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### PROPOSAL OF A NEW SYSTEM OF NOMENCLATURE FOR PHYLOGENETIC SYSTEMATICS

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#### **ABSTRACT**

After a brief study of the main concepts of the intuitive set theory, formal definitions of taxon, morphospecies and eidophoront are given. Follows a critical study of the creation of the Linnaean categories and why they cannot be maintained, and of the three different meanings of «genos» in evolutionary taxonomy (C-genos, P-genos and inf (P-genos)). Then, a new system of nomenclature is proposed for phylogenetic systematics, in which, without ever creating new names, all the species and all the proper subsets of a phylogenetic system are named. As the nomenclatural system becomes isomorphic with the phylogenetic system, the classification retrieves all the phylogenetic information, in the same order. The new system is based on the principle of absolute priority of names and, analogously, on Hennig's theory of phylogenetic systematics. Two taxa A and B are distinct if they possess nominal heterobathmy, i.e., if A possesses an autaponomastic and B possesses another; monophyly of A and B is indicated by the possession of a synaponomastic, which is formed by taking the name which has priority, adding a negative index: the synaponomastic of A and B will be automatically the autaponomastic of the immediate ancestral species of A and B. The process goes on until the species ancestral to the entire group is named. Many other conventions are established for the use of the system, including cases of species fusion, hybrids, polypatrid species, fossil species, subgenera. The last section deals with the stability of nomenclature, showing that this new method insures that desideratum.

Keywords: Phylogenetic systematics, new system of nomenclature, set-theory.

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#### 1. INTRODUCTION

"La théorie de l'histoire naturelle n'est pas dissociable de celle du langage. Et pourtant, il ne s'agit pas, de l'une à l'autre, d'un transfer de méthode. Ni d'une communication de concepts, ou des prestiges d'un modèle qui, pour avoir 'réussi' d'un côté serait essayé dans le domaine voisin. Il ne s'agit pas non plus d'une rationalité plus générale qui imposerait des formes identiques à la réflexion sur la grammaire et à la *taxinomia*. Mais d'une disposition fondamentale du savoir qui ordonne la

connaissance des êtres à la possibilité de les représenter dans un système de noms (p.170). L'histoire naturelle est contemporaine du langage: elle est de même niveau que le jeu spontané qui analyse les représentations dans le souvenir, fixe leurs éléments communs, établit des signes à partir d'eux, et impose finalement des noms. Classer et parler trouvent leur lieu d'origine dans ce même espace que la représentation ouvre à l'intérieur de soi parce qu'elle est vouée au temps, à la mémoire, à la réflexion, à la continuité. Mais l'histoire naturelle ne peut et ne doit exister comme langue indépendante de toutes les autres que si elle est langue bien faite. Et universellement valable. (...) L'histoire naturelle ne sera une langue bien faite que si le jeu est formé: si l'exactitude descriptive fait de toute proposition un découpage constant du réel (si on peut toujours attribuer à la représentation ce qu' on y articule) et si la désignation de chaque être implique de plein droit la place qu'il occupe dans la disposition générale de l'ensemble (pp. 171-172). Entre le langage et la théorie de la nature, il existe donc un rapport qui est de type critique; connaître la nature, c'est en effet bâtir à partir du langage un langage vrai mais qui découvrira à quelles conditions tout langage est possible et dans quelles limites il peut avoir un domaine de validité (p. 175)".

MICHEL FOUCAULT, 1966. Les mots et les choses (Chap. V: Classer; vii. Le discours de la nature).

"What's the use of their having names, the Gnat said, «if they won't answer to them?» «No use to *them*», said Alice, «but it's useful to the people that name them, I suppose. If not, why do they have names at all?"

LEWIS CARROLL, Through the Looking Glass

"Peut-être l'exposition que nous venons de faire des systèmes auquels on a été obligé d'avoir recours, disposera-t-elle nos Lecteurs à juger avec plus d'indulgence du nôtre. En tout cas, nous ne prétendons pas assurément le donner ni comme prouvé ni comme à l'abri de toutes objections. Dans une matiere aussi ténébreuse, nous serons contens si ce que nous proposons est sujet à moins de difficultés, ou moins éloigné de la vraissemblace, que ce qu'ont proposé les autres (XIII). Qu'on ne s'alarme pas par les mots que je viens de prononcer: qu'on ne croie pas que je veuille établir ici une opinion dangereuse. J'entends déjà murmurer tous

ceux qui prennent pour un pieux zele l'opiniâtreté dans leur sentiment, ou la difficulté qu'ils ont à recevoir de nouvelles idées. (...). Mais je les prie de m' ècouter, & de me répondre (XV)"

MAUPERTUIS, 1754. Systême de la Nature

\*

The inadequacy of Linnaeus' system of categories, already serious in classical (Aristotelic-Linnaean) taxonomy, becomes acute when a phylogenetic framework is employed. The problem was examined very lucidly by Willmann (1989: 275-277):

"Evolutionary classification is a system of taxa arranged in a Linnaean hierarchy" (Bock 1977: 869). A quite similar view has long been held among phylogenetic systematists as many cladists stated that sistergroups must be assigned the same categorial rank (e.g. Ashlock 1974: 94; Hennig 1966: 139,193; Hennig & Schlee 1978: 8; Schoch 1986: 261, 265; Willmann 1981: 62-63) with which they meant 'Linnaean categorial ranks' -otherwise, according to the common belief, it would be impossible to recognize a pair of sistergroups as such in a written system (or at least their status as a pair of adelphotaxa would be veiled). As each hierarchic level deserves a particular categorial rank, and as dichotomous splitting is the most common cladogenetic process, a particular rank can usually only be used twice along a particular evolutionary lineage.

It has been argued that this leads to an unbearable increase in the number of categories, to changes, whenever new taxa are detected, and often to a drastic change of current ranks of higher taxa which makes the written fixation of the phylogenetic system impractical. It may be impractical indeed, but the real question is, whether Linnaean categorial ranks are justified in modern biosystematics at all. The aim of biosystematics as a branch of natural science is not a classification of the biotic diversity but a systematization (Griffiths 1974, 1976) -a representation of the reconstruction of the system as it is in itself as a result of phylogenesis (Ax 1984, 1988: 6). But the Linnaean categorial ranks were not introduced to indicate sistergroup relationships, and they were originally not linked with the idea of organismic evolution. They were introduced to serve as

classification of the organisms on the basis of Aristotelian logic (Griffiths 1974: 118,1976). Now that we know that (and how) the biotic diversity is underlain by a natural system, categorial ranking in the form used by Linné contradicts our knowledge about the structure of the living world and must be abandoned. Lack of well founded knowledge of the sistergroup relationships during the late 19th and early 20th centuries had allowed further use of the Linnaean hierarchy which should expressly not reflect 'speculations' about phylogenetic relationships. This resulted in more securely establishing the use of Linnaean categories until recently. Now it is possibly due to the power of tradition that only few systematists dare to propose abandonment of the Linnaean categories, some of which are even obligatory according to the codes of nomenclature.

(...). Abandoning the Linnaean categorial names may elicit objections (1) by those who are not aware of the difference between classification and systematization (for details see Griffiths 1974, 1976; Ax 1984, 1987, 1988: 6, 19-20), (2) by those systematists who still do not reconstruct natural taxa but tend to determine extensions of taxa subjectively while neglecting the underlying phylogeny totally or in part, and (3) in general, because one is used to them. The latter is, of course, a psychological foundation wich is not related to the intensions of natural science, and should not be justified at all. But it cannot be denied that subjective reasons are behind numerous decisions in cultural endeavours where one should expect objectivity.

(...). Renunciation of the Linnaean categories implies a simplification of the written classification insofar, as redundant taxonomic names (see Wiley 1981: 200 for the term) are avoided. If there is only one species as the adelphotaxon of a species-rich group, this species is not to be classified as a family, suborder, order etc., of its own, each category corresponding to a taxonomic name -and in a written fixation of the system only this name would appear and refer to one of the basic adelphotaxa of the superordinate monophylum.

(...). It may well be that some authors view the codes of nomenclature in their present form as kind of a sacred cow which should not be touched. However, one should consider the fact that the rules date back to the time when systematics was not completely integrated into evolutionary theory and are not at all related to the current understanding of the nature of natural taxa (Willmann, 1987)".

It is not our intention here to present a historical view and exegesis of the latest tentatives to improve the code of zoological nomenclature, trying to adapt it (after more than a century) to the evolutionary thinking and specially to phylogenetic systematics. The reader may consult, for that purpose, among others, the papers by de Queiroz & Gauthier (1990, 1992). All those tentatives, however, suffer from the centuries-old confusion between the intensional and extensional aspects of the taxa, and from the confusion among what we define herein as C-genos, P-genos and inf(P-genos). Moreover, those systems do not name all the taxa involved in a phylogeny.

Our new system of nomenclature, besides the restriction of the use of Linnaean categories, names not only all the species of a phylogeny, but yet all the proper subsets of a phylogenetic system, without ever creating new names. Our system is isomorphic with the phylogenetic system, thus retrieving all the phylogenetic information, in the same order.

We think that the words of Lao Tsu (Tao Te King, ch. I; cf. Blakney, 1955: 53) describe very well our proposal:

There are ways but the Way is uncharted;
There are names but not nature in words:
Nameless indeed is the source of creation
But things have a mother and she has a name.
The secret waits for the insight
Of eyes unclouded by longing;
Those who are bound by desire
See only the outward container.

Those two come paired but distinct But their names. Of all things profound, Say that their pairing is deepest, The gate to the root of the world.

#### 2. BASIC CONCEPTS OF SET THEORY

In this chapter the fundamental concepts of intuitive set theory are introduced. They will be used throughout the article. Our intention is not to be the rigorous or exhaustive; we only present a minimum of information that may help to follow the reasonings of the forthcoming sections. The interested reader may obtain further information about the subject in the book of Abe & Papavero (1991) or any other reference treatise.

#### 2.1. Sets; logical connectives

For our purposes, a set is any collection of objects (of our perception or understanding); the objects are called *elements* or *members* of the set. The symbol

$$x \in A$$

means that x is an element of the set A (or that x belongs to A). If x is not an element of A, we write

#### x ∉ A.

A set is determined by its elements, that is, two sets A and B are identical (in symbols, A = B) if and only if they share the same elements. A set is generally defined as a collection that satisfies a certain property P; thus, the expression  $\{x \mid P(x)\}$  show us the set of all x such that P(x) is true, and the symbol  $(x \mid P(x))$  reads 'for all that satisfy'.

There is a set called the *empty set* (symbolized by  $\emptyset$ ), which has no elements. This set is obtained from any contradictory properties, for example:

$$\emptyset = \{ x \mid x \neq x \}.$$

A set that has only one element is called a *unitary set*. Example:  $A = \{a\}$  (A is the unitary set of a). The only element of a unitary set may also be a set  $(A = \{\{a\}\}; A \text{ is the unitary set of the unitary set of a; notice that, in this case, <math>\{a\} \in A$ ).

The logical connectives (or operators), and their respective symbols, are:

- ∧ That reads 'and';
- That reads 'or' in the meaning of 'either or , or both);
- That reads 'no'
- → That reads 'if , then ', or 'implies that';
- ∃ That reads 'exists' (at least one); this is the so-called *existential* quantifier («∃!» means 'there exists only one');
- ∀ That reads 'for every'; this is the so-called *universal* quantifier.

#### 2.2 Intension and extension of a set

Given a concept, it has two sets associated with it: one that is the intension of the concept and other that is the extension of the concept. The intension of a concept is the set of all the properties or attributes that characterize the concept; or, in other words, its definition. The extension of a concept is the set of all objects that satisfy the definition of that concept.

#### 2.3. Subsets

If A and B are sets,  $A \subset B$  denotes the *inclusion*; that is, that A is a *subset* of B. This means that all the elements of A are also elements of B.

The *equality* of the sets A and B (denoted by A=B) is verified if and only if  $A \subset B$  and  $B \subset A$ . If A is not equal to B, we then write  $A \neq B$ .

If  $A \subset B$  and  $A \neq B$ , we say that A is a proper part, or proper subset or that A is properly included in B; this is denoted by writing  $A \subseteq B$ .

If it is not true that  $A \subset B$ , we write  $A \not\subset B$ .

Given a set A, if  $a_1 \in A$ ,  $a_2 \in A$ , ...,  $a_n \in A$  ( $n \ge 2$ ), we write that abbreviately as  $a_1, a_2, ..., a_n \in B$ ; also, if  $A_1 \subset B$ ,  $A_2 \subset B$ , ...,  $A_n \subset B$  ( $n \ge 2$ ), we write simply  $A_1, A_2, ..., A_n \subset B$ .

Given to sets A and B, if  $A \subset B$  or  $B \subset A$ , we say that A and B are *comparable*. When A and B are comparable (say  $A \subset B$  and  $A \neq B$ ), we represent that through a *linear diagram* (Fig. 2.1):



Figure 2.1.

If  $A \not\subset B$  and  $B \not\subset A$ , we say that the sets A and B are *non-comparable*.

#### 2.4. Operations with sets

Let U be a fixed set (called the *universal set* of a discourse or simply universe) such that  $A \subseteq U$ .

(i) The *complement*  $\overline{A}$  of A (in relation to U) is defined thus:

$$\overline{A} = \{x \in U \mid x \notin A\}.$$

(ii) Intersection. If A and B are sets, their intersection (denoted by A ∩ B) is the set of all the elements that belong to A and B. In symbols:

$$A \cap B = \{x \mid x \in A \land x \in B\}.$$

If  $A \cap B = \emptyset$ , we say that A and B are disjunct.

(iii) *Union*. The union of two sets A and B (denoted by  $A \cup B$ ) is the set of all the elements that belong to A or to B. In symbols:

$$A \cup B = \{x \mid x \in A \lor x \in B\}.$$

(iv) Difference. The difference between the sets A and B is thus defined:

$$A - B = \{x \mid x \in A \land x \notin B\}.$$

#### 2.5. The power set

If A is a set, then P(A) denotes the set of all the subsets of A:

$$P(A) = \{x \mid x \subset A\}$$

P (A) is called the *power set* of A. Notice that  $\emptyset$ ,  $A \in P(A)$ .

#### 2.6. Cartesian product

If A and B are sets, the Cartesian product  $A \times B$  of A and B is defined as the set of all ordered pairs (a, b), [also written (a, b)] with  $a \in A$  and  $b \in B$ . In symbols:

$$A \times B = \{(a, b) \mid x \in A \land b \in B\}.$$

#### 2.7. Graphs and relations

Let  $A \times A$  be the Cartesian product of A by A. Any subset G of  $A \times A$  is called a graph. In symbols:

G is a graph 
$$\Leftrightarrow$$
  $(\forall z) (z \in G \rightarrow (\exists x) (\exists y) (z=(x,y)).$ 

Let G be a graph. The *domain* of a graph is the set of all the first elements of all the ordered pairs belonging to G, *i.e.*, Dom  $(G) = \{x \mid \exists y \text{ such that } (x, y) \in G\}$ . The *image* of a graph is the set of all the second elements of all the ordered pairs belonging to G, *i.e.*, Im  $(G) = \{y \mid \exists x \text{ such that } (x,y) \in G\}$ .

Given a graph, if a property P uniting the first (x) and the second (y) components of all the ordered pairs (x,y) belonging to G(i.e., P(x,y)) is necessarily true, we say that the graph G is a relation on a set A and denote it by R.

Relations on a set A may be classified as follows:

#### (a) Reflexive

A relation R on A is called *reflexive* if, for every  $x \in A$ , we have x R x.

#### (b) Irreflexive

A relation R on A is called *irreflexive* if, for every  $x \in A$ , we have  $x \not k x$ .

#### (c) Symmetric

A relation R on A is called *symmetric* if,  $\forall x, y \in A$ , if x R y, then y R x.

#### (d) Anti-symmetric

A relation R on A is called anti-symmetric if,  $\forall x, y \in A$ , if x R y and y R x, then x=y.

#### (e) Asymmetric

A relation R on A is called asymmetric if,  $\forall x, y \in A$ , if x R y then y  $\not\in X$  x.

#### (f) Transitive

A relation R on A is called *transitive* if,  $\forall x$ , y,  $z \in A$ , if x R y and y R z, then x R z.

#### (g) Intransitive

A relation R on A is called *intransitive* if,  $\forall x, y, z \in A$ , if x R y and y R z, then x  $\not x$  z.

#### 2.8. Partially ordered sets

Let A be a set. A relation R on A is called a partial order on A if

- a) R is reflexive;
- b) R is anti-symmetric;
- c) R is transitive.

We symbolize by  $\leq$  any partial order on A.  $x \leq y$  reads: «x is smaller than or equal to y», or «x precedes y». [Conversely,  $y \geq x$  reads «y is greater than or equal to x», or «y succeds x»].

Let  $\leq$  be a partial order relation on a set A. The ordered pair  $\langle A, \leq \rangle$  is called a partially ordered system.

Also, given  $x, y \in A$ , if  $x \le y$  or  $y \le x$ , we say that x and y are *comparable*; if  $x \le y$  and  $y \le x$ , we say that x and y are *non-comparable*.

Let  $\langle A, \leq \rangle$  be a finite partially ordered system. If  $x \leq y$ , they are graphically represented as follows (Fig. 2.2)



Figure 2.2.

If  $x \le y$  and  $x \le z$ , and  $y \not\le z$  and  $z \not\le y$ , the graphic representation is as follows (Fig. 2.3):

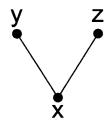


Figure 2.3.

The above diagrams are called *Hasse diagrams*.

#### 2.9. Totally ordered sets, strict order

A partially ordered system  $\langle A, \leq \rangle$  is said to be a *totally ordered system* (or a *chain*) if any two elements of A are comparable. Example: the following ordered system, given by the Hasse diagram of Fig. 2.4, is a totally ordered system.

We symbolize by < any strict order on A. x < y reads: < x is strictly smaller than y> x or < x strictly precedes y> x. (Conversely, y> x reads: < x is strictly greater than x> x or < x strictly succeds < x in the relation < x has the following properties:

- a)  $x \not < x$  (< is irreflexive);
- b) if x < y, then  $y \le x$  (< is assymmetric);
- c) if x < y and y < z, then x < z (< is transitive).

A system <A,< > that satisfies the above conditions is called a *strictly ordered system*.

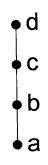
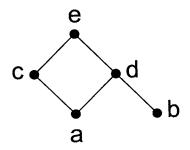


Figure 2.4



maximum = e minimum : ∄ maximal element = e minimal elements = a, b

Figure 2.5

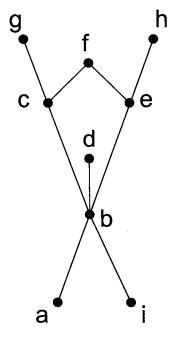
#### 2.10. Noteworthy elements of an ordered set

Let  $\langle A, \leq \rangle$  be a partially ordered system.

- a) Maximum and minimum. An element  $a \in A$  is called the *maximum* of  $\langle A, \leq \rangle$  if  $a \geq x, \forall x \in A$ . An element  $b \in A$  is called the *minimum* of  $\langle A, \leq \rangle$  if  $b \leq x, \forall x \in A$ .
- b) Maximal and minimal elements. An element a
   ∈ A is called a maximal element of < A, ≤> if ∀
   x ∈ A, if x ≥ a then x = a (i.e., there is no element
   x of A strictly greater than a).

An element  $b \in A$  is called a minimal element of  $< A, \le >$  if  $\forall x \in A$ , if  $x \le b$  then x = b (i.e., there is no element x of A strictly smaller than b).

The following examples illustrate the above concepts (Figs. 2.5, 2.6):



maximum: † minimum: † maximal elements = g, f, h, d minimal elements = a, i

Figure 2.6

Now let B be a subset of a partially ordered system  $< A, \le >$ .

 c) Majorants (or upper bounds) and minorants (or lower bounds).

An element  $a \in A$  is called a majorant (or upper bound) of B if  $a \ge x$ ,  $\forall x \in B$ .

An element  $b \in A$  is called a *minorant* (or lower bound) of B if  $b \le x$ ,  $\forall x \in B$ .

d) Supremum (or least upper bound) and infimum (greatest lower bound)

An element  $a \in A$  is called the *supremum* (or *least upper bound*) of B if a is the minimum of the set the majorants (or upper bounds) of B.

An element  $b \in B$  is called the *infimum* (or greatest lower bound) of B if b is the maximum of the set of the minorants (or lower bounds) of B.

#### Example (Figure 2.7):

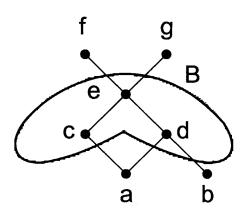


Figure 2.7

majorants of B = e, f, g minorant of B = asupremum of B = einfimum of B = a

#### 2.11. Sup-lattices and sup-semilattices

A partially ordered system  $< A, \le >$  is called a *sup-lattice* if  $\forall x, y \in A$ , there exists sup  $(\{x, y\})$ .

Notice that the supremum, if it exists, is unique.

A sup-lattice such that  $\forall x, y \in A, x \neq y, \nexists$  inf  $(\{x, y\})$  is called a *sup-semilattice* (Figure 2.8):

#### 2.12. Inf-lattices and inf-semilattices

A partially ordered system  $< A, \le >$  is called an *inf-lattice* if  $\forall x, y \in A, \exists \inf (\{x, y\})$ . Notice also that the infimum, if it exists, is unique.

And inf-lattice such that  $\forall x, y \in A, x \neq y, \nexists$  sup ( $\{x, y\}$ ) is called an *inf-semilattice* (Fig. 2.9):

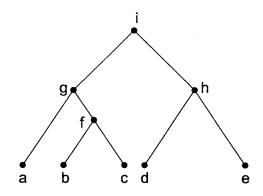


Figure 2.8

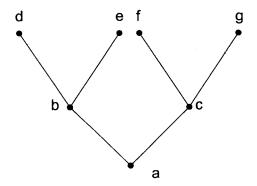


Figure 2.9

#### 2.13. Lattices

A partially ordered system < A,  $\le$  > is called a *lattice* if < A,  $\le$  > is simultaneously a sup-lattice and an inf-lattice (Figures 2.10 and 2.11):

Every totally ordered set is a lattice (Fig. 2.11), but not all lattices are totally ordered (Fig. 2.10).

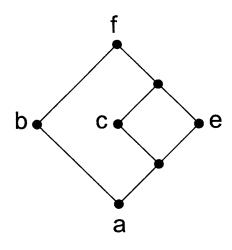


Figure 2.10

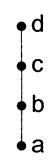


Figure 2.11

#### 2.14. Partition of a set

We call *partition* of a non-empty set A every non-empty collection **P** of subsets of A such that

- a) If  $X \in P$ , then  $X \neq \emptyset$
- b) If  $X, Y \in P$ , such that  $X \neq Y$ , then  $X \cap Y = \emptyset$

c) UX = A.

 $X \in P$ 

#### 2.15. Functions

Let A and B be sets. A function f of A in B (f:  $A \rightarrow B$ ) is a relation  $f \subset A \times B$  such that

- a)  $\forall x \in A, \exists y \in B \text{ such that } (x, y) \in f.$
- b) If  $(x, y) \in f$  and  $(x, y') \in f$ , then y = y'.

Notice that if  $(x, y) \in f$ , we also write f(x) = y.

Example Let  $A = \{a,b,c,\}, B = \{1,2,3,4\}.$ Then  $f_1 = \{(a,1), (b,2), (c,4)\}$  is a function of A in B. Also  $f_2 = \{(a,1), (b,1), (c,3)\}$  is a function of A in B (Figure 2.12):

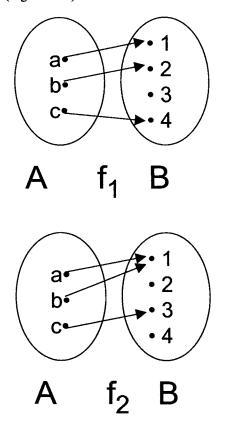


Figure 2.12

#### 2.16. Injective, surjective and bijective functions

A function f: A  $\rightarrow$  B is said to be *injective* if  $f(x_1) = f(x_2)$  implies that  $x_1 = x_2$ .

A function f:  $A \rightarrow B$  is said to be *surjective* if Im (f) = B.

A function  $f: A \rightarrow B$  is said to be *bijective* if it is simultaneously injective and surjective.

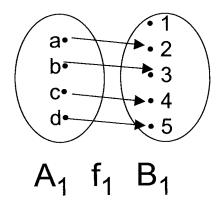


Figure 2.13

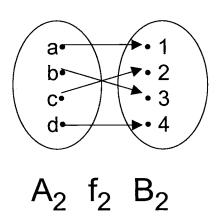


Figure 2.14

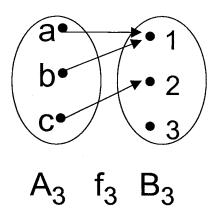


Figure 2.15

Example: Let's examine the following cases (Figures 2.13, 2.14, 2.15)

In Figure 2.13  $f_1$  is injective, but not surjective (as im(f))=  $\{2,3,4,5\} \neq B$ ); consequently  $f_1$  is not bijective. In Figure 2.14  $f_2$  is injective and surjective simultaneously, so  $f_2$  is bijective. In Figure 2.15  $f_3$  is not injective, (as f(a) = f(b), but  $a \neq b$ );  $f_3$  is not surjective (as  $f(a) \neq f(b)$ ); consequently,  $f_3$  is not bijective.

## 2.17. Order-preserving functions, isomorphisms of order, immersions

Let < A,  $\le$  > and < B,  $\le$  > be partially ordered sets. A function f: A  $\rightarrow$  B is said to be an *order-preserving function* if it satisfies the following condition:

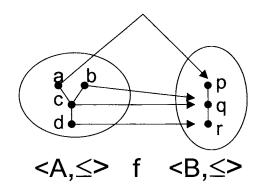


Figure 2.16

 $\forall x, y \in A, x \le y \text{ implies that } f(x) \le f(y)$  (Figure 2.16):

A function  $f: A \to B$  is a strict orderpreserving function if

 $\forall x, y \in A, x < y \text{ implies that } f(x) < f(y).$ 

Let < A,  $\le$  > and < B,  $\le$  > be partially ordered sets. An order preserving function  $f: A \to B$  is said to be an *isomorphism* [of order] if:

a) it is bijective, and

b)  $\forall x, y \in A, x \le y \text{ if and only if } f(x) \le f(y)$ (Figure 2.17)

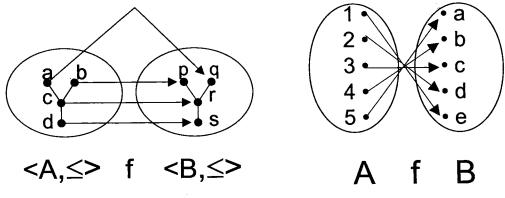
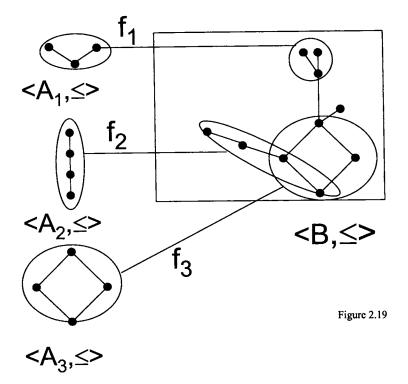


Figure 2.17

Figure 2.18

Let  $< A, \le >$  and  $< B, \le >$  be partially ordered systems. If there exists a function  $f: A \to B$  such that  $\forall x, y \in A, x \le y$  implies that  $f(x) \ge f(y)$ , this function is called a *decreasing function* (Figure 2.18)

Let < A,  $\le$  > and < B,  $\le$  > be partially ordered systems. If there exists an order preserving function f: A  $\rightarrow$  B such that f: A  $\rightarrow$  Im (f) constitutes an isomorphism between < A,  $\le$  > and < Im(f),  $\le$  >, we say that < A,  $\le$  > is *immersible* in < B,  $\le$  >. In this case we say that f is an *immersion* of < A,  $\le$  > in <B,  $\le$  > (Figure 2.19):



#### 3. TAXON AND RELATED CONCEPTS

#### 3.1. Definition of taxon

In order to adequately define the concept of taxon, let's introduce a relational system of taxa (for the complete version see Papavero & Llorente-Bousquets, 1993g). We will employ the language of the usual set theory without extensive comments.

**Definition 3.1.1.** A relational system of taxa is the ordered quintuple

$$A_1 = < O, O, N, N, T>,$$

such that the following axioms are verified:

A, ) O is a non-empty finite set.

The elements of O are called *material* objects (in the particular case of living material objects they are called *organisms*) and are denoted by o -with or without numerical subscripts.

 $A_2$ )  $O \subset (P(O) - \{\emptyset\})$  [P(O) stands for the power set of O] and  $O \neq \emptyset$ .

The elements of O are called *lots* (in the particular case of organisms they are called *populations*) and are denoted by o -with or without numerical subscripts.

A, N is a non-empty finite set.

The elements of N are called *notes* (the expressions 'attributes', 'characters', 'characteristics', 'characters states' are also used in particular cases) and are denoted by n -with or without numerical subscripts.

 $A_{H} N \subset (P(N) - \{\emptyset\})$  [P(N) stands for the power set of N] and  $N \neq \emptyset$ .

The elements of N are called sets of notes and are denoted by n -with or without numerical subscripts.

 $A_{s}$ )  $T \subset A O X N$  and  $T \neq \emptyset$  [O X N stands for the Cartesian product of O and N].

The elements of T are called *taxa* (see Definition 3.1.2 below).

**Definition 3.1.2.** Given a relational system of taxa, the elements of T are called *taxa*; they are called *biological taxa* when the objects are organisms; taxa are denoted by (o, n), or by twith or without numerical subscripts.

Given a taxon (o, n), o is called the *extension* of the taxon and n is called the *intension* or *comprehension* of the taxon.

#### 3.2. Definition of morphospecies

Let  $t_1 = (o_1, n_1)$  and  $t_2 = (o_2, n_2)$  be any two distinct taxa.

**Definition 3.2.1.** The taxon  $t_1$  is said to be a morphospecies in relation to the taxon  $t_2$  if  $n_1 \not\subset n_2$  and  $n_2 \not\subset n_3$ .

**Lemma 3.2.1.** If the taxon  $t_1$  is a morphospecies in relation to a taxon  $t_2$ , then  $t_2$  is also a morphospecies in relation to  $t_1$ .

Corollary 3.2.1. The relation "to be a morphospecies" over the set of taxa S constitutes a symmetric relation.

Now let  $S = \{t_1, t_2, ..., t_n\}$   $(n \ge 2)$  be a set of taxa.

**Definition 3.2.2.** A taxon  $t = \{o, n\}$  is said to be a morphospecies in relation to a set of taxa S if t is a morphospecies in relation to any of the elements of S, i.e., if

 $\forall n_i \ (n_i \text{ being the intension of } t_i, \ \forall t_i \in S), n \not\subset n_i \text{ and } n_i \not\subset n.$ 

Lemma 3.2.2. If a taxon t is a morphospecies in relation to a set of taxa S, then each taxon belonging to S is also a morphospecies in relation to t.

#### 3.3. Definition of eidophoront

Hennig (1966, 1968) called semaphoront each

morphological phase of an organism in different times in which it is examined during its lifetime (for a definition of *semaphoront* see Papavero & Llorente-Bousquets, 1993g). Semaphoronts are interconnected in the physical individual by ontogenetic relations; these relations allow us to connect apparently distinct semaphoronts which compose the vital cycle of an individual, *e.g.*, egg, caterpillar, pupa and adult of a determined species of butterfly. Semaphoronts of the same individual form a totally ordered temporal linear system or temporal chain; the foregoing example may be graphically represented as in Figure 3.1.

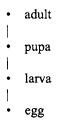


Figure 3.1. Semaphoronts of an insect

Shifting now from an individual to an evolutionary lineage, this lineage may change in form through time, without dividing itself, analogously to the morphological transformations occurring in an organism during its ontogenetic development. To the phenomenon of the appearance of morphological changes in an evolutionary lineage, that is, to the appearance of autapomorphies, the name *anagenesis* is given.

#### Mayr (1981: 38-39) comments:

"Many evolutionists view speciation as a dual phenomenon, the 'dual dimensions' of speciation (Ross, 1974: 58). The first of these dimensions is lineage splitting (cladogenesis). The second is said to be sequential production of species within a single evolutionary lineage. This has been variously termed 'transformation of species in time' (Romanes, 1897), 'phyletic evolution' (Simpson, 1961) and 'phyletic speciation' (Mayr, 1963). Mayr (1963: 424-425) provides a hypothetical example [Figure 3.2]:

"An isolated population on an island, for instance, might change in the course of time from

species a through b and c into species d without ever splitting.

The new species produced in this fashion are variously termed 'successional species' or 'paleospecies' (Simpson, 1961) or 'allochronic species' (Mayr, 1949). The extinctions caused by this speciation are usually termed 'taxonomic extinctions'".

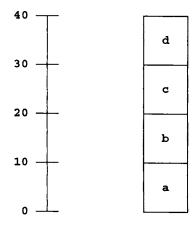


Figure 3.2. Mayr's example of allochronic speciation; the time axis in millions of years at the left; small letters denote 'species'.

