AN EMPIRICAL SYSTEM OF RANKING OF BIOLOGICAL CLASSIFICATIONS USING BIOGEOGRAPHIC COMPONENTS

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ABSTRACT. The Linnaean system of taxa and categories is philosophically based on an Aristotelian idealistic vision of the world. The phylogenetic system differs from the Linnaean system basically because it assumes that taxa at and above the species level correspond to entities in the real, material world. No adequate solution was proposed up to now for the problem of ranking in the phylogenetic system. A method of systematization is herein proposed in which a label corresponding to the biogeographic component of each taxonomic level is added to the name of the taxon. The name of the category itself may be omitted in the system, although the names of the taxa at the group of the family or below follow the rules of the code of nomenclature. This method corresponds to the association of information about the evolution of the ecosystems in which the ancestral species of the taxa lived to the history of genealogical relationships among the taxa. It includes information in the systematization additional to that of merely informing relative level of subordinated taxa. Also, it does not at all interfere with the names of the taxa in pre-existing classifications, as well as with the proposed Linnaean categories. Examples are given in the systematizations of the Anisopodoidea, Ditomyiidae, Scatopsidae (Diptera), and Fagaceae.

KEYWORDS. CLASSIFICATION; CATEGORY; SYSTEMATICS; BIOGEOGRAPHY; EVOLUTION.

INTRODUCTION

One of the most important contributions of the work of Willi Hennig was the proposal that the biological reference system - the classification of the organisms - should be a partially ordered system in which groups reflect precisely genealogical relationships among term-taxa. Phylogenetic systematics has stimulated the discussion of the basis of the biological classification. A series of papers have been published defining particular concepts about the structure of the classifications (HENNIG, 1966, 1969; NELSON, 1972, 1974, 1979; GRIFFITHS, 1974a, b, 1976; FARRIS, 1976, 1979; WILEY, 1979; etc.) and establishing measurements of its information (FARRIS, 1973, 1983; MICKEVICH, 1978; NELSON & PLATNICK, 1981; COLLESS, 1981; MICKEVICH, 1981; MICKEVICH & FARRIS, 1981; MICKEVICH & PLATNICK, 1989; ROHLF, 1982; etc.).

The information content of a classification may be understood as the information expressed through ranks and indentations of a set of terminal taxa placed into groups (MICKEVICH & PLATNICK, 1989). Most of the recent discussion about the information content of biological classifications has been focused on the information given by the groups, little attention being given to the problem of ranking. This is rather expected, since the groups are the very essence of the classifications. However, ranking, as part of the classification, adds information to the system and

the final content of the classification in certainly affected by the way groups are ranked.

A hierarchy, from the logical point of view, is an ordered system. Ordered systems can be partially or fully ordered. In most systems proposed of biological classifications the information about ranking is given through the addition of the name of a "category" or an index to the name of a taxon which shows only its relative position in the hierarchy. Hence, a classification is an association between a fully ordered system (the hierarchy of categories) to a partially ordered system (the hierarchy of taxa).

Actually, the word category originally meant in Greek "predicate" or "accusation". The original Linnaean hierarchy of categories included four levels: (1) the supreme genus, which is not a species of any higher genus; (2) the genera which are not the supreme genus, but whose species are also genera; (3) the genera whose species are not genera; (4) the species which are not genera. These levels were named, respectively, Class, Order, Genus, and Species (PAPAVERO, pers. comm.). It is obvious that LINNAEUS (1758) discovered levels of similarity relationships other than these four, as in plants and in insects, but they were not transformed into categories. This system is perfectly adequate for an idealist model of the world. In a non-idealistic model of the world, however, the set of taxa placed at the same category actually compose a class of entities which has no existence in the real world.

The ranking of taxa since the *Systema Naturae* has always had the problem of representing a larger number of discovered levels than the number of categories available. A solution later proposed has been the creation of an additional number of categories and the omission of many recognized levels in the classifications (with consequent loss of information). In practice, the Linnaean system of categories sometimes seems to have a "phenetic" approach: depending on how far a specialist is able to recognize a taxon, a higher or lower category that taxon will be placed in. A numerical, objective method could be eventually developed to apply consistently such "phenetic" criterion of ranking. However, the categories would still correspond to Aristotelian classes, with neither beginnings nor ends in time (GRIFFITHS, 1974b), and they would have no correspondence in the material, evolving world. Furthermore, it would add little qualitative information to the system in use as a whole.

