ADVANCES IN SYSTEMATIC MAMMALOGY

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INTRODUCTION

It seems to me that it is not only an impossible task but a bit presumptive to think that a short paper such as this can do justice to the subject of advances in systematic mammalogy. Additionally, if they are truly significant "advances" it is unlikely that any one person is capable of properly presenting a balanced presentation and perspective overview. Therefore the reader should understand that the opinions below are biased from a single person's viewpoint and the literature cited is not intended to be comprehensive. With these protective caveats I make the following observations.

The changes in systematic mammalogy have been on many fronts ranging from the changes (and in some cases advances) in the philosophy of systematics, to high tech methodologies. I shall try to touch on the full spectrum.

PHILOSOPHY AND APPROACH TO DETERMINING RELATIONS

I think that most systematic mammalogists agree that a systematic classification should reflect evolutionary history and common ancestry. However, even if we knew the true family tree of all mammals, I think that there would be disagreement among mammalogists on how to convert such a tree into the categories: genera, families, orders, and so forth. Not only do we not know the true family tree, we also have the problem that many currently recognised genera, families, orders, and other categories have a history of being defined from a Gestalt, often with little agreement as to their limits. Systematics has often been as much art as science and higher taxonomic categories have simply been what taxonomists have called them. Therefore, it should not be surprising that in systematics there have been repeated efforts to make classification methodologies more scientific.

The two most recent attempts have been numerical taxonomy or phenetics (Sneath and Sokal, 1973; Rohlf and Sokal, 1981) and cladistics (Hennig, 1966; Farris, 1979; Funk and Brooks, 1981; Platnick and Funk, 1983). Thank goodness, it is far beyond the scope of this paper to deal with the details of these two camps of thought, but the reader is referred to the numerous, often heated, discussions published during the last ten years in the journal, Systematic Zoology. Basically phenetics and numerical taxonomy would classify taxa based on how similar they are without regard to whether the similarities are primitive or derived. Alternatively cladistics associates taxa only if they share derived character states. Additionally, cladistics embraces the ideas of parsimony and outgroups (Wiley, 1981; Watrous and Wheeler, 1981; Farris, 1982; Maddison et al., 1984; Smith and Hood, 1984).

Several points appear to me to be worthy of note. First, a significant number of the persons who favour either cladistics or phenetics often border on a religious commitment to these ideas. In my opinion, there is no place in science for such a fanatic attitude and I do not think that systematics is better off as a result of these over zealous people. It is ironic that such a religious fervor is associated with an attempt to be more scientific. Second, as far as mammals are concerned, very few papers have successfully employed these techniques to a point where a superior classification has resulted. To some extent this is because there is a large gap between theory and application. The bottom line is, however, that the theories of numerical taxonomy and cladistics had little impact on development of the currently accepted mammalian classification (Anderson and Jones, 1984). Third, one extremely valuable aspect of cladistical analysis is that it provides a measure of convergences and/or reversals. For example for chromosomal rearrangements identifiable with G-bands, convergent evolution seems to be a significant problem (Robbins and Baker, 1981; Rogers, 1983; Hood et al., 1984). However, not until anatomical, electrophoretic, DNA as well as other types of data sets are analysed under similar methods will it be apparent if convergence is less a problem for these data sets. Fourth, I would also like to note that although earlier taxonomists may not have understood our "more modern" techniques, I have been impressed with how accurate some of these early works have proven when tested with more recently developed methods. Examples are Osgood's (1909) revision of Peromyscus and Miller's (1907) revision of the families and genera of bats.

On a more specific level, for G-band chromosomal data generated in my laboratory we have attempted to use the cladistical methods (Patton and Baker, 1978; Baker and Bass, 1979; Baker et al., 1983; Haiduk and Baker, 1982, 1984; Stangl and Baker, 1984). Hood and Smith (1982) also used a cladistic analysis of the histology and anatomy of the female reproductive tracts of bats. An example of biochemical data being cladistically analysed is Goodman et al. (1982a), who produced a hypothesised phylogenetic tree for the mammalian orders and fairly
detailed study of many primates. In all of these studies, there is generally a good agreement with existing classifications and in several examples where previous classifications have been poorly defined the new study also was indecisive.

**Computers and Number Crunching**

As data sets become more complex and varied it is only natural that computers and associated statistical programmes would be critical to systematic analysis, regardless of the philosophy that is favoured. Just as each data set (morphological, chromosomal, genetic, and others) has its own strengths and limitations, so does each statistical programme and a most critical aspect of successful utilisation is the proper choice of the programme for a specific question involving a specific data set. From my perspective, one needs a computer just to keep up with the available programmes and my understanding of what these programmes can do is primarily faith in the word of statisticians and computer types. Nonetheless here is my limited overview.

Basically there are two broad categories of systematic methods for dealing with multivariate data sets—clustering and statistical. Typically (although not necessarily) the statistical techniques are considered to be part of phenetic methodology, and involve some type of analysis of overall similarities. Clustering methods may be phenetic (based on overall similarities) or cladistic (based on shared derived similarities). Neff and Marcus (1980) provided an overview of systematic philosophies, algorithms, and available computer programmes.

During the past decade or so a number of computer programmes and programme packages have been developed and distributed in order to ease analysis of data and to proliferate the systematic philosophies of the programmes' authors. Three widely used cladistic packages available are PAUP (David L. Swoford), PHYSYS (James S. Farris), and Joe Felsenstein's package. Each of these does Wagner-type clustering under a number of user-defined constraints, and various of them will also do other types of analyses (For example, character compatibility, user-defined tree analysis).

Notwithstanding the availability of these and other programmes for some years, few cladistic studies of mammals have utilised them. Carleton (1980), in his study of cricetine rodents, utilised and compared results from Prim networks, Weighted Invariant Step Strategy (WISS) trees, and Wagner trees based on morphologic data.

Phenetic clustering methods have been more commonly used in mammalian systematic studies, perhaps due in part to the widespread availability of the NTSYS package developed by Rohlf, Kishpaugh, and Kirk. This package provides a number of clustering programmes as well as principal components analysis and minimum spanning network. Authors who have used various of these techniques in systematic studies include Findley (1972), Genoways (1973), Best (1978), and Carleton (1980). Other statistical methods used less typically or for more specific application include discriminant analysis (Smith and Starrett, 1979), and analysis of variance (Owen and Webster, 1983).

A ubiquitous concern in systematic analysis of mammal data sets is that of size. Lemen and Freeman (1984), in an analysis of bat data, provide a discussion of the taxonomic meaning carried by the size and shape components of a morphometric data set. The usual approach to the “problem” of size has been an attempt to remove the effect of size by the use either of ratios or removal of the first principal component (for example, Best, 1978; Douglas, et al., 1984). However, use of either of these techniques assumes linearity of size relationships among taxa (Pimentel, 1979), and Atchley (1978) has raised other objections to the use of ratios. Wood (1983) suggested that the systematist's real objective should not be to remove the effect of size, but rather that portion of the data set variance, which he called the "common part"; he further outlined a regression procedure to accomplish this.

One of the potential problems of the incorporation of complex computer-aided data analyses is that the researcher may depend too heavily on a posteriori reasoning. Often, the hypotheses tested are generated after the data analysis has been performed. The danger in such processes is that the investigations become data oriented and the study is not conceived as an integral part of the scientific method. In order for the field of systematic biology to advance significantly as a recognised science greater emphasis must be placed on experimental design and adherence to scientific principles.

**Newer Types of Data for Systematics**

An old cliche in systematics is that “systematists aren’t proud, and they will use any data available.” With the expanding horizons of biotechnology the potential data are mind boggling. Cellular structure, subcellular structure, and biochemical studies have all recently been interpreted in a systematic framework. Studies on sperm morphology (Forman and Genoways, 1979), ultrastructure and light microscopic histology of the alimentary canal (Phillips et al., 1984), surface structure of arvicoline rodent teeth (Koenigswald, 1980), and hair structure in heteromyids (Homan and Genoways, 1978) serve as examples of the types of morphological data used in a systematic context.
Electrophoresis

Protein electrophoresis is by far the most commonly used technique for determining the genetic relatedness of taxa. As a result of electrophoretic studies there have been assessments and reviews of genetic variation in natural populations (Nevo, 1978) and the reader is referred to Smith et al. (1982). Prior to electrophoretic studies of natural populations, it was generally accepted that species of animals contained little genetic variability. Smithes (1955) and Lewontin and Hubby (1966) demonstrated that organismal populations did indeed contain high levels of genetic variability. Additionally, electrophoretic studies of this variability have clearly documented that the populational structures over short geographic distances are much more complex than previously thought (Selander, 1970, Chesser, 1983; Ryman et al., 1980).

Because of the amount of variability found in natural populations, the systematic value of electrophoretic studies in mammals has generally been most valuable to the lower taxonomic levels (species and closely related genera) rather than in relations of higher levels (such as orders and families).

The primary problems associated with electrophoresis are that it is difficult to be sure that the identical migration of a band on a gel indicates genetic identity, as well as and the inability to make comparisons between distantly related taxa. Nonetheless because electrophoresis is relatively inexpensive and easily performed from a technical standpoint, it will continue to be a widely utilised technique.

Immunology

One of the oldest biochemical techniques used to study systematic relationships of mammals has been immunology. Probably the most significant results of the immunological studies is the development of the molecular clock hypothesis (Sarich, 1969; Wilson et al., 1977; Sarich and Cronin, 1980), which has resulted from micro-complement fixation studies (Sarich and Wilson, 1966). Because immunological studies have considerable resolving power for both closely and distantly related taxa and because the techniques are relatively well understood, I suspect that the technique will continue to be used in mammalian systematics (Arnold et al., 1982; Baker et al., 1981; Fuller et al., 1984). Nonetheless, the immunological techniques have the problems of 1) only estimating how different the proteins are from different taxa (Sarich and Wilson, 1966); 2) examples of well documented non-clock like evolution (Arnold et al., 1982); and, 3) a reduced resolving power because of variation of reciprocity studies (Sarich and Cronin, 1980).

Sequencing of Amino Acids of Proteins

One of the types of data that has been most successfully converted into systematic hypothesis is that generated from amino acid sequences analyses from polypeptide chains (Goodman, et al., 1982a, 1982b, 1982c). Data from such studies have the advantage of being discrete, readily analysed by cladistical methods, and sufficiently conservative in rate of evolution that comparisons between higher taxa (such as orders and classes) can be made. Because there are literally thousands of available proteins, the theoretical limit for such studies is boundless (Goodman, 1982). However, because these studies are relatively expensive and technically complicated, it is likely that such studies will be performed in a limited number of laboratories and on a relatively small number of proteins and taxa.

DNA Analysis

As DNA is the genetic material, there is considerable anticipation in the development of the various techniques required to produce the type of data needed for systematic work. Although this is a relatively new field some of the first studies have been most promising (for instance see the DNA/DNA hybridisation studies of Brownell, 1983 and Sibley and Ahlquist, 1984; the restriction endonuclease maps of Templeton, 1983; the mitochondrial DNA studies on primates by Brown et al., 1982, Peromyscus by Avise et al., 1979 and Lansman et al., 1983, and Geomyys by Avise et al., 1979; DNA spacer sequences studies of Apfel and Honeycutt, in press; and studies on the genomes of closely related species, Dover et al., 1980). There are several problems associated with DNA studies (Dover, 1980), however, it appears to me that the number of laboratories, and number of productive scientists, and the magnitude of medical and scientific funding of DNA biochemistry will result in an immediate significant volume of literature, some of which will be systematic in nature. Certainly this is the hottest area of systematic research.

Chromosomal Studies

Ever since chromosomal data have been available, they have been interpreted as having systematic value. Newer techniques for mammalian chromosomes produce differential staining which is thought to document genetic homology (Haiduk and Baker, 1984). At this time, it is probably safe to conclude that non-differentially stained chromosomes and C-bands (regions of highly repetitive DNA sequences) will have very limited systematic value (Baker et al., 1983). Of the various types of differential staining techniques, G-bands appear to be the most useful to systematics. With the advent of bone matrow
methods (Lee and Elder, 1980), field techniques (Baker et al., 1982), and high resolution banding (Yunis et al., 1980; Yunis and Prakash, 1982) the potential uses are great. The primary problems associated with determining G-band homology are that in some closely related taxa the G-band sequences can be radically rearranged (Baker and Bickham, 1984), genetic homology is assumed but not proven, and convergent evolution has been found in a number of cases. Chromosomal G-bands have been used to provide systematic hypotheses in a number of papers (Yunis et al., 1980; Baverstock et al., 1983; Baker and Bass, 1979; Baker et al., 1983). Additionally, chromosomal data have some value in defining cryptic species (Baker, 1984; Capanna, 1982).

ROLE OF MUSEUMS

One final note about the role of museums in systematic studies involving the more recent advances in biotechnology. The need for voucher specimens deposited in reputable museums is imperative. Museum personnel can play a most valuable and critical role in being sure that proper data are obtained, in order that specimens used in the newer types of studies are clearly referenced as a tissue source for specific systematic studies. Problems associated with such systematic studies and vital tissue collections are addressed in Dessauer and Hafner (1984) and Baker and Haiduk (1985). It is my opinion that we are at a most exciting time for discoveries in the area of mammalian evolution and systematics and the museums of the world are a most critical component to the proper scientific procedures associated with such discoveries.

SUMMARY

As new scientific methods have been developed that provide more detailed information on molecular and cellular biology of mammals, it is only logical that such methods be used to generate data for systematic studies. For maximum value such studies must not only maintain a state of the science for these modern techniques but they also must conform to modern museum standards. Proper voucher specimens must be prepared in a way to document which tissues and types of data were taken and what studies were made. If a museum contains specimens with such data, it significantly increases the value of that collection.

Methods that are commonly used include: differentially stained chromosomes, electrophoretic definition of proteins, immunological studies on proteins, amino acid sequences for a specific protein, DNA hybridization, and mitochondrial DNA studies by restriction endonuclease. How to evaluate the results of such studies and problems in establishing a credible data set are discussed. All techniques that have been extensively studied, show areas where that technique can provide definition in some parts of the classification of mammals. However, all techniques that have been extensively studied also show areas in which they provide little or no resolution. Clearly, knowing the strengths and weaknesses for any given method is critical to designing proper systematic research programmes. Within most mammalian taxonomic groups, systematic schemes are in need of critical test and the future belongs to a balanced study from a variety of systematical techniques including data from the classical, skin, skull, and other anatomical methods as well as those from more sophisticated molecular techniques that are now becoming available.

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REFERENCES


Baker: Advances in Systematic Mammalogy


