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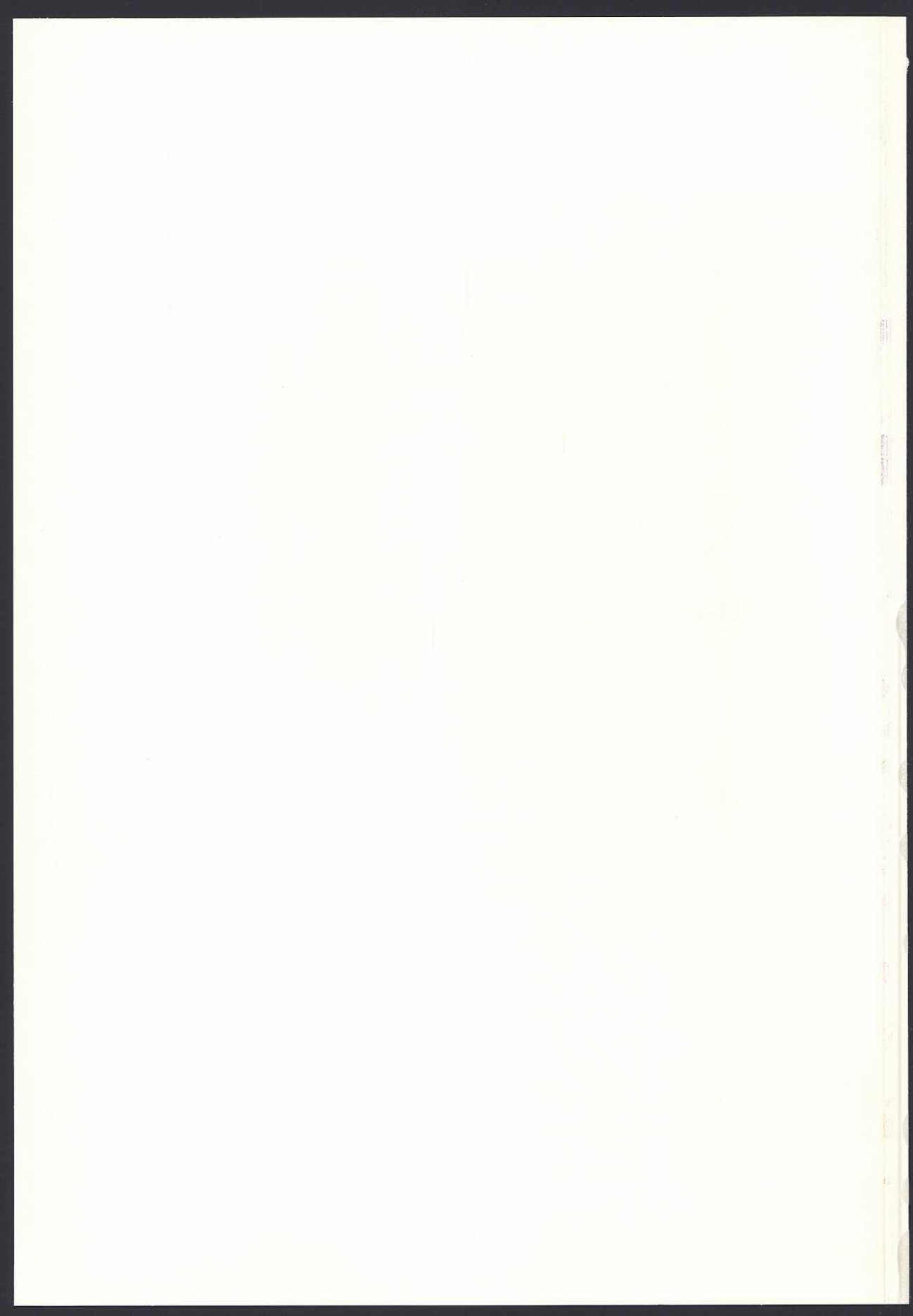
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TREE-THINKING
AND NEMERTEAN SYSTEMATICS

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Tree-thinking

and Nemertean Systematics

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Dissertation

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Fakultetsopponent: Dr. Jon L. Norenburg, Department of Invertebrate Zoology,
Smithsonian Institution, Washington D.C., USA.

"Jag sa: Kom så ger vi fan i debatten om betydelsen i konsten.
Här har vi penslar och färg, det räcker till och vi målar liksom som vi vill.
För livet är lek och spel, och vi leker våra spel, och går en stund på jorden,
ja vi går en stund på jorden".

Ulf Lundell - Och går en stund på jorden (1976)

"Du kan foga dej i flocken
Du kan kuva ner din kraft
Men aldrig se dej i dom ögon
du en gång haft"

Ulf Lundell - Laglös (1982)

"The act of arranging things into groups seems virtually indispensable to every sort of intellectual endeavor. In all branches of learning we encounter kinds and classes. Chemists have their molecules and elements, botanists their phanerogams and cryptogams, moralists their sins and peccadillos, grammarians their nouns and verbs, dramatists their comedies and tragedies. It is hard to imagine how we could get along without classifying. We cannot generalize when we concern ourselves merely with single objects. Even where we are mainly interested in one individual thing, we compare it and its attributes to others. Whatever the topic of discourse - be it gods, organisms, or statues - we inevitably talk and think about groups. Hence the problems of classification should interest everyone who seeks to view the various branches of knowledge in a larger perspective"

Michael T. Ghiselin (1980)

Tree-thinking and Nemertean Systematics

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Abstract: Classification and systematization are fundamentals in the organismal world because they form the basis for our ability to generalize and distinguish various things. Systematics is thus of major importance in biology.

This thesis is a result of phylogenetic and biogeographic studies of a group of marine nemerteans (Nemertea, Hoplonemertea, Eurentantia). The main theme is trees and tree-thinking, covering aspects of phylogenetic systematics like homology vs. homoplasy (I), cladistic analysis (II, III), historical biogeography (III, IV), and philosophy of taxonomy and systematics (V, VI).

Using a set of more than 100 cladistic analyses (I) we show that nemerteans are no more homoplastic than any other groups of animals or plants. Furthermore, we argue that homoplasy and homology are a strictly historical concepts without relevance outside a phylogenetic hypothesis. Hence, a phylogenetic analysis is a prerequisite for all homology/homoplasy statements.

The cladistic analysis of the eurentantic nemerteans (II) is the first phylogenetic hypothesis of the group and shows that the previous classification, in many parts, is non-monophyletic. Hence there are no logical arguments for keeping the old classification. Therefore, the hypothesis is used as the basis for a systematization of these nemerteans (VI), where all names strictly refers to monophyletic assemblages. In the same paper (VI) I also provide a historical and theoretical account of tree-thinking in nemertean systematics. Paper V explores the philosophy of names and is thus a theoretical basis for the systematization in paper VI. The evolution of the eurentantic nemerteans is studied from a biogeographical point of view in paper III. Eastern Indian Ocean is suggested as the most likely present area being a part of the ancestral area (sea) of the Eurentantia. Besides studying the evolution of the Eurentantia, I present a hypothesis of the historical relationships between the modern oceans. This latter hypothesis, is based on a cladistic biogeographic analysis of a combined data set of eurentantic nemerteans and acanthuroid fishes. I also provide a discussion on concepts and components in cladistic biogeography (IV).

Key words:- Cladistics, Phylogeny, Classification, Systematics, Systematization, Taxonomy, Homology, Homoplasy, Taxa, Clade, Evolution, Reference, Meaning, Individual, Philosophy, History, Names, Definition, Diagnosis, Biogeography, Evolution, Nemertea, Hoplonemertea, Polystilifera, Eurentantia

This thesis is based on the following papers, referred to by their Roman numerals in the text. HÄRLIN and SVENSSON refers to the same person.

- I. SUNDBERG, P., AND M. SVENSSON. 1994. Homoplasy, character function, and nemertean systematics. *Journal of Zoology, London* **234**: 253-263.
- II. HÄRLIN, M., AND P. SUNDBERG. 1995. Cladistic analysis of the eureptantic nemerteans (Nemertea, Hoplonemertea). *Invertebrate Taxonomy* **9**: 1211-1229.
- III. HÄRLIN, M. 1996. Biogeographic patterns and evolution of the eureptantic nemerteans. *Biological Journal of the Linnean Society* (In press).
- IV. HÄRLIN, M. (submitted). Concepts and components in cladistic biogeography.
- V. HÄRLIN, M., AND P. SUNDBERG. (submitted). Taxonomy and philosophy of names.
- VI. HÄRLIN, M. 1996. Tree-thinking and nemertean systematics, with a systematization of the Eureptantia. *Hydrobiologia* (accepted).

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Front cover by Carina Härlin

Preface

In October 1791 George Cuvier wrote a letter to Christian Heinrich Pfaff expressing his views on Jussieu's work. "His merits is not really in very detailed descriptions, or in a large number of species being described, which is often only a sign of a lack of criticism, but it is in the philosophical manner of seeing things, and finding the delicate threads by which plants may be held together, making the whole a painting" (from Stevens, 1994).

My impression is that something similar goes for the present thesis, even though not claiming that it is comparable to the work of Jussieu. Nevertheless, the merits of this thesis is not in the descriptions of nemertean morphology, others have done, and continue to do that much better than I do, but rather in the study of relationships among natural groups. One often hears that no hypothesis is stronger than the observations (data) used to erect the hypothesis with the corollary that we must study our organisms more carefully. This is probably true, but it is based on the notion that observation and theory are independent. However, I believe it is equally true that no observations (data) are stronger than the hypothesis within which the observations are made. Thus, there are no such things as theory independent observations. My hope is that the reader will keep this in mind when browsing this thesis.

Mikael Härlin
Göteborg
February, 1996

"The great tree of life which fills with its dead and broken branches the crust of the earth, and covers its surface with its ever branching and beautiful ramifications"

(Darwin, 1859)

Introduction

Natural order, in various guises, was the aim for scientists long before Darwin. The Greeks searched for the great chain of being (*scala naturae*), where continuity of characters and taxa from "simple" to more complex were of paramount importance. This idea have persisted consciously, or unconsciously, as a central tenet in western philosophy of natural order ever since (Lovejoy, 1936; Stevens, 1994). In France during the 18th and 19th centuries Lamarck, Jussieu, and to some extent de Candolle and Cuvier strived to represent the natural order as a continuous series of taxa from simple to complex in their classifications, that is, the *scala naturae* was the world-view for them and their contemporaries. It was, however, becoming common to view natural order as an analogy with geographic maps. de Candolle and Cuvier, for instance, argued more in favour of discontinuities but without making a clear brake with the tradition of continuity (Stevens, 1994). Stevens (1994) even argues that the notion of continuity lived on, at least unconsciously, well into the 20th century. Examples of this can be seen within nemertean systematics (paper VI; Sundberg *et al.*, 1996). Jussieu's work is generally acknowledged to be the most influential of early attempts to elucidate the structure of natural relationships. His approach was widely adopted by botanists and it also influenced zoologists like Cuvier. By the end of the 18th century it had become commonplace to claim that analytical classifications (systems), in which groups where successively subdivided, were necessarily artificial while the formation of successively larger groups (upward classification, method or synthesis), was believed to lead to natural arrangements of organisms (Stevens, 1994). Outside France, scientists at this time did not discuss the natural system explicitly even though their systems more or less were reflections of the *scala naturae*, or at least of the continuity of taxa and characters. It was not until 1859, when Darwin published his now famous *The Origin of Species*, the world-view changed and the tree of life became the metaphor of natural groups, and evolutionary history have occupied the human mind ever since. Geological information and the geographic distribution of organisms, among other things, led Darwin to introduce an evolutionary world-view and among "... historians of science, the 'Darwinian revolution' has always ranked alongside the 'Copernican revolution' as one of those episodes in which a new scientific theory symbolizes a wholesale change in cultural values" (Bowler, 1989). Biogeographic data was of major importance for Darwin

when reaching his evolutionary theory. Ghiselin (1969) even argues that "In *The Origin of Species*, the strongest positive argument for evolution is the geographical one ...". Darwin (1859: 300-303) himself wrote "In considering the distribution of organic beings over the face of the globe, the first great fact which strikes us is, that neither the similarity nor the dissimilarity of the inhabitants of various regions can be wholly accounted for by climatal and other physical conditions" and continues "A second great fact which strikes us in our general view is, that barriers of any kind, or obstacles to free migration, are related in a close and important manner to the differences between the productions of various regions" and "A third great fact ... is the affinity of the products of the same continent or of the same sea, though the species themselves are distinct at different points and stations". He concludes "We see in these facts some deep organic bond, throughout space and time, over the same areas of land and water, independently of physical conditions. The naturalist must be dull who is not led to inquire what this bond is. The bond is simply inheritance, the cause which alone, as far as we positively know, produces organisms quite like each other, or, as we see in the case of varieties, nearly alike". For Darwin and contemporaries like Wallace, biogeographic distributions was used as an argument for evolution while today, phylogenies are also used to study the historical distributions of biological clades (III, IV).

Darwin used a single illustration in *The Origin of Species* - a phylogenetic tree. The metaphorical tree was important for Darwin when describing and discussing the evolutionary history of species, and it was furthermore the beginning of what now is known as phylogenetic systematics. Even though systematists grasped the theory of evolution and incorporated it into their work, they did so only as an after-the-fact explanation of their taxonomic groups. Thus, the same taxa that was recognized before Darwin were still valid after Darwin's book. Evolution was only used to explain their existence. It took almost 100 years from the publication of *The Origin of Species* until someone provided a method for detecting natural relationships. Zimmerman (1931) and Hennig (1950, 1966) developed a method, or rather, a philosophy for how to detect genealogy (phylogeny). They were the first who clearly distinguished monophyly from paraphyly and argued that only monophyletic assemblages are natural groups. If Darwin started a revolution in human thinking in general and biological thinking in particular, Hennig provided the basis for a revolution within biological systematics. Today, phylogenetic systematics qualifies as a school book example of a scientific revolution *sensu* Kuhn (1970). Anomalies are accumulating and basic concepts like species, taxon, homology are questioned and rapidly changing meaning. Present tree-thinking is quite different from Darwin's and his contemporary practising taxonomists (paper VI). Species concepts within the Darwinian paradigm may serve as the best example of a scientific revolution; from a biological or neo-darwinistic species concept to the cladistic or phylogenetic species concepts discussed today (e.g. Ehreshefsky, 1992; Baum and Donoghue, 1995). One major advantage to be gained from these discussions is the importance to distinguish phylogeny from taxonomy (VI) and thus relegating the ranking

problem to a secondary and arbitrary endeavour. The result will be that we get over rather than solve the problems with species concepts and taxa in general. Hence, "... intellectual progress usually occurs through sheer abandonment of questions together with both the alternatives they assume - an abandonment that results from their decreasing vitality and a change of urgent interest. We do not solve them: we get over them. Old questions are solved by disappearing, evaporating, while new questions corresponding to the changed attitude of endeavour and preference take their place" (Dewey, 1910).