The traditional system has resulted in very different ways of dealing with the same categories in the classification of different groups, from protozoans to arthropods or chordates. In the Callitrichidae (Primates), for example, the category "family" is associated with a rather small part of the Neotropical taxon Platyrrhini, which has an Afro-Oriental sister group. The maximum age of the Callitrichidae is about Lower Cretaceous and it includes less than 50 known species. In the Tipulidae (Diptera), on the other hand, the family rank is applied to a group including maybe at least 50 subordinated taxa, each of which probably had an ancestral species already present on Pangaea. The minimum age of this group is Lower Triassic or Upper Permian and it includes today about 14,000 known species. There are certainly "families" still more restricted than the Callitrichidae, and some others larger and older than the Tipulidae. These

differences must be considered excessive if categories are supposed to have any more consistent meaning other than to give the relative hierarchical positions between subordinated taxa.

THE PHYLOGENETIC-LINNAEAN SYSTEM
AND OTHER SYSTEMS PROPOSED

HENNIG (1966) tried to develop a truly phylogenetic system of classification regarding the problem of categories. He seems to have understood that temporal sequences corresponds to a natural fully ordered system which can be associated with the Linnaean hierarchy of categories. In his system, the traditional categories corresponded to given periods of time, obtained through paleontological information.

His system had no practical acceptance, except for the approximation given by MATILE (1990). Objections to a general acceptance of HENNIG's (1966) system are of different kinds: (1) to many authors, it seems reasonable to associate the Linnaean system - based on an Aristotelian idealist logic - to entities belonging to a temporal model of the world; (2) whatever period to which the traditional categories are fixed the whole system presently in use would suffer enormous changes; (3) many groups have no paleontological record available and they would have their minimum age obtained from distantly related taxa; (4) because of limitations of the fossil record, our paleontological knowledge for nearly all groups will probably expand quite slowly, but continuously - this successive approximation to the actual age of the groups results in changes in the classification and it would probably take too much time for the classification to reach a reasonable stability, if ever. GRIFFITHS (1976) has partially developed HENNIG's (1966) system with some modifications, but some limitations still persist.

Other methods of ranking have been proposed. HENNIG (1969) has used numerical indices to indicate ranking, which led to long series of numbers to substitute names of categories (e.g., "2.2.2.2.4.6.2.2. Diptera"). HENNIG (1969) originally used this system for the classification of "orders" of insects. WILLMANN (1989) more recently applied this system to Mecoptera. LOVTRUP (1977) modified this system reducing the length of the index. The worse problem is that numbers correspond to a linear sequence that do not fit well with branching structures which are continuously growing. Categories or indices can be also eliminated, expressing ranking exclusively through indentations across pages (see WILEY, 1981:205).

More recently, phylogenetic classifications have been erected with two different methods: sequencing and subordination (see NELSON, 1974). Both have been used adopting the Linnaean basic system of categories using at some levels traditional ranks as points of departure. To reflect unequivocally phylogenetic relationships among term-taxa in a classification, modifications have been proposed by FARRIS (1976), PATTERSON & ROSEN (1977), WILEY (1979), and AMORIM (1982a; in press) to solve particular internal limitations of both systems. However, all these systems, with the exception of HENNIG's (1966), are limited by the meaning of relative and artificial categories.

BIOLOGICAL CLASSIFICATIONS INCLUDING
BIOGEOGRAPHIC INFORMATION

An alternative way of erecting phylogenetic systems could be through an association of categories and biogeographical components. This system could be applicable to any group for which phylogenetic and biogeographical analyses have been undertaken. Different from HENNIG's (1966) system, it could be constructed entirely independently from the fossil record (although this information is always welcome to biogeographical analyses).

Some limitations to this system are immediately detectable and require solutions: (1) the system is now applicable only to taxa more recent than the Upper Triassic; (2) strong disagreements still exist between biogeographical reconstructions proposed by authors from different schools; and (3) any direct association between Linnaean categories and biogeographical components would promote radical changes to the traditional system.

The first of these problems, at least for the time being, apparently has no solution, since no biogeographical reconstructions are presently available for the period prior to the division of Pangaea. YOUNG (1986) has proposed an area cladogram for the Paleozoic, but it is based entirely on geological data. Although theoretically possible, reconstruction of biogeographical history of groups before the Triassic depends on detailed paleontological data presently unavailable for most groups of organisms. This is a considerable limitation, since there is a long period of organismic evolution between the Pre-Cambrian and the Triassic. All taxonomic levels in the hierarchy included in this period would have to be ranked using an arbitrary system of ranks or be referred using to an estimate of the minimum age based on fossils, if at all available.

The second problem has hardly a solution, but it is a matter of point of view. The application of biogeographical methods based on vicariance biogeography - panbiogeography (CROIZAT, 1958, 1964, 1976; CRAW, 1979, 1982, 1983), cladistic biogeography (ROSEN, 1978; PLATNICK, 1981; NELSON & PLATNICK, 1981; HUMPHRIES, 1981; PLATNICK & NELSON, 1984; HUMPHRIES & PARENTI, 1986), and its modifications (PAGE, 1987, 1988; WILEY, 1988a, b) - seem to have resulted in largely congruent reconstructions for many groups. Most of the recent disputes among these methodological variations are basically focused on how to interpret cases of incongruence, rather than on the congruent patterns. These reconstructions seem to largely agree about the existence of a long series of vicariant Mesozoic-Tertiary events caused by tectonic movements in the history of many groups of taxa with worldwide distributions.

The more serious problem concerns the prior biogeographical reconstructions, namely, dispersionism and refugianism. Vicariant theories predict that increasing numbers of known patterns of distribution will provide greater strength to the proposed reconstructions. Therefore, there is less and less space for prior reconstructions and imprecise criticisms made by these schools to vicariant methodologies. It is quite improbable that strongly competing "biogeographical classifications" can be produced by dispersionists or refugianists . The biogeographical reconstructions proposed by these schools push indiscriminantly termi-

nal speciation events as evidenced in biological cladograms to a short period of time at the Upper Tertiary-Quaternary boundary. Their methodological tools have not acquired sufficient precision to construct a system of biogeographical ranking as herein is proposed.

Different biogeographical reconstructions may indeed be proposed by authors using different vicariant methods. However, it can be expected that disagreements in the association between vicariant events and geological events in different reconstructions will refer to a limited number of components. The use of artifacts in the systematization may help to discern between patterns with large agreement from others with strong incongruencies. On the other hand, it is necessary to recognize that such an exaggerated expectancy of stability in biological classifications sustained many times in the literature seems to be a by-product of a Platonic-Aristotelian idealist vision of the world.

Finally, the question of how to associate components and ranks has a solution. Instead of changing radically the Linnaean system, the entire traditional structure of the names of the taxa can be maintained (if truly phylogenetic) and only labels corresponding to the biogeographical component would be *added* to the name of the taxa. This independence between Linnaean categories and biogeographical information in the systematization has strong advantages for the progressive development of a new biological reference system: (1) traditionalists may simply not use the biogeographical labels; (2) the use of the system would not affect the groups for which this knowledge is unavailable; (3) an eventual instability promoted by changes in the biogeographical reconstructions would not alter the taxonomic nomenclature; and (4) modifications of the Linnaean categorization in given classifications (particularly involving the categories at or below the group of the family) would have no consequences at all for biogeographical ranking.

The addition of a name to the "category plus taxon" set will not necessarily render classifications cumbersome. There seems to be little emphasis nowadays on higher categories (which can be actually ignored). At the family level and below, on the other hand, rigidly ruled by the international codes of nomenclature, the endings and italics on the name of the taxa make names of categories of family and genus groups virtually superfluous.