Mayr (1963) commented that Darwin confounded two essentially distinct problems under the unique epigraph of 'origin of species'. Darwin was interested in, primarily, demonstrating the evolutionary changes proper. Such a process was appropriately designated by Romanes (1897) 'transformation of the species in time' and by Simpson (1944) 'phyletic evolution', both terms being synonyms of anagenesis. The other process is cladogenesis.

Mayr (1963) argumented that such transformations of a species along time are totally independent of the origin of discontinuities, and they do not lead to the multiplication of species; an isolated species could evolve along geological time, gradually, becoming a very distinct species - morphologically speaking- without originating separate biological species (reproductively isolated).

Let's now consider the following hypothetical cladogram (Figure 3.3):

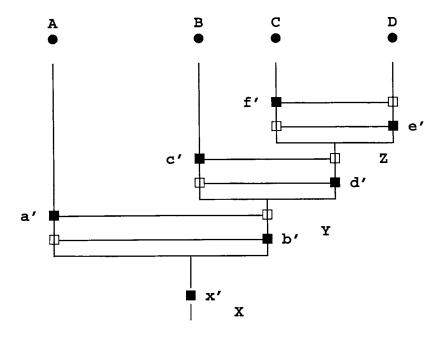


Figure 3.3. A hypothetical cladogram

A, Y, B, Z, C and D are considered species, as, taken two at a time, they possess heterobathmy and are monophyletic, by possessing at least one synapomorphy.

But let us consider, for instance, a totally ordered proper subset of that cladogram, formed, for instance, by the taxa X, Y, Z and D (Figure 3.4)

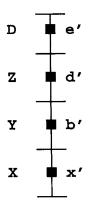


Figure 3.4 Diagram representing anagenesis or phyletic evolution. X, Y, Z and D are eidophoronts.

This is a typical case of anagenesis or phyletic evolution. In this situation, what are X, Y, Z and D? They are not separate species, according to evolutionary systematics, as there is no interruption of gene flow among the taxa. Let us notice that, set-theoretically,

$$X = \{x'\},$$
  
 $Y = \{x', b'\},$   
 $Z = \{x', b', d'\},$   
 $D = \{x', b', d', e'\},$ 

We thus have a chain, ordered by intensional inclusion and ordered temporally.

How should we call each element of this chain (in our example of Figure 3.4 the taxa X, Y, Z and D)? We propose to call them *eidophoronts* (Papavero & Llorente-Bousquets, 1992a; 1993g).

**Definition 3.3.1.** Two distinct taxa  $t_1 = (o_1, n_1)$  and  $t_2 = (o_2, n_2)$  are said to be *eidophoronts* if

their intensions are comparable, i.e., if  $n_1 \subseteq n_2$  or  $n_2 \subseteq n_1$ .

**Definition 3.3.2.** A taxon t = (o, n) is said to be an *eidophoront* in relation to a set of taxa  $S = \{t_1, t_2, ..., t_n\}$   $(n \ge 2)$  if t and any element of S are eidophoronts, i.e., if

 $\forall n_i (n_i \text{ being the intension of } t_i, \forall t_i \in S), n \subseteq n_i \text{ or } n_i \subseteq n$ 

#### 4. THE LINNAEAN CATEGORIES

#### 4.1. Logical division or diairesis

Given a certain concept - 'Animals', for instance, we may divide it, extensionally speaking, into two or more concepts, adding some characteristics. Thus, we may divide 'Animals' into 'blooded animals' (Enaima) and 'bloodless animals' (Anaima), as did Aristotle.

'Animals', in such a case, is taken as logical genus or *genos*. The union of the set of characters of a *genos* with the set of differences (*diaphorá*) gives us a logical species or *eidos*.

We may then take the species (eide) 'blooded animals' and 'bloodless animals' as genera

(gene) and divide them in species, adding more differences. Thus, 'blooded animals' may be divided into 'viviparous blooded animals', 'ovoviviparous blooded animals', and 'oviparous blooded animals'.

Each of these three species may be again taken as *gene* and be further subdivided into *eide*, by the addition of other *diaphorá*.

The logical division or diairesis process can proceed in this manner until we can no longer subdivide the concepts, reaching the level of physical individuals. Then the process ends.

Given a certain universe of discourse, there is always a concept which is a genos and never an eidos; such a concept was called a supreme genus (genus summum or genus generalissimum) (in our example, the supreme genus is 'Animals'). And there are concepts which are always eide and never gene; these are called infimous or atomic species (speciei infimae, atomicae or specialissimae).

All the other intermediary concepts are either *gene* or *eide*, alternately, depending on how we regard them. Thus, in Figure 4.1, for instance,

t<sub>1</sub> is the supreme genus - it is always a *genos* (in this universe of discourse), but never an *eidos*.

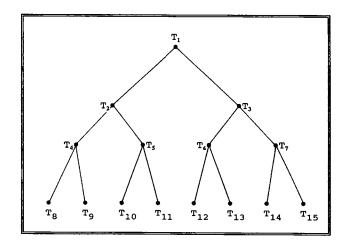


Figure 4.1. Diagram representing diairesis or logical division.

 $t_{s}$ ,  $t_{s}$ ,  $t_{10}$ ,  $t_{11}$ ,  $t_{12}$ ,  $t_{13}$ ,  $t_{14}$ ,  $t_{15}$  are infimous species - they are always *eide*, but never *gene*.

 $t_1$  may be considered an *eidos* in relation to  $t_1$  ( $t_3$  is also an *eidos* of  $t_1$ ), but  $t_2$  is a *genos* in relation to  $t_4$  and  $t_5$  ( $t_5$  is a *genos* in relation to  $t_6$  and  $t_7$ ).

 $t_{1}$  is an eidos of  $t_{3}$ , but a genos in relation to the eide (in this case infimous species)  $t_{14}$  and  $t_{15}$ .

In order to avoid this inconvenience in designating intermediary taxa of a classification, Linnaeus had the idea of a system of categories (later denominated *Linnaean* or taxonomic categories). Linnaeus published his system of categories for the first time in the first edition of his Systema Naturae (1735).

#### 4.2. Definition of Linnaean category

To adequately define what a 'Linnaean category' means, we must first introduce some basic definitions, mostly adapted from Williams (1970).

**Definition 4.2.1.** A line of sequence from taxon t' to taxon t' (denoted by S(t', t'')) is any non-empty and finite set of taxa  $t', t_i, t_j, ..., t_k, t_{k+1}, t''$  such that  $t' = t_i, t'' = t_{k+1}$  ( $k \ge 1$ ), and for every i such that  $1 \le i \le k$ ,  $t_i <_i t_{i+1}$  ( $<_i$  means 'is the immediate ancestor of').

**Example 4.2.1.** Let be the ordered system of taxa <T,  $\le$  >, ordered by the diagram of Figure 4.1. The line of sequence from taxon  $t_s$  to taxon  $t_i$ , that is,  $S(t_s, t_i) = \{t_s, t_s, t_i\}$ .

**Definition 4.2.2.** S(t', t'') is said to have *length* i if there are i + 1 taxa in S(t', t'').

**Example 4.2.2.** Let  $S(t_8, t_1) = \{t_8, t_4, t_2, t_1\}$  as in the previous example;  $S(t_8, t_1)$  has length 3.

**Definition 4.2.3.** A taxon t" is an *i-supe*rior of a taxon t' if there exists a line of sequence S(t', t'') of length i from t' to t".

**Example 4.2.3.** Let be S(t', t'') as in the preceding examples.  $t_1$  is the 3-superior of  $t_s$ .

**Definition 4.2.4.** A taxon t' is an *i-inferior* of t" if t" is an i-superior of t'.

**Example 4.2.4.** In relation to example 4.2.3,  $t_s$  is a 3-inferior of  $t_i$ .

Now let T be a non-empty and finite set of taxa.

**Definition 4.2.5.** A taxon t" is an i-superior of T if,  $\forall$  t'  $\in$  T, t" is an i-superior of t'.

Example 4.2.5. Let be the ordered

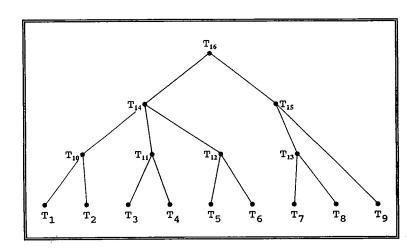


Figure 4.2 Diagram representing an ordered system of taxa.

system of taxa  $\langle T, \leq \rangle$ , ordered by the diagram of Figure 4.2.  $t_{14}$  is a 2-superior of  $T = \{t_1, t_2, t_3, t_4, t_5\}$ . Taxon  $t_{16}$  is a 3-superior of  $T = \{t_1, t_2, t_3, t_4, t_5, t_6, t_7, t_8\}$ . But notice that  $t_{16}$  is a 2-superior of taxon  $t_5$ .

**Example 4.2.6.** Let be the ordered system of taxa < T,  $\le >$ , ordered by the diagram of Figure 4.3. The taxa  $t_6$ ,  $t_7$ ,  $t_8$  and  $t_9$  are 3-superiors of taxon  $t_7$ ;  $t_8$ ,  $t_9$ ,  $t_{11}$ , are the 2-superiors of  $t_1$ ;  $t_8$  and  $t_9$  are the 1-superiors of  $t_8$ , such as  $t_8$  and  $t_9$  are the 1-superiors of  $t_8$ .

**Definition 4.2.6.** A clan of taxa determined by T (denoted by  $K_T$ ) is any set of taxa t" such that

(i)  $t'' \in T$ , or

(ii) t" is an i-superior of T ( $i \ge 1$ ).

**Example 4.2.7.** Let be the ordered system of taxa <T,  $\le$  >, ordered by the diagram of figure 4.3, and  $T = \{t_i\}$ .  $K_T$ , in this case, is the set  $\{t_i, t_2, t_3, t_4, t_5, t_6, t_7, t_8, t_9, t_{10}, t_{11}\}$ . Let's put now  $T = \{t_2, t_5\}$ ; then  $K_T = \{t_2, t_3, t_3, t_4, t_5, t_7, t_8, t_9, t_{10}, t_{11}\}$ .

**Example 4.2.8.** Let be the ordered system of taxa <T,  $\ge>$ , ordered by the diagram of Figure 4.2. Let  $T = \{t_1, t_2, t_3, t_4\}$ ; then  $K_T = \{t_1, t_2, t_3, t_4, t_{10}, t_{11}, t_{14}, t_{16}\}$ . Let  $T = \{t_{14}, t_{13}\}$ ; then  $K_T = \{t_{14}, t_{13}, t_{15}, t_{16}\}$ . Consequently, given a set T whatsoever, we

can talk about the first level of the clan  $K_{\tau}$  (that is, the set of all the 1-superiors of T), of the second level of the clan  $K_{\tau}$  (that is, the set of all the 2-superiors of T) and so forth. The i-th level of  $K_{\tau}$  will be denoted by  $K_{\tau}(i)$  (i 3 1).  $K_{\tau}(0)$  will denote the set T proper (i.e., the 0-th level of  $K_{\tau}$ ).

**Definition 4.2.7.** The *i-th level* of the clan  $K_{\tau}$  is the set of all the i-superiors of  $K_{\tau}(0)$ .

This set is denoted by  $K_{\tau}(i)$  ( $i \ge 1$ ).

**Example 4.2.9.** In relation to Figure 4.3, let  $T = \{t_1\}$ . The second level of clan  $K_{\tau}(i.e., K_{\tau}(2))$  is the set  $\{t_s, t_s, t_{10}, t_{11}\}$  and the third level of clan  $K_{\tau}(i.e., K_{\tau}(3))$  is the set  $\{t_s, t_s, t_s\}$ .

**Example 4.2.10.** Let's consider Figure 4.2 and  $T = \{t_1, t_{11}\}$ ;  $K_T(2)$ , in this case, is the set  $\{t_{14}, t_{16}\}$ .

**Definition 4.2.8.** A taxon  $t'' \in K_r(i)$   $(i \ge 1)$  if there exists  $t' \in K_r(0)$  such that t'' is an i-superior of t'.

We can now introduce the definition of Linnaean category and some other concepts. For that, let's postulate that T is the set of all the infimous species.

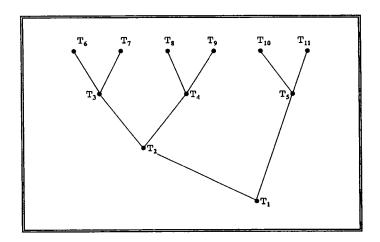


Figure 4.3. Diagram representing an ordered system of taxa.

**Definition 4.2.9.** Given a level  $K_r(i)$  ( $i \ge 0$ ), a *Linnaean category* is the set of all the taxa t belonging to  $K_r(i)$ .

A Linnaean category will be denoted by C.

**Definition 4.2.10.** A Linnaean hierarchy is a non-empty and finite set of categories  $\{C', C_o, C_i, C_2, ..., C_k, C_{k+1}, C''\}$  such that  $C' = C_o, C'' = C_{k+1}$   $(k \ge 0)$ , and, for every i, such that  $0 \le i \le k$ ,  $C_i < C_{i+1}$ .

A Linnaean hierarchy is denoted by S(C', C")

**Observation 4.2.1.** A Linnaean hierarchy of categories is a chain (or totally ordered linear system), ordered by a strict relation of order.

**Definition 4.2.11.** S(C', C'') has *length i* if there are i+1 categories in S(C', C'').

**Definition 4.2.12.** A category C" is an *i-superior* of C' if there exists a Linnaean hierarchy S(C', C") of length i from C' to C".

**Definition 4.2.13.** A category C' is an *i-inferior* of C' if C' is an i-superior of C'.

**Example 4.2.11.** Let be the diagram of Figure 4.4 and let  $t_s$ ,  $t_o$ ,  $t_{10}$ ,  $t_{11}$ ,  $t_{12}$ ,  $t_{13}$ ,  $t_{14}$ , and  $t_{15}$  be infimous species. We have here four categories:  $C_o$ ,  $C_1$ ,  $C_2$ ,  $C_3$ , which are, in this particular case, the following sets of taxa:

$$C_{0} = \{t_{8}, t_{9}, t_{10}, t_{11}, t_{12}, t_{13}, t_{14}, t_{15}\};$$

$$C_{1} = \{t_{4}, t_{5}, t_{6}, t_{7}\};$$

$$C_{2} = \{t_{2}, t_{3}\};$$

$$C_{3} = \{t_{1}\}.$$

Accordingly, S(C<sub>o</sub>, C<sub>3</sub>) has length 3.

Let it be observed that taxa form a supsemilattice (when ordered extensionally) and that the categories form a chain. We have here a case of a function which preserves order strictly (cf. section 2.17).

#### 4.3. The five primitive Linnaean categories

Linnaeus must have perceived in his youth, some time before the publication of his *Systema Naturae* in 1735, that, if he began with the infimous species, only four levels of taxa sufficed to reach the supreme genus (the fifth level), which he called Kingdom (*Regnum*). Linnaeus probably came to this conclusion because he used very few external morphological characters when classifying natural objects. He then admitted that for minerals, plants and animals, a hierarchy of length 4 was the rule (that is, a chain with 5 elements, the categories  $C_0$ ,  $C_1$ ,  $C_2$ ,  $C_3$  and  $C_4$ ).

He called category C<sub>0</sub> (which includes all the infimous species -which are always *eide* and

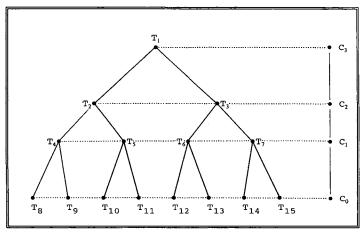


Figure 4.4. Relations between levels of taxa and categories

never gene) species (plural speciei, in Latin).

To the category C<sub>1</sub> he gave the name *genus* (proper) (plural *genera*, in Latin). This category is then the *genus proximum* (because it immediately succeeds the species category). It must be noticed that the taxa belonging to this category are *gene* relative to the infimous species, but are *eide* in relation to the immediately superior taxa.

Category C<sub>2</sub> was called *order* by Linnaeus (*ordo*, plural *ordines*, in Latin). Any taxon included in this category is a *genos* in relation to the Linnaean *genera*, but are an eidos of some taxon of immediately superior level.

Category C, was called by Linnaeus class (classis, plural classes, in Latin). Each taxon belonging to this category is an eidos of the immediate superior taxon and a genos in relation to two or more Linnaean ordines.

Finally, category C<sub>4</sub> was designated by the name kingdom (regnum, pl. regna, in Latin). As a supreme genus, the kingdom is always a genos and never an eidos. Linnaeus ignored the fact that the three kingdoms he used were eide of the genos 'material being' and, following the traditional usage, accepted the kingdoms 'minerals', 'plants', and 'animals'.

The five Linnaean categories form a totally ordered linear system (ordered by the strict relation of order):

species < genus < ordo < classis < regnum, or, graphically (Figure 4.5):

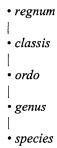


Figure 4.5. The chain of Linnaean categories.

Such a hierarchy (with five categories), apparently, applied marvelously to the 'Regnum Lapideum' such as classified by Linnaeus in 1735. Thus (Figures 4.6 and 4.7) the mineral kingdom could be divided into three classes: Petrae, Minerae and Fossilia. Each one of these classes could be divided into ordines; Petrae was divided into the ordines Apyri, Calcarii and Vitrescentes; Minerae into the ordines Salia, Sulphura and Mercurialia; the ordines Terrae. Concreta and Petrificata were the divisions of the classis Fossilia. Then followed the genera of each order (in a total of 50) and finally the speciei (or infimous species) (not represented, of course, in Figure 4.6, for economy's sake; in Figure 4.7 we represent only the species of the genera of the order Petrificata).

### 4.4. Criteria of validity for the application of Linnaean categories

A taxon, as seen in Chapter 3, is a concept applicable to material objects, and possesses an extension and an intension (or comprehension).

A genos ( $\gamma \epsilon v \circ \zeta$ ) or logical genus is, by definition:

- 1) The non-empty intersection of the intensions of two or more distinct eide or logical species. It is absurd for a genos to be the intersection of two identical species (that is, of a species with itself) as, for every  $A, A \cap A = A$ , we would arrive at the absurdity that every species is a genus (and then that every genus is an order, every order a class, and so forth);
- 2) The *union* of the *extensions* of those two or more *eide* or distinct logical species.

An intensional classification of taxa results in an inf-semilattice, and an extensional classification of the same taxa results in a supsemilattice. There is, consequently, between the two, a decreasing function (cf. section 2.17). Let's illustrate this point: let be the taxa t<sub>1</sub>, t<sub>2</sub>, t<sub>3</sub>, t<sub>4</sub>, t<sub>5</sub>, t<sub>6</sub>, t<sub>7</sub>. Let's suppose that, once classified extensionally,

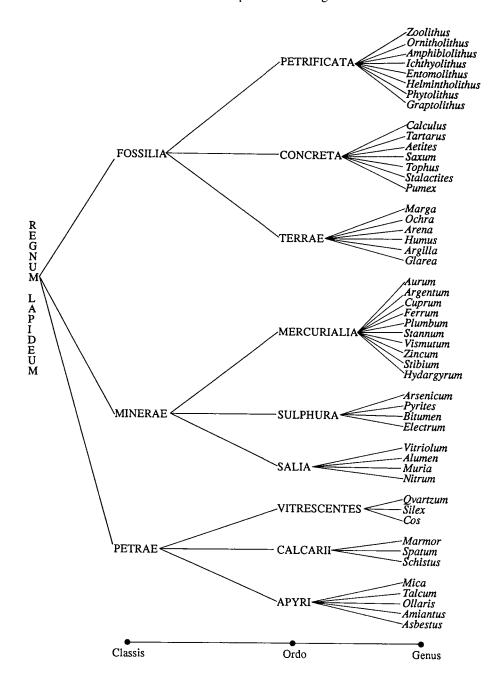


Figure 4.6. Logical division of the 'Regnum Lapideum' according to Linnaeus (1735).

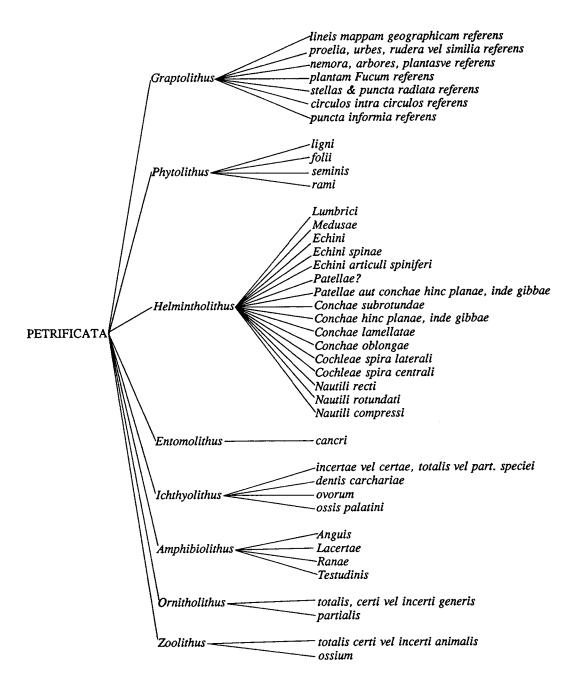


Figure 4.7. Species of the genera of the Order Petrificata (Linnaeus, 1735).

they form the diagram of Figure 4.8 (a supsemilattice).

It is obvious that, in the Aristotelian system of logical division, their intensional classification is the opposite order (Figure 4.9).

Between the extensional and the intensional classifications there exists a decreasing function (Figure 4.10).

Let's denote by A an inf-semilattice

whatsoever representing the logical division or diairesis of a certain universe of discourse of natural history; let this inf-semilattice be an intensional classification.

Let's denote by X any non-empty proper subset of A such that

- (i) X is a sequence of taxa S(t', t");
- (ii) the supreme of X (sup(X)) coincides with a maximal taxon of A and the infimum of X (inf(X)) coincides with the minimum element of A (min(A)).

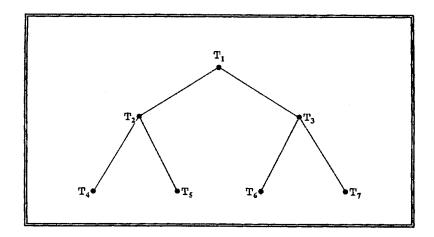


Figure 4.8. A sup-semilattice of extensionally ordered taxa.

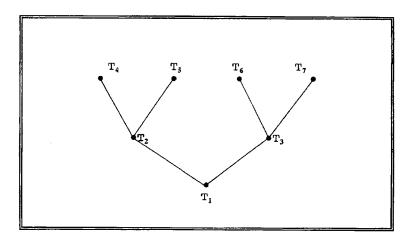


Figure 4.9. An inf-semilattice of intensionally ordered taxa.

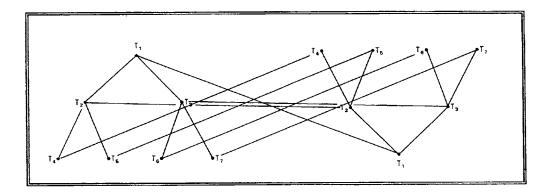


Figure 4.10. Descreasing function from the sup-semilattice of expensionally ordered taxa into the inf-semilattice of intensionally ordered taxa.

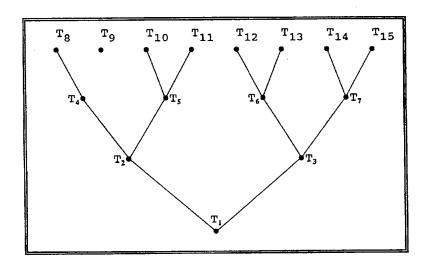


Figure 4.11

**Example 4.4.1.** Let A be the inf-semilattice given by the diagram of Figure 4.11:

We have 8 proper subsets of A satisfying conditions (i) and (ii) above, namely

$$X_1 = \{t_1, t_2, t_4, t_8\};$$

$$X_2 = \{t_1, t_2, t_4, t_5\};$$

$$X_3 = \{t_1, t_2, t_5, t_{10}\};$$

$$X_4 = \{t_1, t_2, t_3, t_{11}\};$$

$$X_5 = \{t_1, t_3, t_6, t_{12}\};$$

$$X_6 = \{t_1, t_3, t_6, t_{13}\};$$

$$X_7 = \{t_1, t_2, t_1, t_{14}\};$$

$$X_{s} = \{t_{1}, t_{2}, t_{3}, t_{5}\};$$

Finally, let's denote by H the chain of the five primitive Linnaean categories (a hierarchy of categories).

Definition 4.4.1. The Linnaean system of

categories is employed validly if:

(i) Every taxon t (except the maximal taxa in an intensional classification)  $\in C_i(0 \le i \le n)$  is related to at least two distinct taxa belonging to the immediately superior category (i. e.,  $C_{i+1}$ ), that is,

$$\begin{split} \forall t (\text{not maximal}) \in \ C_i \ (0 \leq i \leq n), \ \exists t_i, \ t_2, \\ ..., \ t_m \ (m \geq 2) \in \ C_{i+1}, \ t_i, \ t_2, \ ..., \ t_m \neq t, \ \text{such that} \end{split}$$

$$t < t_1, t_2, ..., t_m$$

In other words, every proper subset X of A (such as defined above) must have the same length i.

(ii) For every proper subset X of A, there exists a

function  $f: X \to H$  such that it preserves order strictly.

## 4.5. Difficulties encountered by Linnaeus in the application of his system of categories.

Already in the first edition of his Systema Naturae (1735) Linnaeus felt the practical problem of applying his system of categories. Let's examine a few examples.

Example 4.5.1. In the case of the Petrificata (Figure 4.7) axiom (i) of Definition 4.4.1 was violated. The genus *Entomolithus* includes only one species: *Entomolithus cancri*. Notice that, intensionally speaking, *Entomolithus* = {*Entomolithus cancri*}.

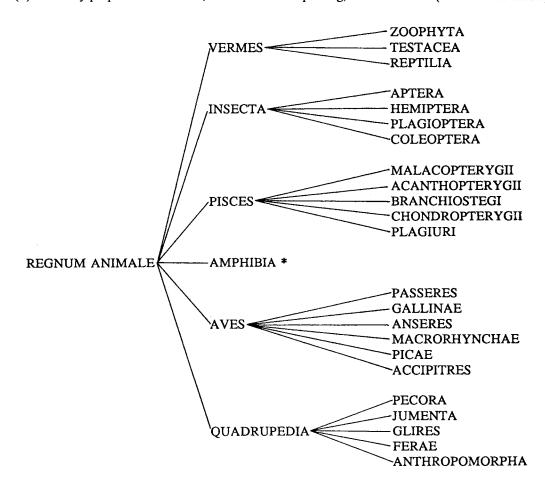


Figure 4.12. Classification of the Animal Kingdom down to the level of order (after Linnaeus, 1735). The classification of the Class Amphibia down to the level of species is shown in Figure 4.13.

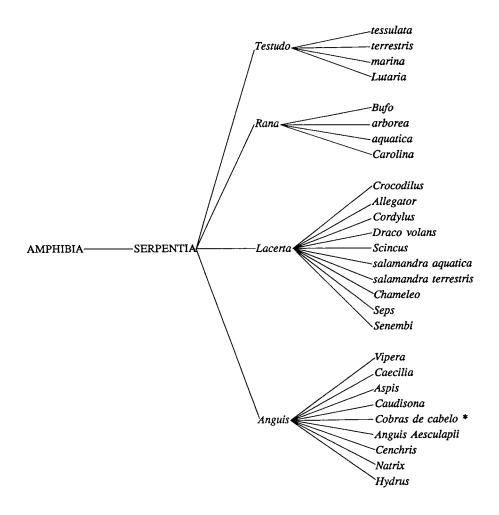


Figure 4.13. Classification of Amphibia down to species level (after Linnaeus, 1735). (\*) In Portuguese in Linnaeus' original. Linnaeus intended to say "cobras de capelo" (i. c., najas), and not "cobras de cabelo" (hair snakes).

**Example 4.5.2.** A similar situation occurs in the case of the 'Regnum Animale' (Figures 4.12 and 4.13) -Amphibia has only one order, Serpentia. Intensionally, Amphibia = {Serpentia}.

**Example 4.5.3.** In the case of the 'Regnum Vegetabile' the situation is disastrous. Axioms (i) and (ii) of Definition 4.4.1 are violated several times (cf. Figures 4.14 and 4.15).

That Linnaeus was conscious of the problems caused by his stubborn adherence to the system of categories will be made clear in the next

section, where we shall see the devices he used in trying to circumvent those problems; he created, instead, worse difficulties.

### 4.6. Devices used by Linnaeus to circumvent the problem of the use of the system of categories

On several occasions, including his 10th edition of the Systema Naturae (1758), Linnaeus used several devices to circumvent the inadequacy in the application of his system of categories to classifications. A few examples will illustrate this.

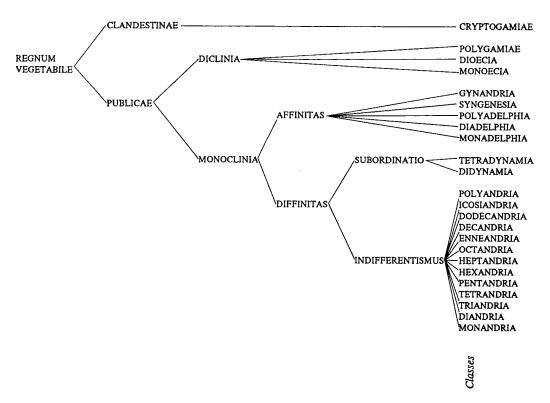


Figure 4.14. Classification of the Plant Kingdom down to the level of 'Classes' (apud Linnaeus, 1735).

**Example 4.6.1.** Let's consider the *genus Curculio* (Insecta, Coleoptera) such as it appears in the *Systema Naturae* of 1758. Linnaeus divided it as in Figure 4.16:

But the correct logical division is that shown in Figure 4.17. There are, according to the correct logical division, two additional levels, and, consequently, two categories more, between the infimous species and *Curculio*. This latter taxon would belong, following Linnaeus' system, in the category *classis*, and never in the category *genus*. This would ruin the entire system of categories within the Animal Kingdom. Linnaeus tried to eliminate this problem doing a false logical division of the '*genus*' Curculio.

**Example 4.6.2.** Another artifice commonly employed by Linnaeus is illustrated by the case of *Entomolithus cancri*, aforementioned. Let us establish a set-theoretical basis to explain what we consider was the intuitive reasoning of Linnaeus.

Let's denote the taxa Graptolithus, Phytolithus, Helmintholithus, Entomolithus, Ichthyolithus, Amphibiolithus, Ornitholithus and Zoolithus, respectively, by their initial letters; let's give them an extension (denoted by o) and an intension (denoted by n), in the following manner:

G = 
$$(o_{G}, n_{G})$$
,  
P =  $(o_{P}, n_{P})$ ,  
H =  $(o_{H}, n_{H})$ ,  
E =  $(o_{E}, n_{E})$ ,  
I =  $(o_{I}, n_{I})$ ,  
A =  $(o_{A}, n_{A})$ ,  
O =  $(o_{O}, n_{O})$ ,

 $Z = (o_z, n_z).$ 

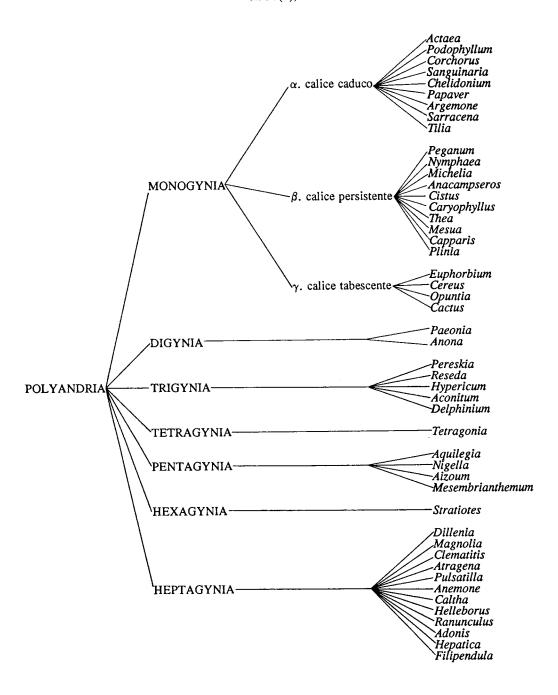


Figure 4.15. Classification of the Polyandria down to the level of genera (apud Linnaeus, 1735).

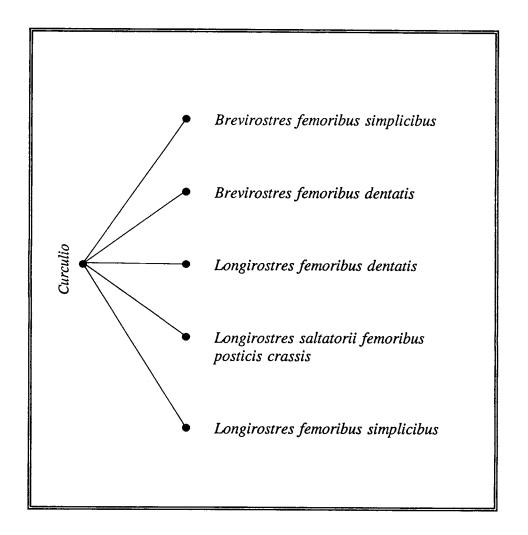


Figure 4.16. Division of the 'genus' Curculio in eide, such as it appears in Linnaeus' Systema Naturae (1758).

Next, let's attribute hypothetical notes to the several intensions:

$$n_{\rm G} = \{a, b, c\}$$
  
 $n_{\rm P} = \{a, d, c\}$   
 $n_{\rm H} = \{a, f, g\}$ 

$$n_{\rm E} = \{\{a, h, i\}\}$$

$$n_1 = \{a, j, k\}$$

$$n_A = \{a, l, m\}$$

$$n_0 = \{a, n, o\},\$$

$$n_z = \{a, p, q\}.$$

Notice that  $\{a, h, i\}$  is the (hypothetical) set of notes attributed to *Entomolithus cancri*, the sole species of *Entomolithus*. To obtain the distinct set *Entomolithus* (to maintain a certain symmetry in the system of categories), Linnaeus had to transform (so as to say) *Entomolithus* into the unitary set of the set  $\{a, h, i\}$ , that is, *Entomolithus* (or, better saying,  $n_E$ ) =  $\{\{a, h, i\}\}$ .

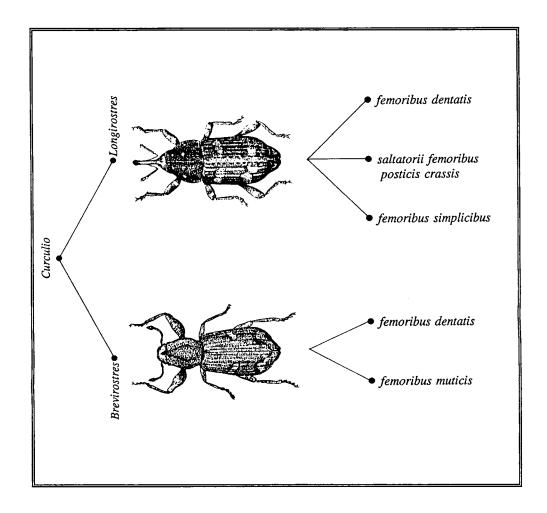


Figure 4.17. The correct logical division of the 'genus' Curculio, using the characters employed by Linnaeus in 1758.

Doing this, Linnaeus created serious problems:

- (i) He broke the relation of (intensional) order which orders the classification. Notice that *Entomolithus cancri*, understood as the intensional set {a, h, i} is *not* included in *Entomolithus*, taken as the set {{a, h, i}}, but *belongs* to it ({a, h, i} Î {{a, h, i}}). Consequently, Linnaeus would not have a classification.
- (ii) He could never have obtained 'Petrificata' as the non-empty intersection of the

intensions of G, P, H, E, I, A, O and Z. E (or, more appropriately,  $n_{\rm p}$ ) = {{a, h, i}} is disjunct from each of the intensional sets  $n_{\rm c}$ ,  $n_{\rm p}$ ,  $n_{\rm q}$ ,  $n_{\rm p}$ ,  $n_{\rm o}$ , and  $n_{\rm z}$ , as there is no element in common between  $n_{\rm e}$  and those sets (the only element of the set {{a, h, i}} is the set {a, h, i}, which is exclusive of E).

The taxon *Entomolithus*, therefore, should be left out of the classification. This absurd result is necessary, if one adopts such a Linnaean artifice.

**Example 4.6.3.** The same reasoning applies to the case of the Amphibia (Figures 4.12 and 4.13):

Serpentia would belong to Amphibia (Amphibia understood as {Serpentia}) and Amphibia would be intensionally disjunct from Vermes, Insecta, Pisces, Aves and Quadrupedia. In short, Amphibia should be excluded from the Animal Kingdom!

Example 4.6.4. The most desperate artifice used by Linnaeus to maintain his absurd system of categories was employed in his most beloved kingdom -the Plants. As the distinct  $X_i \subseteq A$ , in this case, have different lengths, Linnaeus attributed categories to taxa in an arbitrary form, whilst leaving many taxa without a corresponding category (e.g., in Figure 4.14, the taxa he called Publicae, Clandestinae, Monoclinia, Diclinia, Diffinitas, Affinitas, Indifferentismus and Subordinatio). He attributed the category classis to many groups which occupy different levels in the diairesis. In the case of the Polyandria (Figure 4.15) he just ignored the intermediary level (an additonal category) between the Monogynia and the 'genera'. In short, in total desperation, he used the categories as he wanted, without logical bases!

Example 4.6.5. One last example will illustrate another forceful device used by Linnaeus to maintain his system of categories. In the first edition of his Systema Naturae (1735), in the chapter "Observationes in Regna iii. naturae", in the paragraph 15 he states: "Lapides crescunt. Vegetabilia crescunt & vivunt. Animalia crescunt, vivunt & sentiunt. Hinc limites inter haecce Regna constituta sunt."

Consequently, these three taxa form a totally ordered system (if arranged intensionally), or a chain (a "scala naturae"). Therefore, the three cannot be "kingdoms", as, to belong to the same category, taxa must be intensionally non-comparable. In this case, the taxon "Lapides" is properly included in the taxon "Vegetabilia", which, in its turn, is properly included in the taxon "Animalia" (intensionally speaking) (Figure 4.18). If "Animalia" is a member of the category "Kingdom", then, according to Linnaeus' system, "Vegetabilia" should be a "Class" and "Lapides" an "order"!

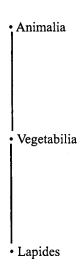


Figure 4.18. The true order of Animalia, Vegetabilia and Lapides, according to the characters given by Linnaeus (1735).

#### 4.7. Conclusion

Instead of abandoning the system of categories, provedly inadequate to reality, Linnaeus adhered stubbornly to it, originating many absurds. To complicate the situation, subsequent authors have created more and more categories (Phylum, Cohort, Family, Tribe, and so on), using prefixes (super, sub-, infra-, etc.) to facilitate the proliferation of categories.

The number of categories may grow indefinitely -they will always form a chain. The number of taxa may grow indefinitely -they will always form (taken intensionally) an inf-semilattice. What will never exist, between this inf-semilattice and the chain formed by categories, is a strict order-preserving function.

To maintain the Linnaean system of categories (otherwise called the system of taxonomic categories) is absurd - unless it be used, as still do taxonomists, in an entirely arbitrary manner. It is incredible that this lack of sense has been perpetuated (and aggravated) in taxonomy.

#### 4.8 A Post-Script

The problem posed by the Linnaean system of categories was considered before by J. R. Gregg in his classic *The language of taxonomy* (1954). The so-called "Gregg's paradox" aroused much discussion in the literature. Sklar (1964), Van Valen (1964) and Buck and Hull (1966) commented it. There was an answer from Gregg (1968). Then entered in the discussion Hull and Snyder (1969), Buck and Hull (1969) and Ruse (1971). We shall not occupy ourselves here with the opinions of those authors, who, according to us, entirely missed the issue. The interested reader may compare those papers with our treatment of the problem.

### 5. THE EQUIVOCAL USAGE OF THE CONCEPT OF 'GENOS'

### 5.1. The concept of 'genos' (γενος) in classical taxonomy

Let us suppose, initially, four 'Linnaean species'  $S_1$ ,  $S_2$ ,  $S_3$  and  $S_4$ . Let's denote by  $n_1$ ,  $n_2$ ,  $n_3$  and  $n_4$  the respective *intensions* of those species, such that

$$n_1 = \{n_1, n_3\},$$
  
 $n_1 = \{n_1, n_2, n_4\},$ 

$$n_3 = \{n_1, n_2, n_5, n_6\},$$

$$n_4 = \{n_1, n_2, n_3, n_7\}.$$

Let's denote by  $o_1$ ,  $o_2$ ,  $o_3$  and  $o_4$  the respective extensions of the species  $S_1$ ,  $S_2$ ,  $S_3$  and  $S_4$ .

We have already seen that, in a purely logical classification, a logical genus or genos is

- (i) Intensionally speaking, the non-empty intersection of the intensions of two or more distinct logical species; and
- (ii) Extensionally speaking, the union of the extensions of those two or more distinct logical species.

It follows, then, that the species  $S_1$ ,  $S_2$ ,  $S_3$  and  $S_4$ , in our case, will show the following aspect, if ordered intensionally (Figure 5.1):

There exist three 'logical genera' (gene):  $X_1$ ,  $X_2$  and  $X_3$ , whose respective intensions are  $nx_1$ ,  $nx_2$  and  $nx_3$ , such that

$$n_{x_1} = n_x \cap n_x$$
,  
 $n_{x_2} = n_x \cap n_x$ , (that is,  $n_x \cap n_y \cap n_y$ ),  
 $n_{x_3} = n_x \cap n_x$ , (that is,  $n_x \cap n_y \cap n_y \cap n_y$ ).

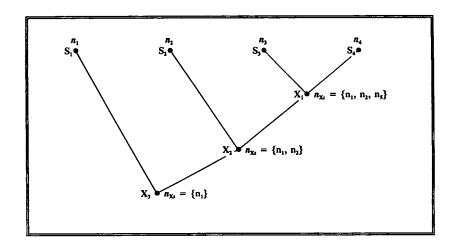


Figure 5.1. Intensional inf-semilattice formed by four terminal species; three logical genera result from the intersections.

Now, extensionally, we have a supsemilattice (Figure 5.2):

Notice that:

$$o_{x_1} = o_3 \cup o_4$$
  
 $o_{x_2} = o_2 \cup o_{x_1}$  (that is,  $o_2 \cup o_3 \cup o_4$ ),  
 $o_{x_3} = o_1 \cup o_{x_2}$  (that is,  $o_1 \cup o_2 \cup o_3 \cup o_4$ ).

Another way of representing this is (Figure 5.3):

Between the extensional sup-semilattice and the intensional inf-semilattice, as commented in the previous chapter, there exists a decreasing function (Figure 5.4).

This is the type of classification normally used in the traditional or 'Linnaean' taxonomy.

Let's examine an example of such a classification. Let the 'logical genus' X<sub>3</sub> of Figure 5.2 be the 'Order' Palaeognathiformes (Aves). Let the 'logical species' S<sub>1</sub> be the 'Suborder' Tinami and the 'logical genus' X<sub>2</sub> the 'Suborder' Ratiti. Let the 'logical genus' X<sub>1</sub> be the 'Infraorder' Struthiones and the 'logical species' S<sub>2</sub> the

'Infraorder' Apteryges. Finally, let the 'infimous species' S<sub>3</sub> and S<sub>4</sub> (of our example) be, respectively, the 'Families' Casuariidae and Struthionidae.

If it is a Linnaean classification, we may represent it graphically, using the *extension* of those concepts, as shown in Figure 5.5:

In this case we may say, extensionally, that

- (i) The 'order' Palaeognathiformes *includes* the 'suborders' Tinami and Ratiti;
- (ii) The 'suborder' Ratiti *includes* the 'infraorders' Struthiones and Apteryges;
- (iii) The 'infraorder' Struthiones *includes* the 'families' Casuariidae and Struthionidae:
- (iv) Tinami, Apteryges, Casuariidae and Struthionidae are included in Palaeognathiformes.

Intensionally speaking, however, the 'order' Palaeognathiformes is included in the 'suborders' Tinami and Ratiti; Apteryges and Struthiones include Ratiti; Casuariidae and Struthionidae include Struthiones; and Paleognathiformes is included in Tinami, Apteryges, Casuariidae and Struthionidae (Figures 5.6 and 5.7).

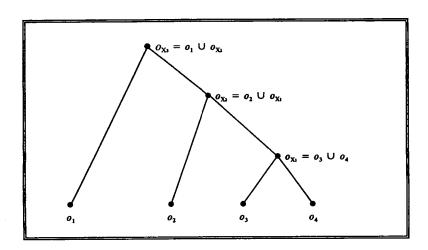


Figure 5.2. Extensional sup-semilattice formed by four species. Three logical genera result from the unions.

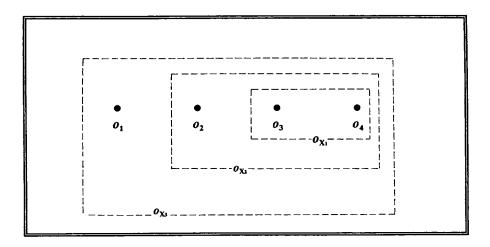


Figure 5.3. Another representation of the relation of extensional inclusion of the classes of Figure 5.2

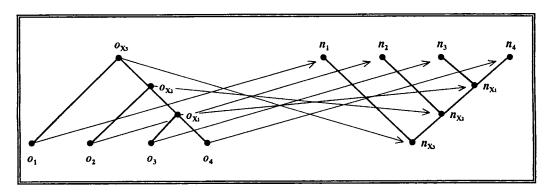


Figure 5.4. Decreasing function from the extensional sup-semilattice in to the intensional inf-semilattice, obtained in classical taxonomy.

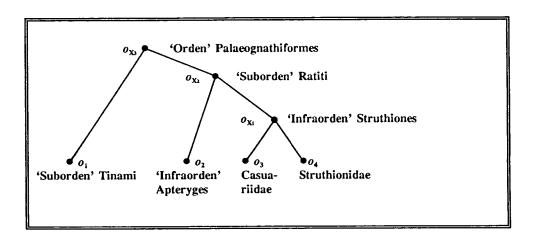


Figure 5.5. Extensional classification of the 'order' Palaeognathiformes.

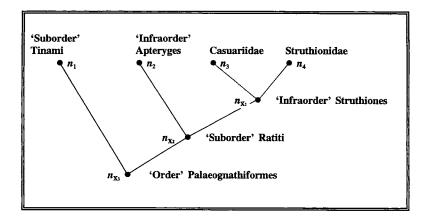


Figure 5.6. Intensional classification of the 'order' Palaeognathiformes.

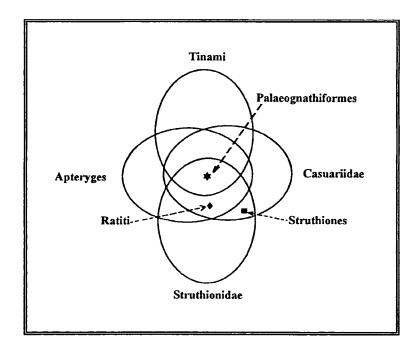


Figure 5.7. Euler-Venn diagram of the intensional classification of the 'order' Palaeognathiformes.

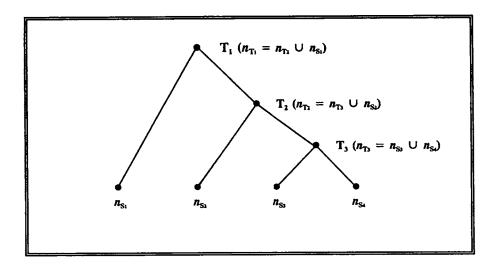


Figure 5.8. Intensional sup-semilattice formed by 'monophyletic-groups'

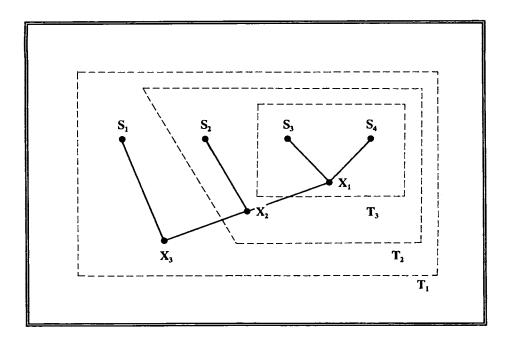


Figure 5.9. Another graphic representation of the intensional sup-semilattice formed by 'monophyletic groups' shown in Figure 5.8, with 'ancestral cidophoronts'  $(X_3, X_2, X_1)$ .

## 5.2. What happened to the 'logical genera' in evolutionary taxonomy

We may now consider the changes introduced in taxonomy with the advent of the Theory of Evolution.

1. Given two or more distinct species, the nonempty intersection of the *intensions* of those species came to be considered the *intension of an ancestral* species (of an eidophoront, in our terminology, ancestral to those species). Thus, in our example of Figure 5.1, the intension of the eidophoront  $X_1$  $(n_{x_1})$  is the set  $\{n_1, n_2, n_5\}$ ; the intension of the eidophoront  $X_2$   $(n_{x_2})$  is the set  $\{n_1, n_2\}$ ; notice that  $n_{x_2}$  is also equivalent to  $n_2 \cap n_3 \cap n_4$ ); and that the intension of the eidophoront  $X_3$   $(n_{x_3})$  is the unitary set  $\{n_1\}$ , which is equivalent to  $n_1 \cap n_{x_2}$   $(= n_1 \cap n_2 \cap n_{x_3} \cap n_4)$ .

From the set-theoretical point of view, be it in Linnaean taxonomy, or in evolutionary taxonomy, the species system, ordered intensionally by the relation of proper inclusion, will always result in inf-semilattices. The difference lies in the underlying ontology. In Linnaean taxonomy, the non-empty intersections of two or more species are logical 'genera' or gene; in evolutionary taxonomy, they are considered 'ancestral species' (or, in our terminology, ancestral eidophoronts) - real entities, then, and no longer abstractions - which existed in time and space.

2. Given two or more distinct morphospecies with non-empty intensional intersection, the *union* of their *intensions* is now, in evolutionary taxonomy, considered a *monophyletic group*. Thus, in relation to the previous example, we have the following (Figure 5.8):

Representing together the system of the species and the system of the 'monophyletic groups' we have the aspect exhibited in Figure 5.9:

Notice that the intensions of the sets  $t_1$ ,  $t_2$  and  $t_3$  are, respectively:

$$n_{T1} = \{n_1, n_2, n_3, n_4, n_5, n_6, n_7\};$$

$$n_{77} = \{n_1, n_2, n_4, n_5, n_6, n_7\};$$

$$n_{T3} = \{n_1, n_2, n_5, n_6, n_7\}.$$

Remember that  $n_1 = \{n_1, n_3\}$ ,  $n_2 = \{n_1, n_2, n_4\}$ ,  $n_3 = \{n_1, n_2, n_3, n_4\}$  and  $n_4 = \{n_1, n_2, n_3, n_4\}$ , which are the respective intensions of S<sub>1</sub>, S<sub>2</sub>, S<sub>3</sub> and S<sub>4</sub>.

Now let's return to the example of the Palaeognathiformes. Let's postulate that this group presents only the taxa represented in Figure 5.6, for brevity's sake.

In evolutionary taxonomy, intensionally speaking, we have that the name 'Palaeognathiformes' designates the set called  $t_1$  in our Figure 5.8; in the Linnaean system it designates (still intensionally) the 'genos'  $X_3$  of Figure 5.1, and extensionally the element  $o_{x3}$  of the supsemilattice shown in Figure 5.2.

'Tinami', as we had convened, is the name of the 'species' S<sub>1</sub>.

'Ratiti', intensionally, in evolutionary taxonomy, corresponds to the taxon  $t_1$  of Figure 5.8; in the Linnaean taxonomy, it denotes the 'genos'  $X_2$  (Figure 5.1) and the element  $o_{x2}$  of the supsemilattice of Figure 5.2.

'Apteryges' is the name of S<sub>1</sub>.

'Struthiones' denotes the set  $t_3$  (Figure 5.8) and the 'genos'  $X_1$  of Figure 5.1 (or the element  $o_{x_1}$  of the sup-semilattice of Figure 5.2).

Finally, 'Casuariidae' corresponds to  $S_3$  and 'Struthionidae' to  $S_4$ .

We now see why the same name of a 'suprageneric category' is used, in a preposterous way, to denote the entire monophyletic system and to denote exclusively the eidophoront which is ancestral to all other taxa of that same monophyletic system. Pure and simply because of confusion between concepts used in Linnaean taxonomy and evolutionary taxonomy.

Let's denote, now, respectively, by  $o_p$ ,  $o_g$ ,  $o_s$ ,  $o_T$ ,  $o_A$ ,  $o_c$  and  $o_s$ , the extensions of the taxa Palaeognathiformes, Ratiti, Struthiones, Tinami,

Apteryges, Casuariidae and Struthionidae. The ordered system results as in Figure 5.10, in evolutionary systematics. We have the same result in Linnaean taxonomy.

But if we compare it to the sup-semilattice obtained with the *intensions* of the same taxa in evolutionary taxonomy, we will note that there is an *isomorphism of order* between the two, and no longer a decreasing function, as happened with Linnaean taxonomy (Figure 5.4). Figure 5.11 represents the isomorphism of order existing between the extensional sup-semilattice and the intensional sup-semilattice of the same taxonomic group in evolutionary taxonomy.

The *species*, in evolutionary taxonomy, ordered by the relation of intensional inclusion, will always form an inf-semilattice.

Monophyletic groups will always result, ordered by the relation of intensional or extensional inclusion, in sup-semilattices, in evolutionary taxonomy.

## 5.3. The three different meanings of 'genus'

Due to the confusion generated in evolutionary taxonomy as regards the 'supraspecific categories', three different meanings of the concept of 'genus' (and the same can be said of all the other 'suprageneric categories') exist. We will call them C-genos, P-genos and inf(P-genos).

- 1. Given a phylogeny (with 3 or more taxa), a *C*-genos is the set of all the terminal species (the maximal elements of the inf-semilattice obtained by intensional inclusion). This is the concept of 'genus' (and other categories) appearing in catalogues -that's why we call this concept a C-genos.
- 2. Given a phylogeny (with 3 or more taxa) a *P*-genos is the set of all the taxa (species and eidophoronts) of that phylogeny.
- 3. Finally, the *inf(P-genos)* is the eidophoront which is ancestral to all the other taxa of a phylogeny. Let's illustrate this with an example (Figure 5.12):

When a phylogeneticist says 'the phylogeny of the 'genera' *M-us*, *N-us* and *X-us*', he actually means 'the phylogeny of the ancestral eidophoront of the monophyletic groups *M-us*, *N-us* and *X-us*'.

Another example to illustrate the confusion among these three concepts.

Let's postulate the existence of the following hypothetical species and their respective sets of apomorphies:

$$X$$
-us  $a$ -us =  $\{n_1, n_2\}$ ;

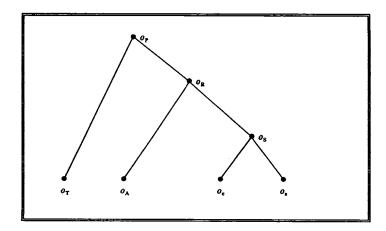


Figure 5.10. Extensional sup-semilattice formed by the 'monophyletic groups' of the 'Order' Palaeognathiformes.

$$X$$
-us  $b$ -us = { $n_1$ ,  $n_2$ ,  $n_4$ };

$$X$$
-us  $c$ -us = { $n_1$ ,  $n_2$ ,  $n_5$ ,  $n_6$ };

$$X$$
-us  $d$ -us = { $n_1$ ,  $n_2$ ,  $n_5$ ,  $n_7$ }.

The phylogeny results as in Figure 5.13:

X-us can be interpreted in three different manners, as explained above:

- 1. As a C-genos, it includes 4 morphospecies (the terminal species of the phylogeny);
- 2. As a P-genos, it includes 7 taxa;
- 3. As an  $\inf(P-genos)$  it is identical with the eidophoront  $X_1$ .

As regards the *intension*s of these three meanings, *X-us*, considered either as a C-genos or as a P-genos, has the same intension ( $\{n_1, n_2, n_3, n_4, n_5, n_8, n_7\}$ ), but as an inf(P-genos) its intension is  $\{n_1\}$ .

## 5.4. On how even Hennig became equivocated

In *Phylogenetic Systematics* (1966: 70-72) W. Hennig declared:

«Two different graphic representations of a hierarchic system are contrasted in Fig. 18 [our Figure 5.14]. Comparison shows that they correspond exactly to one another: every fact that can be inferred from I is also expressed in II; the only difference is the way in which the phylogenetic relationships of the individual species are expressed. In II the phylogenetic relationships between a species (stem species) and its successor species are indicated by arrows. In I they can be recognized equally well from the fact that the symbolic boundary lines of the stem species have been drawn around their successor species. The form of representation I has a particular significance because it shows how the boundaries of the higher taxa must be drawn in the phylogenetic system: in I the symbols for the 'stem species' 1, 2, 3, 4, coincide with the boundaries of the higher taxa in which the species that arose from them are collected in groups in the phylogenetic system [and here Hennig was equivocated, as will be demonstrated presently]. From this it is evident that to every higher taxon in the phylogenetic system there corresponds a 'stem species' from which all the species included in the taxon have arisen. It is also evident that in the phylogenetic system the species included in each higher taxon must be derivable from a common stem species, and that no species having arisen from this stem species can be placed outside this taxon.

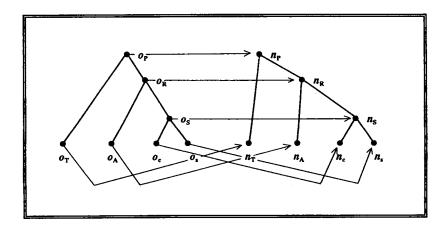


Figure 5.11. Isomorphism of order from the extensional sup-semilattice into the intensional sup-semilattice formed by the 'monophyletic groups' of the 'Order' Palaeognathiformes, obtained in phylogenetic systematics.

From the fact that in diagram I the boundaries of a 'stem species' coincides with boundaries of the taxon that includes all its successor species [Hennig's equivoque], it follows that the 'stem species' itself belongs in this taxon. But since, so to speak, it is identical with all the species that have arisen from it [sic], the 'stem species' occupies a special position in this taxon. If, for example, we knew with certainty the stem species of the birds (and it is only from such a

premise that we can start in theoretical considerations), then we would have to include it in the group 'Aves'. But it could not be placed in any of the subgroups of the Aves. Rather we would have to express unmistakably the fact that in the phylogenetic system it is equivalent to the totality of all species of the group [sic]» (italics ours).

Let's redraw Hennig's phylogeny, naming its constitutive taxa, and giving them apomorphies, as in Table 5.1 and Figure 5.15.

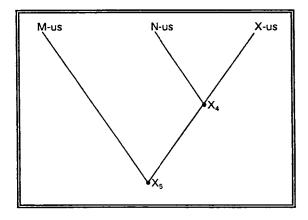


Figure 5.12. 'Phylogeny' of three hypothetic 'genera', M-us, N-us and X-us.

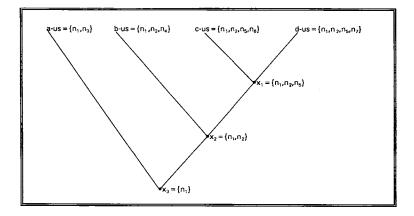


Figure 5.13. 'Phylogeny' of a hypothetical group.

TABLE 5.1. Hypothetical intensions of the 23 taxa included in Hennig's Figure 18 (1966: 71). Compare with figures 5.14 and 5.15.

 $= \{n_i\}$  $= \{\mathbf{n}_1, \mathbf{n}_2\}$  $= \{\mathbf{n}_1, \, \mathbf{n}_3\}$  $= \{\mathbf{n}_1, \mathbf{n}_2, \mathbf{n}_4\}$  $= \{n_1, n_2, n_3\}$  $= \{\mathbf{n}_{\scriptscriptstyle 1},\,\mathbf{n}_{\scriptscriptstyle 2},\,\mathbf{n}_{\scriptscriptstyle 5},\,\mathbf{n}_{\scriptscriptstyle 6}\}$  $= \{n_1, n_2, n_3, n_4\}$ =  $\{n_1, n_2, n_5, n_6, n_8\}$  $= \{n_1, n_2, n_3, n_4, n_6\}$  $= \{n_1, n_2, n_4, n_{10}\}$  $= \{n_1, n_2, n_4, n_{11}\}$  $= \{n_1, n_2, n_3, n_4, n_8, n_{12}\}$ =  $\{n_1, n_2, n_5, n_6, n_8, n_{13}\}$  $= \{n_1, n_2, n_5, n_6, n_9, n_{14}\}$  $= \{n_1, n_2, n_5, n_6, n_9, n_{15}\}$  $= \{\mathbf{n}_{1}, \, \mathbf{n}_{2}, \, \mathbf{n}_{5}, \, \mathbf{n}_{7}, \, \mathbf{n}_{16}\}$ =  $\{n_1, n_2, n_3, n_7, n_{17}\}$  $= \{n_1, n_3, n_{18}\}$  $= \{n_1, n_2, n_{10}\}$  $= \{n_{1}, n_{3}, n_{18}, n_{20}\}$  $= \{\mathbf{n}_{1}, \, \mathbf{n}_{3}, \, \mathbf{n}_{18}, \, \mathbf{n}_{21}\}$  $= \{n_1, n_3, n_{19}, n_{22}\}$  $= \{n_1, n_2, n_{10}, n_{13}\}$ 

Our Figure 5.15 corresponds to Hennig's 'interpretation II' (cf. Hennig, 1966, Fig. 18).

In our Figure 5.16 we represent graphically the interrelationships among the 'supraspecific taxa' relative to the same phylogeny. This corresponds to Hennig's 'interpretation I' (cf. Hennig, 1966, fig. 18; our Figure 5.14).

Let's now suppose that this phylogeny presented by Hennig refers to the Palaeognathiformes, in order to use the data seen before.

The Hennigian eidophoront S<sub>1</sub> (Figure 5.15) is the infimous element of the *intensional* inf-semilattice formed by the taxa, either in Linnaean taxonomy or in Phylogenetic Systematics.

However, in Linnaean taxonomy (but *not* in phylogenetic systematics), S<sub>1</sub> corresponds to the maximum element of the *extensional* sup-semilattice formed by the taxa. In Linnaean taxonomy, therefore, S<sub>1</sub> (extensionally) would be named 'Order Palaeognathiformes'. In the phylogenetic system, 'Palaeognathiformes' would denote the set A<sub>1</sub> (Figure 5.15). Notice that, in the Linnaean system, the intension of 'Palaeognathiformes', understood

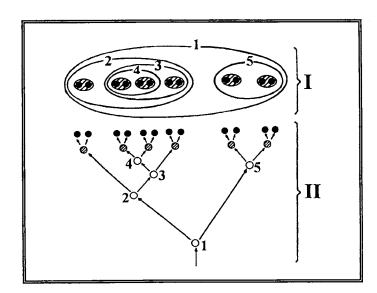


Figure 5.14. The phylogenetic kinship relations between the species of a monophyletic group, represented in two different ways (apud Hennig, 1966: 71, Fig. 18).

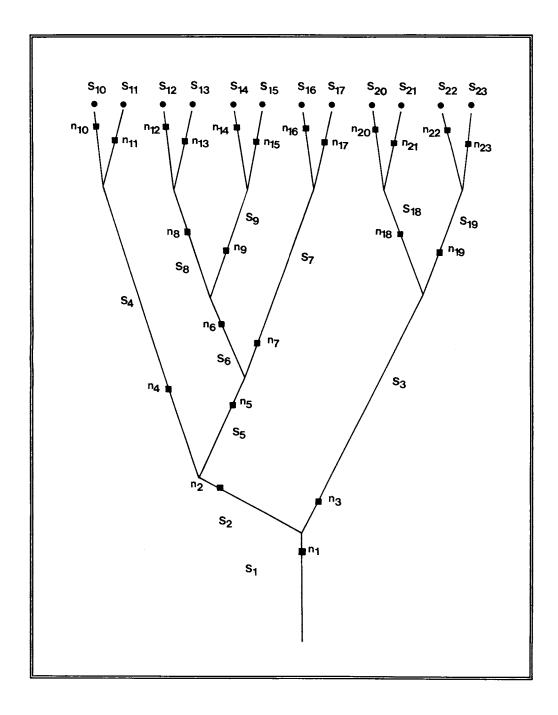


Figure 5.15. Another representation of Hennig's Figure 18 (1966: 71), with hypothetical autapomorphies of the 23 taxa involved.

as  $S_1$ , is  $\{n_1\}$ ; in the phylogenetic system, 'Palaeognathiformes', understood as the set  $A_1$ , has as intension the set  $A_1 = \{n_1, n_2, n_3, n_4, n_5, n_6, n_7, n_9, n_{10}, n_{11}, n_{12}, n_{13}, n_{14}, n_{15}, n_{16}, n_{17}, n_{18}, n_{19}, n_{20}, n_{21}, n_{22}, n_{23}\}$ .

As the same *name*, in our case 'Palaeognathiformes', is equivocally applied to the *eidophoront* S<sub>1</sub> from the Linnaean point of view, and to *all the taxa* of the phylogeny, i. e., the set A<sub>1</sub>, from the phylogenetic point of view, Hennig reached the false conclusion that "the original species, in the corresponding phylogenetic system, is equivalent to all the remaining species of the group".

What Hennig called 'species 1' in his 'interpretation I' is equivalent, in reality, to set A<sub>1</sub> of our Figure 5.16, and never to the 'species 1' of his 'interpretation II'. Because of the *names*, probably, Hennig confounded two distinct sets (and two distinct schools -his own and the Linnaean).

The same happens with the other

'supraspecific taxa'. In relation to Figure 5.16, we would have:

 $A_1 = Palaeognathiformes;$ 

 $A_{,} = Ratiti;$ 

 $A_1 = Struthiones;$ 

 $A_2 - A_3 = Apteryges;$ 

 $A_{\lambda} = Struthionidae;$ 

 $A_1 - A_4 = Casuariidae;$ 

 $A_s = Tinami.$ 

Consequently, the 'species 2' of 'interpretation II' is *not* equivalent to the 'species 2' of 'interpretation I' (the latter is our set  $A_2$ ). The 'species 3' of 'interpretation II' is *not* equivalent to the 'species 3' of 'interpretation I' (which is our set  $A_3$ ). And so forth.

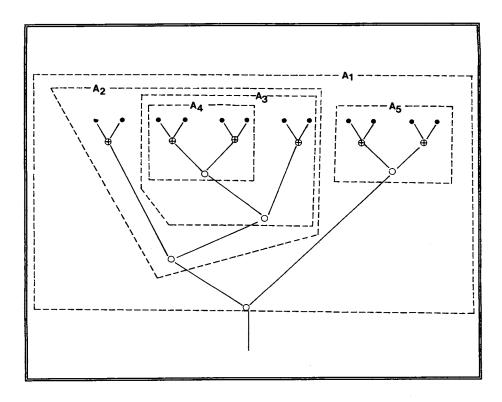


Figure 5.16. Hypothetical intensions of the monophyletic groups of Hennig's Figure 18 (1966: 71).  $A_1 = \{n_1, n_2, n_3, n_4, n_5, n_6, n_7, n_8, n_9, n_{10}, n_{10}$ 

6. GENERAL CONVENTIONS OF THE NEW SYSTEM OF NOMENCLATURE FOR PHYLOGENETIC SYSTEMATICS

In the sequence we present some conventions for the new system of nomenclature. Then we will show examples on how to work with the ancient 'supraspecific categories'.

Convention 1. Morphospecies which are not ancestors of other morphospecies, be they living, fossil or extinct, are named by Linnaean binomina, in the traditional manner; these binomina are always written in italics, or any other type different from the remaining text.

**Example 6.1.** When we write *Musca domestica* Linnaeus, 1758, we know it is a morphospecies which is not ancestor of other morphospecies.

**Convention 2.** The singular name in the nominative case forming the first part of a *binomen* is called a *praenomen* -the ancient expression 'generic name' is abandoned. We are here following Griffiths (1974: 120), who, for other reasons, declares:

"It will avoid confusion if we refer to the first name in species names as the forename or *praenomen*, not as the generic name."

**Example 6.2.** Given the binomen *Musca domestica* Linnaeus, 1758, *Musca* Linnaeus, 1758 is a *praenomen*.

Convention 3. 'Ancestral species' (eidophoronts), be they hypothetical or real, may be named either by a *praenomen* or by a *binomen*. In both cases those names are *not* written in italics or in any other type different from the remaining text.

Example 6.3. Musca domestica, Linnaeus, 1758 and Oestrus, Linnaeus, 1758, are names of (hypothetical) 'ancestral species' (ancestral eidophoronts).

Using, then, either *praenomina*, or specific names, we may now introduce our proposed new system of nomenclature for phylogenetic systematics.

This system is analogous to Hennig's Theory

of Phylogenetic Systematics, in the meaning that apomorphies are substituted by names (onomastics); therefore, where autapomorphies exist, we employ autaponomastics and where synapomorphies exist we employ synaponomastics. The usage of these terms is based upon the following requirements and conditions asked from a biological classification:

- 1. That it produces the least possible quantity of new names;
- 2. That it may apply names to all the taxa composing a phylogeny;
- 3. That it may represent an isomorphism of order between the inf-semilattice representing the phylogeny and the inf-semilattice representing the nomenclature, thus retrieving, in the most exact manner, the phylogenetic information.

Using an example, we may see how simply our new system works. But before proceeding, let's give some basic principles:

- a) Given two distinct taxa A and B, A and B are nominally distinct if they possess *nominal heterobathmy*, i.e., if A has an autaponomastic and B has another;
- b) A and B are considered monophyletic, from the nomenclatural point of view, if they possess a *synaponomastic*; in order to obtain a 'synaponomasia', we proceed in the following way: we take the name (either a *praenomen* or a specific name) that has priority (year, page, paragraph, line) and give to it the index '-1': that name is attributed to both taxa, constituting a 'synaponomasia'; as a 'synaponomasia' (analogously to a synapomorphy) is an autaponomasia of the immediate ancestral eidophoront, the latter is automatically named in this way, without creating a new name.

As example, let's consider the phylogeny of the 'genera' (ancestral eidophoronts of the 'genera' of the 'tribe' Erodiscini (Coleoptera, Curculionidae) (Vanin, 1986). We see in Figure 6.1 that the ancestral eidophoronts have no name.

In order to give names to the ancestral eidophoronts and in order to maintain the relation

of order (by inclusion) of such a phylogeny, we use the following procedures:

- 1. We take the terminal taxa with the greatest number of ancestral elements (in our case Hammatostylus and Lancearius, with 5 ancestors each);
- 2. We take Hammatostylus and Lancearius (no italics) as autaponomastics, respectively, of the taxa N and O (of Figure 6.1) -thus we have a nominal heterobathmy between those two species (Figure 6.2):
- 3. Next we take the name that has priority, i.e., *Hammatostylus* Champion, 1903, and give to it the index «-1». Hammatostylus, is now considered to be the 'synaponomasia' of the species N and O (Figure 6.3). As the synaponomasia of these two species is the autaponomasia of the immediate ancestral eidophoront (M in our example), this taxon is then called Hammatostylus, Champion, 1903. No new name is necessary (Figure 6.4)
- 4. The same procedure goes on successively. As seen in Figure 6.5, we now have two sister-species, L (Sicoderus) and M (Hammatostylus<sub>-1</sub>), with nominal heterobathmy. We take next the oldest name, in our example *Hammatostylus*, and, adding the index «-2», transform it into the synaponomasia of the species L and M, and into the autaponomasia of the ancestor eidophoront K (Figure 6.6).
- 5. Now, the species J and K present nominal heterobathmy (Figure 6.7). Ludovix Laporte, 1840 has priority over Hammatostylus Champion, 1903; hence, the synaponomasia of both species will be Ludovix. Laporte, 1840, which is the autaponomasia of the eidophoront I (Figure 6.8).
- 6. The species H and I now present nominal heterobathmy (Figure 6.9). As *Ludovix* Laporte, 1840 has priority over *Prosicoderus* Vanin, 1986, Ludovix<sub>2</sub> Laporte, 1840 will be the synaponomasia of H and I and the autaponomasia of the ancestral eidophoront C (figure 6.10):
- 7. To go on with our process, we need an autaponomastic for B. As we don't know it, we need to start the process again with other terminal elements (the species F, G and D). Ecnomorhinus and Pimelerodius, with nominal heterobathmy, have

the greatest number of ancestral eidophoronts - consequently we begin our process with them. Now those *praenomina* were published by the same author in the same publication -we establish priority using page precedence: *Pimelerodius* is the *praenomen* with page precedence. The ancestral eidophoront E will be then called Pimelerodius<sub>.1</sub> (Figure 6.11). Thus we will obtain nominal heterobathmy between E and D (Erodiscus Schoenherr, 1825). As *Erodiscus* has priority over *Pimelerodius*, E and D will have as synaponomastic Erodiscus<sub>.1</sub>, which is the name of the ancestor eidophoront B (Figure 6.12)

8. Finally, we have obtained nominal heterobathmy between B and C, and, as *Erodiscus* has priority over *Ludovix*, the synaponomasia of the species B and C will be Erodiscus<sub>2</sub>, also the autaponomastic of the ancestral eidophoront A (Figure 6.13).

Figure 6.14 shows the complete cladogram, with all the autaponomastics. Notice that F, G and D are topologically equivalent to the cladogram of Figure 6.1.

In our new system, no new names are needed; based on the names of the terminal species, we can name all the ancestor eidophoronts of a given phylogeny. One additional advantage of this system is that, due to the strict isomorphism between nomenclature and phylogeny, the latter may be retrieved from the classification.

The classification of the phylogeny used in the foregoing example will be thus expressed:

- 1. Erodiscus, Schoenherr, 1825
- 2. Erodiscus, Schoenherr, 1825: Ludovix, Laporte, 1840
- Erodiscus Schoenherr, 1825: Pimelerodius, Vanin, 1986
- 4. Pimelerodius Vanin, 1986: Ecnomorhinus Vanin, 1986
- 5. Ludovix., Laporte, 1840: Prosicoderus Vanin, 1986
- 6. Ludovix Laporte, 1840: Hammatostylus.<sub>2</sub> Champion, 1903
- 7. Hammatostylus., Champion, 1903: Sicoderus Vanin, 1986

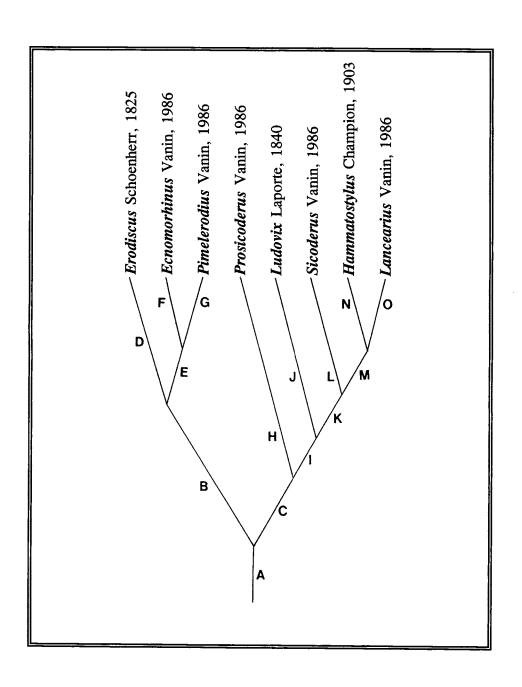


Figure 6.1. Phylogeny of the 'genera' of Erodiscini (Coleoptera, Curculionidae) (after Vanin, 1986).

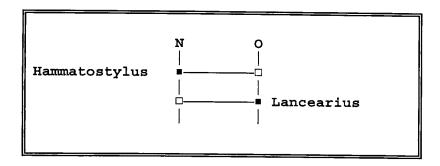


Figure 6.2. Nominal heterobathmy between lineages N and O.

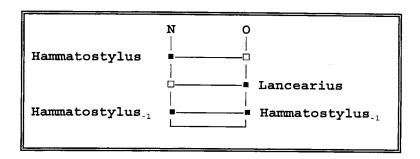


Figure 6.3. Establishment of the synaponomasia of lineages N and O.

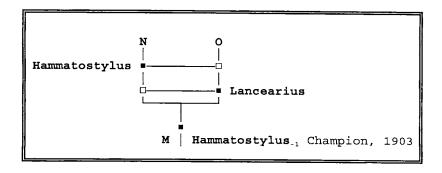


Figure 6.4. The synaponomasia of lineages N and O becomes the autaponomasia of the ancestral lineage M.

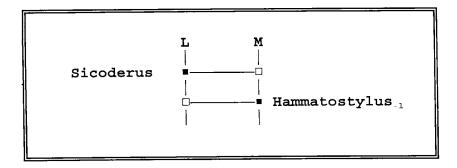


Figure 6.5. Nominal heterobathmy between lineages L and M.

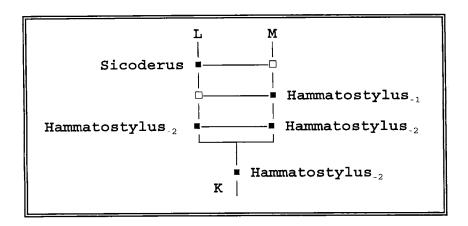


Figure 6.6. The synaponomasia of lineages L and M becomes the autaponomasia of lineage K.

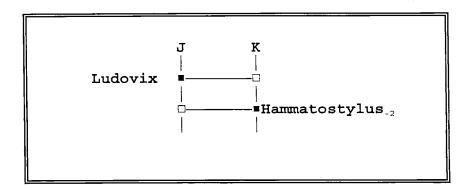


Figure 6.7. Nominal heterobathmy between lineages J and K.

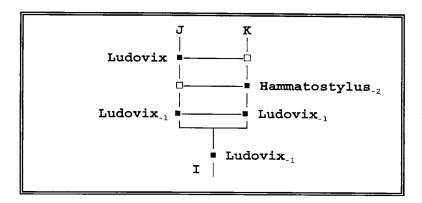


Figure 6.8. The synaponomasia of J and K becomes the autaponomasia of I.

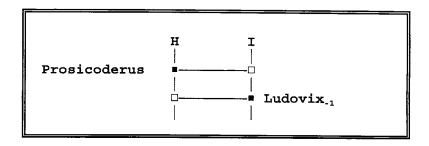


Figure 6.9. Nominal heterobathmy between lineages H and I.

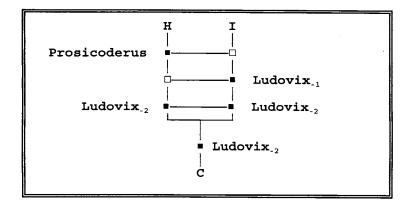
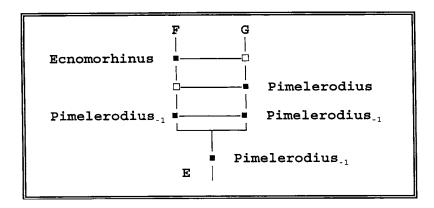


Figure 6.10. The synaponomasia of H and I becomes the autaponomasia of C.



 $\label{eq:Figure 6.11.} Figure 6.11. \ Nominal \ heterobathmy \ between \ F \ and \ G \ . The \ synaponomasia \ of \ F \ and \ G \ becomes the \ autaponomasia \ of \ E.$ 

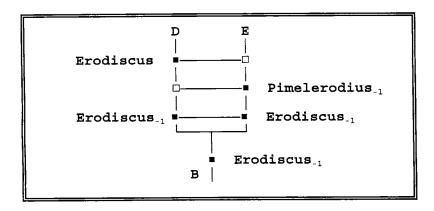


Figure 6.12. Nominal heterobahtmy between D and E. The synaponomasia of D and E becomes the autaponomasia of B.

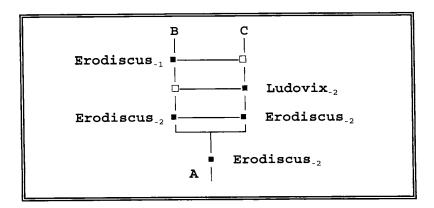


Figure 6.13. Nominal heterobathmy between B and C. The synaponomasia of B and C becomes the autaponomasia of E.

8. Hammatostylus Champion, 1903 : Lancearius Vanin, 1986

By convention, in each line of the classification, we always cite first the name that has priority; the symbol «:» indicates that the names united in a given line belong to sister-species.

The first line of the classification refers to the ancestor (eidophoront) of all the taxa of a monophyletic group.

The second expresses the primary division of the ancestor, the third line the divisions of the 1-descendants of the first ancestor, and so on, until we come to the terminal species.

From such a simple classification we may retrieve the phylogeny of the group. Figures 6.15 to 6.18 ilustrate, step by step, the process of retrieving the phylogenetic relationships from the classification used as an example.

With the new system herein proposed, not only do we retrieve the genealogical information, but we give names to every taxon in a phylogeny, be it terminal or ancestral. Another advantage of the new system is that we may refer to any non-empty subset of an ordered phylogenetic system. In Figure 6.19, for example, we have 22 different subsets of taxa in the phylogeny represented in Figure 6.1. These 22 subsystems (called by capital Latin letters) are classified in the following manner:

- A. Erodiscus, Schoenherr, 1825
- B. Erodiscus, Schoenherr, 1825
- C. Ludovix, Laporte, 1840
- D. Erodiscus Schoenherr, 1825
- E. Pimelerodius, Vanin, 1986
- F. Ecnomorhinus Vanin, 1986
- G. Pimelerodius Vanin, 1986
- H. Prosicoderus Vanin, 1986
- I. Ludovix, Laporte, 1840
- J. Ludovix Laporte, 1840

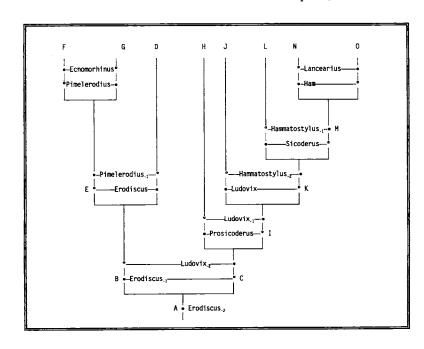


Figure 6.14. Phylogeny of basal groups of Erodiscini, showing autaponomasia of all the taxa involved.

- K. Hammatostylus, Champion, 1903
- L. Sicoderus Vanin, 1986
- M. Hammatostylus, Champion, 1903
- N. Hammatostylus Champion, 1903
- O. Lancearius Vanin, 1986
- P. Erodiscus. Schoenherr, 1825 Erodiscus Schoenherr, 1825: Pimelerodius. Vanin, 1986 Pimelerodius Vanin, 1986: Ecnomorhinus Vanin, 1986
- Q. Pimelerodius. Vanin, 1986
  Pimelerodius Vanin, 1986: Ecnomorhinus Vanin, 1986
- R. Ludovix, Laporte, 1840
  Ludovix, Laporte, 1840: Prosicoderus Vanin, 1986
  Ludovix Laporte, 1840: Hammatostylus,
  Champion, 1903
  Hammatostylus, Champion, 1903: Sicoderus
  Vanin, 1986
  Hammatostylus Champion, 1903: Lancearius
  Vanin, 1986
- S. Ludovix., Laporte, 1840 Ludovix Laporte, 1840: Hammatostylus.

Champion, 1903 Hammatostylus., Champion, 1903: Sicoderus Vanin, 1986

Hammatostylus Champion, 1903: Lancearius Vanin, 1986

- T. Hammatostylus. Champion, 1903

  Hammatostylus. Champion, 1903: Sicoderus
  Vanin, 1986

  Hammatostylus Champion, 1903: Lancearius
  Vanin, 1986
- U. Hammatostylus. Champion, 1903
   Hammatostylus Champion, 1903: Lancearius
   Vanin, 1986
- V. Erodiscus. Schoenherr, 1825
  Erodiscus. Schoenherr, 1825: Ludovix. Laporte, 1840
  Erodiscus Schoenherr, 1825: Pimelerodius.
  Vanin, 1986
  Pimelerodius Vanin, 1986: Ecnomorhinus Vanin, 1986
  Ludovix. Laporte, 1840: Prosicoderus Vanin, 1986
  Ludovix Laporte, 1840: Hammatostylus.
  Champion, 1903
  Hammatostylus. Champion, 1903: Sicoderus Vanin, 1986
  Hammatostylus Champion, 1903: Lancearius Vanin, 1986

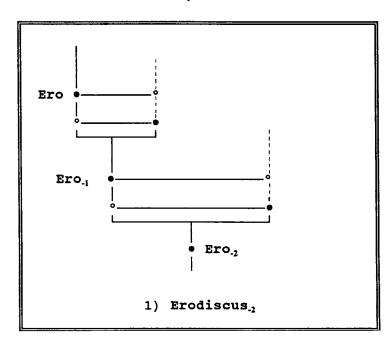


Figure 6.15. Retrieval of the phylogeny from the classification (cont.)

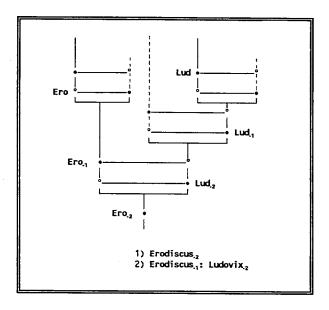


Figure 6.16. Retrieval of the phylogeny from the classification (cont.).

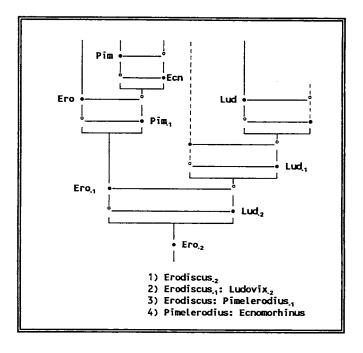


Figure 6.17. Retrieval of the phylogeny from the classification (cont.).

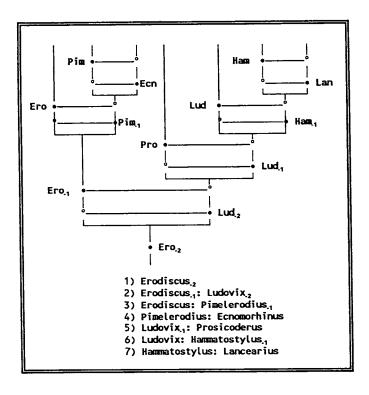


Figure 6.18. Retrieval of the phylogeny from the classification (concl.).

The same is to be done when we use specific names, as can be seen in Figures 6.20 to 6.21. In the example there is an instance of *trichotomy* (Figure 6.21). Notice also that the relation of order (by inclusion) is maintained among the several taxa involved, when transformed into onomastic sets (cf. Figure 6.22).

Figure 6.22 gives the onomastic sets involved in the phylogeny shown in Figure 6.21, retrieved from the classification shown in Figure 6.20:

a. antilope 6

b. antilope s: analis tringa tringa

c. antilope : ciconia

d. antilope : appendiculatus

e. antilope\_: delaunayi

f. antilope\_1: tinamus

g. antilope: ibis

h. analis\_1: subcoronatus

i. analis: hirsutus

j. tringa<sub>2</sub>: granatensis<sub>1</sub>

k. tringa\_i: bicolor

1. tringa: mollicomus

m. granatensis: convexipennis.

n. convexipennis: nodieri\_1

o. nodieri: labidus

Figure 6.20. Classification of the 'genus' Sicoderus (adapted from Vanin, 1986). (Note: The terminal elements of this classification (also in Figure 6.21) are not the terminal species of the phylogeny of Sicoderus as presented in Vanin's original 1986 paper; we are just taking them as terminal species in this example to simplify the matter). Terminal species (of this example) are in italics. Numbers between parentheses used as 'powers' indicate the number of terminal species of which the name affected by the 'power' is the ancestor. Names of authors and dates omitted for brevity's sake.

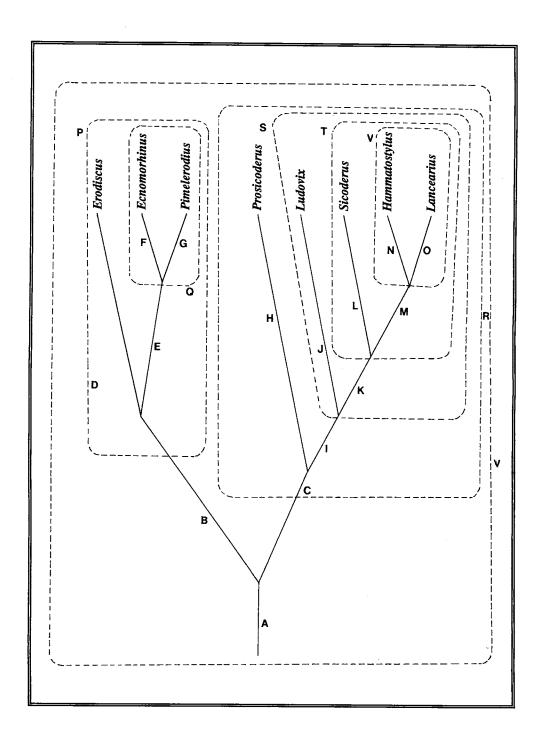


Figure 6.19. The 22 different subsets of taxa (A to V) of the phylogeny presented in Figura 6.1.

Let's examine now some other conventions:

Convention 4. The 'supraspecific categories' of the ancient taxonomy are abolished, but their traditional names may be used under certain constraints (see convention 5). The 'categories' and their names are maintained, of course, in classical taxonomy.

Convention 5. Any monophyletic group with three or more taxa, forming an intensional inf-semilattice is called a *P-genos*. If a P-genos has a traditional name, this name may be used to designate it or any of its proper subsystems, using the following devices:

- (i) A 'P' is added as a prefix to the traditional name (to indicate that the name now refers to a monophylum or monophyletic group);
- (ii) The P-genos being designated can be *any* non-empty subsystem of an ordered system, but must include the infimous element of the P-genos which is being considered as the universe of discourse;
- (iii) After the name of the P-genos, between parentheses and as 'power', we indicate the number of maximal elements involved in the phylogeny presented, and, between square brackets (also as 'power') the number of maximal elements and the number of ancestral eidophoronts. Thus we may identify the different subsystems of a system, using the same traditional name. If all the known terminal species are included in the phylogeny, we indicate these by putting, between parentheses, the number of maximal elements followed by an asterisk (\*).
- (iv) The traditional name *cannot* be used, however, to indicate the inf(P-genos) (i.e., the ancestral eidophoront of all the monophyletic group).

**Example 6.4.** Let's consider again the phylogeny show in Figure 6.19. Given this universe of discourse, we may have several subsystems, as follows:

- 1. The entire universe of discourse;
- 2. The proper subsystem {A, B, C};
- 3. The proper subsystem {A, B, C, D, E, H, I};
- 4. The proper subsystem {A, B, C, D, E, H, I, J, K};
- 5. The proper subsystem  $\{A, B, C, D, E, F, G, H, I, J, K\}$ ;

The proper subsystem {A, B, C, D, E, F, G, H, I, J, K, L, M}.

We can use the same name 'Erodiscini' to indicate all those different subsystems, in the following way, using Convention 5:

Case 1. Classification of P-Erodiscini (8)[15] sensu Vanin, 1986

Erodiscus, Schoenherr, 1825

Erodiscus, Schoenherr, 1825: Ludovix, Laporte, 1840 Erodiscus Schoenherr, 1825: Pimelerodius, Vanin, 1986 Pimeledorius Vanin, 1986: Ecnomorhinus Vanin, 1986 Ludovix, Laporte, 1840: Prosicoderus Vanin, 1986 Ludovix Laporte, 1840: Hammatostylus, Champion, 1903

Hammatostylus. Champion, 1903: Sicoderus Vanin, 1986

Hammatostylus Champion, 1903 : Lancearius Vanin, 1986

Case 2. Classification of P-Erodiscini<sup>(2)[3]</sup> sensu Vanin, 1986

Erodiscus, Schoenherr, 1825: Ludovix, Laporte, 1840

Case 3. Classification of P-Erodiscini<sup>(4)(7)</sup> sensu Vanin, 1986

Erodiscus, Schoenherr, 1825

Erodiscus Schoenherr, 1825: Ludovix Laporte, 1840 Erodiscus Schoenherr, 1825: Pimelerodius Vanin, 1986 Ludovix Laporte, 1840: Prosicoderus Vanin, 1986

Case 4. Classification of P-Erodiscini<sup>(5)[9]</sup> sensu Vanin, 1986

Erodiscus, Schoenherr, 1825

Erodiscus, Schoenherr, 1825: Ludovix, Laporte, 1840 Erodiscus Schoenherr, 1825: Pimelerodius, Vanin, 1986 Ludovix, Laporte, 1840: Prosicoderus Vanin, 1986 Ludovix Laporte, 1840: Hammatostylus, Champion, 1903

Case 5. Classification of P-Erodiscini<sup>(6)[11]</sup> sensu Vanin, 1986

Erodiscus<sub>-2</sub> Schoenherr, 1825

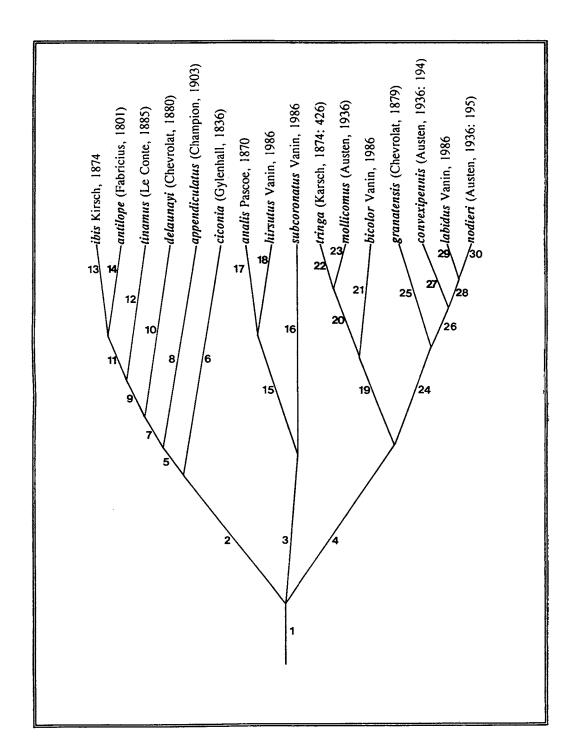


Figure 6.21. Phylogeny of the species of the genus Sicoderus (adapted from Vanin, 1986) (See note under Fig. 6.20).

```
= {antilope }
                                                     = {antilope<sup>-6</sup>, antilope }
= {antilope<sup>-6</sup>, analis }<sup>-5</sup>
= {antilope<sup>-6</sup>, tringa<sup>-2</sup>}
  2
  3
  4
                                                       = {antilope<sup>-6</sup>, antilope<sup>-5</sup>, antilope<sup>-5</sup>, ciconia}<sup>4</sup>
  5
    6
                                                       = {antilope 6, antilope 5, antilope , antilope }
    7
7 = {antilope<sup>-6</sup>, antilope<sup>-5</sup>, antilope<sup>-4</sup>, appendiculatus}
8 = {antilope<sup>-6</sup>, antilope<sup>-5</sup>, antilope<sup>-4</sup>, antilope<sup>-3</sup>, anti
      15 = {antilope<sup>-6</sup>, analis , analis }

16 = {antilope<sup>-6</sup>, analis<sup>-2</sup>, subcoronatus}
      17 = {antilope-6, analis-2, analis, analis}
      18 = {antilope<sup>-6</sup>, anali <sup>-7</sup>, analis <sup>-1</sup>, hirsutus}
19 = {antilope<sup>-6</sup>, tringa <sup>-1</sup>, tringa <sup>-1</sup>}
         20 = {antilope<sup>-6</sup>, tringa<sup>-3</sup>, tringa<sup>-2</sup>, tringa }
    21 = {antilope<sup>-6</sup>, tringa<sup>-3</sup>, tringa<sup>-2</sup>, bicolor} }
22 = {antilope<sup>-6</sup>, tringa<sup>-3</sup>, tringa<sup>-2</sup>, tringa , tringa}
23 = {antilope<sup>-6</sup>, tringa<sup>-3</sup>, tringa<sup>-2</sup>, tringa<sup>-1</sup>, mollicomus}
  23 = {antilope*, tringa*, tringa*, mollicomus}
24 = {antilope*, tringa*, granafensis} -1
25 = {antilope*, tringa*, granatensis*, granatensis}
26 = {antilope*, tringa*, granatensis*, convexipennis}
27 = {antilope*, tringa*, granatensis*, convexipennis*, convexipennis}
28 = {antilope*, tringa*, granatensis*, convexipennis*, nodieri}
29 = {antilope*, tringa*, granatensis*, convexipennis*, nodieri*, labidus}
30 = {antilope*, tringa*, granatensis*, convexipennis*, nodieri*, no
```

Figure 6.22. Taxa of the phylogeny shown in Figure 6.21 transformed into onomastic sets.

Erodiscus\_, Schoenherr, 1825: Ludovix\_, Laporte, 1840 Erodiscus Schoenherr, 1825: Pimelerodius\_, Vanin, 1986 Pimelerodius Vanin, 1986: Ecnomorhinus Vanin, 1986 Ludovix\_, Laporte, 1840: Prosicoderus Vanin, 1986 Ludovix\_ Laporte, 1840: Hammatostylus\_, Champion, 1903

Case 6. Classification of P-Erodiscini<sup>(7)[13]</sup> sensu Vanin, 1986

Erodiscus\_2 Schoenherr, 1825: Ludovix\_2 Laporte, 1840 Erodiscus Schoenherr, 1825: Ludovix\_2 Laporte, 1840 Erodiscus Schoenherr, 1825: Pimelerodius\_1 Vanin, 1986 Pimelerodius Vanin, 1986: Ecnomorhinus Vanin, 1986 Ludovix\_1 Laporte, 1840: Prosicoderus Vanin, 1903 Ludovix\_1 Laporte, 1840: Hammatostylus\_2 Champion, 1903 Hammatostylus, Champion, 1903: Sicoderus Vanin, 1986

Example 6.5. The classification of P-Oestridae<sup>(31\*)(60)</sup> sensu Papavero, 1977 is given in Table 6.1. The 'power' (31\*) indicates that we are dealing here with *all* the known terminal species of the P-genos.

Example 6.6. The classification of P-Brachycera (106)[204] is given in Table 6.3.

Let's consider now the case of a proper subsystem of a P-genos which is also a P-genos (i.e., a monophyletic group or monophylum) but that *does not* include the infimous element of the P-genos which is being taken as the universe of discourse. For example, in relation to Figure 6.14,

let's consider the proper subsystem (monophyletic group) whose classification is the following:

Ludovix Laporte, 1840

Ludovix Laporte, 1840 : Hammatostylus<sub>.2</sub> Champion, 1903

Hammatostylus. Champion, 1903: Sicoderus Vanin, 1986

Hammatostylus Champion, 1903: Lancearius Vanin, 1986.

This subsystem does not have a traditional taxonomic name. We may then create a code-name to refer to it, in the following manner:

- (i) We add to the name of its infimous element the prefix 'P' (to indicate that it is a monophyletic group having as an infimous element the name cited (in our case we would have 'P-Ludovix,');
- (ii) We add to that name thus formed, as 'powers', an 'upright' arrow (to indicate that two or more taxa are included in the phylogeny, then (in parentheses) the number of terminal morphospecies, and finally (in square brackets), the total number of the taxa involved (including the infimous element) (in our case we would then have: 'P-Ludovix, <sup>1(4)(7)</sup>').

Thus we would have a name for the monophylum. Therefore, the classification of P-Ludovix, 1(447) is:

Ludovix\_ Laporte, 1840

Ludovix Laporte, 1840 : Hammatostylus<sub>.2</sub> Champion, 1903

Hammatostylus., Champion, 1903: Sicoderus Vanin, 1986

Hammatostylus Champion, 1903: Lancearius Vanin, 1986.

One additional example: P-Erodiscus, f(3)[5] would denote the monophyletic group whose classification is:

Erodiscus, Schoenherr, 1825

Erodiscus Schoenherr, 1825: Pimelerodius, Vanin, 1986

Pimeledorius Vanin, 1986: Ecnomorhinus Vanin, 1986.

Convention 6. Any monotypic taxon belonging, in the ancient taxonomy, to a 'supraspecific category' is named with the binomen of its unique species (in italics or some other type if the species is not ancestral, without italics if the species is ancestral, in the case that the specific name is still associated to the praenomen where it was originally included).

**Example 6.7.** The 'family' Heterostomidae of the ancient taxonomy (cf. Nagatomi, 1977, 1981, 1982) includes only one species, *Heterostomus curvipalpis* Bigot, 1857; the name of this taxon is therefore *Heterostomus curvipalpis* Bigot, 1857 (the name 'Heterostomidae' is abandoned).

Thus, as already quoted, Willmann (1989: 277) comments: 'If there is only one species as the adelphotaxon of a species-rich group, this species is not to be classified as a family, suborder, order, etc., of its own, each category corresponding to a taxonomic name. There is only one name required and justified for the species -its proper name- and in a written fixation of the system only this name would appear and refer to one of the basic adelphotaxa of the superordinate monophylum.'

Convention 7. In cases where the praenomen is associated to only one specific name, and the latter has been transferred from a previous praenomen to the present one, the present praenomen in cited first, with author and date, followed, between parentheses, by the name of the species, with author and date, between parentheses.

**Example 6.9.** In Figure 6.23, we have, for instance:

Tracheomyia Townsend, 1916 (T. macropi (Frogatt, 1913)).

We thus know that this is the only species associated with the *praenomen Tracheomyia*, but that the specific name is no longer in the original combination.

Convention 8. The name of the ancestral 'species' of an entire P-genos which, in the ancient taxonomy, was considered a 'genus' is named with the *binomen* having priority within this group, with a negative numeral as index, or only with a

praenomen also affected by a negative index (in both cases the names are written using the same type of the text, never with italics or any other different type).

Exercise 6.1. Let's do an exercise to train the new system of nomenclature and the conventions seen up to now. Figures 6.23 to 6.25 show the phylogeny of the species of the 'family' Oestridae (Papavero, 1977). There are 31 terminal (nonancestral) species and 15 praenomina. The species Pharyngobolus africanus Brauer, 1866 has maintained the original combination (of the praenomen with the specific name), whereas Tracheomyia macropi (Froggatt, 1913) changed the praenomen (Figured 6.23). The same happens (Figure 6.24) with Procephenemyia stimulatrix (Clark, 1977) and Acrocomyia auribarbis (Meigen, 1824). We have to cite, first, the present praenomen (with author and date) and then the binomen of the species, as indicated in the figures mentioned.

Let's now examine Figure 6.25. Gedoelstia cristata Rodhain & Bequaert, 1913, has priority over Gedoelstia haessleri Gedoelst, 1915. The name of the ancestor eidophoront of those two species is, then, Gedoelstia cristata. Rodhain & Bequaert, 1913 (cf. Convention 3).

Gedoelstia cristata, Rodhain & Bequaert, 1913 is the sister-species of Cephalopina titillatrix (Clark, 1816). But those two species have different praenomina. We continue the process of naming the ancestors using only the praenomina -we substitute the name Gedoelstia cristata, Rodhain & Bequaert, 1913 (remember it is the name of an ancestral eidophoront, and therefore does not come in italics) by the praenomen Gedoelstia Rodhain & Bequaert, 1913 (no italics, again), and we employ for its sister-species the praenomen Cephalopina Strand, 1928 (no italics). As Gedoelstia has priority over Cephalopina, the ancestor eidophoront of those two species will be named Gedoelstia, Rodhain & Bequaert, 1913. And then we continue, in a likely fashion, naming all the other taxa, until we arrive to the eidophoront which is ancestral to all the other taxa of this monophyletic group, which is called Oestrus, Linnaeus, 1758 (Figure 6.23).

TABLE 6.1. Classification of P-Oestridae<sub>F</sub> sensu Papavero, 1977 (Figures 6.23 to 6.25).

- 1. Oestrus<sub>8</sub><sup>(31)</sup> Linnaeus, 1758 (= Oestrus<sub>F</sub> Linnaeus, 1758)
- 2. Oestrus, Linnaeus, 1758 : Cephenemyia, (10) Latreille, 1818
- 3(2). Cephenemyia, Latreille, 1818:
  Pharyngomyia Schiner, 1861
  (= Pharyngomyia picta, (Meigen, 1824))
- 4(3). Pharyngomyia picta (Meigen, 1824): Pharyngomyia dzerenae Grunin, 1950
- 5(3). Cephenemyia. Latreille, 1818: Acrocomyia Papavero, 1977 (A. auribarbis (Meigen, 1824))
- 6(5). Cephenemyia Latreille, 1818 (= C. trompe<sub>4</sub> (Modeer, 1786)): Procephenemyia Papavero, 1977 (P. stimulatrix (Clark, 1815))
- 7(6). Cephenemyia trompe<sub>.</sub>, (Modeer, 1786): Cephenemyia phobifera (Clark, 1815)
- 8(7). Cephenemyia trompe<sub>2</sub> (Modeer, 1786): Cephenemyia pratti, Hunter, 1915
- 9(8). Cephenemyia pratti Hunter, 1915 : Cephenemyia apicata Bennett & Sabrosky, 1962
- 10(8). Cephenemyia trompe<sub>.1</sub> (Modeer, 1786): *Cephenemyia jellisoni* Townsend, 1941
- 11(10). Cephenemyia trompe (Modeer, 1786): Cephenemyia ulrichi Brauer, 1862
- 12(2). Oestrus<sub>6</sub> Linnaeus, 1758 : *Pharyngobolus africanus* Brauer, 1866
- 13(12). Oestrus, Linnaeus, 1758 : Tracheomyia Townsend, 1916 (*T. macropi* (Froggatt, 1913))
- 14(13). Oestrus Linnaeus, 1758 : Kirkioestrus Rodhain & Bequaert, 1914 (= K. blanchardi, (Gedoelst, 1914))
- 15(14). Kirkioestrus blanchardi (Gedoelst, 1914): Kirkioestrus minutus (Rodhain & Bequaert, 1915)
- 16(14). Oestrus, Linnaeus, 1758 : Gedoelstia, Rodhain & Bequaert, 1913
- 17(16). Gedoelstia Rodhain & Bequaert, 1913 (= G. cristata, Rodhain & Bequaert, 1913): Cephalopina Strand, 1928 (C. titillatrix (Clark, 1816))
- 18(17). Gedoelstia cristata Rodhain & Bequaert,

- 1913: Gedoelstia haessleri Gedoelst, 1915
- 19(16). Oestrus<sub>2</sub> Linnaeus, 1758 : Rhinoestrus<sub>2</sub> Brauer, 1886
- 20(19). Rhinoestrus. Brauer, 1886: Suinoestrus Papavero, 1977 (S. nivarleti (Rodhain & Bequaert, 1912))
- 21(20). Rhinoestrus Brauer, 1886 (= R. purpureus<sub>.2</sub> (Brauer, 1858)): Gruninia Papavero, 1977 (*G. tshernyshevi* Grunin, 1951)
- 22(21). Rhinoestrus purpureus. (Brauer, 1858): Rhinoestrus hippopotami, Gruenberg, 1904
- 23(22). Rhinoestrus purpureus (Brauer, 1858): Rhinoestrus usbekistanicus, Gan, 1947
- 24(23). Rhinoestrus usbekistanicus Gan, 1947: Rhinoestrus vanzyli Zumpt & Bauristhene, 1964
- 25(22). Rhinoestrus hippopotami<sub>.2</sub> Gruenberg, 1904: *Rhinoestrus antidorcitis* Zumpt & Bauristhne, 1962
- 26(24). Rhinoestrus hippopotami. Gruenberg, 1904: Rhinoestrus latifrons Gan, 1947
- 27(26). Rhinoestrus hippopotami Gruenberg, 1904: Rhinoestrus steyni Zumpt, 1958
- 28(19). Oestrus. Linnaeus, 1758 : Loewioestrus Townsend, 1918 (*L. variolosus* (Loew, 1863))
- 29(27). Oestrus Linnaeus, 1758 (= Oestrus ovis<sub>2</sub> Linnaeus, 1758) : Oestroides Gedoelst, 1912 (O. macdonaldi (Gedoelst, 1912))
- 30(28). Oestrus ovis, Linnaeus, 1758 : Oestrus aureoargentatus Rodhain & Bequaert, 1912
- 31(30). Oestrus ovis Linnaeus, 1758 : Oestrus caucasicus Grunin. 1948

Convention 9. The name of the ancestral eidophoront of two or more morphospecies with distinct *praenomina* takes the *praenomen* which has priority, affected by a negative numeral.

Observation 6.1. An additional advantage of this new system of nomenclature is that we can work with the ancient «supraspecific categories» even in the absence of a knowledge of the phylogeny of its species, as long as we are sure it is a monophyletic group. For example, if we do not know the phylogeny of the species of the 'genus' *Oestrus* L., 1758, but we have evidence that it is a monophyletic group, we can work with the ancestral eidophoront of that monophyletic P-genos, whose name is Oestrus L., 1758. The same

procedure may be adopted in relation with any other 'supraspecific category' besides the 'genus'. As the *praenomen* included in a monophyletic group having priority over all the other *praenomina* will automatically be the name of the ancestor eidophoront of the P-genos, we can always name the ancestor. To indicate to which 'category' of the ancient taxonomy the P-genos belonged (and to indicate, at the same time, that the phylogeny of its species is not known), we use as indices the initial letter(s) of the ancient category, preceded or not by prefixes, as will be seen in the sequence.

Convention 10. If a P-genos is in all probability monophyletic, but we do not know the phylogeny of its species, we may work with its ancestral eidophoront. Its ancestral eidophoront will be named with the *praenomen* included in the P-genos which has priority over all the other *praenomina*, with an index indicating to which 'category' the P-genos belonged in the ancient taxonomy.

The list of some those indices is the following (plus some prefixes) is given in Table 6.2):

Table 6.2. Indices and prefixes for denoting categories

C	Classis	P	Phyllum
Co	Cohorte	p	prae
D	Divisio	R	Regnum
F	Family	S	Super
Fo	Form	s	sub
g	group	$S_{_{\rm E}}$	series
i	infra	St	Sectio
O	Ordo	T	Tribus

## Example 6.9. Accordingly, we have that:

(i) Araneus<sub>R</sub> Clerck, 1757 is the name of the ancestral eidophoront of all the animals (the ancient 'Animal Kingdom'). Araneus Clerck, 1757 has, by force of the international rules of zoological nomenclature, priority over all the other praenomina used for animals, as the work of Clerck on spiders of Sweden (1757) is the only one considered valid before the publication of Linnaeus Systema Naturae in 1758.

- (ii) Araneus, Clerck, 1757 is the name of the ancestral eidophoront of all the taxa before united under the 'Phyllum Arthropoda'.
- (iii) Araneus<sub>F</sub> Clerck, 1757 is the name of the ancestral eidophoront of all the taxa included in the 'family' Araneidae.
- (iv) Araneus Clerck, 1757 is the name of the ancestral eidophoront of all the species before included in the 'genus' *Araneus* Clerck, 1757.

We give, in the sequence, some names of ancestral eidophoronts of some monophyletic P-gene:

Homo, Linnaeus, 1758 (of the Phylum Chordata)

Homo<sub>c</sub> Linnaeus, 1758 (of the Classis Mammalia)

Homo<sub>o</sub> Linnaeus, 1758 (of the Ordo Primates)

Homo Linnaeus, 1758 (of the Genus Homo)

Homo<sub>T</sub> Linnaeus, 1758 (of the Tribus Hominini)

Homo<sub>se</sub> Linnaeus, 1758 (of the Superfamilia Hominoidea)

Homo<sub>st</sub> Linnaeus, 1758 (of the Subtribus Hominina)

Vultur<sub>c</sub> Linnaeus, 1758 (of the Classis Reptilia (incl. Aves))

Rana<sub>c</sub> Linnaeus, 1758 (of the Classis Amphibia)

Scarabaeus<sub>o</sub> Linnaeus, 1758 (of the Ordo Coleoptera)

Oestrus<sub>F</sub> Linnaeus, 1758 (of the Familia Oestridae)

Oestrus<sub>o</sub> Linnaeus, 1758 (of the Ordo Diptera).

The greatest advantage of this method is that the ancestor eidophoront of most 'larger groups' will take as a name Linnaean *praenomina*, which are (or should be) familiar to any taxonomist. In appendices I and II we give the list of the *praenomina* published by Linnaeus in the 10th edition of the *Systema Naturae*, organized by order of priority and alphabetically.

This system serves equally to any other group of living beings, as far as it may be worked phylogenetically. Thus, for instance, the ancestral eidophoront of all the plants will be called Canna<sub>R</sub> Linnaeus, 1753.

Exercise 6.2. We may now work with eidophoronts that are ancestral of different P-gene. Figures 6.26 to 6.35 illustrate the process (using eidophoronts ancestral to 'families'), using the phylogeny of ancestral eidophoronts of the 'families' of the 'suborder Brachycera' of the 'order Diptera' (adapted from McAlpine (1989) and Woodley (1989)). In Figure 6.26, when we write Xylophagus, Meigen, 1803, for instance, it means that in the P-genos derived from this eidophoront, there exist at least two praenomina. On the other hand, when we write, for instance, Exeretoneura Macquart, 1846, that there is only this praenomen in the F-genos, but that there are two or more species (terminal species) in the monophyletic group. When we write Heterostomus curvipalpis Bigot, 1857, for instance, this means that this is the only terminal species (and that its name maintains the original combination).

**Observation 6.2.** The most ancient praenomen included in a P-genos is not always the 'type-genus' of a 'suprageneric category'. In Figure 6.27, for example, Cyrtus Latreille, 1796, is the most ancient praenomen of the 'family' Acroceridae (but the 'type-genus' is Acrocera).

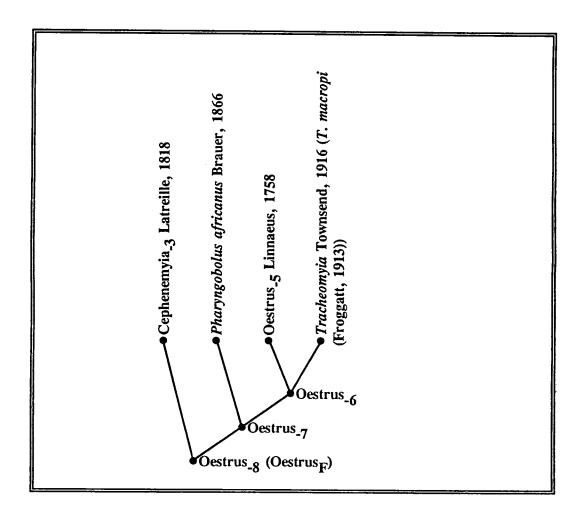


Figure 6.23. Phylogeny of Oestridae (Papavero, 1977) (cont.).

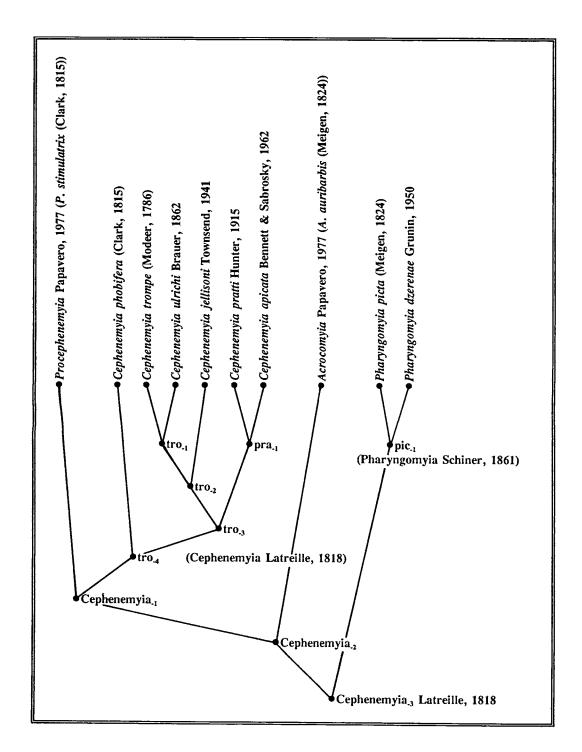


Figure 6.24. Phylogeny of Oestridae (Papavero, 1977) (continuation of Fig. 6.23)

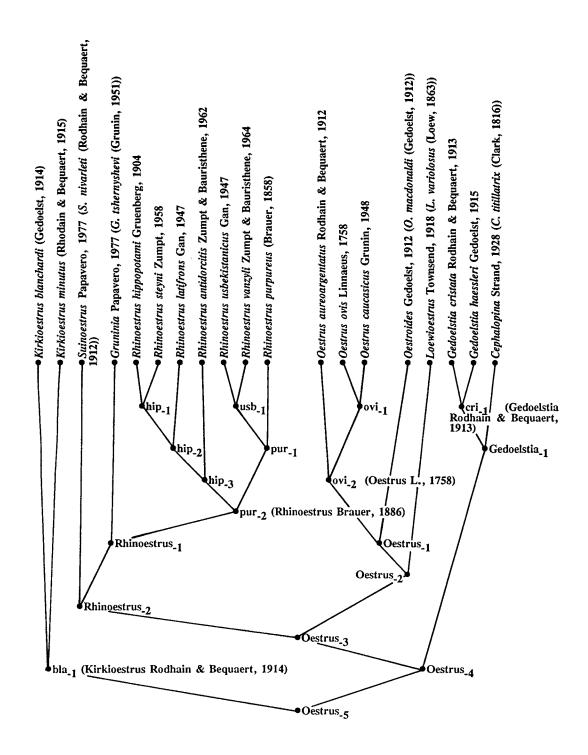


Figure 6.25. Phylogeny of Oestridae (Papavero, 1977) (continuation of Fig. 6.23).

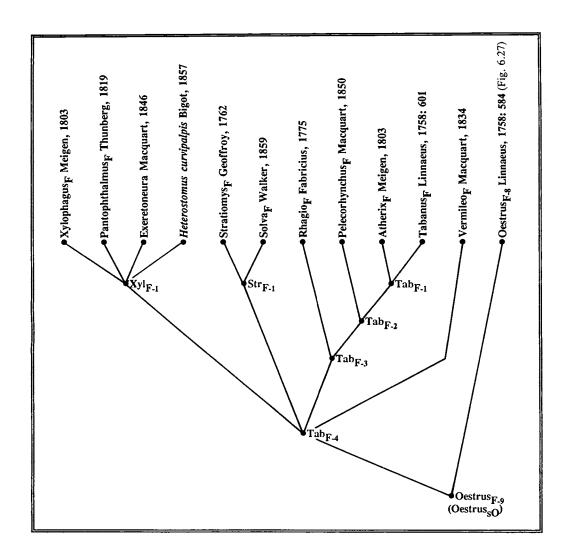


Figure 6.26. Phylogeny of the basal groups of 'Brachycera' (Diptera) (cont.).

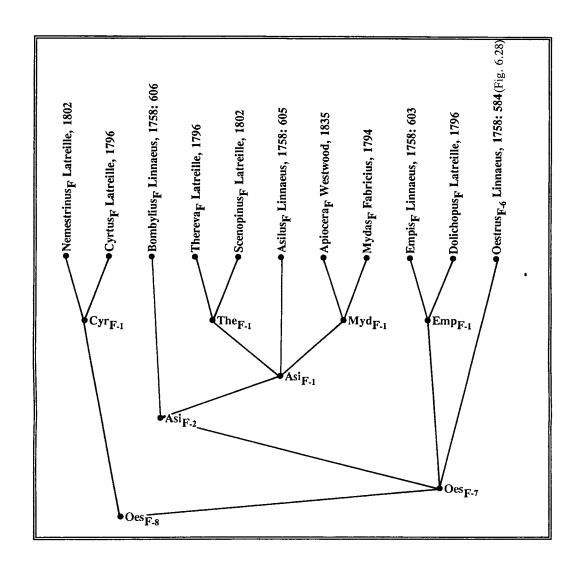


Figure 6.27. Phylogeny of the basal groups of 'Brachycera' (Diptera) (cont.).

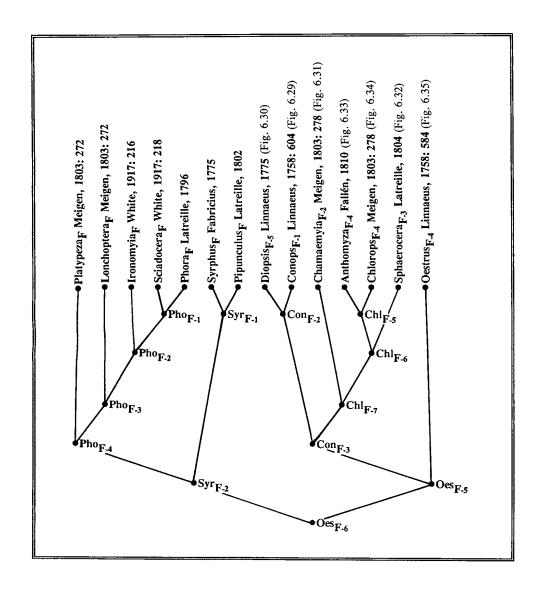


Figure 6.28. Phylogeny of the basal groups of 'Brachycera' (Diptera) (cont.).

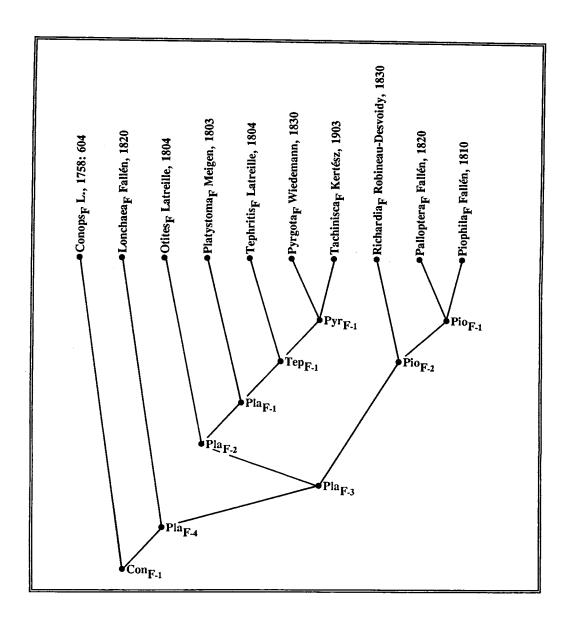


Figure 6.29. Phylogeny of the basal groups of 'Brachycera' (Diptera) (continuation of Fig. 6.28).

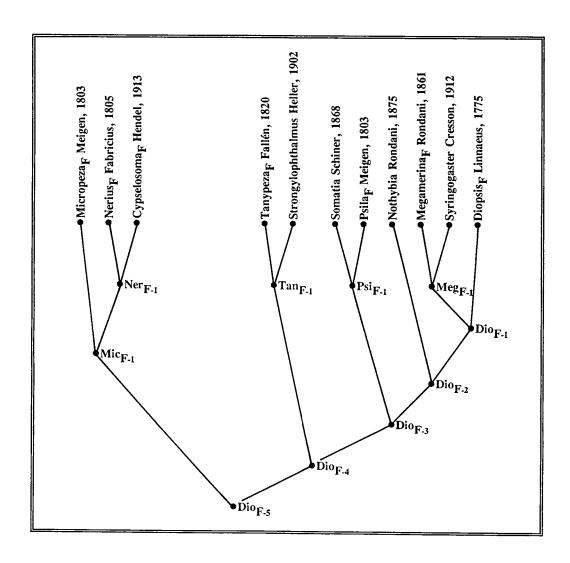


Figure 6.30. Phylogeny of basal groups of 'Brachycera' (Diptera) (continuation of Fig. 6.28).

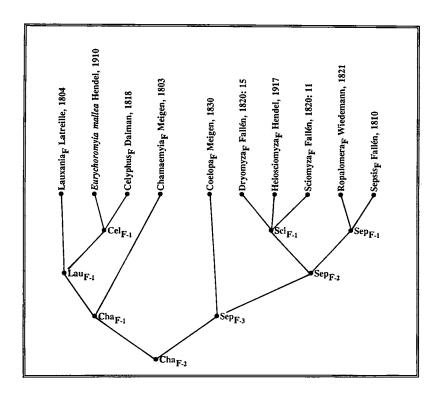


Figure 6.31. Phylogeny of the basal groups of 'Brachycera' (Diptera) (continuation of Fig. 6.28).

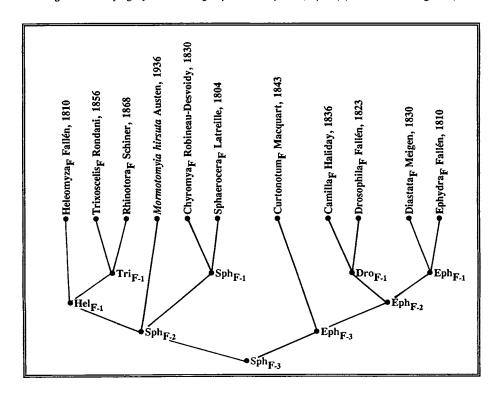


Figure 6.32. Phylogeny of the basal groups of 'Brachycera' (Diptera) (continuation of Fig. 6.28).

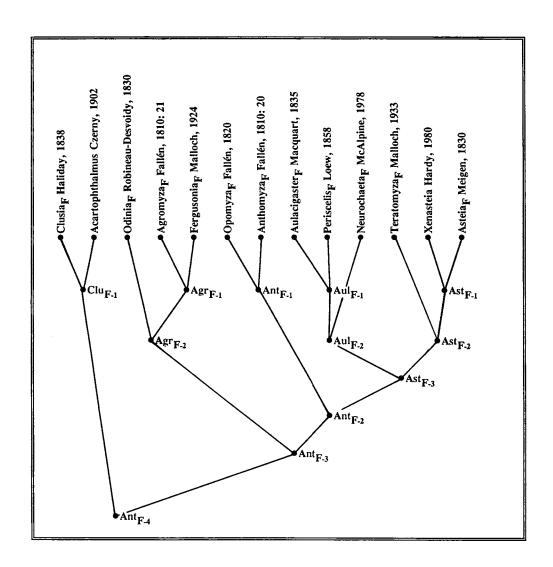


Figure 6.33. Phylogeny of the basal groups of 'Brachycera' (Diptera) (continuation of Fig. 6.28).

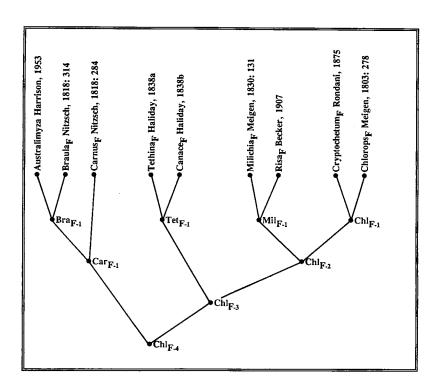


Figure 6.34. Phylogeny of the basal groups of 'Brachycera' (Diptera) (continuation of Fig. 6.28).

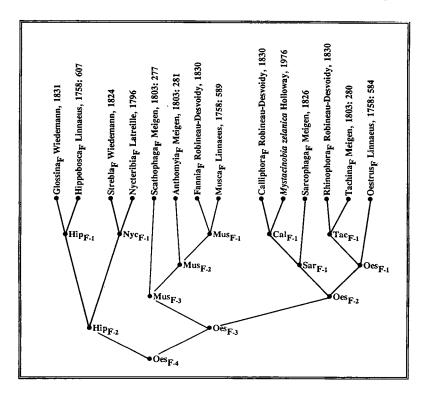


Figure 6.35. Phylogeny of the basal groups el 'Brachycera' (Diptera) (continuation of Fig.6.28).

# TABLE 6.3. Classification of P-Brachycera (106) [204] (Figures 6.26 - 6.35).

- 1. Oestrus<sub>E,0</sub><sup>(106)</sup>Linnaeus, 1758
- 12(1). Oestrus<sub>F.8</sub> (95) Linnaeus, 1758:584 : Tabanus<sub>F.4</sub> (11) Linnaeus, 1758:601
- 3(2). Tabanus<sub>F-3</sub><sup>(4)</sup> Linnaeus, 1758 : Xylophagus<sub>F-1</sub><sup>(4)</sup> Meigen, 1803 : Stratiomys<sub>F-1</sub><sup>(2)</sup> Geoffroy, 1762 : Vermileo<sub>F</sub> Macquart, 1834
- 4(3). Xylophagus, Meigen, 1803:
  Pantophthalmus, Thunberg, 1819:
  Exeretoneura Macquart, 1846:
  Heterostomus curvipalpis Bigot, 1857
- 5(3). Stratiomys<sub>F</sub> Geoffroy, 1762 : Solva<sub>F</sub> Walker, 1859
- 6(3). Tabanus<sub>F-2</sub> Linnaeus, 1758 : Rhagio<sub>F</sub> Fabricius, 1775
- 7(6). Tabanus<sub>F-1</sub> Linnaeus, 1758 Pelecorhynchus<sub>r</sub> Macquart, 1850
- 8(7). Tabanus, Linnaeus, 1758 : Atherix, Meigen, 1803
- 9(2). Oestrus<sub>F-7</sub><sup>(93)</sup> Linnaeus, 1758 : Cyrtus<sub>F-1</sub><sup>(2)</sup> Latreille, 1796
- 10(9). Cyrtus, Latreille, 1796 : Nemestrinus, Latreille, 1802
- 11(9). Oestrus<sub>F-6</sub><sup>(85)</sup> Linnaeus, 1758:584 : Asilus<sub>F-2</sub><sup>(6)</sup> Linnaeus, 1758:605 : Empis<sub>F-1</sub><sup>(2)</sup> Linnaeus, 1758:603
- 12(11). Asilus<sub>F-1</sub> Linnaeus, 1758:605 : Bombylius<sub>F</sub> Linnaeus, 1758:606
- 13(12). Asilus, Linnaeus, 1758: Thereva, Latreille, 1796: Mydas, Fabricius, 1794
- 14(13). Thereva<sub>F</sub> Latreille, 1796 : Scenopinus<sub>F</sub> Latreille, 1802
- 15(13). Mydas<sub>F</sub> Fabricius, 1794 : Apiocera<sub>F</sub> Westwood, 1835
- 16(11). Empis<sub>F</sub> Linnaeus, 1758 : Dolichopus<sub>F</sub> Latreille, 1796
- 17(11). Oestrus<sub>F-5</sub><sup>(78)</sup> Linnaeus, 1758 : Syrphus<sub>F-2</sub><sup>(7)</sup> Fabricius, 1775
- 18(17). Syrphus<sub>F-1</sub><sup>(2)</sup> Fabricius, 1775 : Phora<sub>F-4</sub><sup>(5)</sup> Latreille, 1796
- 19(18). Syrphus, Fabricius, 1775 : Pipunculus, Latreille, 1802
- 20(18). Phora<sub>F.3</sub> Latreille, 1796 : Platypeza<sub>F</sub> Meigen, 1803
- 21(20). Phora<sub>F-2</sub> Latreille, 1796 : Lonchoptera<sub>F</sub> Meigen, 1803
- 22(21). Phora<sub>F-1</sub> Latreille, 1796: Ironomyia<sub>F</sub>

- White, 1917
- 23(22). Phora, Latreille, 1796 : Sciadocera, White, 1917
- 24(17). Oestrus<sub>F-4</sub><sup>(14)</sup> Linnaeus, 1758:584 : Conops<sub>F-3</sub><sup>(64)</sup> Linnaeus, 1758:604
- 25(24). Conops<sub>F-2</sub><sup>(21)</sup> Linnaeus, 1758 : Chlorops<sub>F-2</sub><sup>(43)</sup>Meigen, 1803
- 26(25). Conops<sub>F-1</sub><sup>(10)</sup> Linnaeus, 1758 : Diopsis<sub>F-5</sub><sup>(11)</sup> Linnaeus, 1775
- 27(26). Conops<sub>F</sub> Linnaeus, 1758 : Platystoma<sub>F-4</sub><sup>(9)</sup> Meigen, 1803
- 28(27). Platystoma<sub>F-3</sub> Meigen, 1803 : Lonchaea<sub>F</sub> Fallén, 1820
- 29(28). Platystoma<sub>F-2</sub><sup>(5)</sup> Meigen, 1803 : Piophila<sub>F-</sub>
  , (3) Fallén, 1810
- 30(29). Platystoma<sub>F-1</sub> Meigen, 1803 : Otites<sub>F</sub> Latreille, 1804
- 31(30). Platystoma<sub>F</sub> Meigen, 1803 : Tephritis<sub>F-1</sub> Latreille, 1804
- 32(31). Tephritis, Latreille, 1804: Pyrgota, Wiedemann, 1830
- 33(32). Pyrgota<sub>F</sub> Wiedemann, 1830 : Tachinisca<sub>F</sub> Kertész, 1903
- 34(29). Piophila<sub>F-1</sub> Fallén, 1810 : Richardia Robineau-Desvoidy, 1830
- 35(34). Piophila, Fallén, 1810: Palloptera, Fallén, 1820
- 36(26). Diopsis<sub>F-4</sub><sup>(8)</sup> Linnaeus, 1775 : Micropeza<sub>F-</sub>
  <sup>(3)</sup> Meigen, 1803
- 37(36). Micropeza<sub>F</sub> Meigen, 1803: Nerius<sub>F-1</sub> Fabricius, 1805
- 38(37). Nerius, Fabricius, 1805 : Cypselosoma, Hendel, 1913
- 39(38). Diopsis<sub>F-3</sub><sup>(6)</sup> Linnaeus, 1775 : Tanypeza<sub>F-1</sub> Fallén, 1820
- 40(39). Tanypeza<sub>F</sub> Fallén, 1820 Strongylophthalmus Heller,1902
- 41(38). Diopsis<sub>F-2</sub> Linnaeus, 1775: Psila<sub>F-1</sub> Meigen, 1803
- 42(41). Psila, Meigen, 1803: Somatia Schiner, 1868
- 43(41). Diopsis<sub>F-1</sub> Linnaeus, 1775 : Nothybia Rondani, 1875
- 44(43). Diopsis<sub>F</sub> Linnaeus, 1775 : Megamerina<sub>F-1</sub> Rondani, 1861
- 45(44). Megamerina, Rondani, 1861: Syringogaster Cresson, 1912
- 46(25). Chlorops<sub>F-6</sub><sup>(33)</sup> Meigen, 1803: Chamaemyia<sub>F-6</sub><sup>(10)</sup> Meigen, 1803
- 47(46). Chamaemyia<sub>F-1</sub> Meigen, 1803 : Sepsis<sub>F-1</sub> (6) Fallén, 1810

- 48(47). Chamaemyia, Meigen, 1803: Lauxania, Latreille, 1804
- 49(48). Lauxania, Latreille, 1804 : Celyphus, Dalman, 1818
- 50(49). Celyphus, Dalman, 1818: Eurychoromyia mallea Hendel, 1910
- 51(47). Sepsis<sub>F-2</sub> Fallén, 1810 : Coelopa<sub>F</sub> Meigen, 1830
- 52(51). Sepsis<sub>F-1</sub><sup>(2)</sup> Fallén, 1810 : Sciomyza<sub>F-1</sub><sup>(3)</sup> Fallén, 1820
- 53(52). Sepsis, Fallén, 1810 : Ropalomera, Wiedemann, 1821
- 54(52). Sciomyza, Fallén, 1820:11 : Dryomyza, Fallén, 1820:15 : Helosciomyza, Hendel, 1917
- 55(46). Chlorops<sub>F.5</sub> Meigen, 1803 : Sphaerocera<sub>F.</sub>
  3(11) Latreille, 1804
- 56(55). Sphaerocera<sub>F.2</sub><sup>(6)</sup> Latreille, 1804: Ephydra<sub>F.</sub>
  3<sup>(5)</sup> Fallén, 1810
- 57(56). Sphaerocera<sub>F-1</sub> Latreille, 1804: Heleomyza<sub>F-1</sub> Fallén, 1810: Mormotomyia hirsuta Austen, 1936
- 58(57). Sphaerocera, Latreille, 1804: Chyromya, Robineau-Desvoidy, 1830
- 59(57). Heleomyza, Fallén, 1810 : Trixoscelis, Rondani, 1856
- 60(59). Trixoscelis, Rondani, 1856: Rhinotora, Schiner, 1868
- 61(56). Ephydra<sub>F-2</sub> Fallén, 1810 : Curtonotum<sub>F</sub> Macquart, 1843
- 62(61). Ephydra<sub>F-1</sub> Fallén, 1810 : Drosophila<sub>F-1</sub> Fallén, 1823
- 63(62). Ephydra, Fallén, 1810: Diastata, Meigen, 1830
- 64(63). Drosophila, Fallén, 1823 : Camilla, Haliday, 1836
- 65(55). Chlorops<sub>F-4</sub><sup>(9)</sup> Meigen, 1803: Anthomyza<sub>F</sub><sub>4</sub><sup>(13)</sup> Fallén, 1810
- 66(65). Anthomyza<sub>F-3</sub><sup>(11)</sup> Fallén, 1810 : Clusia<sub>F-1</sub> Haliday, 1838
- 67(66). Clusia, Haliday, 1838 : Acartophthalmus Czerny, 1902
- 68(66). Anthomyza<sub>F-2</sub><sup>(8)</sup> Fallén, 1810:20 : Agromyza<sub>F-2</sub> Fallén, 1810:21
- 69(68). Agromyza<sub>F-1</sub> Fallén, 1810 : Odinia<sub>F</sub> Robineau-Desvoidy, 1830
- 70(69). Agromyza, Fallén, 1810 : Fergusonia, Malloch, 1924
- 71(68). Anthomyza<sub>F-1</sub><sup>(2)</sup> Fallén, 1810 : Asteia<sub>F-3</sub><sup>(6)</sup> Meigen, 1830

- 72(71). Anthomyza, Fallén, 1810 : Opomyza, Fallén, 1820
- 73(71). Asteia<sub>F-2</sub><sup>(3)</sup> Meigen, 1830 : Aulacigaster<sub>F-2</sub><sup>(3)</sup> Macquart, 1835
- 74(73). Aulacigaster<sub>F-1</sub> Macquart, 1835 : Neurochaeta, McAlpine, 1978
- 75(74). Aulacigaster, Macquart, 1835: Periscelis, Loew, 1858
- 76(73). Asteia<sub>F-1</sub> Meigen, 1830 : Teratomyza<sub>F</sub> Malloch, 1933
- 77(76). Asteia, Meigen, 1830: Xenasteia Hardy, 1980
- 78(65). Chlorops<sub>F-3</sub><sup>(6)</sup> Meigen, 1803 : Carnus<sub>F-1</sub><sup>(3)</sup> Nitzsch, 1818
- 79(78). Carnus, Nitzsch, 1818:284 : Braula, Nitzsch, 1818:314
- 80(79). Braula<sub>F</sub> Nitzsch, 1818 : Australimyza Harrison, 1953
- 81(78). Chlorops<sub>F-2</sub> Meigen, 1803: Tethina<sub>F-1</sub> Haliday, 1838a
- 82(81). Tethina, Haliday, 1838a : Canace, Haliday, 1838b
- 83(78). Chlorops<sub>F-1</sub> Meigen, 1803: Milichia<sub>F-1</sub> Meigen, 1830
- 84(83). Chlorops, Meigen, 1803: Cryptochetum, Rondani, 1875
- 85(83). Milichia, Meigen, 1830: Risa, Becker, 1907
- 86(24). Oestrus<sub>F-3</sub><sup>(10)</sup> Linnaeus, 1758:584 : Hippobosca<sub>F-2</sub><sup>(4)</sup> Linnaeus, 1758:607
- 87(86). Hippobosca<sub>F-1</sub> Linnaeus, 1758: Nycteribia<sub>F-1</sub> Latreille, 1796
- 88(87). Nycteribia, Latreille, 1796 : Strebla, Wiedemann, 1824
- 89(87). Hippobosca, Linnaeus, 1758 : Glossina, Wiedemann, 1831
- 90(86). Oestrus<sub>F-2</sub><sup>(6)</sup> Linnaeus, 1758:584 : Musca<sub>F-3</sub><sup>(4)</sup> Linnaeus, 1758:589
- 91(90). Musca<sub>F-2</sub> Linnaeus, 1758 : Scathophaga<sub>F</sub> Meigen, 1803
- 92(91). Musca<sub>F-1</sub> Linnaeus, 1758 : Anthomyia<sub>F</sub> Meigen, 1803
- 93(92). Musca, Linnaeus, 1758 : Fannia, Robineau-Desvoidy, 1830
- 94(90). Oestrus<sub>F-I</sub> Linnaeus, 1758 : Sarcophaga<sub>F-I</sub> Meigen, 1826
- 95(94). Sarcophaga, Meigen, 1826: Calliphora, Robineau-Desvoidy, 1830
- 96(95). Calliphora, Robineau-Desvoidy, 1830 : *Mystacinobia zelanica* Hollowy, 1976

97(94). Oestrus, Linnaeus, 1758 : Tachina, Meigen, 1803

98(97). Tachina, Meigen, 1803: Rhinophora, Robineau-Desvoidy, 1830: 280

Exercise 6.3. In a similar way, we can work with ancestral eidophoronts of P-gene which were considered 'orders' in ancient taxonomy. Figures 6.39 to 6.42 illustrate the process (phylogeny of the ancestral eidophoronts of the 'orders' of the 'Class Insecta', according to Hennig, 1981).

It must be noticed that, for example, when we write Zorotypus Silvestri, 1913 (Figure 6.41) we mean that this eidophoront is ancestral of a P-genos which includes only this *praenomen*, but which includes two or more terminal species; when we write, on the other hand, Psocus<sub>o</sub> Fabricius, 1798, we mean that this eidophoront is ancestral of a P-genos which in the ancient system was considered an 'order' including two or more *praenomina*.

Observation 6.3. We must be careful, when

TABLE 6.4 HENNIG'S SYSTEM OF CLASSIFICATION FOR THE CLASS INSECTA (1981) (Figures 6.36-6.38)

1. Entognatha	2.2.2.23.22. Condylognatha
1.1. Diplura	2.2.2.23.22.1. Thysanoptera
1.2. Ellipura	2.2.2.2.3.22. Hemiptera
1.2.1. Protura	2.2.2.3.22.1. Heteropteroidea
1.2.2. Collembola	2.2.2.3.22.1.1. Coleorhyncha
2. Ectognatha	2.2.2.3.22.1.2. Heteroptera
2.1. Archaeognatha (Microcoryphia)	2.2.2.3.22.2. Sternorhyncha
2.2. Dicondylia	2.2.2.3.22.2.1. Aphidomorpha
2.2.1. Zygentoma	2.2.2.3.22.2.1.1. Aphidina
2.2.2. Pterygota	2.2.2.3.22.2.1.2. Coccina
2.2.2.1. Palaeoptera	2.2.2.3.22.2.2. Psyllomorpha
2.2.2.11. Ephemeroptera	2.2.2.3.22.2.2.1. Aleyrodina
2.2.2.12. Odonata	2.2.2.2.3.22.2.2.2. Psyllina
2.2.2. Neoptera	2.2.2.3.22.2.3. Auchenorhyncha
2.2.2.1. Plecoptera	2.2.2.3.22.2.3.1. Fulgoriformes
2.2.2.2. Paurometabola	2.2.2.2.3.22.2.3.2. Cicadiformes
2.2.2.2.1. Embioptera	2.2.2.2.4. Holometabola
2.2.2.2.2. Orthopteromorpha	2.2.2.2.4.1. Neuropteroidea
2.2.2.22.1. Blattopteriformia	2.2.2.24.11. Megaloptera
2.2.2.2.2.1.1. Notoptera (Grylloblattodea)	2.2.2.24.12. Raphidioptera
2.2.2.22.1.2. Dermaptera	2.2.2.2.4.13. Planipennia
2.2.2.22.1.3. Blattopteroidea	2.2.2.2.4.2. Coleoptera
2.2.2.22.1.3.1. Mantodea	2.2.2.2.4.3. Strepsiptera
2.2.2.22.1.3.2. Blattodea	2.2.2.2.4.4. Hymenoptera
2.2.2.22. Orthopteroidea	2.2.2.24.5. Siphonaptera
2.2.2.2.2.2.1. Ensifera	2.2.2.24.6. Mecopteroidea
2.2.2.2.2.2. Caelifera	2.2.2.24.61. Amphiesmenoptera
2.2.2.2.2.2.3. Phasmatodea	2.2.2.24.61.1. Trichoptera
2.2.2.3. Paraneoptera	2.2.2.24.61.2. Lepidoptera
2.2.2.3.1. Zoraptera	2.2.2.2.4.62. Antliophora
2.2.2.3.2. Acercaria	2.2.2.24.62.1. Mecoptera
2.2.2.3.21. Psocodea	2.2.2.24.62.2. Diptera

putting names in ancestral eidophoronts of P-gene before considered 'orders', that it is the oldest *praenomen* included in that group. Thus, in Figure 6.41, let it be observed that Chermes<sub>o</sub> Linnaeus, 1758, is the name of an eidophoront ancestral of a P-genos called by Hennig 'Psyllina' -it happens that *Chermes* Linnaeus, 1758 is the oldest *praenomen* included in 'Psyllina' (and not *Psylla*).

Observation 6.4. Hennig's system of classification for phylogenies (let's consider the particular case of the phylogeny of the 'orders' of the 'Class Insecta' such as appearing in Hennig, 1981) (cf. Table 6.4 and Figures 6.36 - 6.38) is not adequate, because, rigorously speaking, it results into a chain and not into an inf-semilattice, as Hennig uses a lexicographic system (1 strictly precedes 1.1, which strictly precedes 1.2, and so forth). If we ignore this, it has the advantage, like our system, of being isomorphic with the phylogeny. As a serious disadvantage, Hennig's system has two drawbacks: it is necessary to create a quantity of new names (or cumbersome numerical systems) for the 'categories' and these names, as seen before, are equivocal -we don't know whether they denote the entire P-genos or the ancestral eidophoront exclusively; in the second place, if they denote the P-gene, the ancestral eidophoronts remain unnamed (and vice-versa) and if they denote both concepts, it is an absurd.

TABLE 6.5. Clasification de P-Insecta<sup>(38)(73)</sup> sensu Hennig, 1981 (Figures 6.39 to 6.41)

- 1. Scarabaeus<sub>0.6</sub><sup>(38)</sup> Linnaeus, 1758 (Scarabaeus, Linnaeus, 1758)
- 2(1). Scarabaeus<sub>0.3</sub><sup>(35)</sup> Linnaeus, 1758:345 : Podura<sub>0.2</sub><sup>(3)</sup> Linnaeus 1758:608b
- 3(2). Podura<sub>o.1</sub> Linnaeus, 1758 : Campodea<sub>o</sub> Westwood, 1842
- 4(3). Podura<sub>o</sub> Linnaeus, 1758 : Acerentomon<sub>o</sub> Silvestri, 1907
- 5(2). Scarabaeus<sub>0.4</sub><sup>(34)</sup> Linnaeus, 1758 : Machilis<sub>0</sub> Latreille, 1802
- 6(5). Scarabaeus<sub>0.3</sub><sup>(33)</sup> Linnaeus, 1758:345 : Lepisma<sub>0</sub> Linnaeus, 1758:608a
- 7(6). Scarabaeus<sub>0.2</sub><sup>(31)</sup> Linnaeus, 1758:345 : Libellula<sub>0.1</sub> Linnaeus, 1758:543
- 8(7). Libellula Linnaeus, 1758:543:

- Ephemera<sub>o</sub> Linnaeus, 1758:546 9(7). Scarabaeus<sub>o.1</sub>(11) Linnaeus, 1758:345:
- Perla<sub>o</sub> Geoffroy, 1762 : Forficula<sub>o</sub>,<sup>(8)</sup>
  Linnaeus, 1758:423 : Cicada<sub>o</sub>,<sup>(11)</sup>
  Linnaeus, 1758:434
- 10(9). Forficula<sub>0-2</sub> Linnaeus, 1758 : Embia<sub>o</sub> Latreille, 1829
- 11(10). Forficula<sub>0-1</sub><sup>(4)</sup> Linnaeus, 1758:423 : Gryllus<sub>0-1</sub><sup>(3)</sup> Linnaeus, 1758:425a
- 12(11). Forficula<sub>o</sub> Linnaeus, 1758:423 : Grylloblatta<sub>o</sub> Walker, 1914 : Blatta<sub>o-1</sub> Linnaeus, 1758:424
- 13(12). Blatta<sub>o</sub> Linnaeus, 1758:424: Mantis<sub>o</sub> Linnaeus, 1758:425
- 14(11). Gryllus<sub>o</sub> Linnaeus, 1758:425a : Acrida<sub>o</sub> Linnaeus, 1758:425b : Phasma<sub>o</sub> Lichtenstein, 1796
- 15(9). Cicada<sub>0.4</sub> Linnaeus, 1758 : Zorotypus<sub>0</sub> Silvestri, 1913
- 16(15). Cicada<sub>o.3</sub> Linnaeus, 1758 : Psocus<sub>o</sub> Fabricius, 1798
- 17(16). Cicada<sub>o-2</sub> Linnaeus, 1758:434 : Thrips<sub>o</sub> Linnaeus, 1758:457
- 18(17). Cicada<sub>0-1</sub> Linnaeus, 1758:434 : Notonecta<sub>0-1</sub> Linnaeus, 1758:439 : Aphis<sub>0-2</sub> Linnaeus, 1758:451
- 19(18). Cicada<sub>o</sub> Linnaeus, 1758 : Laternaria<sub>o</sub> Linnaeus, 1764
- 20(18). Notonecta<sub>o</sub> Linnaeus, 1758 : Peloridium<sub>o</sub> Breddin, 1897
- 21(18). Aphis<sub>o.1</sub> Linnaeus, 1758:451 : Chermes<sub>o.</sub> Linnaeus, 1758:453
- 22(21). Chermes<sub>o</sub> Linnaeus, 1758 : Aleyrodes<sub>o</sub> Latreille, 1796
- 23(21). Aphis<sub>o</sub> Linnaeus, 1758:451 : Coccus<sub>o</sub> Linnaeus, 1758:455
- 24(9). Scarabaeus<sub>o</sub> Linnaeus, 1758:345:
  Hemerobius<sub>o-1</sub> Linnaeus, 1758:549:
  Xenos<sub>o</sub> Rossi, 1794: Pulex<sub>o</sub> Linnaeus,
  1758:614: Papilio<sub>o-2</sub> Linnaeus, 1758:458
  : Cynips<sub>o</sub> Linnaeus, 1758:553
- 25(24). Hemerobius<sub>o</sub> Linnaeus, 1758:549 : Raphidia<sub>o</sub> Linnaeus, 1758:552 : Corydalus<sub>o</sub> Latreille, 1802
- 26(24). Papilio<sub>o.</sub>, Linnaeus, 1758:458 : Panorpa<sub>o.</sub> Linnaeus, 1758:551
- 27(26). Papilio<sub>o</sub> Linnaeus, 1758:458 : Phryganea<sub>o</sub> Linnaeus, 1758:547
- 28(26). Panorpa<sub>o</sub> Linnaeus, 1758:551 : Oestrus<sub>o</sub> Linnaeus, 1758:584

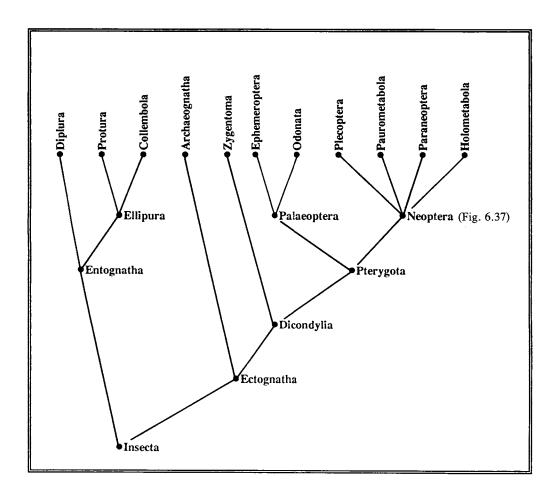


Figure 6.36. Phylogeny of the 'orders' of Insecta (Hennig, 1981) (cont.).

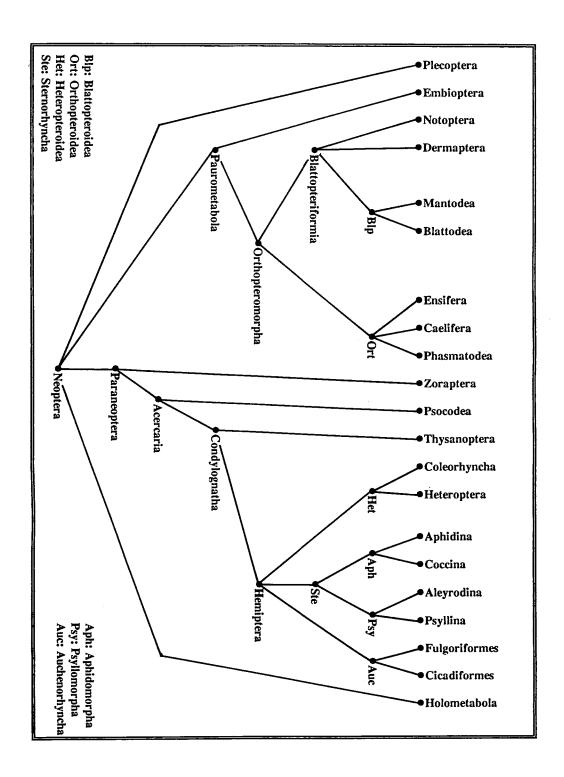


Figure 6.37. Phylogeny of the 'orders' of Insecta (Hennig, 1981) (continuation of Fig. 6.36).

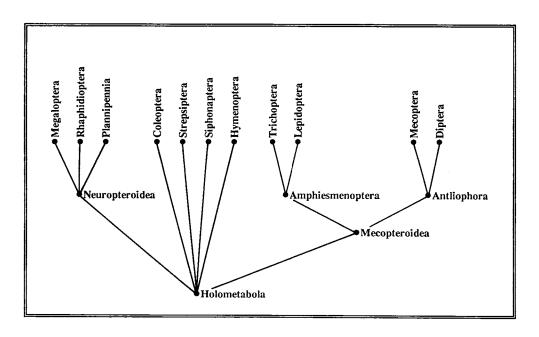


Figure 6.38. Phylogeny of the 'orders' of Insecta (Hennig, 1981) (continuation of Fig. 6.37).

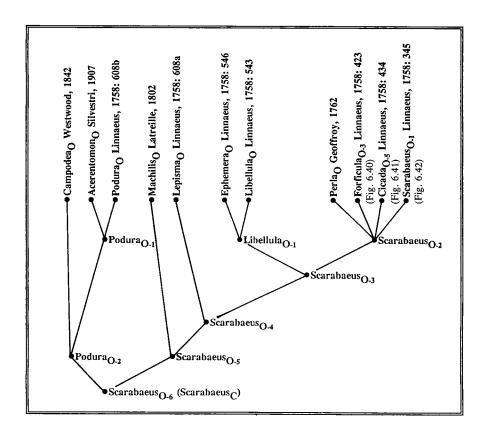


Figure 6.39. Phylogeny of the basal groups of Insecta, using the new system of nomenclature (cont.).

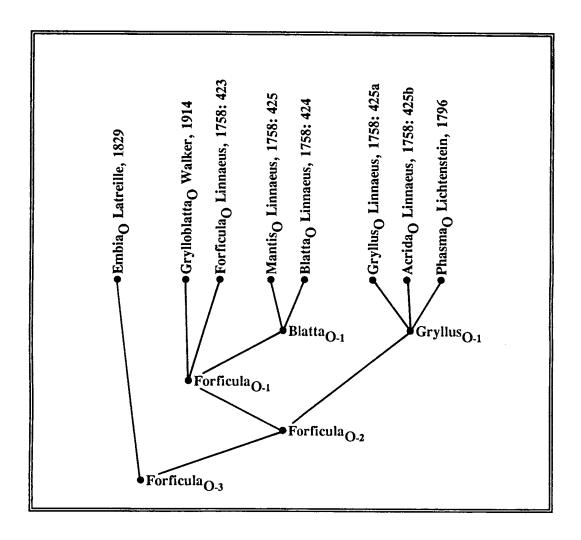


Figure 6.40. Phylogeny of the basal groups of Insecta, using the new system of nomenclature (continuation of Fig. 6.39).

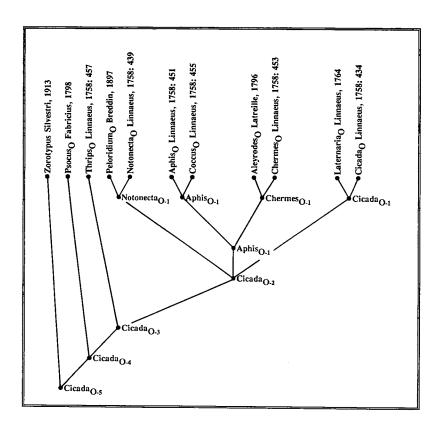


Figure 6.41. Phylogeny of the basal groups of Insecta, using the new system of nomenclature (continuation of Fig. 6.39).

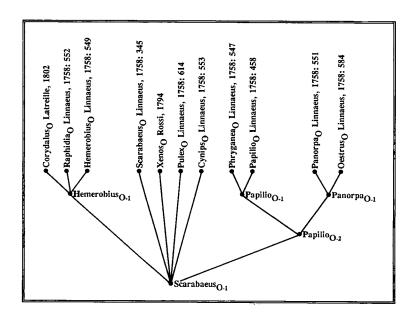


Figure 6.42. Phylogeny of the basal groups of Insecta, using the new system of nomenclature (continuation of Fig. 6.39).

#### 7. PHYLOGENIES WITH SPECIES FUSION

Mayr (1979: 429) commented that «The most extreme degree of introgression would be the complete fusion of two species. Such a fusion is, so to speak, the reverse of multiplication of species. (...); occasionally a previously existing reproductive isolation breaks down and two previously distinct sympatric\* [sic] species merge.»

Mayr (1. c.) adverted that the frequency of such a fact is very much in question. The majority of the cases cited in the literature allow different interpretations.

In Figure 7.1 we show the fusion of two species in a schematic way.

This figure -if inverted- gives us an event of cladogenesis, with the formation of two clades\*\*. Species fusion, as noticed by Mayr, is the reverse of species multiplication, but is also a phenomenon of cladogenesis, as there is the formation of a new clade, from two or more pre-existing clades, which cease to exist after becoming fused in the new clade. We may therefore introduce two new concepts:

**Definition 7.1.** We call *inf-cladogenesis* the phenomenon of the formation of two (or more)

clades from a single clade previously existent.

Let's suppose a clade  $C_1$ , existing during an interval of time  $T_1$ . If a physical barrier divides it into two, each one of the descendant populations originating from this division,  $C_2$  and  $C_3$ , in  $T_2$ , if they remain sexually isolated, will originate a new clade.  $C_1$  is related to  $C_2$  and  $C_3$  by tocogenetic relations, and as it precedes  $C_2$  and  $C_3$  in time, those three sets (of individuals) form an inf-semilattice; for this reason this process of cladogenesis will be called inf-cladogenesis (Figure 7.2).

**Defintion 7.2.** We call *sup-cladogenesis* the phenomenon of formation of a clade from two or more clades previously existent.

As mentioned by Mayr, in order that a supcladogenesis may exist, it is necessary that two or more clades which were in allopatry become fused. Here we have the reverse of the process of infcladogenesis; therefore, set-theoretically speaking, we have a sup-semilattice (Figure 7.3).

**Definition 7.3.** Species-fusion or supcladogenesis refers exclusively to those phenomena where the resulting clade is restricted to only one geographical area, that is, if the newly formed clade does not occupy two or more disjunct areas.

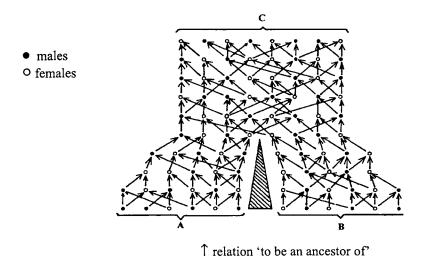


Figure 7.1. Fusion of two species; adapted (from Hennig, 1968: 26, fig. 4).

<sup>\*</sup> For comments on the incorrectness of expressions such as 'sympatric', 'allopatric', etc., see Papavero, Llorente & Abe, 1994.

<sup>\*\*</sup> For a more complete treatment of the concepts of 'clade' and 'cladogenesis' consult Papavero, Abe & Llorente-Bousquets, 1993a, 1993b.

This remark is important to establish an operational distinction between the concepts of supcladogenesis and hybridization; in the latter case, a certain species, formed from two or more species, occupies two or more disjunct geographical areas, as it is formed by *polygenism* (cf. ch. 8).

Now a sup-cladogenesis may assume two distinct forms; in order to facilitate the discussion, let's consider only the case of two preceding species:

- 1) Two morphospecies become fused, disappear and originate a new clade (for instance, as in Figures 7.16 and 7.17)
- 2) Two morphospecies become fused and originate a new clade, but the 'preceding' morphospecies apparently remain, contemporaneously with the new clade; that is, the new clade was formed from the fusion of segments or parts of the two 'parental' morphospecies.

Mayr commented (1968: 443) that it is less probable the origin of a new species by the fusion of segments of two parental species together with the persistence of those parental species. Such a process has been postulated in a number of cases, but those who propose it forget that they have to explain the two problems that always occur in speciation, namely, the acquisition of ecological compatibility and reproductive isolation. If the two parental species are so little isolated reproductively that they produce hybrids, their reproductive isolation with the resulting hybrids will be still lesser. The problem is, therefore, to segregate such a population of hybrids and to maintain them segregated until they acquire reproductive isolation. No mechanism is known that may effectuate this but geographical isolation.

Let's take a hypothetical example to see how a process of type 2) (see above) could occur. Let's initially consider two distinct morphospecies, S<sub>1</sub> and S<sub>2</sub>, which are allopatrid, separated by a physical barrier BI (Figure 7.4).

Let's suppose next that S<sub>1</sub> undergoes an inf-cladogenesis, due to a barrier BII and that the same happens -contemporarily or not- with S<sub>2</sub>, in this case due to a barrier BIII. Four clades would

ensue, geographically isolated (Figure 7.5).

The morphospecies  $S_1$  and  $S_2$  became extinct when they generated, respectively, the clades  $C_1$ - $C_2$  and  $C_3$ - $C_4$  (phylogenetic extinction of  $S_1$  and  $S_2$ ). But, morphologically speaking,  $C_1$ ,  $C_2$  and  $S_1$  are identical, and the same occurs with  $C_3$ ,  $C_4$  and  $S_2$ . According to the essencialist traditional taxonomy, there are only two species (morphospecies). Biologically and historically, however, we have the phylogenetic extinction of  $S_1$  and  $S_2$  and the appearance of four geographically isolated clades, and, consequently, reproductively isolated clades.

During a third episode, let's suppose that clades C<sub>2</sub> and C<sub>3</sub> dispersed and became fused, generating a new clade C<sub>5</sub>. This was due, let's say, to the disappearance of the 'northern' part of barrier BI. We finally have the following aspect of the entire evolutionary process (Figure 7.6):

In the instant of time  $T_3$  we have three distinct morphospecies coexisting:  $C_1$ ,  $C_2$  and  $C_4$ ; in the instant of time  $T_2$  there existed four clades  $(C_1, C_2, C_3, C_4)$ , but only two morphologically distinct sets  $(C_1 = C_2 \text{ and } C_3 = C_4)$ , as they would be confounded from the essencialist taxonomy's point of view with the morphospecies  $S_1$  and  $S_2$ , which existed in the instant of time  $T_1$ . Let's insist that  $S_1$  and  $S_2$  became extinct phylogenetically after suffering inf-cladogenesis;  $C_2$  and  $C_3$  became phylogenetically extinct during the process of sup-cladogenesis.

The subset with two elements  $\{C_2, C_5\}$  is totally ordered; it forms a chain with two eidophoronts. Let's represent this chain by  $C_2 < C_5$ ;  $C_2 < C_5$  is the sister-group of  $C_1$ . Similarly,  $C_3 < C_5$  is the sister-group of  $C_4$ .

Once this said, let's see how we proceed to put names in all those clades, using the new system of nomenclature. To do that, let's employ some real data.

Mayr (1968: 443) declared that

"Patterson and Stone (1952) postulate a hybrid origin for *Drosophila americana*, because it united orderings of genes from *D. novamexicana* and *D.* 

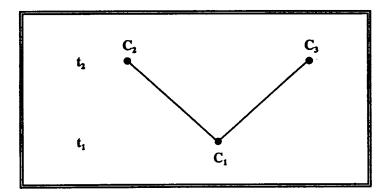


Figure 7.2. An event of inf-cladogenesis.

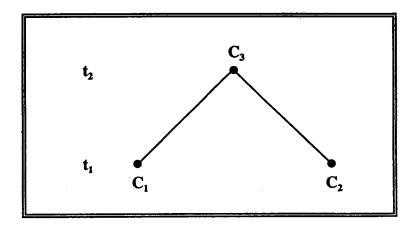


Figure 7.3. An event of sup-cladogenesis, compare with Fig. 7.1

texana. But the essential chromossomic resemblance of the western populations of *D. americana* with *D. novamexicana* and of the eastern ones of *D. americana* with *D. texana* suggest a different interpretation (Mayr, 1957, fig. XV-2; our Figure 7.7)".

We may speculate that the history shown in Figure 7.6 has occurred with this group of drosophilas, and that C<sub>1</sub> corresponds to Drosophila novamexicana Patterson, 1941, C<sub>3</sub> to Drosophila americana Patterson, 1938, and C<sub>4</sub> to Drosophila texana Spencer, 1940. Let's see the conventions which must be employed to put names in all the clades preceding those species.

Let be the diagram of Figure 7.8.

We begin with the terminal species with the

greater number of ancestors; in our case, D. americana Patterson, 1938. As this species was formed from two other, by sup-cladogenesis, it is necessary that we indicate, through appropiate names, that C, and C, are included in D. americana; we do this in the following manner: the autaponomastic of C, will be D. americana, Patterson, 1938 -the symbol 'λ' (lambda) indicating that this nominal species is included in D. americana and that it is placed, in the diagram, to the left (Greek λαιός, α,ον, left, placed to the left of) of the species in which it is included, relative to the reader. The autaponomastic for C, will be D. americana, Patterson, 1938 -the symbol 'δ' (delta) indicating that this nominal species is placed below and to the right (Greek δεξιός, α, ov, right, to the right of) the species in which it is included in the diagram.

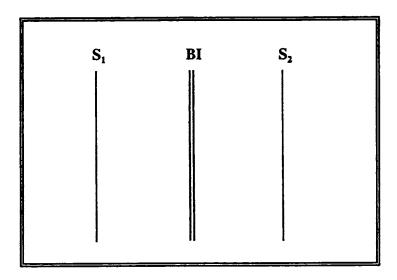


Figure 7.4. Two allopatrid species,  $S_1$  and  $S_2$ , separated by the physical barrier BI (schematic).

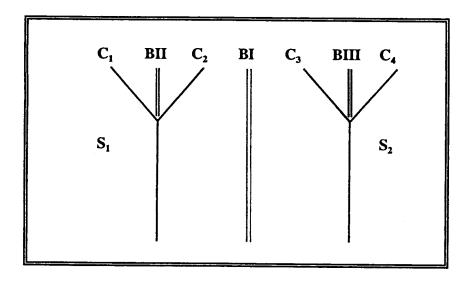


Figure 7.5. Scheme representing inf-cladogenesis of  $S_{1}$  (caused by barrier BII) and inf-cladogenesis of  $S_{2}$  (caused by barrier BIII).

D. americana $_{.1\lambda} < D$ . americana Patterson, 1938 is the sister-group of D. novamexicana Patterson, 1941. As the eidophoront D. americana, has priority over D. novamexicana Patterson, 1941, the synaponomastic of these species will be D. americana, Patterson, 1938, and, consequently, the autaponomastic of  $S_1$ .

D. americana $_{.18}$  < D. americana Patterson, 1938 is the sister-group of D. texana Spencer, 1940. As the eidophoront's name D. americana $_{.18}$  Patterson, 1938 has priority over D. texana Spencer, 1940, the synaponomastic of both species will be D. americana $_{.28}$  Patterson, 1938, and, consequently, the autaponomastic of S<sub>2</sub>.

That way we now obtain the scheme of Figure 7.9.

By convention, when we have two species with the same name, with distinct numerical indexes or not, one of them affected by a  $\lambda$  and the other by a  $\delta$ , which are sister-species, the name with a  $\delta$  has priority, notwithstanding the negative numeral that it has. This will be illustrated in the exercises at the end of this chapter.

Before proceding, let's examine another

advantage of the new nomenclatural system proposed. With this method we can now talk about the past biogeographical history of a group much more clearly, as we may refer ourselves to ancestral eidophoronts by their names. Let's suppose that the history of these three species of *Drosophila* before mentioned has really been as shown in the diagram of Figure 7.9. We may discuss the biogeographical history with more commodity, as illustrated in Figures 7.10-7.13.

In order to illustrate how our method operates, let's consider the hypothetical example of Figure 7.14, which includes those three recent species of *Drosophila*. The classification of this (hypothetical) monophyletic group will be thus expressed:

- 1) Drosophila americana, Patterson, 1938
- 2) D. americana, Patterson, 1938: D. a-ana P., 1945
- 3) D. americana A Patterson, 1938 : D. americana Patterson, 1938
- 4) D. americana<sub>.1x</sub>< D. americana Patterson, 1938: D. novamexicana Patterson, 1941
- D. americana<sub>.3δ</sub> Patterson, 1938 : D. c-ana S., 1942
- D. americana<sub>.2δ</sub> Patterson, 1938 : D. d-ana<sub>.1</sub> P., 1944

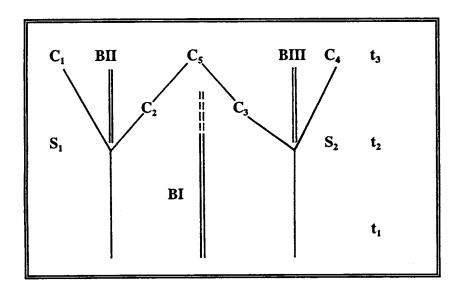


Figure 7.6. Scheme representing sup-cladogenesis of C and C3, forming the new clade C.

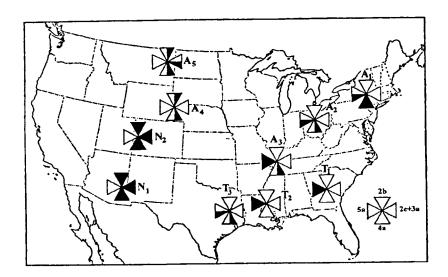


Figure 7.7. Distribution of some gene arrangements in *Drosophila americana* (A -A), *D. texana* (T -T), and *D. novamexicana* (N -N). Presence of the inversions 2b, 2c + 3a, 4a, and 5a are indicated by black, absence by white arms of the crosses (key on the right). A half-filled arm indicates polymorphism. The western populations of *americana* (A, A) have the gene arrangements of *novamexicana*, the eastern populations (A, A, A) those of *texana*. (From Mayr, 1957; 1979: Fig. XV-2).

7) D. americana<sub>.18</sub>< D. americana Patterson, 1938: D. texana Spencer, 1940

8) D. d-ana P., 1944: D. e-ana S., 1949

To prove that the onomastic sets obtained by our system result into an inf-semilattice such as that of Figure 7.14, we invite the reader to do a settheoretical exercise with them. Here they are:

 $E_i = \{americana_{ss}\}$ 

 $E_{a} = \{americana_{ss}, a-ana\}$ 

E, = {americana\_s, americana\_s}

 $E_{i} = \{americana_{ss}, americana_{ss}, americana_{ss}\}$ 

E = {americana a americana a, americana a}

 $E_6 = \{americana_{.5}, americana_{.5}, americana_{.2},$ 

novamexicana}

 $E_{\tau} = \{americana_{sd}, americana_{.sd}, americana_{.zl}, americana_{.zl}\}$ 

 $E_s = \{americana_{.5s}, americana_{.5s}, americana_{.4s}, c_{-ana}\}$ 

E<sub>9</sub> = {americana<sub>ss</sub>, americana<sub>ss</sub>, americana<sub>ss</sub>, americana<sub>ss</sub>,

E<sub>10</sub> = {americana<sub>ss</sub>, americana<sub>ss</sub>, americana<sub>ss</sub>, americana<sub>ss</sub>,

E<sub>11</sub> = {americana<sub>36</sub>, americana<sub>36</sub>, americana<sub>46</sub>, americana<sub>36</sub>}

E<sub>12</sub> = {americana<sub>48</sub>, americana<sub>58</sub>, americana<sub>48</sub>, americana<sub>48</sub>

E<sub>13</sub> = {americana<sub>66</sub>, americana<sub>56</sub>, americana<sub>46</sub>, americana<sub>46</sub>, d-ana<sub>1</sub>, d-ana}

E<sub>14</sub> = {americana <sub>66</sub>, americana <sub>36</sub>, americana <sub>46</sub>, americana <sub>36</sub>, texana}

E<sub>15</sub> = {americana<sub>66</sub>, americana<sub>36</sub>, americana<sub>46</sub>, americana<sub>36</sub>}

E<sub>16</sub> = {americana<sub>.56</sub>, americana<sub>.56</sub>, americana<sub>.26</sub>, americana<sub>.18</sub>, americana<sub>.36</sub>, americana<sub>.36</sub>, americana<sub>.36</sub>, americana<sub>.18</sub>, americana}

In the sequence we present some exercises which the reader may do. The answers are presented in the end of this chapter.

**Exercise 7.1.** Let be the cladogram of Figure 7.15. Draw, step by step, the process of putting names in the ancestral species.

Exercise 7.2. Let be the cladogram of Figure 7.15. Give the classification of this monophyletic group.

**Exercise 7.3.** Given the classification of the monophyletic group of Exercise 7.2, draw, step by

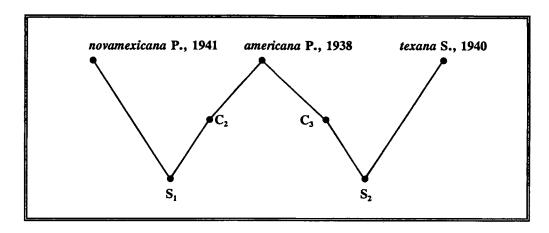


Figure 7.8. Speculative history of the formation of the three species of Drosophila. Ancestors still unnamed.

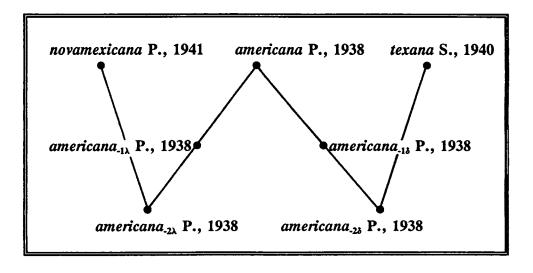


Figure 7.9. Speculative history of the formation of the three species of *Drosophila*, with ancestors named with the new system of nomenclature.

step, the process of retrieval of the corresponding cladogram.

Exercise 7.4. Transform into onomastic sets all the species of the cladogram of Figure 7.15.

Exercise 7.5. Given the cladogram of Figure 7.16, name the unnamed ancestors. Notice that the species M. n-us R., 1933, has no priority over its ancestor species M. l-us J., 1920 and M. n-us K., 1930, which are supposedly known as ancestors. The convention used will be seen in the answer.

**Exercise 7.6.** Give the classification of the monophyletic group of Figure 7.16.

**Exercise 7.7.** Transform into onomastic sets each one of the species of the cladogram of Figure 7.16.

**Exercise 7.8.** Given the cladogram of Figure 7.17, name the unnamed ancestors.

**Exercise 7.9.** Transform into onomastic sets each one of the species of the cladogram of Figure 7.17.

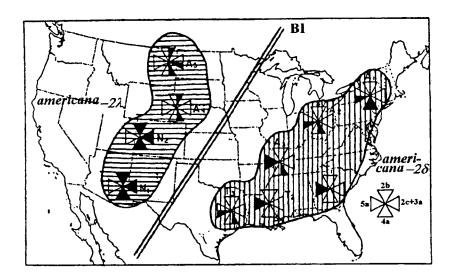


Figure 7.10. Speculative history of the evolution of a group of *Drosophila* species. Two species, D. americana- $_{25}$  and D. americana- $_{25}$  were in allopatry, in a time period  $T_1$ , separated by a physical barrier (BI).

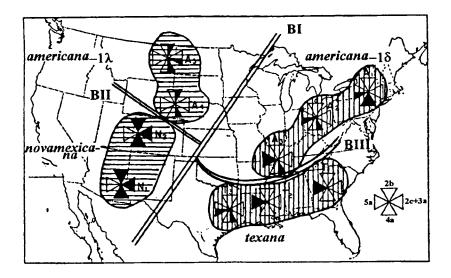


Figure 7.11. Speculative history of the evolution of a group of *Drosophila* species. D. americana<sub>.18</sub> suffered inf-cladogenesis, due to the appearance of a barrier (BII), originating D. americana<sub>.18</sub> and D. novamexicana. D. americana<sub>.28</sub> also suffered inf-cladogenesis (Barrier BIII), originating D. americana-<sub>18</sub> and D. texana.

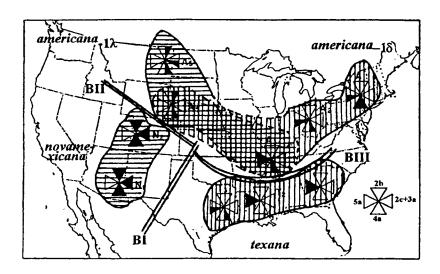


Figure 7.12. Speculative history of the evolution of a group of *Drosophila* species. D. americana and D. americana dispersed, entering in sympatry, due to the disappearance of the northern tract of Barrier BI.

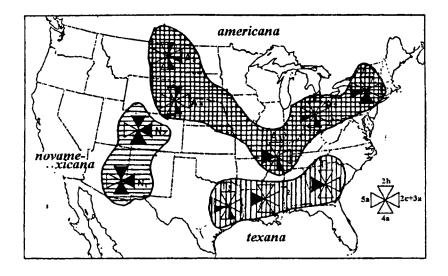


Figure 7.13. Speculative history of the evolution of a group of Drosophila species. Complete fusion (sup-cladogenesis) of D. americana<sub>.iv</sub> and D. americana<sub>.iv</sub> forming the present species D. americana.

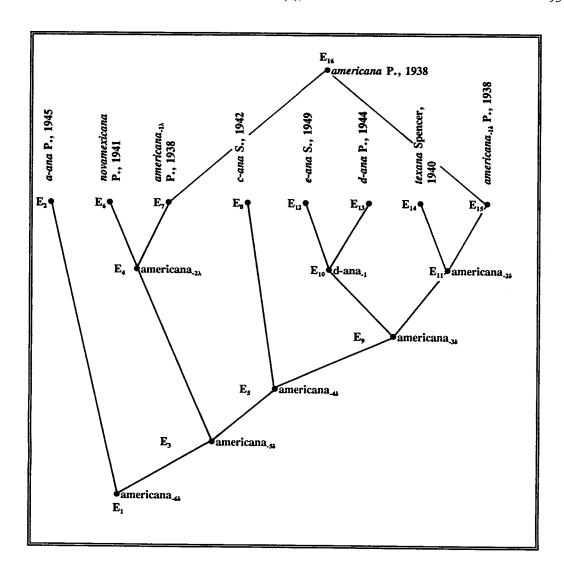


Figure 7.14. Hypothetical phylogeny of a group of *Drosophila* species, illustrating the conventions of the new system of nomenclature regarding species fusion.

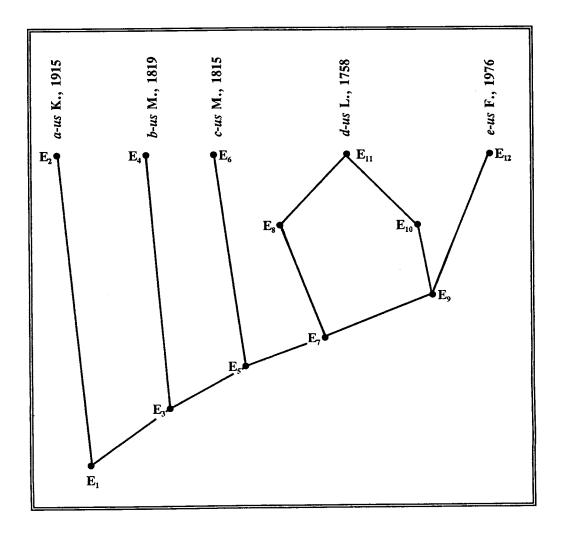


Figure. 7.15

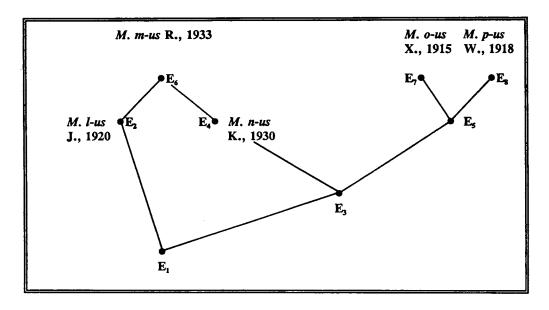


Figure. 7.16

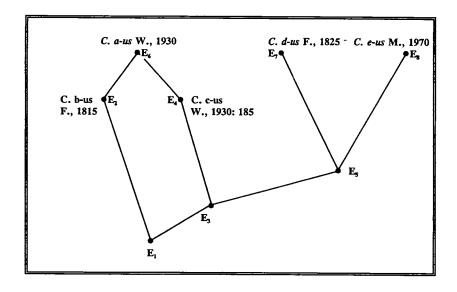


Figure 7.17

## ANSWERS TO THE EXERCISES

**Exercise 7.1.** See Figures 7.18-7.24

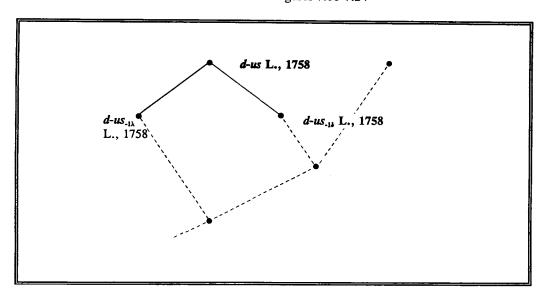


Figure. 7.18

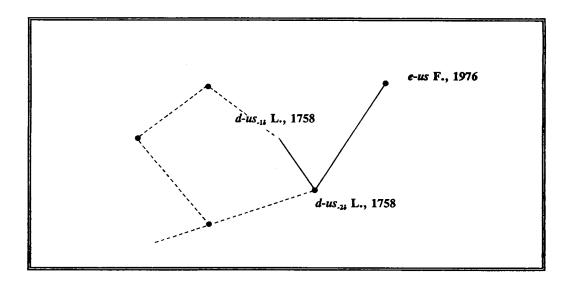


Figure. 7.19

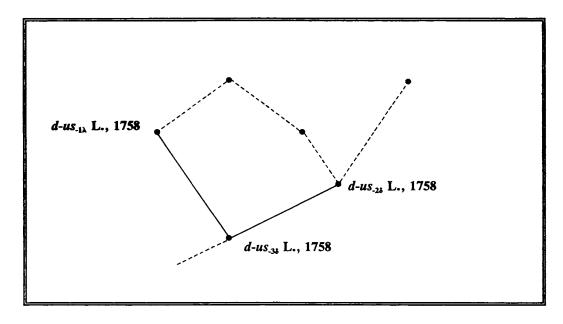


Figure 7.20

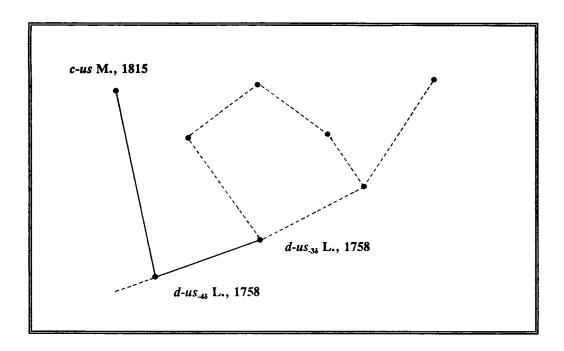


Figure 7.21

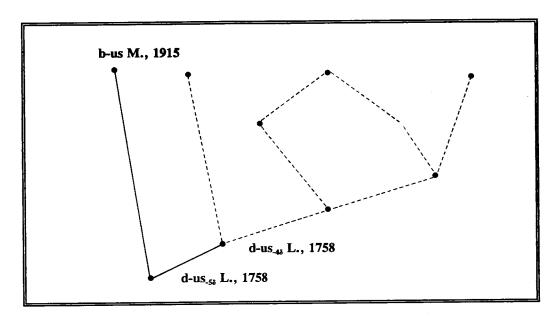


Figure 7.22

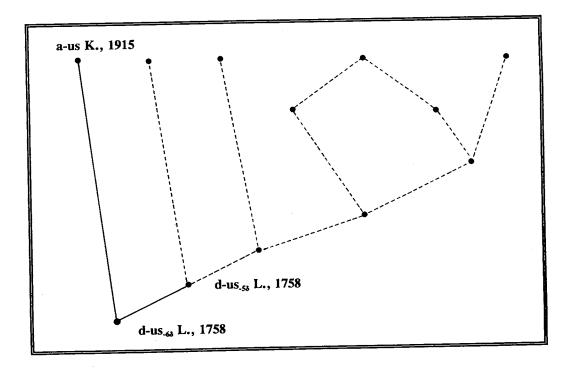


Figure 7.23

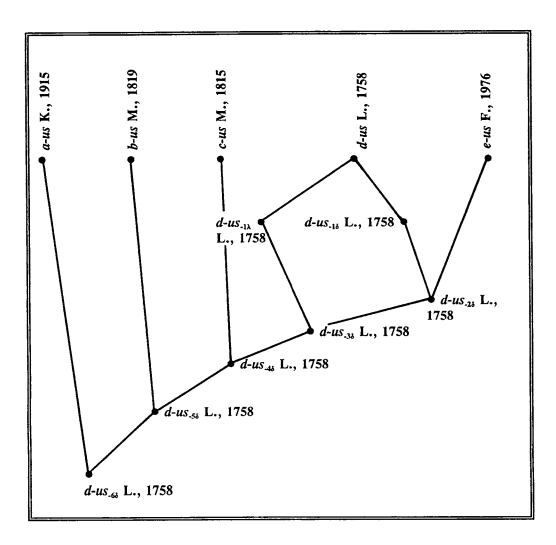


Figure 7.24

## Exercise 7.2:

- 1) d-us<sub>-68</sub> L., 1758
- 2) d-us<sub>.58</sub> L., 1758: a-us K., 1915
- 3) d-us<sub>46</sub> L., 1758: b-us M., 1819
- 4) d-us<sub>38</sub> L., 1758: c-us M., 1815
- 5) d-us<sub>.18</sub> L., 1758: d-us<sub>.1λ</sub> < d-us L., 1758 6) d-us<sub>.18</sub> < d-us L., 1758 : e-us F., 1976

## **Exercise 7.3.** See Figures 7.25-7.27.

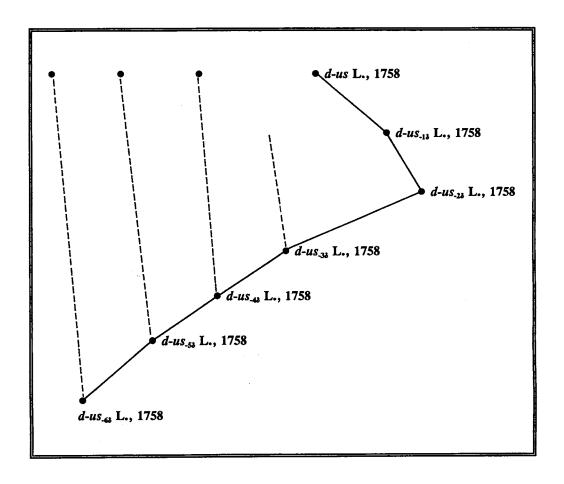


Figure 7.25 1) d-us<sub>-68</sub> L., 1758

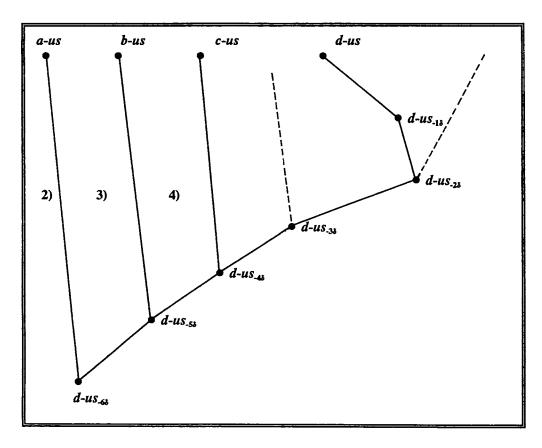


Figure 7.26 2) d-us<sub>.ss</sub> L., 1758 : *a-us* K., 1915 3) d-us<sub>.ss</sub> L., 1758 : *b-us* M., 1819 4) d-us<sub>.ss</sub> L., 1758 : *c-us* M., 1815

### Exercise 7.4:

```
\begin{split} E_1 &= \{\text{d-us}_{.65}\} \\ E_2 &= \{\text{d-us}_{.65}, \, a\text{-us}\} \\ E_3 &= \{\text{d-us}_{.65}, \, \text{d-us}_{.56}\} \\ E_4 &= \{\text{d-us}_{.65}, \, \text{d-us}_{.56}, \, \text{b-us}\} \\ E_5 &= \{\text{d-us}_{.65}, \, \text{d-us}_{.56}, \, \text{d-us}_{.46}\} \\ E_6 &= \{\text{d-us}_{.65}, \, \text{d-us}_{.56}, \, \text{d-us}_{.46}, \, \text{c-us}\} \\ E_7 &= \{\text{d-us}_{.65}, \, \text{d-us}_{.56}, \, \text{d-us}_{.46}, \, \text{d-us}_{.36}\} \\ E_8 &= \{\text{d-us}_{.65}, \, \text{d-us}_{.56}, \, \text{d-us}_{.46}, \, \text{d-us}_{.36}, \, \text{d-us}_{.12}\} \\ E_9 &= \{\text{d-us}_{.66}, \, \text{d-us}_{.56}, \, \text{d-us}_{.46}, \, \text{d-us}_{.36}, \, \text{d-us}_{.26}\} \\ E_{10} &= \{\text{d-us}_{.66}, \, \text{d-us}_{.56}, \, \text{d-us}_{.46}, \, \text{d-us}_{.36}, \, \text{d-us}_{.26}, \, \text{d-us}_{.16}, \, \text{d-us}_{.16}\} \\ E_{11} &= \{\text{d-us}_{.66}, \, \text{d-us}_{.56}, \, \text{d-us}_{.46}, \, \text{d-us}_{.36}, \, \text{d-us}_{.16}, \, \text{d-us}, \, \text{d-us}_{.16}, \, \text{d-us}_{.26}, \,
```

## Exercise 7.5. See Figure 7.28

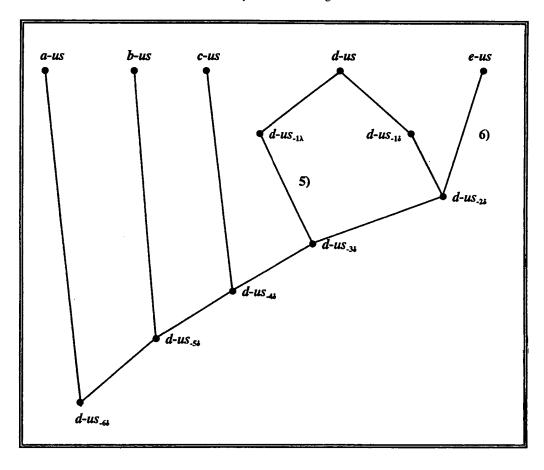


Figure 7.27. 5) d-us<sub>.18</sub> L., 1758 : d-us<sub>.18</sub> < *d-us* L., 1758 6) d-us<sub>.18</sub> < *d-us* L., 1758 : *e-us* F., 1976

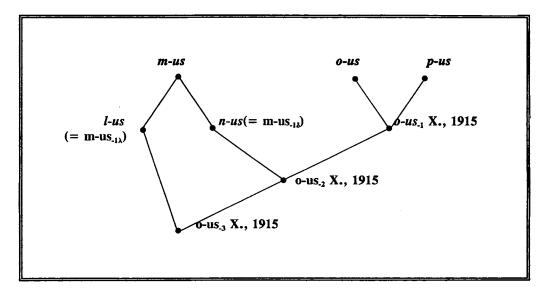


Figure 7.28

Note: A species (morphospecies) generated by species fusion does not have nominal priority over its ancestral species, and in the classification the synonyms are cited between parentheses, according to the conventions  $(\delta,\lambda)$  previously cited (see Exercise 7.6).

#### Exercise 7.6:

- 1) o-us, X., 1915
- 2) o-us<sub>.2</sub> X., 1915 : *l-us* J., 1920 (= m-us<sub>.1 $\lambda$ </sub>) < *m-us* R., 1933
- 3) o-us<sub>.1</sub> X., 1915 : n-us K., 1930 (= m-us<sub>.1 $\theta$ </sub>) < m-us R., 1933
- 4) o-us X., 1915 : p-us W., 1918

#### Exercise 7.7:

$$\begin{split} E_{1} &= \{\text{o-us}_{.3}\} \\ E_{2} &= \{\text{o-us}_{.3}, l\text{-}us (= \text{m-us}_{.18})\} \\ E_{3} &= \{\text{o-us}_{.3}, \text{o-us}_{.2}\} \\ E_{4} &= \{\text{o-us}_{.3}, \text{o-us}_{.2}, n\text{-}us (= \text{m-us}_{.18})\} \\ E_{5} &= \{\text{o-us}_{.3}, \text{o-us}_{.2}, \text{o-us}_{.1}\} \\ E_{6} &= \{\text{o-us}_{.3}, l\text{-}us (= \text{m-us}_{.12}), m\text{-}us, n\text{-}us (= \text{m-us}_{.18}), \\ \text{o-us}_{.2}\} \\ E_{7} &= \{\text{o-us}_{.3}, \text{o-us}_{.2}, \text{o-us}_{.1}, o\text{-}us\} \\ E_{8} &= \{\text{o-us}_{.3}, \text{o-us}_{.2}, \text{o-us}_{.1}, p\text{-}us\} \end{split}$$

#### Exercise 7.8. See Figure 7.29

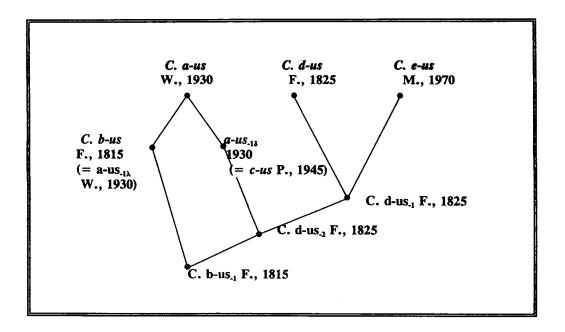


Figure 7.29

```
\begin{split} E_1 &= \{b\text{-}us_{.1}\} \\ E_2 &= \{b\text{-}us_{.1}, b\text{-}us (= a\text{-}us_{.1\lambda})\} \\ E_3 &= \{b\text{-}us_{.1}, d\text{-}us_{.2}\} \\ E_4 &= \{b\text{-}us_{.1}, d\text{-}us_{.2}, a\text{-}us_{.1\delta} (= c\text{-}us)\} \\ E_5 &= \{b\text{-}us_{.1}, d\text{-}us_{.2}, d\text{-}us_{.1}\} \\ E_6 &= \{b\text{-}us_{.1}, b\text{-}us (= a\text{-}us_{.1\lambda}), a\text{-}us, a\text{-}us_{.1\delta} (= c\text{-}us), d\text{-}us_{.2}\} \\ E_7 &= \{b\text{-}us_{.1}, d\text{-}us_{.2}, d\text{-}us_{.1}, d\text{-}us\} \\ E_8 &= \{b\text{-}us_{.1}, d\text{-}us_{.2}, d\text{-}us_{.1}, e\text{-}us\} \end{split}
```

#### 8. THE QUESTION OF HYBRIDS

In the sixth chapter of his Animal species and evolution (1979: 118-125), Mayr describes several cases of hybridization. Let's quote some of them:

1. In the case of *Passer domesticus* and *Passer hispaniolensis*, Mayr says (1979: 119):

«In southern Europe and western Asia there are two closely related and widespread species of sparrows, the House Sparrow (Passer domesticus) and the Willow Sparrow (Passer hispaniolensis). In most areas the two species coexist side by side without any signs of interbreeding [Our Figure 8.1]. In such areas the House Sparrow is associated with human habitations while the Willow Sparrow lives in willow groves or other kinds of woods in river bottoms. Such sharp separation occurs in Spain, Morocco, the Balkans, Asia Minor, Iran, and Turkestan. However, in a few areas the barrier between the two species has broken down and more or less unrestricted hybridization between them is taking place (Meise, 1936). One of these areas is Tunisia, another is Italy and adjacent islands (Sicily, Corsica), a third is Crete. Conditions are different from place to place. Sometimes one species prevails, while the other is rare and occasional hybrids appear. More frequently the hybrid population includes phenotypically the two parental species and all conceivable combinations of the parental characters with indication of complete random mating. Finally, there are some areas, like Italy and the oases of southern Tunisia, where an intermediate hybrid type has become stabilized and the parental extremes have disappeared. A clue to the origin of the hybridization is provided by the fact that the Willow Sparrow occupies the ecological niche of the House Sparrow (human habitations!) in certain areas, such as Sardinia, eastern Tunisia, and Cyrenaica. Where the aggressive House Sparrow invades such areas, the conditions are present, in the absence of ecological separation, for a breakdown of reproductive isolation».

2. In the case of Terpsiphone rufiventer, Terpsiphone rufocinerea and Terpsiphone viridis, Mayr declares (1979: 119, 121):

«Chapin (1948) describes a particularly interesting case from tropical Africa. There are three African species of Paradise Flycatchers (Terpsiphone) of which two, rufiventer and rufocinerea, live in the rain forest, while the third. viridis, lives in second growth woods and in savanna forest. In most areas where these species come into contact with each other they live side by side without any signs of intergradation or hybridization, each one restricted to its own habitat. However, along the edge of the African rain forest there are many areas where parts of the forest have been partially or completely cleared in recent years, and in such areas viridis interbreeds with the two forest species, particularly with rufiventer. As a result there are now three areas with hybrid populations: one in northwestern Angola (T. rufocinerea rufocinerea X T. viridis plumbeiceps), one in West Africa (T. rufiventer rufiventer X T. v. viridis), and one in Uganda (T. rufiventer somereni X T. viridis ferreti). In each case the hybrid population has settled down to a reasonable constancy, so that the new stabilized hybrid populations were at first considered separate species or subspecies: bannermani in Angola, nominate rufiventer at the Gambia River, and emini, poliothorax, and albiventris in Uganda. Where much of the original rain forest is left, hybrids are sporadic; where it has been destroyed and the remaining stands have been invaded by T. viridis, complete hybrid populations have evolved. The available evidence suggests to Chapin that the hybridization is quite recent, being in all cases due to the clearing of the forest by the African natives».

3. Finally, let's consider the spectacular case of *Pipilo* in Mexico (Mayr, 1979: 121):

«Perhaps the most thoroughly analyzed case of the breakdown of isolation between two species of birds in that of two members of the genus *Pipilo* in Mexico (Sibley, 1950, 1954; Sibley and West, 1958). The red-eyed Towhee (*P. erythrophthalmus*) and the Collared Towhee (*P. ocai*) are more or less widespread as 'pure' species [Our Figure 8.2]. *Pipilo ocai* occurs from Oaxaca to Jalisco. *Pipilo erythrophthalmus* is widespread in North America and extends south as far as Chiapas and Guatemala. In Oaxaca the two species live side by side without



Figure 8.1. Largely sympatrid distribution of the House Sparrow, *Passer domesticus* (horizontal hatching) and the Willow Sparrow *P. hispaniolensis* (vertical hatching). Hybridization and introgression (black) in various Mediterranean and North African areas (After Meise 1936) [after Mayr, 1979: 120, Fig. 6-1).

intermixing. In Puebla 16 percent of the 117 known specimens show evidence of hybridization. In the other states of the Mexican plateau from northern Puebla through Nayarit and Michoacan to Jalisco a series of introgressed hybrid populations is found, which in the east and north are similar to P. erythrophthalmus and toward the south and west are similar to P. ocai. If a hybrid index is designated which gives pure erythrophthalmus the value of 24 and pure ocai the value 0, an east-west chain of populations is found with the mean values 22.4-19.8-16.9-15.8-13.5-7.8-4.0, and north-south chain with the values 23.5-22.8-22.6-13.7-8.0-2.8-0.17. The variation within a local population is great but does not span the total range. In a population with a mean index of 13.7 it varied from 6 to 20 in 76 specimens; in another with a mean of 8.0 it varied from 3 to 16 among 58 specimens. If it were not for the pronounced differences between the species and their sympatry in Oaxaca, one might be tempted to consider them conspecific. Sibley's original paper must be consulted for many other interesting aspects of this hybridization. Again, it is apparently a very recent event, caused by man's agricultural activities, and not dating back further than 300-500 years».

It follows, from the foregoing examples, that a 'species' resulting from hybridization is characterized, generally, by:

- 1. Occupying two or more disjunct geographical areas (polypatry);
- Presenting those two or more areas situated in the zone of sympatry of the two species which originated it;
- Presenting those two or more geographical areas as a result of the break of an ancient reproductive isolation due to ecological or ethological causes.

Consequently, a hybrid 'species' appears by polygenism and that its populations may be formed synchronically or allochronically (see Figure 8.3). Hence, a hybrid 'species' is merely a morphological class, or a 'Linnaean' species, which does not fit in the phylogenetic system.

The system of nomenclature proposed by us applies exclusively to the components of a phylogeny; it does not apply, then, to classes or Linnaean species. However, it is useful to indicate that, given a certain monophyletic group, there are phenomena of hybridization involved. To represent them, the following conventions are used:

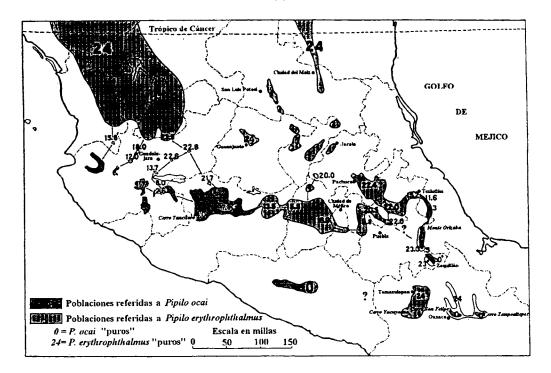
- The phylogeny of the group is reconstructed, including all the 'Hennigian' species; then one proceeds as indicated in the preceding chapters.
- 2. Afterwards the hybrid 'species' are placed in the phylogeny by means of interrupted lines linking the species which produced them. In the case of hybrids, the names of hybrid species are not used for priority's sake, although they are, as sets of characters, maximal elements of an infsemilattice.

In the example of Figure 8.4 this process is illustrated: we construct the phylogeny of the species of the C-genos 'X' without including the hybrid species. Then, by means of interrupted lines, the cases of hybridization are added. In this hypothetical case, X. x a-us 1753, which is, let's suppose, the type-species of the 'genus', has priority over all the remaining species of the group, but, as it is a Linnaean species, it is not considered in the new system of nomenclature. Figure 8.5 illustrates another hypothetical case, with three cases of hybridization.

\*

A few considerations about the problem of hybridization:

- 1. What is called 'hybridization between two species' means, in reality, 'hybridization between certain pairs of individuals belonging to two distinct morphospecies', as a hybrid 'species' results from polygenism.
- 2. The situation is different when we come to 'intergeneric hybrids'. Linnaean genera are abstractions, and therefore do not occupy time nor space. How can 'genera' copulate and produce (or not) offspring? This is one more of the absurds of the Linnaean taxonomy. Only physical individuals belonging to distinct morphospecies can form hybrids. This conceptual aberration is unfortunately very



Populations in relation to *Pipilo ocai*Populations in relation to *Pipilo erythrophthalmus*0= P. ocai «pures»
24=P. erythrophthalmus «pures»

Figure 8.2 Distribution of the Red-eyed Towhees (*Pipilo*) in Mexico. Pure *erythrophthalmus* (24) in the north and southeast. Pure *ocai* (0) in the south and southeast. The numbers (from 0 to 24) indicate the mean character indices of various hybrid populations. Note the sympatry of the two species at several localities in the southeast (From Sibley 1954) [after Mayr, 1979: 122, Fig. 6-2].

common among botanists; Wagner Jr. (1983: 76), says, for example:

"Intergeneric hybrids [sic] can be designated by a 'generic name', which is considered to be a condensed formula. This contracted formula is a combination of the names (or parts of them but not all of both of them) of the parental genera [sic], preceded by the multiplication sign (e. g., X Quercifagus)".

It would be more appropriate to say: hybrid between species (in the sense defined above, in consideration 1), belonging to distinct 'genera'.

Hybrid 'genera' (such as X Quercifagus) are mere abstractions, or sets of morphological classes; consequently, there is no phylogeny of such 'genera'. Therefore, only in the context of

traditional taxonomy the assertion of Wagner Jr. (1. c.) may be accepted:

"All hybrids between species of the same two different genera must be placed under the hybrid genus name".

An additional confusion arose in the Codes of Nomenclature (both botanical and zoological), which are still impregnated of scholastic taxonomy. Let's examine another declaration of Wagner Jr. (l. c.):

"Guides to forming the names for trigeneric and more complex hybrids are given in the Code. No description or diagnosis is required for publishing: the name of a hybrid genus; it is considered validly published if only the names of the parent genera are given at the time of publication".

males

In our new system of nomenclature, hybrids between species belonging to distinct 'genera' or to any other 'supraspecific category' are treated in the same manner as hybrids between species with the same praenomen, i.e., they are indicated by means of interrupted lines linking the species which 'hybridized'. The 'intergeneric' hybrids are denoted, for instance, in the following ways:

Quercus a-us X Fagus m-us (no longer X Quercifagus), or

Quercus m-us X Fagus x-us X Quercus a-us.

We have, therefore, only hybrids between 'species', or *nothospecies*, as they are called by botanists (Wagner Jr., 1983: 76; from the Greek  $vo\theta \delta \varsigma$ , bastard, of illegitimate birth).

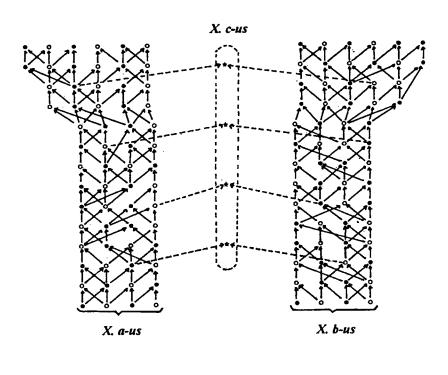


Figure 8.3. Schematic representation of the formation, by polygenism, of a hybrid species.

o females

o relation 'to be parent of'

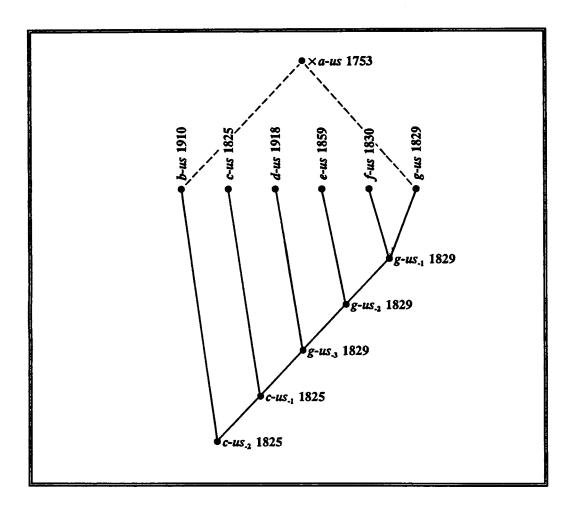


Figure 8.4. Hypothetical phylogeny, with a case of hybridization. The classification results as follows: 1) X. c-us<sub>.2</sub> 1825; 2) X. c-us<sub>.1</sub> 1825: X. b-us 1910; 3) X. c-us<sub>.1</sub> 1825: X. g-us<sub>.2</sub> 1829; 4) X. g-us<sub>.2</sub> 1829: X. d-us 1918; 5) X. g-us<sub>.1</sub> 1829: X. e-us 1859; 6) X. g-us 1829: X. f-us 1830; 7) X. b-us  $1910 \times X$ . g-us  $1829 = X \times a$ -us 1753.

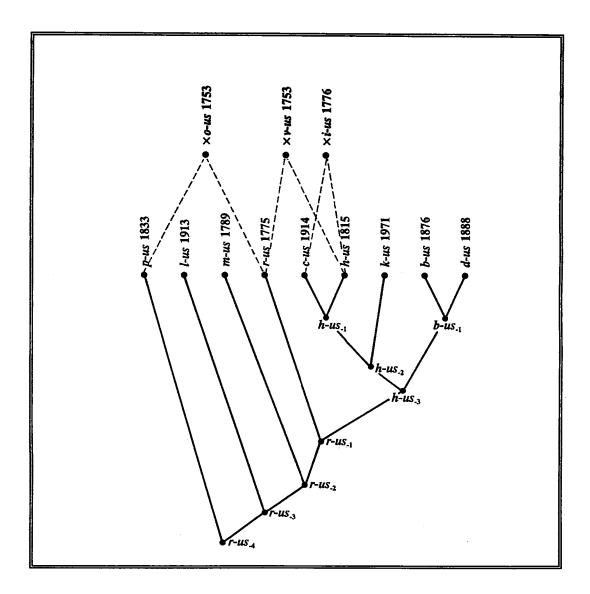


Figure 8.5. Hypothetical phylogeny with three cases of hybridization. The classification results as follows: 1) A. r-us<sub>1</sub> 1775; 2) A. r-us<sub>1</sub> 1775: A. p-us<sub>1</sub> 1833; 3) A. r-us<sub>1</sub> 1775: A. l-us<sub>1</sub> 1913; 4) A. r-us<sub>1</sub> 1775: A. m-us<sub>1</sub> 1789; 5) A. r-us<sub>1</sub> 1775: A. h-us<sub>1</sub> 1815; 6) A. h-us<sub>1</sub> 1815: A. b-us<sub>1</sub> 1876; 7) A. h-us<sub>1</sub> 1815: A. k-us<sub>1</sub> 1971; 8) A. h-us<sub>1</sub> 1815: A. c-us<sub>1</sub> 1914; 9) A. b-us<sub>1</sub> 1876: A. d-us<sub>2</sub> 1888; 10) A. p-us<sub>1</sub> 1833  $\times$  A. r-us<sub>2</sub> 1775 = A.  $\times$  o-us<sub>2</sub> 1753; 11) A. r-us<sub>2</sub> 1775  $\times$  A. h-us<sub>3</sub> 1815: A.  $\times$  us<sub>4</sub> 1775  $\times$  A. h-us<sub>5</sub> 1753; 12) A. c-us<sub>5</sub> 1914  $\times$  A. h-us<sub>6</sub> 1815 = A.  $\times$  i-us<sub>7</sub> 1776.

### 9. POLYPATRID SPECIES

We will call polypatrid species those species which, from the point of view of Phylogenetic Systematics, are well defined through autapomorphies, but which occupy two or more clearly defined disjunct distributional areas.

According to the canons of Phylogenetic Systematics, we may be dealing with only *one* species, but, from the evolutionary point of view, a polypatrid species may be considered as *two or more* 'biological species', if the allopatrid populations do not exchange genes -if they are reproductively isolated.

Polypatrid species are not uncommon in nature. Lee et al. 1980 (see also Wiley and Mayden, 1985: 599, figs. 1, 2, 27, 28) represented the areas of distribution of the fishes Fundulus sciadicus, and Fundulus catenatus, Eurycea lucifuga, a salamander, and the spectacular case of the polypatrid species Percina evidens, distributed in no less than 19 disjunct areas.

Now, how can we distinguish nominally the

'biological species' of a polypatrid species? By referring to their respective geographical areas, in the following way: we denote each geographical area by S<sub>1</sub>, S<sub>2</sub>, ..., S<sub>n</sub> and then those symbols are added to the name of the biological species that occupies each of these areas. Thus we have for instance, (see Wiley & Maiden, 1985: 599, fig. 1) the areas of distribution occupied by Fundulus sciadicus-S<sub>1</sub>, Fundulus sciadicus-S<sub>2</sub> and Fundulus sciadicus-S<sub>3</sub>. (Three allopatrid populations).

Two possibilities exist concerning the history of the polypatrism of *Fundulus sciadicus* - either we know the vicariant events which have brought about this distribution, or we don't.

a) In the first case -we know the biogeographical history of this polypatrid species - we employ the convention used in Figure 9.1.

Let it be observed that the arrows of the diagram are directed 'downward', as the inf-semilattice is ordered by the inverse relation of proper inclusion ( $\supseteq$ ); thus, for instance, *F. sciadicus*-S<sub>2</sub>  $\cup$  S<sub>3</sub> properly includes *F. sciadicus*-S<sub>2</sub> and *F. sciadicus* S<sub>3</sub>.

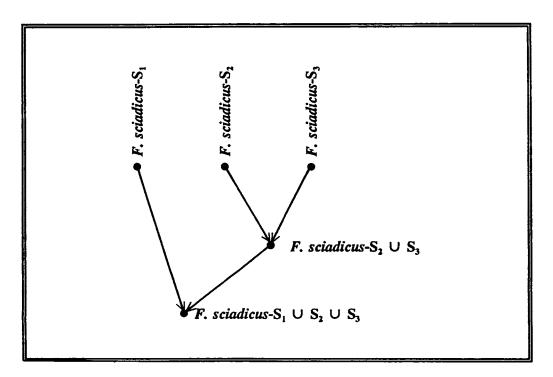


Figure 9.1. Convention used in the new method of nomenclature for representing a polypatrid species whose biogeographic history is known.

b) In the second case -we don't know the biogeographical history of the group- the biological species of the polypatrid species are placed in the diagram polytomically. In the particular case of F. sciadicus, we would have the cladogram shown in Figure 9.2.

In either case, we have to have the maps with the areas of geographical distribution of the biological species of a polypatrid species.

Let's now suppose that the phylogeny of the group that includes F. sciadicus is the following (Figure 9.3):

We add to that phylogeny the sequence of the phenomena of geographical partititon (biological speciation) which occurred with the terminal (morphological) species F. sciadicus (case a) or just place them polytomically, in the absence of such a knowledge (respectively, Figures 9.4 and 9.5).

The corresponding classification of the phylogeny given in Figure 9.4 is this:

- 1) F. a-us
- 2) F. a-us: F. b-us.
- 3) F. b-us: F. sciadicus- $S_1 \cup S_2 \cup S_3$
- 4) F. sciadicus-S<sub>1</sub>: F. sciadicus-S<sub>2</sub>

The corresponding classification of the phylogeny given in Figure 9.5 is the following:

- 1) F. a-us
- 2) F. a-us: F. b-us,
- 3) F. b-us: F. sciadicus- $S_1 \cup S_2 \cup S_3$
- 4) F. sciadicus-S<sub>1</sub>: F. sciadicus-S<sub>2</sub> ∪ S<sub>3</sub> 5) F. sciadicus-S<sub>2</sub>: F. sciadicus-S<sub>3</sub>

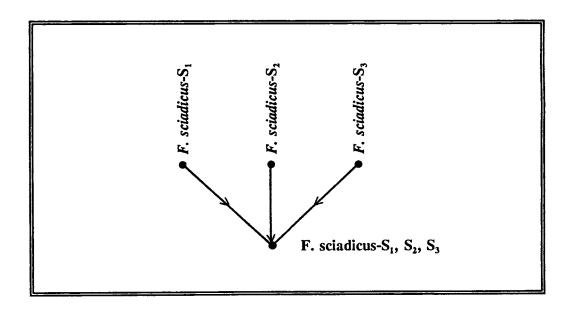


Figure 9.2. Convention used in the new method of nomenclature for representing a polypatrid species whose biogeographic history is unknown.

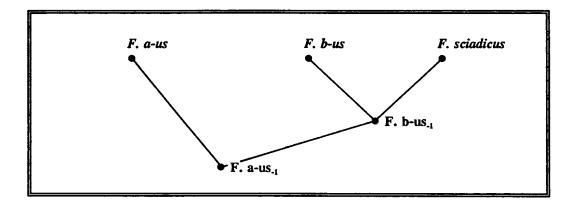


Figure 9.3. Hypothetical phylogeny, including F sciadicus.

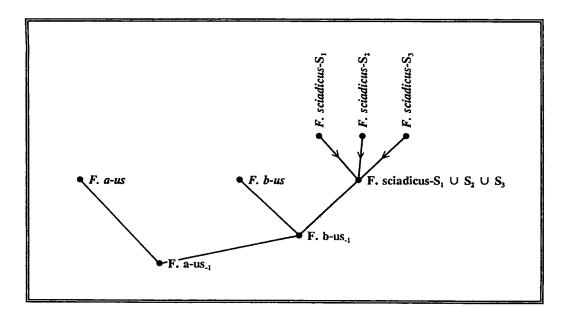


Figure 9.4. Convention used for polypatrid species with unknown biogeographical history.

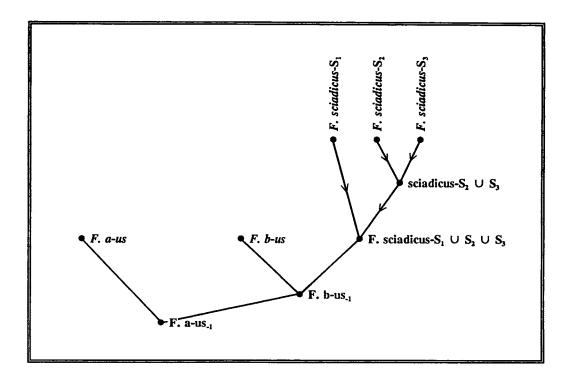


Figure 9.5. Conventions used for polypatrid species with known biogeographical history.

### 10. FOSSIL SPECIES

Before commenting on phylogenies which include fossil species, let's distinguish two types of species based on fossil remains:

- There are species based upon relatively perfectly preserved specimens, such as the insects preserved in amber, which allow us the detection of almost all morphological characters, just like they were recent specimens;
- 2) Most of the species based upon fossil remains, however, are defined by very few characters, as only parts of the organism became preserved, or the process of preservation was such that it allows only the detection of few characters.

Let's examine then the different cases.

## 10.1. Terminal species based on well-preserved specimens

There is no problem in treating terminal fossil species -they are treated in the same way as the recent species- only their name is preceded by the traditional sign of dagger (†) used for fossils. Figures 10.1 and 10.2 illustrate the procedure to be adopted, using hypothetical cases:

# 10.2. Fossil species, based on well-preserved specimens, which are immediate ancestors of at least two morphospecies

Let's now suppose that a certain fossil species is surely known as the immediate ancestor of two or more morphospecies. We then proceed analogously to the cases of phylogenies with species fusion (see Chapter 7). The example of Figure 10.3 illustrates the process:

In this latter case, the resulting classification is the following:

- 1) X. v-us, 1809
- 2) X. v-us., 1809 (= †e-us 1975): X. r-us., 1914
- 3) X. r-us 1914 : X. s-us 1988
- 4) X. v-us., 1809 : X. t-us 1898
- 5) X. v-us 1809 : X. z-us 1945

# 10.3. Fossil species, based on well-preserved specimens, which are not immediate ancestors of at least two morphospecies

Kraus (1989: 20-22) commented that:

"Neontologists applying the biospecies concept (...) are operating horizontally at the Recent time-level. In contrast to problems known from angiosperm taxonomy, zoologists normally have no problems in ascertaining biospecies. Palaeontologists, however, have to deal with a third, vertical dimension: time. Ax (1984), Wiley (1981) and, especially, Willmann (1985) followed Hennig's arguments (e.g., 1982: 62) and explained in detail that a species can only be defined in space and time by the beginning and the end of its existence. This coincides with two succeeding events: one event in which a species has originated as a genetically intercommunicating unit (which is reproductively isolated from other such units), and a second, in which the descendants of a continous sequence of generations ceased to form a single reproductive unit. This may happen by way of a succeeding speciaton event - or by way of extinction. This biological species definition has now generally been accepted as the *evolutionary* species concept.

The terms 'evolutionary species' and 'chronospecies' make two fundamentally different approaches in paleontology. The evolutionary species concept integrates continuous but not necessarily constant changes in the appearance of a species during the course of its existence. Chronospecies, in contrast, are typological units: their borders in time and space are arbitrarily fixed by morphological data (see Willmann, 1985: 185). The arbitrariness of the distinction of three succeeding species of man, *Homo habilis*, *H. erectus* and *H. sapiens*, is a good example of such typologically defined 'chronospecies'.

The only possible means of delimiting 'chronospecies' within an evolutionary continuum, e.g., Homo sapiens s. str. from the earlier 'H. erectus', are convention and some kind of hiatus in the known fossil record. But there is no reason to assume that any speciation event has happened since the existence of H. habilis (or any other representative of the australopithecine stage group closely related to H. habilis). Then, we have to assume an uninterrupted sequence of approximately 200 000 generations. Therefore, a single evolutionary species, Homo sapiens, has to be postuladed. There has been a considerable change in the characters during the existence of this species; the names habilis, erectus and sapiens s. str. therefore simply refer to succeeding gradual stages of one and the same evolutionary species».

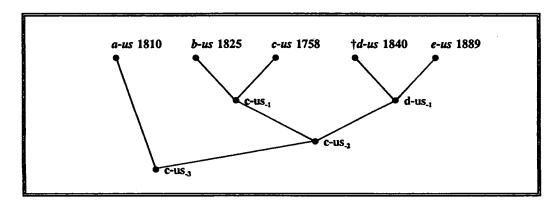


Figure 10.1. Conventions used in the new system of nomenclature for phylogenies including terminal fossil species based on well-preserved specimens.

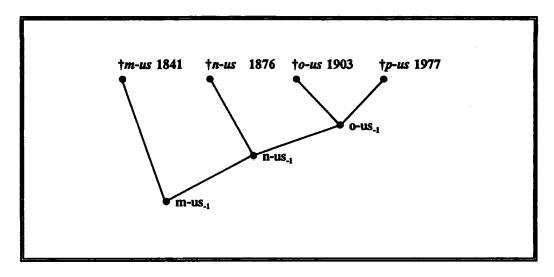


Figure 10.2. Conventions used in the new system of nomenclature for phylogenies including terminal fossil species based on well-preserved specimens.

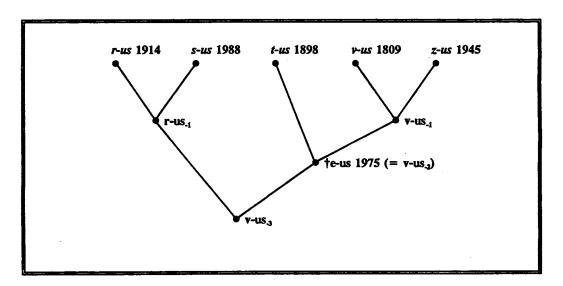


Figure 10.3. Conventions used in the new system of nomenclature for phylogenies including fossil species, based on well-preserved specimens, which are immediate ancestors of at least two morphospecies.

Let's suppose that the taxa Homo habilis, H. erectus and H. sapiens are a lineage of three eidophoronts, and that this lineage is the sistergroup of a (hypothetical) species Homo y-us (a fossil species). Let's suppose that the fossil taxa are based upon well-preserved specimens. Finally, let's suppose that their intensions are as follows:

Homo y-us = 
$$\{a, b, c\}$$
,  
Homo sapiens =  $\{a, b, d, e, f\}$ ,

Homo erectus = 
$$\{a, b, d, e\}$$
,  
Homo habilis =  $\{a, b, d\}$ .

We would therefore have the phylogeny shown in figure 10.4:

Figure 10.4 shows the conventions adopted in this case: the terminal species †*Homo y-us* and *Homo sapiens* Linnaeus, 1758 have their names written in italics; Homo erectus and Homo habilis

are both ancestral eidophoronts of *Homo sapiens* their names, therefore, are *not* written in a type different from the remainder text; as they are *not* immediate ancestors of at least two morphospecies, we indicate this fact by putting a ' $\chi$ ' before their names - this indicates that they are *chronospecies* (in the traditional sense used in palaeontology). Notice that  $\chi$ Homo erectus is a morphospecies in relation to †*Homo y-us*; the same happens with  $\chi$ Homo habilis. The valid name for the entire lineage (or clade) is, however, Homo sapiens L., 1758 (i.e., the maximal element's name), and the ancestral eidophoront of both *Homo sapiens* L., 1758 and †*Homo y-us* is Homo sapiens, Linnaeus, 1758.

As palaentologists have names, in certain cases, for fossil eidophoronts which are not immediate ancestors of two or more morphospecies, with this convention we retrieve the information and add to our knowledge the steps which led to the terminal species.

Let's now imagine that those chronospecies, due to new discoveries of fossils, became the ancestor eidophoronts of two more morphospecies. Figure 10.5 illustrates the conventions that should be used:

The classification relative to figure 10.4 would be:

- 1) Homo sapiens, L., 1758
- 2) Homo sapiens L., 1758 (⊃ χHomo erectus ⊃ χHomo habilis): †Homo y-us

The classification relative to Figure 10.5 would be the following:

- 1) Homo sapiens, Linnaeus, 1758
- 2) Homo sapiens. Linnaeus, 1758 (= †Homo habilis): †Homo y-us
- 3) Homo sapiens. Linaeus, 1758 (= †Homo erectus): †Homo w-us
- 4) Homo sapiens Linnaeus, 1758: †Homo z-us

## 10.4. Fossil species based on poorly preserved specimens

In this case, we normally have that the species presents some of the synapomorphies of a monophyletic group, but no autapomorphy. Then we include the species in the phylogeny by means of a partially interrupted line, such as shown in Figure 10.6. Its uncertain position in the phylogeny (and therefore in the classification) may be indicated by a question mark (?).

In this case the name of the fossil species of uncertain position is not taken into consideration for priority purposes.

The resulting classification will be like this:

- 1) X. d-us., 1845
- 2) X. d-us<sub>2</sub> 1845 : ? †X. a-us 1830
- 3) X. d-us<sub>1</sub> 1845 : X. b-us 1922
- 4) X. d-us 1845 : X. c-us 1931

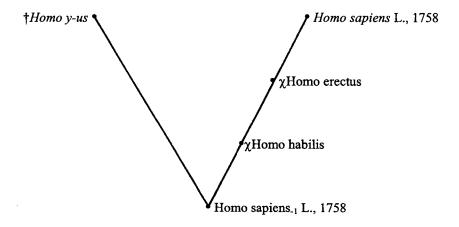


Figure 10.4. A hypothetical phylogeny of two species of *Homo*, including fossil eidophoronts which are not ancestors of two or more morphospecies, showing conventions used.

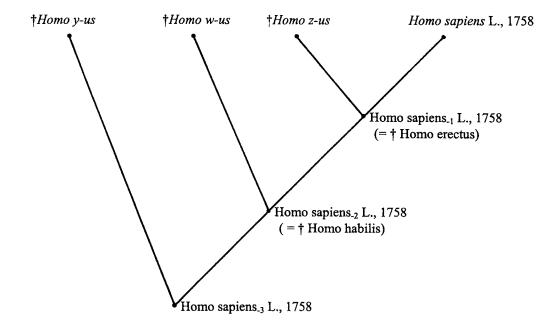


Figure 10.5. A hypothetical phylogeny of species of *Homo* including fossil eidophoronts which are ancestor of two or more morphospecies, showing conventions used.

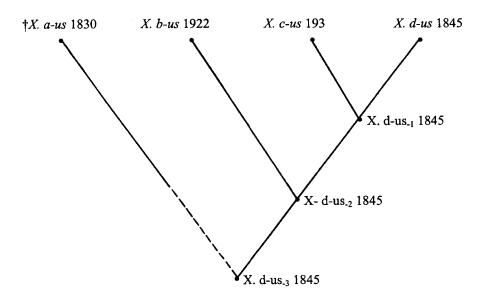


Figure 10.6. Hypothetical phylogeny including fossil species based on poorly preserved specimens, showing conventions used.

### 11. THE QUESTION OF THE 'SUBGENERA'

### 11.1. Paraphyletic 'subgenera'

Let's examine the example of Figure 11.1. Let's suppose that a-us, b-us, c-us, d-us and e-us are the species of a 'genus' A-us.

Let's suppose now that A-us is divided into two 'subgenera': a-us and b-us belonging to the nominal 'subgenus' A-us, and c-us, d-us and e-us to the 'subgenus' B-us. The 'subgenus' A-us is clearly paraphyletic, in Hennig's sense, being based solely upon symplesiomorphies, while B-us is a monophyletic P-genos.

In cases like that, the convention that must be adopted is the synonymy of the names *A-us* and *B-us*.

The same procedure is employed, of course, also in relation to the hypothetical example of Figure 11.1, if a-us and b-us belong to a 'subgenus' B-us and the remaining morphospecies to a 'subgenus' A-us.

### 11.2. Monotypic 'subgenera'

Let's take as example the phylogeny of the species of the 'genus' *Heterandria* Agassiz, 1853, such as presented by Rosen (1979), in his classical work. There the 'genus' *Heterandria* is divided into two 'subgenera':

(i) Heterandria (sensu stricto), with only one species:

Heterandria (H.) formosa Agassiz, 1853;

- (ii) Pseudoxiphophorus Bleeker, 1860, with 8 species:
- 1. Heterandria (P.) attenuata Rosen & Bailey, 1979:
- 2. Heterandria (P.) jonesi (Günther, 1866);
- 3. Heterandria (P.) litoperas Rosen & Bailey, 1979;
- 4. Heterandria (P.) obliqua Rosen, 1979;
- 5. Heterandria (P.) anzuetoi Rosen & Bailey, 1979;
- 6. Heterandria (P.) cataractae Rosen, 1979;
- 7. Heterandria (P.) dirempta Rosen, 1979;
- 8. Heterandria (P.) bimaculata (Heckel, 1848).

Our next step will be the transformation of those species in intensional sets (sets of apomorphies)

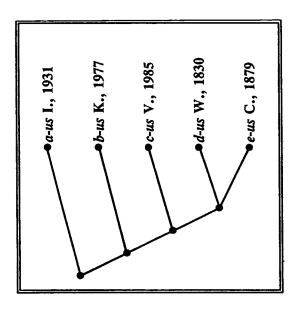


Figure 11.1. Hypothetical phylogeny of the species of the genus A-us.

(Table 11.1) - the numbers designate apomorphic characters, such as employed by Rosen (1979).

#### TABLE 11.1.

Intensions (sets of apomorphies) of the species of *Heterandria* (after Rosen, 1979)

$$formosa = \{1, 2, 3, 4, 5, 28, 29, 30, 31, 32, 33\}$$

The phylogeny results, consequently, as shown in Figure 11.2, if we take the sets of Table 11.1.

If we want to maintain the 'subgenera', the following happens:

- (i) The 'subgenus' *Pseudoxiphophorus* Bleeker, 1860, will be the non-empty intersection of the intensions of its terminal species the 8 species previously listed. