYMENT *et al.*, 1984; MARCUS, 1991) is the science which deals with a kind of data which investigates variation in size and shape. Theriologists (and rodent students) have traditionally showed a major interest in multivariate morphometrics, as can be seen by all the workshops, books and primers developed ad hoc during mammalian meetings (e.g. NEFF & MARCUS, 1980; MARCUS & CORTI, 1989; CORTI, 1992) and by the considerable number of articles published in Mammalian journals.

However there has only been a limited number of papers which have explicitly concentrated on the central concept of allometry, i.e. on how variation in size and shape, the relative proportions, varies across organisms.

Allometry was defined formally by HUXLEY in 1932, and although his book has been quoted on thousands of occasions over the years, it has probably only been read from cover to cover only by few people. A more precise definition of allometry has been made recently by GOULD (1966) and KLINGENBERG (1996). Allometry can be considered either with respect to development, i.e. comparing individuals at different ages *(growth allometry),* or to variation within the same age class *(static allometry),* or with respect to evolution, i.e. comparing the same age classes of related species *(evolutionary allometry)* (HERSH, 1941).

To build up a rodent classification scheme, we need to compare allometric patterns between taxa. This is what morphometrics is intended for.

One of the first papers was published in 1952 by VON BERTALANFFY & PIROZINSKY. Although limited to a single species (albino rats), they were able to show how body proportions change during growth. They produced a series of plots between body weight and organ weight and compared them with known data for other mammals and showed how ontogenetic allometry does not correspond with interspecific allometry.

However, many studies on morphometric and craniometric variation have been hampered by scanty data sets (this is frequent when collecting in the field), lack of computing instruments, and by a consequent inadequacy, in the partitioning of nongeographic (sex and growth) and geographic effects in the data. Consequently this has limited most analyses (either univariate or multivariate) to simple discrimination purposes. Even when computers became progressively available, they were only used to produce discriminant function scores to classify specimens, The attitude (out of discriminant functions) towards discrimination was exemplified in the pioneer study of Michael FESTING in 1973. In laboratory strains of mice, he was able to distinguish between strains using mandible measurements. Further insight into non-genetic effects (ontogeny, sexual dimorphism) on (multivariate) shape and size changes came from a series of papers by LEAMY (1975, 1977).

In natural population studies, however, the major aim is the identification of patterns and causes of species differences (history and lor ecology) or, in within-species studies, processes of divergence (clines or step clines) with the eventual occurrence of races or subspecies (ENDIER, 1986). This is particularly important in comparisons of closely related species, because morphometric characters are influenced both by historical (i.e. phylogenetic) and adaptive effects (THORPE, 1983). The assessment of morphometric differences due to cladogenesis can be seriously hampered by homoplasies, i.e. adaptation to similar changes in current conditions or sampling from similar areas. Moreover, non-geographic effects, such as allometric growth, can alter the assessment of taxa similarities; this has generally been neglected in rodent multivariate morphometrics, although a general multivariate solution to the problem was produced by BURNABY (1966) and ROHLF & BOOKSTEIN (1987).

Discrimination attitudes, leading to the identification of homogeneous taxa (which is classification but in statistics only) has always been the main goal for many rodent morphometrics practitioners. Even if it has generally been possible to assign specimens to their correct group, many results are only indications for a proper use in taxonomy because they are limited to small areas of the range and therefore cannot be interpretable in a more general context of geographic variation.

GENOWAYS & JONES (1971) carried out one of the first multivariate morphometrics studies where a clear distinction between non-geographic effects (sex and age) on linear measurements was made in which an adequate sample was used. They studied the systematics of the kangaroo rats of the *Dipodomys phillipsii* group in Central America. Their factor analysis showed that all the populations examined should be considered as a single species, with a clinal geographic variation, with *Dipodomys ornatus* being a geographic race of *Dipodomys phillipsii* and not a separate species as previously considered.

Geometric morphometrics

Traditional morphometrics (MARCUS, 1991) is based on linear measurements, whereas this new approach looks at the geometric properties of the form, by recovering them through two- or three-dimensional Cartesian co-ordinates (ROHLF & MARCUS, 1993; MARCUS *et al.*, 1996). This new approach went through an initial experimental phase during the mid-nineties before being perfected (BOOKSTEIN, 1998). Geometric morphometrics has received a close attention from rodent students as it represents an almost definitive solution to the study of size and shape variation across organisms. Several aspects have been attempted, from ontogeny (ZELDITCH *et al.*, 1992; MONTEIRO *et al.*, 1999; HINGST-ZAHER *et al.*, 2000), sexual dimorphism in size and shape (HOOD, 2000), variation within (AUFFRAY *et al.*, 1996; CORTI *et al.*, 1996; CORTI & FADDA, 1996; FADDA & CORTI, 1998) and between species (CORTI *et al.*, 1998, 2000; FADDA & CORTI, 2000).

The study on three species of the African genus *Lophuromys* (CORTI *et al.*, 2000) is a good example. These species are representative of the two subgenera *Lophuromys s.s. (L. flavopunctatus* and *L. sikapusi)* and *Kivumys* (represented by *L. woosnami)* and have been studied by means of a three dimensional approach, which allowed the separate study of size and the reconstruction and visualisation of shape differences in the skull. They found not only significant differences in size among species, but also between age classes (Fig. 4). Furthermore, size is sexually dimorphic in *L. flavopunctatus* and *L. woosnami*. The comparisons of trajectories of size increase during growth for males and females also indicated a common and parallel pattern retained after cladogenesis by the species, females at age class 0 are smaller in size than males, but at age class 1 they become larger. From age class 2 up to age class 4 males become larger.

A principal component analysis of the shape components allowed the distinction of the two subgenera (Fig. 5). There is a high statistical significance between both the subgenera and among the species. Changes in shape are visualised as three dimensional reconstructions with rendering, to provide an aid to the human eye for further interpretation. This represents one of the main features of geometric morphometrics compared to traditional morphometrics where one had to imagine such changes simply by looking at a list of scores. There is a clear distinction in the shape of the rostrum, which is shorter and larger in *Kivumys* and longer and thinner in *Lophuromys s.s.*

Authors interpreted size and shape differences taking into account both phylogeny (i.e. the separation into the two subgenera) and a diet specialisation. This was because the genus is characterised by a strong tendency to insectivority with *Kivumys* being more insectivorous than *Lophuromys s.s.*

The establishment of Rodent cytotaxonomy: a chromosomal Systema Naturae?

BUSH *et al.* (1977) and CAPANNA & CORTI (1991) have highlighted the strict relationship between variation in chromosomal diploid number and the number of species in the major mammalian orders (Fig. 6). The observations concern diploid numbers only, so that only a part of the karyotypic variability is described, i.e. *not* those resulting from inversions,

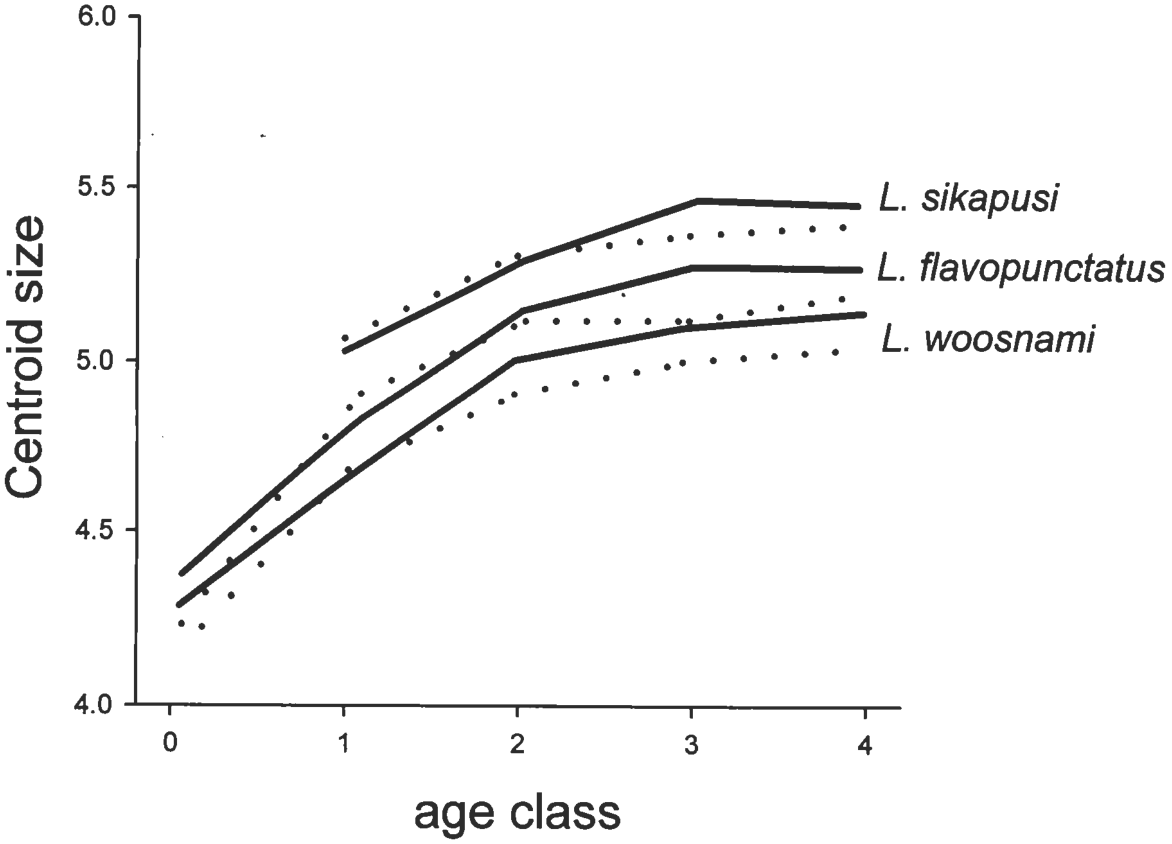

Fig. 4 – Comparisons of mean growth in size among the species from age class 0 to age class 4, in the two sexes. The solid lines are for males and the dotted lines for females.

deletions, etc. which is revealed by banding patterns only. However these observations reveal a direct relationship between the structural reordering of the genome and the prolific speciation occurring in rodents.

Robert MATTHEY in 1949 provided the first review on the karyotypes of Vertebrates, and reported the high number of studies on rodent cytogenetics, which had been investigated up to then. He also hypothesised on the use of these data in a phylogenetic context. However when superimposed on the phylogeny of rodents by WINGE (1924), the variability shown both in diploid and fundamental numbers was so high and overlapping between the families that no conclusion could be drawn.

However, the extensive work carried out in the following years on the pigmy mice *Leggada* and on other rodents by MATTHEY himself (1964) and by many other scholars, showed the occurrence of extensive karyotype polymorphisms within genera and species (see CHIARELLI & CAPANNA, 1973, for a review).

In his chromosome formulae of Eutherian Mammals, MATTHEY (1973) introduced the *Leggada* as *"in this group, the knowledge of the karyotype does not fit with the views of the Taxonomists. There are too many original karyotypes which cannot be referred to a described sp. or ssp. and that I quote as* f.c. *(from French, 'formulae chromosomique'). The polymorphism rests more frequently on Robertsonian processes* (musculoides) *sometimes on pericentric inversions* (oubanguii) *or multiple translocations* (gundae)."

This quote is taken from a chapter of the book "Cytotaxonomy and vertebrate evolution" edited by CHIARELLI & CAPANNA in 1973. The title includes the term "cytotaxonomy" rather than "cytology", and clearly represents the general attitude during the early seventies, when a certain amount of literature on chromosomal polymorphism was already available. It became clear that many species groups are recognisable only on the basis of their karyotypes and that chromosomal rearrangement is not just a new taxonomic character to examine but a possible cause of the high biodiversity and speciation characterising rodents. Consequently followed a suggestion that chromosomes needed to be primarily investigated in every qualified study on rodent species diversity.

BUSH *et al.* (1977) estimated that there are 0.431 karyotypic changes per lineage per million years, and chromosomal speciation became one of the hottest areas in evolutionary biology. Examples from *Spalax* (NEVO, 1991), *Mus* (CAPANNA, 1982), *Rattus* (YONG, 1969; RAMAN & SHARMA, 1977; YOSHIDA, 1980), *Thomomys* (PATTON, 1972), suggested that karyotype rearrangements occur and establish themselves in natural populations and favour speciation by decreasing relative fertility in structural heterozygote hybrids. The book of Michael WHITE "Modes of speciation" (1978) championed these ideas and provided exhaustive samples on rodents, one of the most karyotypically variable order of mammals. Moreover, WHITES' model strongly opposed the classical allopatric model of speciation by MAYR

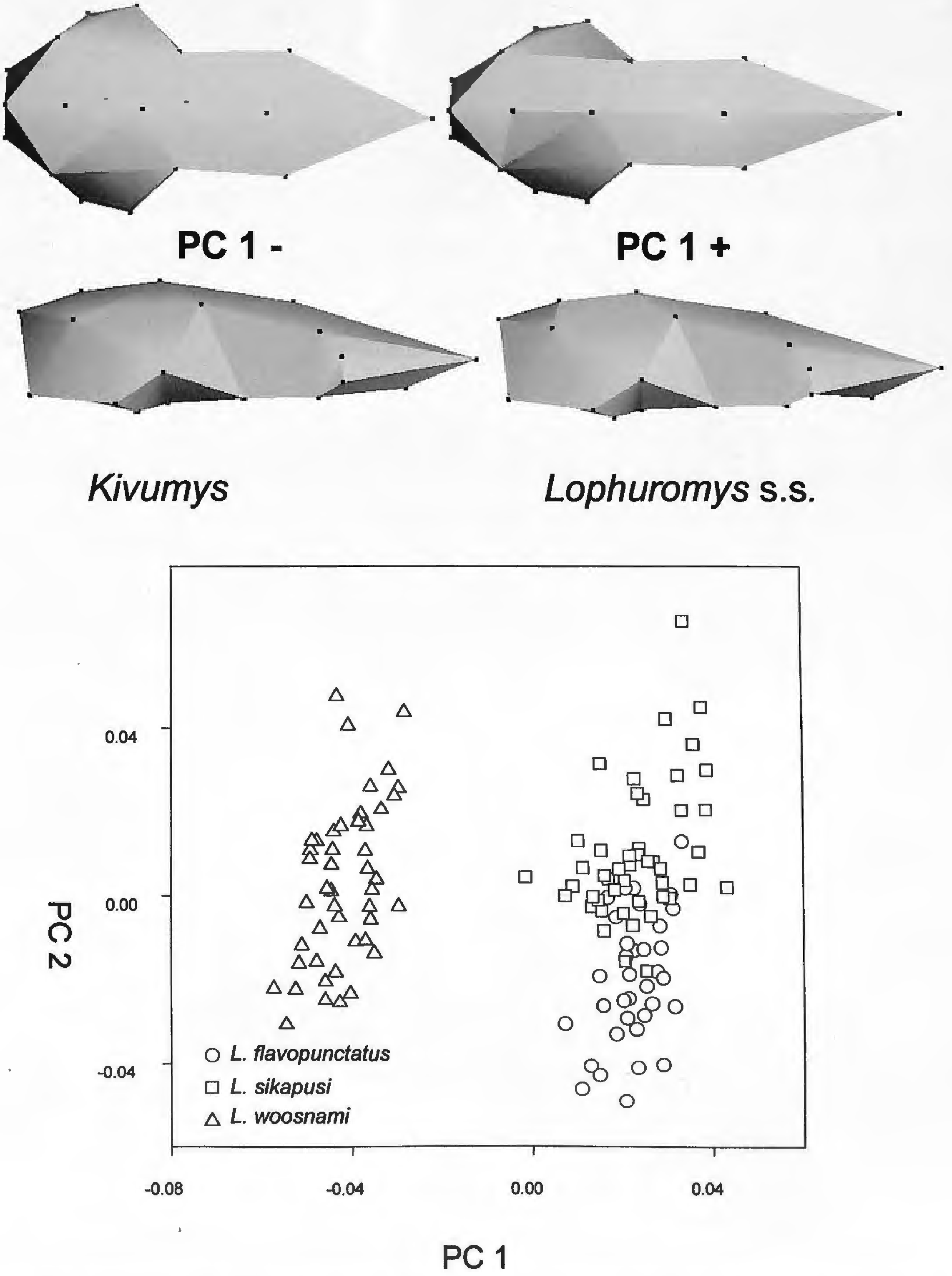

Fig. 5. – Three dimensional study of the shape differences between the two subgenera *Lophuromys* s.s. and *Kivumys*. A principal component scatter plot is shown at the bottom. The shape changes in the upper part are represented as a lateral and dorsal three-dimensional surface reconstruction of the skull relative to the highest (PC 1 +, *Lophuromys* s.s.) and lowest (PC 1 - , *Kivumys*) values of the first vector. Shape changes have been intentionally exaggerated by a factor of 4.

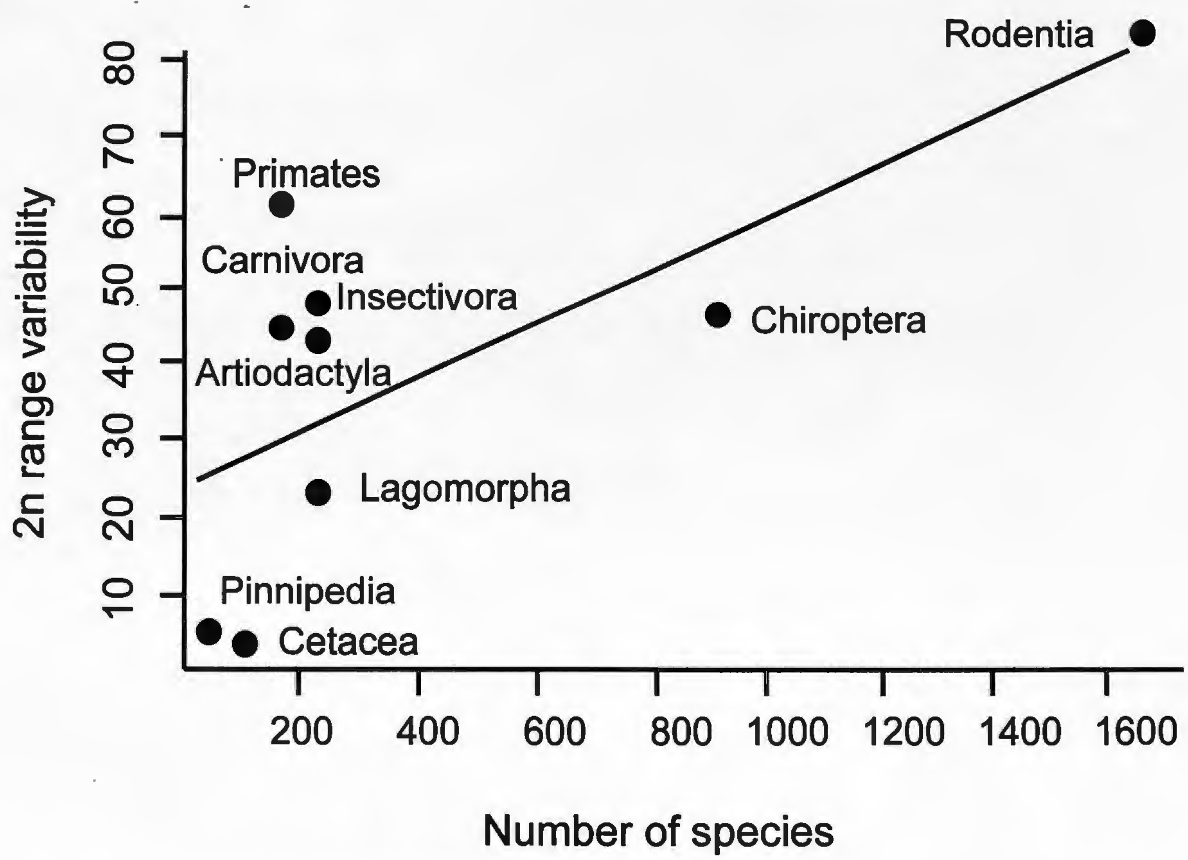

Fig. 6. – The relationship between diploid number variability and the number of species included in some of the major mammalian orders (redrawn from CAPANNA & CORTI, 1991).

Fig. 7. – Left side: G-banded chromosomes of the Apennine races of the house mouse CB (upper row) and CD (lower row). Numbers represent the acrocentric chromosomes fused to give rise to a metacentric. Note that the only homology in fusion found in the two races is between acrocentrics 9 and 16. Right side: meiosis of a structural heterozygote hybrid between the CB and CD races. The long ring is formed by 8 metacentric showing monobranchial homology; the three bivalents are chromosomes 19, 9.16 and the heterochromosomes.

(1963) (the "stasipatric" mode of WHITE, 1978).

One of the most cited examples by WHITE concerns the chromosomal races or species in *status nascendi* of the house mouse, which have been extensively studied by CAPANNA on co-workers (GROPP *et al.*, 1970; CAPANNA, 1982; CORTI *et al.*, 1986).

Figure 7 shows a diakynesis of a male hybrid between two of the many chromosomal races occurring in Italy as well as their G-banded karyotype (the Apennine races CB x CD). During the meiosis of these structural heterozygote hybrids a long multivalent ring is formed, which does not segregate. Meiosis is blocked and the resulting hybrid is sterile. There is a post-mating and sometimes a pre-mating reproductive barrier acting between some of these races (CAPANNA *et al.*, 1984). Chromosomal speciation has been very fast in the house mouse. In fact it did not start in these areas until 7-9000 years ago (CAPANNA, 1982).

A debate arose concerning chromosomal vs. allopatric speciation models (see WHITE, 1978, and MAYR 1991) in promoting biodiversity. From this taxonomic and systematic use of karyotype rearrangements was discussed. During the eighties a good set of qualified studies documented how chromosomal rearrangements can be used as a reliable taxonomic character in rodent taxonomy. These include a study on Nearctic Arvicolidae by MODI (1987) and on speciation and reticulate evolution in the house mouse by CORTI *et al.* (1986) (Fig. 8). The case of the chromosomal races of the house mouse not only documents how fast speciation can occur in rodents, but also provides a taxonomic tool which can be used in the study of the phylogeny of these races. The G-banding patterns were used to identify homologies in chromosomal rearrangements (see Fig. 7 for an example). From that, a phylogenetic hypothesis was then built (Fig. 8). There are some homoplasies in the tree that could only be explained by reticulate evolution (in the form of dashed lines in Fig. 8).

At this point the synthesis between systematics and taxonomy seemed complete: good, reliable taxonomic characters, i.e. chromosomal rearrangements identified on the basis of diploid and arm numbers and different banding techniques, to classify species and to build up reliable schemes of speciation and phylogeny.

Nonetheless, there is strong evidence suggesting that when comparing chromosomal rearrangements above the genus level there are a lot of homoplasies which cannot be detected by usual banding, mainly due to subsequent repattering of the karyotype (see for example WIENBERG & STANYON, 1987). Major criticisms were made on some attempts to reconstruct Rodent phylogenies through karyotype rearrangements (see VIEGAS-PÉQUIGNOT *et al.*, 1986).

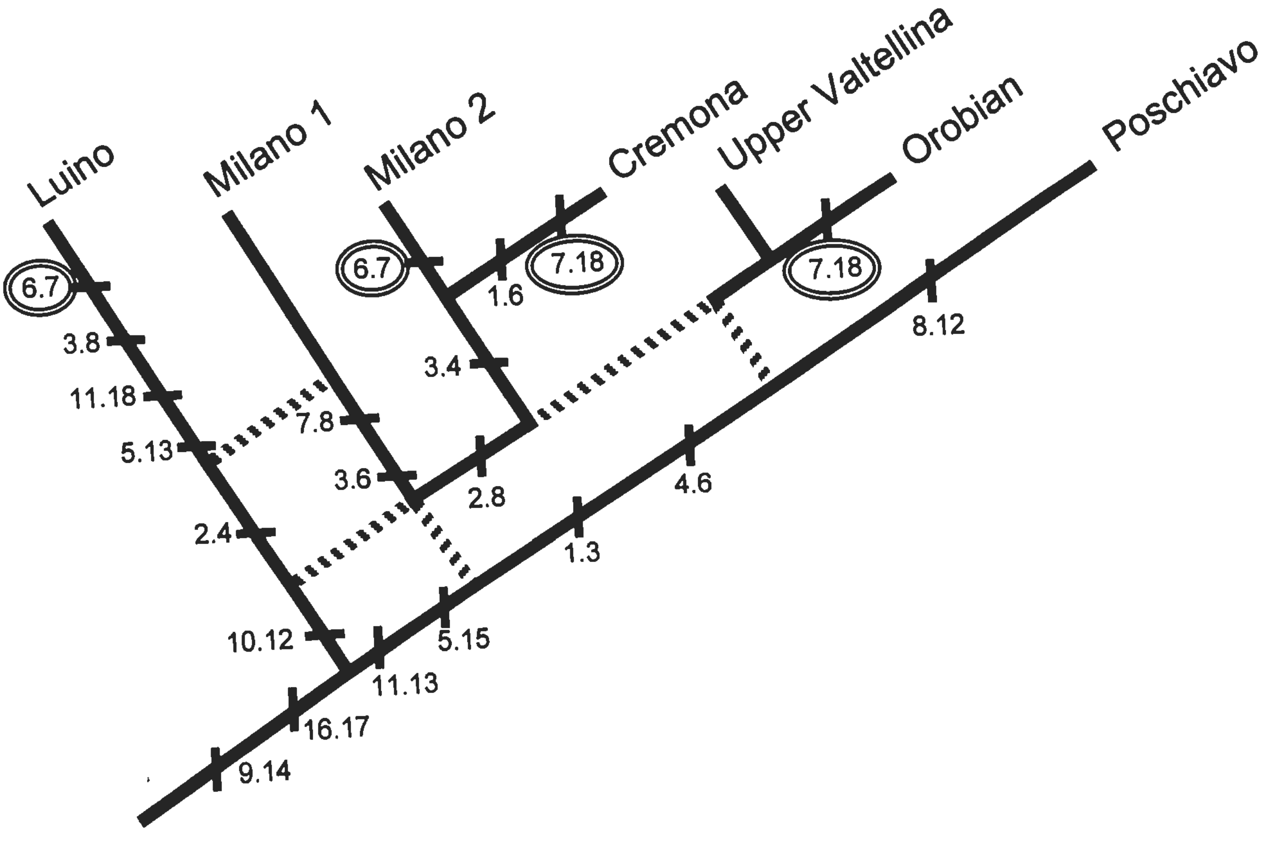

Fig. 8. – Phylogenetic tree of the Alpine chromosomal races of the house mouse (from CORTI, 1991). The occurrence of chromosomal fusion is indicated by two numbers separated by a dot which correspond to the two acrocentrics which are fused into a metacentric (following the Standard Nomenclature for the House Mouse Karyotype). Homoplasies (repeated occurrence of the same fusion into independent branches) are explained through hybridisation events (indicated by dashed lines). There were only two homoplasies in the tree which are enclosed in circles (metacentrics 6.7 and 7.18).

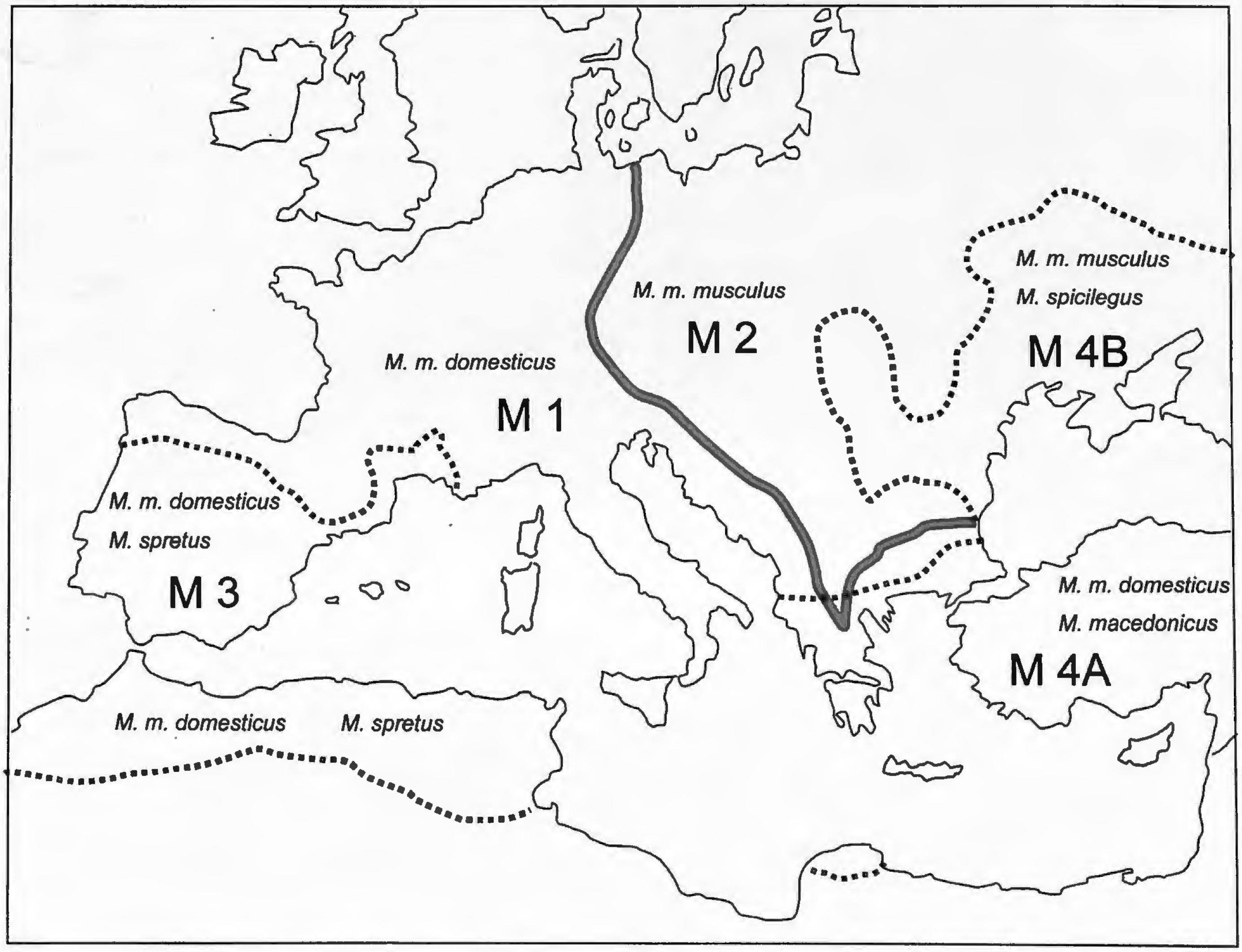

Fig. 9. – Map which shows the five species and subspecies of the genus *Mus* occurring in Europe and the Mediterranean basin and their corresponding biochemical group according to BONHOMME *et al.* (1978). Dotted lines roughly correspond to the limit of the ranges. The grey line indicates the hybridisation zone between *M. musculus domesticus* and *M. musculus musculus*.

Protein electrophoresis

Many of the new insights into rodent taxonomy came from the application of multilocus protein electrophoresis, which became widely diffused in the mid sixties (see AYALA, 1975, 1976). The technique allowed the estimation of gene flow between populations and an estimate of the time of genetic divergence, assuming neutral evolution of structural genes over time. For the first time there was a tool to investigate species systematics and taxonomy which was structurally a central part of the modern Synthesis, i.e. the biological species concept (MAYR, 1963).

One of the first and complete studies came from SELANDER *et al.* (1969) and HUNT & SELANDER (1973) on the two subspecies *Mus musculus musculus* and *Mus musculus domesticus*, which have been hybridising in Central Europe and in the Jutland peninsula for at least 5 000 years. They were able to show the occurrence of a hybrid zone and of an almost unidirectional gene introgression from *domesticus* into *musculus*, suggesting that the separation of the subspecies may have been maintained by a combination of environmental factors and post-mating isolating mechanisms. Genetics was finally able to provide a stronger biological basis to the previously described taxa on the basis of morphological and ecological characters (SCHWARTZ & SCHWARTZ, 1943; URSIN, 1952; ŻIMMERMANN, 1949).

Species boundaries could be then identified through classical population genetics as allozyme variation is inherited in a simple Mendelian fashion. Furthermore processes of within species differentiation (i.e. geographic variation and raciation) could be highlighted and hierarchies based on relative genetic dissimilarity/divergence established.

By the late sixties and the early seventies there was an exponential growth of studies in rodent taxonomy and systematics using protein electrophoresis.

Examples include the studies by JOHNSON & SELANDER (1971) on the kangaroo rats *Dipodomys*, by NEVO & SHAW (1972) on *Spalax ehrenbergi*, and by BONHOMME *et al.* (1978, 1983) on the European and Mediterranean species and subspecies of the genus *Mus*, which led to the identification of at least five biochemical groups, corresponding to the taxa *Mus musculus domesticus* (M 1), *Mus musculus musculus* (M 2), *Mus spretus* (M 3), *Mus macedonicus* (M 4A) and *Mus spicilegus* (M 4B) (Fig. 9).

In 1975 AYALA examined data from allozymic studies on seven genera of rodents and found that the average genetic similarities between species vary from group to group and for some cases they are similar to those found between subspecies. Nonetheless, much of the earlier work in this field proved that electrophoretical determination produce classifications which are in many respects similar to those based on morphological characters. However, it also gave insights into relationships which were not apparent in earlier classifications. We could quote the case of 15 species of *Peromyscus* (AVISE, 1974), where the allozyme relationships "promoted" some subspecies to species, and moved some species from one subgenus into another.

After establishing the occurrence of gene flow, one should question how reliable allozymes are in the study of species relationships. The strong controversy between the selectionist versus the neutralist hypothesis on structural gene evolution went on for over ten years (KIMURA, 1968; KIMURA & MARUYAMA, 1971; NEVO *et al.*, 1974; OHTA & KIMURA, 1975; STEBBINS, 1982).

Historically, the application and growth of the technique of protein electrophoresis has been an extremely powerful tool in solving complex problems at the genus level. However an adequate number of individuals from populations must be analysed in classical Mendelian population genetic framework. It soon became evident however that the technique could not be of great systematic value beyond genus level.

Nuclear and mitochondrial DNA

By the end of the seventies, the use of digestion endonucleases had opened up a new area in rodent taxonomy and systematics (PARKER & WATSON, 1977; AVISE *et al.*, 1979), closely followed by DNA-DNA hybridisation (HUNT *et al.*, 1981) and DNA and RNA sequencing using the PCR technique (GUYER & KOSHLAND, 1989; ARNHEIM *et al.*, 1990). It became possible to include a higher number of geographic localities or species represented by fewer specimens in the analysis, as comparisons at least in a phylogenetic or phylogeographic context could be made not on gene frequencies but between cleavage patterns, distances or sequences, requiring a smaller amount of individuals.

There was a dramatic appearance in the scientific literature of papers dealing with the phylogenetic interpretation of rodent species below and beyond the genus level, and the work by YONEKAWA *et al.* (1981) on cleavage patterns of European and Asian species of *Mus* constitutes one of the first case studies. Others, later attempted to study evolutionary histories of groups (e.g. the South American Akodontinae, SMITH & PATTON, 1993).

Molecular techniques also became an obvious tool which could challenge higher level systematics in Rodents. One of the first attempts to solve the complex problem of rodent family phylogeny was the summary paper by CATZEFLIS *et al.* (1992) through the application of scnDNA hybridisation. They found that the rate of DNA evolution is faster in rodents than in any other order of mammals and birds, and used DNA-DNA hybridisation distances to produce an overall evolutionary tree of the muroid rodents together with a time scale. Their phylogeny seriously contradicted others derived from karyotype rearrangements (e.g. VIEGAS-PEQUINOT *et al.*, 1986), and suggested that the relationship between nucleotide substitution and time is probably curvilinear and not linear, i.e. speciation events dated by palaeontologists are older than those inferred through a linear molecular clock hypothesis.

Several general studies followed the pioneer work by CATZEFLIS and co-workers, using the increasing amount of data made available. These led to many attempts, of variable quality, to solve the complicate matter of rodent families systematics. A good body of literature attempted to question the real monophyly of rodents (GRAUR *et al.*, 1991), contradicting the hypothesis of the uniquely shared characters of the masticatory apparatus of the group. Many fall into the "is the guinea-pig a rodent?" category (GRAUR *et al.*, 1991; LI *et al.*, 1992; MA *et al.*, 1993; D'ERCHIA *et al.*, 1996). This constitutes a clear example of how inappropriate data analysis – even if the data, i.e. mtDNA sequences, are complete and correctly aligned – may cause erroneous interpretations.

Although the story involved an apparent waste of time spent in arguing by supporters of rodent monophyly or polyphyly (together with an increase in Impact Factor), it provides however a clear example of how easily one can violate rigorous assumptions, i.e. all sites are equally variable and evolve at the same rate. This however is not the case of Mammalian mtDNA (YANG *et al.*, 1994; SULLIVAN *et al.*, 1995). A re-examination of the data by omitting the third-codon position (SULLIVAN & SWOFFORD, 1997) through a maximum-likelihood model clearly established the guinea-pig as a rodent so rejecting the polyphyletic origin of the order.

A recent analysis of the 12S RNA (rRNA) by NEDBAL *et al.* (1996) has finally cast some light on the complex phylogenetic relationships between sciurognathous families and Hystricognathi (Fig. 10). They found that the monophyly of Hystricognathi is supported by all analyses (i.e. parsimony and maximum-likelihood, neighbour joining), with the guinea pig failing within the Caviidae family. Furthermore, the analysis also supports a sister-group relationship between Sciuroidea and Aplodontoidea, and for Muroidea and Geomyoidea (with definitive evidence for monophyly for these latter two families). The analysis however on the polytomous relationships among Muroidea, Dipoidea, Geomyoidea, and Pedetoidea, and the unclear placement of Gliroidea and Castoroidea led to some ambiguous results.

An important aspect of Rodents compared to other mammalian orders is their high heterogeneity between lineages, resulting in different branch lengths, with a high rate of among-site variation. This can seriously affect analyses as it may be the result of either differential rates of molecular evolution or ancient divergence, the so called "branch length effect"

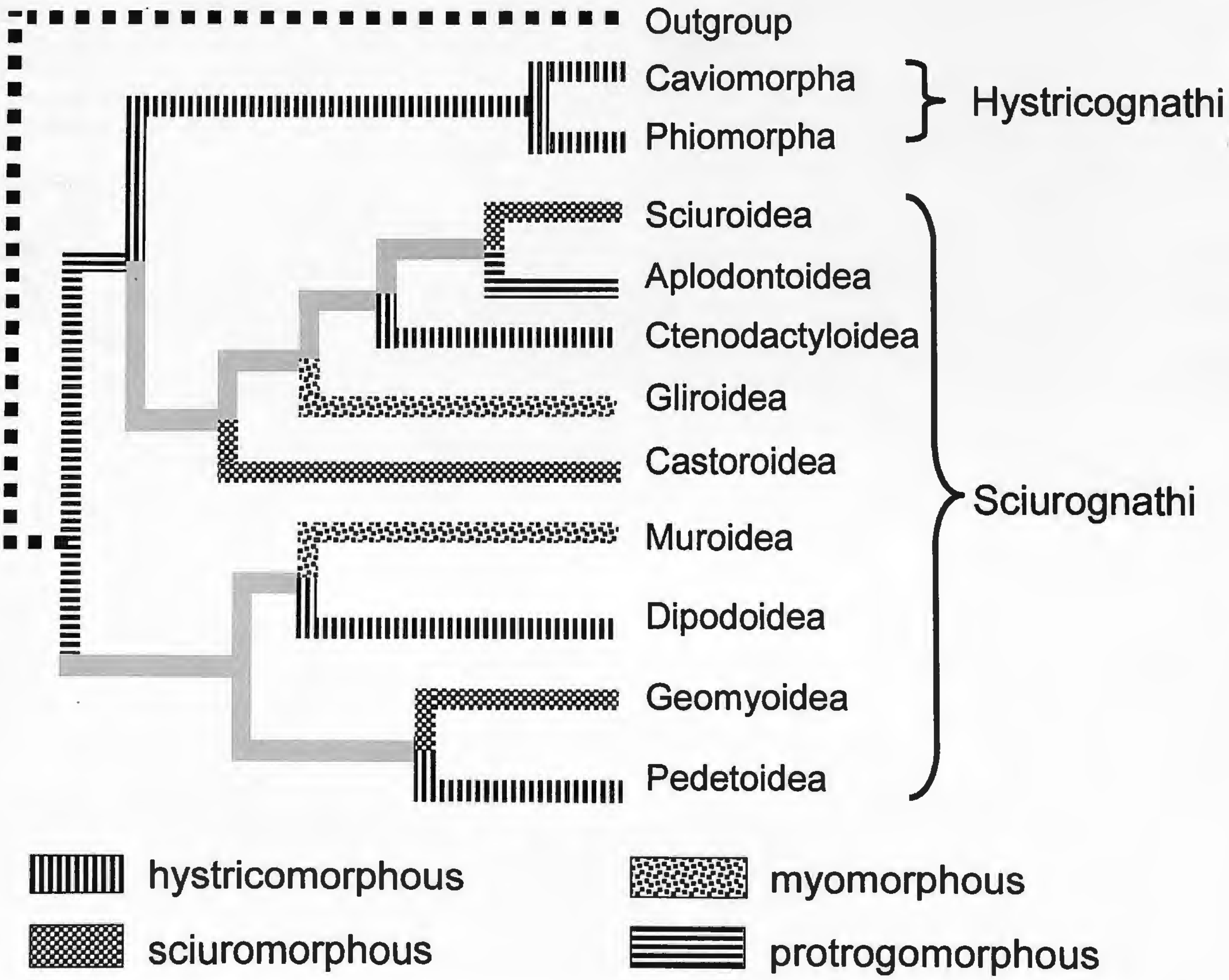

Fig. 10. – The phylogeny of rodent families based on the analysis of the sequence of the 12S RNA (rRNA), after NEDBAL *et al.* (1996). Branch patterns follow the zygomasseteric condition (shown below the tree).

(FELSENSTEIN, 1978; SWOFFORD *et al.*, 1996; but see, for a discussion on the guinea pig, SULLIVAN & SWOFFORD, 1997).

Perspectives

Rodent taxonomy and systematics at the turn of the century is a well established and mature science. Different disciplines including morphology, morphometrics, cytogenetics, genetics, molecular genetics are extensively widespread in many laboratories worldwide and integrated more and more often with each other to produce a consistent scenario of rodent diversity.

Many of the recent multidisciplinary approaches adopted by scientists come from the studies that have carried out for over a century on the rodent faunas of the northern hemisphere. These have provided insights into the richness of species and on many of the biological and geographic factors which have determined such a high diversity. Much still has to be done in the southern part of our globe, where there is the highest demand for rodent taxonomy. There is an obvious practical problem in species identification in the field, as many rats and mice represent real pests for agriculture and are vectors of parasites and micro-organisms which affect livestock and humans. Biodiversity however is also severely disturbed in that part of the world where the deepest environmental crisis since the origin of Neolithic agriculture is taking place. Human population growth and the consequent expansion of agriculture and of other economic activities determine the shrinking and alteration of natural habitats at a faster rate. Rodents represent therefore a key group to be used as a tool for eventual conservation plans of biodiversity.

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