A major problem is how to name components - the biogeographical categories - in the system. An initial possibility would be to use numbers to designate different levels. However, as already noted, numbers do not fit well to hierarchic system. The inclusion of new, intermediate levels would either break the sequence or change the whole numeration below that level. An alternative would be the use of a name derived from the geological nomenclature or, when not misinformative, from geopolitical areas. Modifying GRIFFITHS' (1974b) proposition, the names could be, for example, *Pangaeotaxon, Laurasiotaxon, Gondwanotaxon, Neotropicotaxon,* etc. However, the number of biogeographical components for the whole world between the Triassic and the Recent is certainly too large, demanding a disproportionally large number of complete names. A third alternative would be to use labels which are abbreviations of the geological/geopolitical areas corresponding the components. It would certainly take some time and discussion until

one uniform set of labels could be accepted. However, the existence of one set of divisions in the history of the groups and accumulation of knowledge about patterns promises an acceptable stability to the system in the near future, at least for most levels.

It is interesting to note that a generalized , biological area cladogram (congruent with a geological area cladogram) is a hierarchical system, as with any spatio-temporal evolving entify, in the sense of being a partially ordered system. Consequently, two sister components cannot be attributed to the same level. The real entities which this pair of sister components represent originate simultaneously, but they cease to exist as individuals at different times (if they become further subdivided or extinct). Therefore, the system furnishes ranking, in the sense of a fully ordered system, indirectly through an association of the origin of the components and the levels in the time sequence. From this perspective, the system is a derivative of HENNIG's (1966) proposal.

From the point of view of categories, the method of ranking proposed herein is essentially different from any other proposed until now, except that of HENNIG (1966). The use of biogeographical component information in the biological system correspond to the association of two different hierarchical systems, each of which relates to the real (material) world. One system is the phyletic history of a given taxon, obtained through phylogenetic analysis. The other is the history of the biota in which the ancestral species of that taxon lived earlier, obtained through biogeographical analysis of many groups. Furthermore, the relationship between taxa (phyletic information) and biogeographical components (biotic information) is an clement/system relation (see GRIFFITHS , 1974b) - the phyletic stems are true parts of evolving ecosystems. In other words, it is not an artificial system of ranking. Moreover, the association between these two systems not only fulfills the need of ranking in biological classifications, but also adds information about the history of ecosystems to the content of the classification. All taxa in the system with the same biogeographic label supposedly have belonged to the same entity or system, a biotic ancestral community.

This system is still developed in a limited scope. Components refer to areas in which a set of species have interacted through a period of time. It is theoretically possible to discern even more precisely the ecosystem information in ranking, including, for example, distinctions between marine and continental, terrestrial and fresh-water, or open-formation and forest ecosystems. Biogeographical reconstructions now relate more to space than ecosystems. It seems reasonable to expect that in the future more complex reconstructions for evolution of ecosystems will become available, making it possible to propose a more complete reference system.

ADDITIONAL NECESSARY CONVENTIONS

Peculiarities of individual taxa demand additional conventions. A quite common case is that of biological area cladograms in which two or more levels are "accumulated" because of extinction of taxa (or of sample errors). In the system it is possible to omit or include intermediary levels. The second option is preferred

here, since it is more informative about the previous history of a group. Component labels of intermediate levels can be included together with the labels of term-taxa. This is useful since it allows us to refer to intermediate levels of a phylogeny without creating new taxa.

Another point of concern is area cladograms with "replicated patterns" (about which I will consider in more detail elsewhere). Area cladograms of one or more groups sometimes have components with two or more subcomponents with the same term-information (eventually separated in the same sequence). This is an indication that there was an earlier period of history in an area which included: (1) one or more earlier division events, (2) secondary sympatry in species generated by these earlier events, and (3) division of these two or more sympatrid[1] species by more recent events, which results in the observable disjunctions. The components with sympatrid subcomponents (at the immediate subordinated level), on the one hand, and the components will allopatrid subcomponents, on the other hand, refer to different, although related, historical entities. In the system proposed here when there are two or more replicated levels, the label of the more inclusive one is associated with a number (except for the first) which indicates its position in the replication sequence. Obvious examples of replication patterns are the groups with circum-antarctic distributions (e.g., BRUNDIN, 1966; HUMPHRIES, 1981).

Another point still to be developed is how to indicate cases of dispersion. Dispersion does not correspond to evolution of a system as a whole, so it will have to be indicated as a particular event. Cases of replicated patterns, with evident secondary biotic sympatry, are indicated as above. Cases of individual dispersion are not present in the examples used here, so this problem is left to be handled elsewhere.

EXAMPLES OF APPLICATION OF THE SYSTEM

Applications of this new system are given below for groups which already have proposed biogeographical analyses. A biological area cladogram, based on different partial reconstructions of intercontinental relationships (MUNROE, 1974; PLATNICK, 1976; ROSEN, 1978; HUMPHRIES, 1981; AMORIM, 1982b, 1987) summarized in AMORIM & TOZONI (submitted), is herein used as the basis for the system (Fig. 1). The group$^+$ notation (AMORIM, 1982) is used to name the fully resolved inclusive taxa in sequenced classifications. The group* notation (AMORIM, in press) is used to name inclusive polychotomous taxa in sequenced classifications.

The Linnaean structure of the classification of the Anisopodoidea (Diptera) (Example 1) comes from AMORIM & TOZONI (submitted). The classification of the Ditomyiidae (Diptera) (Example 2) uses most information from MUNROE (1974). The classification of the Rhegmoclematini (Example 3) comes from AMORIM (1982b). The classification of the group *Fagus$^+$* was erected using HUMPHRIES' (1983) phylogeny for the Fagaceae (Example 4). The abbreviations are referred to in the legend of Fig. 1.

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[1] Prof. Nelson Papavero (pers. comm.) correctly observed that the word *sympatric* - largely used in biogeography - actually means "those who have the same father ($\pi\alpha\tau\epsilon\rho$)", while *sympatrid* (as well as allopatrid, or parapatrid, etc.) is the correct form for "those who have the same land of origin ($\pi\alpha\tau\rho\iota\alpha$)".

Example 1 -

P⁴ Anisopodoidea
   P-G Olbiogastridae
       GTe-CAn-NoAuS-NoS new subfamily 1
           Lobogaster
           Carreraia
       GTr Olbiogastrinae
          AfOr new tribe 1 [new genus 1]
          NoAu Olbiogastrini
             AuN new genus 2
             NoN *Olbiogaster*
   P³ group Anisopodidae⁺
      P Anisopodidae
         L *Sylvicola*
         G new genus 3
      P² Mycetobiidae
         P-G-GTr new subfamily 2 [*Valeseguya*]
         P Mycetobiinae⁺
            L Mycetobiinae [*Mycetobia*]
            G-GTr new subfamily 3
               AfOr *Mesochria*
               NoN new genus 4

Example 2 -

P² Ditomyiidae
   P group *Ditomyia*⁺
      L *Ditomyia*
      G group *Nervijuncta*⁺
         GTe-CAn *Nervijuncta*
         GTr group *Asioditomyia*⁺⁺
            AfOr-Or group *Asioditomyia*⁺
               Asioditomayia
               Celebesomyia
            NoAuN-NoN* group *Rhipidita*⁺
               NoN *Rhipidita*
               NoN *Calliceratomyia*
   P group *Symmerus*⁺
      L² *Symmerus*
         L S. (*Symmerus*)
            AA-PaE *S. antennalis*
            EA group *S. lautus*⁺
               PaW group *S. balticus*⁺
                  Plesion *S. balticus*
                  S. annulatus
                  S. nobilis
               NaE *S. lautus*
        L S. (*Psilosymmerus*)
           AA group *coqulus*⁺
             NaW *S. coqulus*
             PaE group *brevicornis**
               S. brevicornis, sed. mut.
               S. nepalensis, sed. mut.
               S. pectinatus, sed. mut.
               S. fuscicaudatus, sed. mut.
               S. elongatus, sed. mut.
           EA-NaE group *vockerothi*⁺
             S. vockerothi
             S. uncatus

G *Australosymmerus*
    GTe-CAn^3 group *A. (Australosymmerus)*[++]
        CAn^2 group *A. (Australosymmerus)*[+]
            CAn *A. (Australosymmerus)*
            CAn *A. (Crionisca)*
        CAn-NoAuS group *A. (Ventrilobus)*[+]
            AuS *A. (Ventrilobus)*
            NoS *A. (Araeostylus)*
    GTr-NoAuN-NoN^2 group *Velliocauda*[+]
        Velliocauda
        Tantrus
        Calosymmerus
        NoN *Melosymmerus*

Example 3 -

P^4 Rhegmoclematini
    P-G-GTe-CAn-NoAuS *Diamphidicus*
        AuS *D. australis*
        NoS *D. chilensis*
    P^3 group *Rhegnoclema*[+]
        P *Rhegnoclema*
        P^2 group *Parascatopse*[+]
            P *Parascatopse*
            P *Rhegnoclemina*
                L *R. (Rhegnoclemina)*
                G-GTr-NoAuN group *Neorhegnoclemina*[+]
                    NoN *Neorhegnoclemina*
                    AuN *Austroclemina*

Example 4 -

P group *Fagus*[+]
    L *Fagus*
    G-GTe *Nothofagus*
        NG/NC4 group *perryi*[+]
            NG/NC-NG *N. perryi*
            NG/NC3 group *nuda*[+]
                NG/NC group *nuda*
                NG/NC2 group *brassii*[+]
                    NG/NC group *brassii*
                    NG/NC-NG group *carrii*
        CAn* group *menziensii*[*]
            CAn group *menziensii, sedis mutabilis*
            CAn group *fusca, sedis mutabilis*
            CAn-NZ group *solandri, sedis mutabilis*
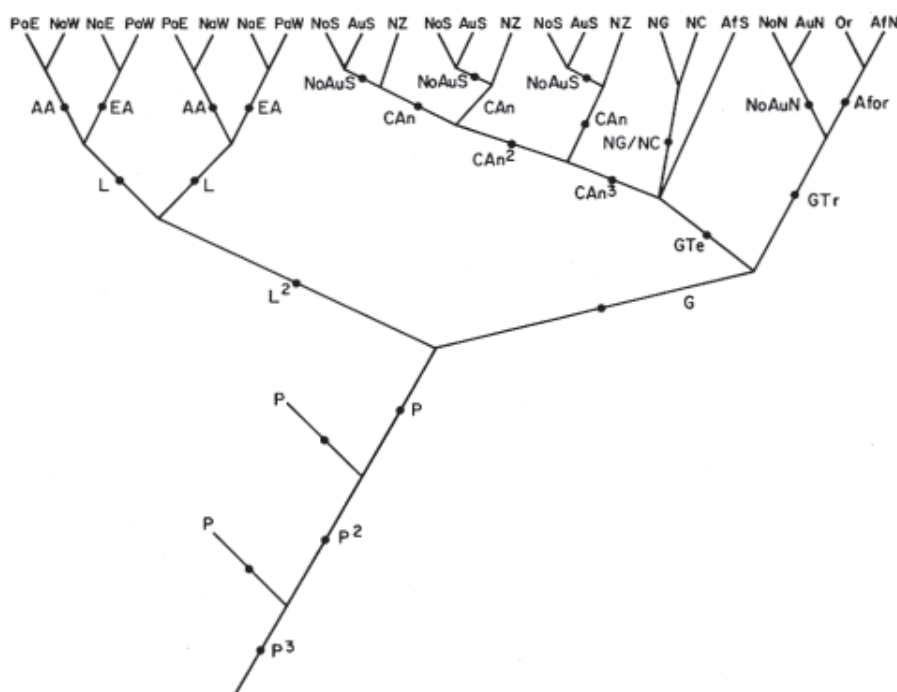   CAn group *pumilio, sedis mutabilis*

Fig. 1 - Area cladogram for the history of intercontinental relationships. Abbreviations of components: AA - Asiamerica; AfN - Northern Afrotropical; AfOr - Afro-Oriental; AfS - Southern Afrotropical; AuN - Northern Australian; AuS - Southern Australian; CAn - Circumantarctic; EA - Euramerica ; G - Gondwana; GTe - Temperate Gondwana; GTr - Tropical Gondwana; L - Laurasia; NaE - East Nearctic; NaW - West Nearctic; NC - New Caledonia; NG - New Guinea; NoAuN - Neotropical-Northern Australian; NoAuS - Neotropical-Southern Australian; NoN - Northern Neotropical; NoS - Southern Neotropical; NZ - New Zealand; Or - Oriental; P - Pangaea; PaE - East Palaearctic; PaW - West Palaearctic. See text for explanations.

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