The main theme in this thesis is trees and tree-thinking, covering aspects like homology and homoplasy (I), cladistic analysis (II, III), historical (cladistic) biogeography (III, IV), philosophy of taxonomy and systematics (V, VI). In this summary I will try to develop some of the ideas in these papers and provide a discussion aiming to put the papers into a broader context. I also give a short review of the phylogenetic and biogeographic results obtained in papers II and III.

Trees and Clades

Beginning with Darwin, the tree-icon have developed into one of the most important and influential illustrations in biology. Darwin argued that descent with modification is the cause for such a tree-like pattern. Fairly little have been devoted to this aspect of evolution compared with how much effort that have been put into the process of natural selection. Haeckel (1866, 1868) developed and discussed the tree-icon of evolutionary history in more detail and was also the one who popularized Darwin's ideas (Oppenheimer, 1987). He transformed Darwin's diagrammatic tree into more tree like pictures like oak trees (Oppenheimer, 1987), thus, in a sense he illustrated Darwin's words (the citation in beginning of this summary may serve as an example of Darwin's writing). Oppenheimer (1987), however, argues that Haeckel rather than trying to illustrate Darwin's words tried to improve on nature. As a skilful artist he was not always so accurate with facts and he was often accused of scientific falsification (Oppenheimer, 1987). The more artistic (or derivations of it) way of illustrating phylogenetic trees have dominated many text books in the 20th century (e.g. Romer and Parsons, 1978; Willmer, 1990) which often makes them difficult to interpret. Cladistics returned to the Darwinian way of illustrating phylogenetic relationships. However, the interpretation of trees have varied (O'Hara, 1992; paper VI) through time. In 1895, for instance Bürger made comments like "*Hubrechtia desiderata* ist die einzige mir bekannte Nemertine, welche die Kluft zwischen Proto- und Heteronemertine überbrückt" and "Mit dieser an Formen ausserordentlich reichen Familie [Lineidae] schliesst die Ordnung der Heteronemertinen ab. Sie steht and der Spitze des einen Hauptastes, welcher von dem kurzen Stamme der Protonemertinen abgeht ...". In a similar vein Brinkmann (1917: fig. 28) argues that "Die Entwicklungsreihe *Probalaenanemertes* - *Balaenanemertes* zeigt auch, was dieses Organ [Blinddarm] betrifft, eine schöne Reihe

fortscreitender Reduktionen...". Similar statements are common at this time and they indicate a core of continuity (*scala naturae*) rather than discontinuities despite their relationship being depicted as a tree (VI), and O'Hara (1992) argues that sequencing of contemporary taxa in a link from primitive to more advanced is a common narrative device in natural history. Nemertean systematics still suffers from a inconsistent interpretation of evolutionary history and a seriously flawed tree-thinking (VI; Sundberg *et al.*, 1996; Sundberg, 1993). One reason for this is the continuous emphasis on anagenetic change as a useful tool in both phylogeny reconstruction and taxonomic practice.

The introduction of cladistic philosophy (Hennig, 1966) changed the way systematists view and interpret phylogenetic trees. Contemporary taxa are no longer sequenced from primitive to advanced. Instead they are viewed as sister taxa sharing a common ancestry. This is a corollary of only cladogenetic events being recognized as important in the sense of conveying evolutionary relationships. Anagenetic change can never be quantified, and in such a continuum only arbitrary delineations can be made (Lidén, 1990; Frost and Kluge, 1994). Cladogenetic events, on the other hand, offer non-arbitrary delineations of historical entities. Given the phylogenetic hierarchy, it is important to distinguish between phylogeny and taxonomy (VI), or, between grouping (phylogeny reconstruction) and ranking (taxonomy) in the words of Donoghue (1985). O'Hara (1988, 1992, 1993) in his historical accounts of systematics called it chronicle and history and identified it as a general distinction made in all historical sciences. A chronicle is a series of statements arranged in chronological order but not accompanied by any explanation or interpretation, while a historical statement contains the explanation of events and interpretations of their significance. Using the terminology of O'Hara (1988), phylogeny is the chronicle and the taxonomy (classification, or rather systematization) is a historical statement representing the phylogeny. A major advantage gained from separating phylogeny from taxonomy is that both can be investigated in some detail, without too much confusion (V). Phylogeny is fractal (self-similar) (Green, 1991) and as such possible to generalize. Given the historical and fractal nature of phylogeny, we must realize that we live in the midst of the evolutionary process giving rise to the ever branching phylogenetic hierarchy and our statements (taxonomy) about segments (clades) of this hierarchy are historically constrained (O'Hara, 1993; Danto, 1985; Atran, 1990). O'Hara (1993) used an analogy between cartography and phylogenetic trees to illustrate the nature of generalizations and their importance for phylogenetic systematics. Just as maps are representations of the earth and subjected to what is called cartographic generalization, so are diagrams of the natural system like phylogenetic trees representations of the evolutionary chronicle. Depending on ones terminal units (genes, organisms, clades) the hypotheses of monophyly may differ. For instance, two genes may have different evolutionary histories and at the level of organism or clade they may lead to different hypotheses of monophyly. Thus, it is important to keep in mind that we search for monophyletic assemblages from an *a priori* chosen starting point, i.e. monophyly is a relative concept (Lidén, 1990; O'Hara, 1993; Frost and Kluge,

1994). Lidén (1990) illustrated this by pointing out that the zygote is not a monophyletic unit itself with regard to its cells, but together with all cells descending from it, it forms a monophyletic assemblage.

How to relate characters and organisms to groups and groups to organisms and characters is an old quest in biological systematics (Stevens, 1984, 1994). A unifying concept in this discussion have been homology. The distinction between affinity (recognized by homology) and parallelism (recognized by analogy) was first made by MacLeay (1821), but later discussed and clarified by Owen (1843) and Strickland (1846). The concept of homology itself is, however, much older and Russell (1916) traces it back to Aristotle. Inference of animal relationships and constructing classifications were, in the early 19th century, based on comparative anatomy as exemplified by the studies of Owen, Cuvier and Geoffroy (see Panchen, 1994 for further discussion). The data were obtained by dissection and close observation. Owen (1843) distinguished analogue (a part or organ in one animal which has the same function as another part or organ in a different animal) from homologue (the same organ in different animals under every variety of form and function). At this time homology was more or less equal to similarity. Hence, if a organ was considered to be similar enough in two species - it was considered homologous. More specifically, according to Owen, two structures are homologous because they are derivations of the same structure in the archetype. Owen's archetype represented a generalized and primitive condition from which, for instance, the skeletons of real vertebrates were derived - the human skeleton, representing the nearest approach to perfection, was furthest removed from the archetype (Panchen, 1994). Rupke (1993) argues that this kind of distinction is of considerable theoretical importance not only to Owen's views but to all non evolutionary explanations of homology. As mentioned by Panchen (1992), Owen's concept is Platonic, i.e. similar to Plato's theory of *forms* or *ideas*. In the beginning these theories were generalizations from classes of objects. Later, however, Plato claimed that the only real things were the *ideas*. This is exemplified by his famous metaphor of the cave, where prisoners in the cave are constrained so that they can see only the wall opposite the entrance; their view of the world outside (the world of *ideas*) is simply that of shadows cast by objects in the real world. The shadows are the objects of sensory perception: the real world consists of *ideas*. Hence, at this time homology was a non evolutionary concept.

For Darwin (1859) the meaning of homology is different. In the glossary he explains homology as "That relation between parts which results from their development from corresponding embryonic parts, either in different animals as in the case of the arm of man, the fore-leg of a quadruped, and the wing of a bird; or in the same individual, as in the case of the fore and hind legs in quadrupeds, and the segments or rings and their appendages of which the body of a worm, a centipede, &., is composed. The latter is called *serial homology*. The parts which stand in such a relation to each other are said to be *homologous*, and one such part or organ is called a *homologue* of the other" (emphasis in original). Analogy, on the other hand is explained as "The resemblance of structures which

depends upon similarity of function, as in the wings of insects and birds. Such structures are said to be *analogous*, and to be *analogues* of each other". Explaining his views further, Darwin (1859:351) argues "... if I do not greatly deceive myself, ... the Natural System is founded on descent with modification;- that the characters which naturalists consider as showing true affinity between two or more species, are those which have been inherited from a common parent, all true classifications being genealogical;- that community of descent is the hidden bond which naturalists have been unconsciously seeking, and not some unknown plan of creation, or the enunciation of general propositions, and the mere putting together and separating objects more or less alike". Thus the Darwinian view of homology is one of characters related through common descent. At some points, Darwin is very close to the phylogenetic view of homology (or rather phylogenetic systematics is very close to Darwin's views) as determined by congruence among all possible characters. He writes "The importance, for classification, of trifling characters; mainly depends on their being correlated with many other characters of more or less importance" (Darwin, 1859). Despite, the Darwinian heritage of a phylogenetic view of homology, the concept is still controversial and often discussed (e.g. paper I, IV; Ghiselin, 1984; Rieppel, 1992; Panchen, 1994; Lauder, 1994; Nelson, 1994). In fact, an edited book was recently devoted to the topic (Hall, 1994). Even among advocates of a phylogenetic or cladistic homology concept, there sometimes is a (maybe unconsciously) echo of pre-Darwinian reasoning. For instance, Lauder (1994) in his discussion of a phylogenetic homology concept agrees with Patterson (1982) who argues that homologous similarities are those that *define* natural or monophyletic groups of organisms. However, natural groups do not possess defining properties (Ghiselin, 1966, 1969, 1981, 1984, 1987, 1995; Hull, 1989; II, IV, V). Natural groups are like individuals rather than classes and as such they cannot be defined, they are whether we find them or not. Concreteness and non-instantiability are the fundamental criteria of individuality (Ghiselin, 1995). The individuality thesis developed by Ghiselin (1966, 1969, 1974, 1987) and later by others (e.g. Hull, 1989) have had major impact on systematic thinking and is also the foundation in the present thesis. It is not only species that are individuals; all taxa are. Even though these ideas are getting more and more general acceptance it is not uncommon that clades (individuals) are defined rather than discovered. I believe it is fundamental to distinguish between two ways of viewing phylogenetic analysis in order to get a better understanding of the groups we are studying and avoid unnecessary class connotations. On the one hand a phylogenetic analysis can be seen as a tree building or reconstruction procedure and on the other as a way of choosing among possible trees. A tree building approach implies that the characters give the tree, i.e. that the clade exists because of the characters supporting it, while in the latter approach congruence among characters are seen as a means for choosing tree(s) from the pool of all possible trees. For a given number of terminal taxa there are a given number of trees, and these trees exist irrespective of the characters. For instance, with three taxa A, B, and C there are only three

possible resolved rooted trees. Either is A sister to B leaving C out, or A is sister to C leaving B out, or B and C are sisters leaving A out (FIG. 1).

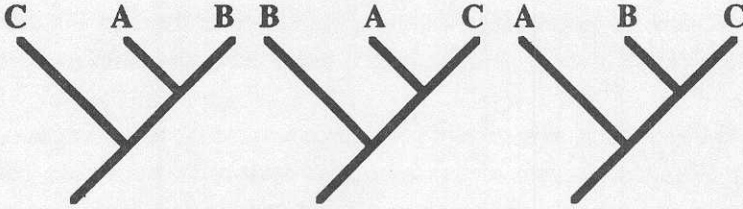


FIGURE 1. The three possible resolved rooted trees, given the terminal taxa A, B, and C.

With more terminal taxa, the number of possible trees soon get astronomically high. Nevertheless, the task of a systematist is to choose among possible trees (II, III). The tree-building approach fails because it does not distinguish between epistemology and ontology. The tree-choosing approach does, and is therefore more in line with the individuality thesis and therefore preferable within an evolutionary paradigm. A corollary of the individuality thesis is that the ordering in phylogenetic systematics should not be viewed as classification but instead as systematization (Griffiths, 1974; de Queiroz, 1988). Classification is the ordering of things into classes defined by their attributes, while systematization is the ordering into systems or wholes where parts are related through a process (Griffiths, 1974; see paper VI for an example and discussion).

Within the phylogenetic framework discussed here, the most logical homology concept is one strictly coupled to tree topology. After an initial observation of structures in two or more organisms, our senses may tell us that the structures look very much the same, which in turn leads us to infer a horizontal similarity relation. These hypotheses, in turn serve as raw data in a congruence analysis (parsimony) of all possible characters which reveal the phylogenetic importance of any given character. The congruent distribution of characters in a phylogenetic tree is the relation called homology (I). Thus, it is not the presence of a specific character in an organism that makes it a homology but rather its congruent relationships with all other possible characters in a tree. While the similarity relation is between two or more organisms in a horizontal fashion, the homology relation is a hierarchical concept based on congruence. This is a crucial advance from the pre-Darwinian homology concepts which only rested on similarity. Ghiselin (1966) puts the problem with similarity like this, "Similarity is a relation; things are not twice as "similar to" any more than they are twice as "around". When I say that x is hotter than y, I do not mean that it contains a greater number of hotter things, or a greater quantity of heat. When I say that rats are similar to mice, I do not mean that they are composed of an equivalent number of comparable entities. If someone says that two organisms differ in 75% of a sample of characters, while two others differ in only 65% of these, he cannot meaningfully assert that

one of these pairs possesses a greater amount of difference, in the same sense that one animal may be said to have more mass than another. One would obtain just as meaningful a figure by adding two oranges, a glass of water, and a telephone number" ... "For this reason, there can be no quantifiable evolutionary rate in either the degree of morphological diversification or the level of anagenesis, and quantitative similarity is a metaphysical delusion".

Trees and tree-thinking have been of major importance in the advancement of biological systematics. With the tree as a central tenet in all systematic endeavours, concepts like homology and taxon have changed into a more precise and evolutionary meaning. Ontological understanding as well as operational discovering procedures of phylogenetic phenomena have gained on the tree-icon.

Not only phylogenetic systematics have gained from the development of tree-thinking, also historical biogeography, the field that meant so much to Darwin when formulating his evolutionary theory (above) have gained tremendous. Biogeographers work under the premises that biological diversity and distributions offer information on the history of geographic areas and waters, but also that geography is a potential explanatory source of biological diversity. With the development of cladistic or phylogenetic systematics both of these approaches have become more explicit. From a phylogenetic tree of the study group(s) a reduced area cladogram is estimated using one (or more) of several methods (e.g. component analysis (Nelson and Platnick, 1981; Page, 1988, 1993), Brooks parsimony analysis (Wiley, 1988; Kluge, 1988; Brooks, 1990), three-area statements (Nelson and Ladiges, 1991)). The main concern of these methods is the study of correlated patterns from independent taxa inhabiting the same areas (e.g. Nelson and Platnick, 1981; Humphries and Parenti, 1986), with the aim to get a general pattern of an areas history. Information from as many independent clades as possible is thus considered important. Bremer (1992) brought back the focus to the study of the origin and evolution within a single clade, and thus closed in on Darwin's original view. He developed a method to estimate how likely it is that a certain area inhabited by extant clade parts was part of the ancestral area (see below and paper III for a discussion and example). Analysing the geographic distribution within a particular clade from a historical perspective contributes to the knowledge of the evolution of the group and have the potential to enhance the general understanding of the evolution of areas.

One problem suffered in cladistic biogeography is that it have relied too much on a "pattern" cladistic approach, not incorporating the individuality thesis (IV). This have caused a confusion of epistemology and ontology and misunderstandings concerning widespread species and areas of endemism (IV).

In conclusion, trees and clades have thus been of paramount importance in more than one historical aspects of biology.

Naming Clades

During the time humans have classified (or systematized) they have also given names to the things classified. Naming is a way of handling our knowledge in order to be able to communicate, while classifications (systematizations) are necessary for generalizations. Single objects alone makes generalizations impossible (Ghiselin, 1980). A world with a name for every unique observation and thing would be a very isolated world. Wittgenstein (1953) developed this to some extent when he explored the possibilities of a private language, something he in the end declared impossible.

How names refer and the difference between meaning and reference are important not only in analytical philosophy. Issues like this may also obscure the advancement of systematics (V). There is an incongruence among systematists and biologists in general in how they use a taxon name when talking about a particular specimen. It is not so common to see that one refers to a specimen of *Homo sapiens* as a **part of** *Homo sapiens*, rather it is much more common to see it referred to as a *Homo sapiens*; implying the existence of several *Homo sapiens*. Rowe (1987) stumbles on a similar problem when arguing that "... one may easily delimit individuals such as Michael Ghiselin from **other** *Homo sapiens*..." (emphasis added). This I believe exemplifies both Ghiselin (1966, 1974) and de Queiroz (1988) point of an failure to distinguish class from individual but also an inability to use the language in a consistent way. The definition of taxon names are often taken for the meaning of the name rather than just being a method of fixing the reference. de Queiroz (1994) explicitly states that "... the meanings of taxon names are stated in terms of phylogenetic relationships rather than on organismal traits...".

Putnam (1975) described the traditional theory of meaning with the following lines: "On the traditional view, the meaning of say, lemon, is given by specifying a conjunction of properties. For each of these properties, the statement 'lemons have the property *P*' is an analytic truth; and if P_1, P_2, \dots, P_n are all of the properties in the conjunction, then anything with all of the properties P_1, \dots , is a lemon is likewise an analytic truth". The conjunction of properties associated with the term is the *intension* and the intension determines the *extension* of the term. Hence, the intension is the definition (meaning) of the name while the extension is everything that fits the definition. Often the intension of a term is taken for the essence of the kind or thing named (Schwartz, 1977), something which also is common in biological taxonomy even though biologists tend to reject the term essence.

Donnellan (1966, 1972) and Kripke (1971, 1980), among others, broke with this traditional view of names. They argued that names lack intension and consequently cannot be defined in a traditional sense. Kripke took his starting point in the notion that identity must exist by necessity, something that rule out contingent identity. While Frege explained contingent identity like " $a = b$ " (given that " $a = a$ " and " $b = b$ ") (see paper V), Kripke argued that it did not exist (yet another example of getting over, rather than solving a problem).

Traditionally, *a priori* and necessity have always walked hand in hand, as have *a posteriori* and contingency. Kripke (1980) argued that this need not be the case, and that both necessary *a posteriori* truths and contingent *a priori* truths are possible. As an example of the relation between contingency and apriority, Kripke (1980) discusses the reference meter in Paris. The argument goes something like this. If we define 'one meter' to be the stick *S* at time t_0 , is it then a necessary truth that stick *S* is one meter at time t_0 ? If we believe that everything we know *a priori* is necessary, we may argue that this is the *definition* of one meter. That is, by definition stick *S* is one meter long at t_0 and conclude that it is a necessary truth. Kripke disagrees, since the use of definition in this case does not *give the meaning* of what is called the 'meter', but it *fixes the reference*. There is a difference between the two statements 'one meter' and 'the length of stick *S* at t_0 '. The first phrase rigidly designates a certain length in all possible worlds, which in the actual world happens to be the length of stick *S* at t_0 . The statement 'the length of stick *S* at t_0 ', on the other hand, does not designate anything rigidly. In some counterfactual situations the stick might have been longer and in others shorter, but the name 'one meter' still refers to the same stick. Hence, it is not a necessary truth that *S* is one meter long at t_0 . The reason is that one designator ('one meter') is rigid and the other designator ('the length of *S* at t_0 ') is not. Epistemologically we have *a priori* knowledge of 'one meter' referring to 'the stick *S* at t_0 ', but this does not necessarily mean that stick *S* at t_0 is one meter long. In this sense we can talk about contingent *a priori* truths. Hence, Kripke argues that names lack intension and thus cannot be defined in a traditional sense.

The referential part of a name is more important to Kripke and Donnellan. They argue that proper names refer independently of identifying (definite) descriptions. Donnellan (1966) showed that reference can take place not only in the absence of identifying descriptions but even when the identifying description associated with the name do not correctly apply to the individual to whom the name refers. Kripke (1980) called such a name a rigid designator since it refers to the same individual in all possible worlds in which it is present. Possible worlds are given by the descriptions we associate with them, i.e., a possible world is stipulated not discovered. In phylogenetic systematics, possible worlds belongs to the pool of all possible trees as discussed below and in paper V. A name (if rigid) will refer to the same individual whether or not he (or she or it) satisfies some list of commonly associated descriptions. When we use a name, Donnellan writes, we use it as a referential description to refer to some definite individual, independently of descriptions. If names are used to refer to whoever fits the identifying descriptions associated with them we get certain paradoxical results. For instance, we might have to conclude that an individual did not exist because he did not fulfil the definite description of his name. It is even impossible to discover things at all about carriers of proper names - because they are their names.

In general, biological taxonomy have not kept up pace with the developments in the philosophy of names. With few exceptions, biological taxonomy is still to a large extent

based on theories of meaning (V). However, early in the development of phylogenetic systematics, Ghiselin (1966, 1969, 1974) claimed that species are individuals rather than classes and argued that their names are proper. He also argued that such names only could be defined ostensively. Thus, the basis for a change in the philosophy of taxonomic names towards a reference system like Kripke's (above and V) have been present just as long as the philosophy for detecting phylogenetic relationships (Hennig, 1966). Despite that, taxon names are commonly defined by the properties of a type specimen. The type specimen, in turn, is used to infer the extension of the taxon. This invokes one immediate problem concerning meaning and reference; they do not have the same extension. The reference is to a particular individual (type specimen) while the meaning of the name covers this specific individual but also other specimen judged similar enough to the type. Furthermore, in this case reference and meaning belongs to two different metaphysical inquiries; the reference is to an individual while the meaning is a class of similar things (V).

In the early 1990's, de Queiroz and Gauthier (1990, 1992, 1994) picked up where Ghiselin left off and approached the problem with a method for *defining* taxon names *phylogenetically*. They proposed three classes of phylogenetic definitions; node-, stem-, and apomorphy based definitions (FIG. 2).

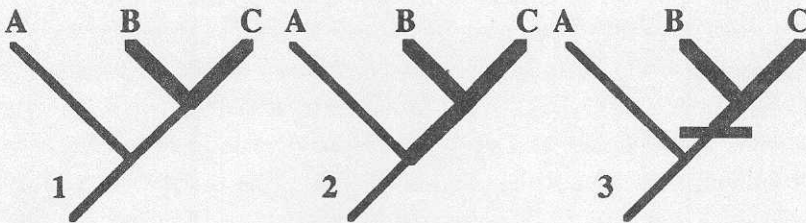


FIGURE 2. The three classes of phylogenetic definitions of taxon names suggested by de Queiroz and Gauthier (1990). A node-based definition (1) can be formulated either as the clade stemming from the most recent common ancestor of B and C (e.g. de Queiroz and Gauthier, 1990, 1992, 1994) or as the least inclusive clade comprising B and C (e.g. Schander and Thollessen, 1995; VI). The stem-based definition (2) can be phrased either in the spirit of de Queiroz and Gauthier like "taxon B and C and all taxa sharing a more recent common ancestor with them than with A" or in the words of Schander and Thollessen (1995) "the most inclusive clade comprising B and C". The apomorphy-based definition (3) refers to the clade stemming from the first ancestor possessing the particular apomorphy (indicated by a black cross-bar). The thicker black lines indicates the inclusiveness resulting from the various types of definitions.

The apomorphy based definition have later been criticized for being ambiguous since it, given a change of phylogenetic hypothesis, can turn out homoplastic (Bryant, 1994; Schander and Thollessen, 1995). Also the stem-based definition have been considered ambiguous since it may refer to a non-existing clade, given a change of phylogenetic hypothesis (Schander and Thollessen, 1995). The node-based definition, however, seems

unambiguous within the system presented by de Queiroz and Gauthier. These effects are due to phylogenetic taxonomy being an application of the traditional theory of names (V). To a large extent, de Queiroz and Gauthier's suggestions have passed rather silently in the literature both practically (but see VI) and theoretically. Besides the contribution of some theoretical comments by de Queiroz (1992, 1994, 1995) himself, few other have entered the discussion (but see Bryant, 1994; Rowe and Gauthier, 1992; Sundberg and Pleijel, 1994; Schander and Tholleson, 1995; Ghiselin, 1995; paper V). The comments that have been made are mainly positive, but none of them (except Ghiselin, 1995; and de Queiroz's own papers in 1992, 1994 and 1995) have considered the philosophical background (V). All of the contributions by the original authors are based on the assumption that common ancestry can be used as *defining properties* of names and de Queiroz (1994) specifically argues that "defining formulas of taxon names can be stated in terms of logically necessary properties, in other words, that the names of taxa have *intension*" (emphasis in original).

de Queiroz and Gauthier's system is an application of the traditional view of names as theories of meaning, although in a phylogenetic suite. Consider the following example. If the meaning of "CD" is given by the definite description "the least inclusive clade comprising C and D" (FIG. 3) the identity judgement "CD is the least inclusive clade comprising C and D" becomes an analytic truth - a tautology; true through linguistic laws. Such statements can be false since it is possible that the specific clade never comprised C and D. In a possible world where another clade comprised C and D, the statement "the least inclusive clade comprising C and D" refers to that clade, while the name "CD" still refers to CD in the actual world. In this sense proper names are rigid designators since they refer to the same individual in all possible worlds (FIG. 3). This is not the case for definite descriptions since they refer to whatever fits the description. The name and the definite description can therefore not have the same meaning.

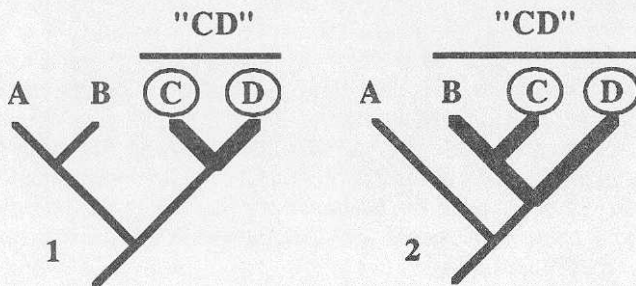


FIGURE 3. CD refers to the least inclusive clade comprising C and D (1). However, C and D are not logically necessary properties of CD since the clade (C, D) does not exist all possible worlds, e.g. tree 2. This is furthermore an example of what can happen if definite descriptions like the least inclusive clade comprising C and D are considered the meaning of the name - the name will refer to whatever clade that fits the description (2).

Possible worlds are stipulated and not discovered, which means should our phylogenetic hypothesis change in a way affecting our named clade so does the resulting possible worlds.

However, it is important that we consider the nature of a phylogenetic individual and what is meant by the same individual if we are to evaluate the two approaches to names and naming. Kripke's philosophy of names stem from a world view where we can observe the individual we name. We observe when a child is borne, and we then decide to give that particular child a name. Phylogenetic individuals, on the other hand, can never be observed since they are historical individuals. Such individuals are nested within larger individuals forming a phylogenetic hierarchy and there are no objective criteria for what clade to name. It is equally logical to name all as none. Furthermore, phylogeny is a ongoing process incorporating both births and deaths of clades. The crucial point, however, is that we never know when we find the true phylogeny and in that sense de Queiroz and Gauthier's system will work as a operational system since it always will refer to a phylogenetic individual, but maybe not the particular one intended in the actual world. Accepting de Queiroz and Gauthier's suggestion we must give up the idea that the clade named (taxon) in the actual world is a real thing, we must accept that it is a human construction made to facilitate communication of phylogeny. One major advantage with this approach is that we gain a sort of operationality but we lose the reality of the clades being named. Kripke's approach, on the other hand, takes for granted that the individuals we have are real and that it is them we refer to by the name. This approach lose in operationality since it is possible that our phylogenetic hypotheses will change with improved methods of inference and with new interpretation of data. A possible way out of this dilemma is to argue that phylogenetic statements like "the least inclusive clade comprising C and D" always refer to the same individual in all possible worlds, even though the inclusiveness of the name will change. Thus even if our knowledge (epistemology) of the clade may change (i.e. inclusiveness), the ontology of the clade will not change. One draw back, of course, is that we then let our language determine what historical individuals to name rather than the individuals being the subject of naming. Hence, we give primacy to names rather than clades. Kripke's philosophy, on the other hand give primacy to the clade being named and also allows for discoveries of new parts of that clade.

de Queiroz and Gauthier (e.g., 1990) tend to confuse epistemology with ontology, and this may be the reason why they argue that taxon names are defined by logically necessary properties. For instance, they claim that phylogenetic definitions of taxon names distinguish between a definition and a diagnosis and argue that this is a difference between an entity itself (ontology) and evidence for its existence (epistemology) (de Queiroz and Gauthier, 1990). I do not agree, both definition and diagnosis are epistemological matters. The ontology of phylogenetic systematics are individuals (clades) and they cannot be defined (Ghiselin 1966, 1969). We can only make more or less accurate reference to particular clades. Furthermore, when arguing in favour of "properties" used in phylogenetic definitions of taxon names being defining and logically necessary properties, de Queiroz

(1995) uses an example aiming to define the name "Mammalia". He writes "Being a part of a particular clade that eventually and contingently gave rise to horses and echidnas in the actual world is what is logically necessary to be a mammal, not being a part of a clade that immediately and necessarily gave rise to horses and echidnas in all possible worlds. Indeed, the existence of horses and echidnas is not even necessary to define the name of the clade/ancestor in question, for house mice and platypuses, or monotremes and therians, would do just as well". This is a confusion of what is *a priori* knowable with what is metaphysical necessary. Contingency and necessity are metaphysical categories; the contingent obtaining in some worlds and the necessary in all. Clades are not necessary since they do not exist in all possible worlds (FIG. 3), unless we accept that whatever the phylogenetic definition of the name refers to is the same individual. Matters of epistemic primacy (what is *a priori* or not) are not questions about worlds but of knowledge. Metaphysical necessity is one thing, epistemic apriority another (Kripke, 1980; Nelson, 1992). The statement "CD refers to the least inclusive clade comprising C and D" (FIG. 3) is a contingent but *a priori* truth. Things could have been different, for instance we could have chosen to give the name "CD" to the least inclusive clade comprising A and B instead. Furthermore, the tree topology could have been different (FIG. 3, right). But given the present situation, the name "CD" is a matter of epistemic apriority, while the fact that it refers to a particular ontological individual is contingent. All clades are contingent and their names are based on *a priori* knowledge of the evolutionary model. Defining and logically necessary properties are not part of a phylogenetic ontology. Hence, it is not a matter of necessity for a horse to be a mammal but given the present usage of the name, it is a matter of *a priori* knowledge.

Phylogeny and Biogeography of the Eureptantia

Eureptantia (Nemertea, Hoplonemertea, Polystilifera) is a group of marine nemerteans distributed world-wide. The Indonesian Archipelago and the Mediterranean Sea are the two main areas of present distribution. Until recently (II, VI), the 46 described species were grouped into 9 families and 24 genera; many of them monotypic. This traditional classification (II, table 1) was mainly constructed on the views of Stiasny-Wijnhoff (1936, and references therein). Recently, we (II) analyzed the cladistic relationship among a majority of the eureptantic species, based on most of the characters that traditionally are used in eureptantic classification. As a comparison, we used the traditional classification as a constraint in an identical cladistic analysis. All genera, families, and higher categories were constrained to be monophyletic, but with their internal relationships unresolved. The original analysis resulted in six, highly congruent, most parsimonious trees with a consistency index (CI) of 0.30, a retention index (RI) of 0.62, and a tree-length of 175 steps. Even though the CI is slightly below the empirically expected (Sanderson and

Donoghue, 1989), it is not significantly lower than in any other group of animals or plants (paper I). The tree distribution is significantly skewed to the left ($g1 = -0.355$), indicating phylogenetic information in the data set (Hillis and Huelsenbeck, 1992).

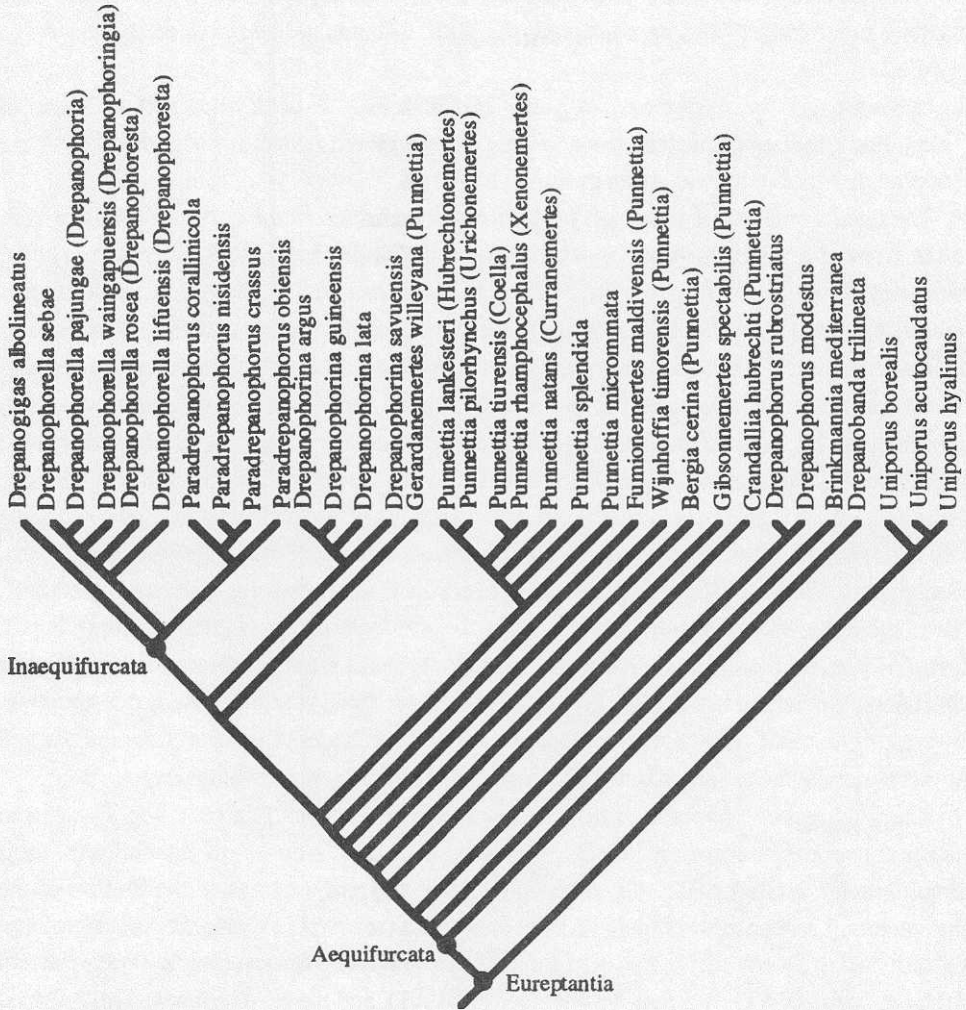


FIGURE 4. Phylogenetic hypothesis of the Eureptantia (II). The names from the systematization in paper VI are used in the tree. For instance, Eureptantia refers to the least inclusive clade comprising Uniporus and Aequifurcata. The old names are mentioned within parenthesis.

Besides, for systematic purposes it is not necessarily a data set with a high CI (i.e. little homoplasy) one need but rather a good possibility for tree choice. "... when actually analysing data cladists probably worry less when they find high levels of homoplasy and

one or a few trees, than when they find hundreds or thousands of equally parsimonious trees. That is the right thing to do" (Goloboff, 1991). Compared with the traditional classification (as resulting from the constrained analysis), the most parsimonious solution is 16 steps shorter. Furthermore, our data set deviate from a random set of characters since on average (based on 5 randomized data sets using the shuffle option in MacClade) such trees are much longer (230 steps), have lower CI (0.24), and are less skewed to the left ($g1 = -0.082$).

In summary, the hypothesis in paper (II) and FIG. 4 offers the best estimate of eurentantic phylogeny presented up to date. Many of the previous recognized taxa are rendered non-monophyletic status as shown in FIG. 4.

The results obtained in paper (II) justifies a reorganization of the eurentantic nemerteans in the form of a systematization (*sensu* Griffiths, 1974; de Queiroz, 1988). A new system of names is suggested in paper (VI, table 1) and shown in FIG. 4, which strictly make reference to phylogeny rather than to organismal traits or Linnean categories. All references are made to nodes in the phylogeny and as many of the traditional names as possible have been kept. However, I am eager to point out that even though some of the names refer to the same species, they do that on totally different grounds. For instance, *Paradrepanophorus* is traditionally *defined* by Stiasny-Wijnhoff (1936) as "Atrium untief oder fehlend. Dorsale Gehirnganglia mit gegabeltem Faserkern. Blinddarm bis neben dem Magen. Enterontaschen alle gleich gestaltet. Periphere Blutgefässanastomosen. Proximale Nephridiopori. Gonadentaschen vielreihig bis paarweise angeordnet, vorzugsweise V-förmig gestaltet". Now, the name *Paradrepanophorus* *refers* to "the least inclusive clade comprising *P. corallinicola* and *P. obiensis*". While the former only make reference (is defined by) a set of characters, the latter make explicit reference to a clade. Thus, the difference is tree-thinking. By making explicit reference to a clade we avoid all unnecessary class connotations and furthermore, we make sure that the reference is to a historically relevant entity.

The phylogenetic hypothesis of the eurentantic nemerteans is a first step towards an increased understanding of their evolution. Another step is to investigate their biogeographic relations (III). Given the phylogeny (II) and the known distribution of the Eurentantia, I recognized six main areas of endemism (see paper IV on areas of endemism); Eastern Indian Ocean (EIO), Western Indian Ocean (WIO), Western Pacific (WP), Eastern Atlantic Ocean (EAT), Western Atlantic Ocean (WAT), and the Mediterranean (ME). Based on Bremer's (1992) ancestral area analysis, I identified EIO as the present area being most likely to be part of the ancestral distribution of the Eurentantia (III).

The reduced area cladogram based on the eurentantic phylogeny (paper III, fig. 3 and FIG. 5) suggests that the evolution of the Eurentantia have been dominated by vicariance events rather than dispersals. This is deduced from the high consistency index (0.87) which suggests a good fit of the characters on the tree topology. Furthermore, the phylogenetic tree (II and FIG. 4) is significantly asymmetric using two of the statistics ($\bar{N} = 11.26$ and $\sigma^2_{\bar{N}} = 5.24$) in Kirkpatrick and Slatkin (1993) with most statistical power for trees with

more than 20 species. One explanation for asymmetric trees could be that species living in geologically active areas experience frequent vicariant events resulting in a biased cladogenesis. A possible cause for the asymmetry in the eurentic evolution could be that many clades evolved in south-east Asia, which is, and have been, a geologically active area. The many autapomorphies on the EIO branch (III, fig. 3 and FIG. 5) indicate the high cladogenesis in that area during the last 20-30 million years.

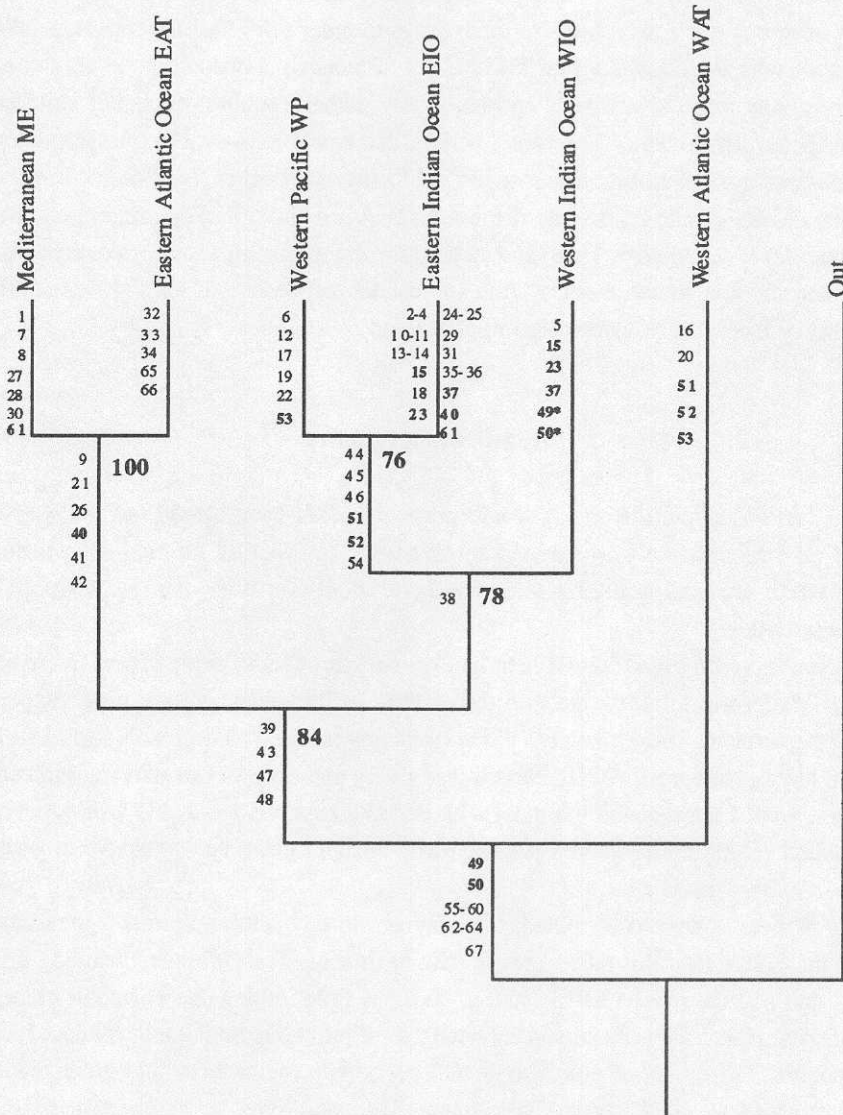


FIGURE 5. Reduced area cladogram based on the phylogeny of the eurentic nemerteans (III).

Summary

Humans tend to classify or systematize most things, from the less important like nemerteans (e.g. paper VI) to more essential things in life like Scotch single-malt whiskies (e.g. Lapointe and Legendre, 1994). This is not surprising since systematics and taxonomy are more than biological fields of inquiry, they are part of "a fundamental operation in the acquisition of knowledge" (Ghiselin, 1981). "Taxonomy is [even] older than thinking" (Ghiselin, 1981). However, it is important to keep in mind that there is not just a vast number of things to classify, but also many ways to order things into groups depending on the purpose with the classification. There is not necessarily a bad and good way or a right and wrong way to do systematics and taxonomy, rather certain approaches suite certain purposes better than others. Therefore, I believe that being consistent in ones approaches to taxonomy and systematics, and thus avoid confusing approaches, is of major importance. For instance, we should realize the distinction between classification and systematization (Griffiths, 1974; de Queiroz, 1988) and stop criticizing a classification for not doing the job of a systematization, and vice versa. Both approaches can be kept as long as we maintain an awareness of their totally different assumptions and possibilities.

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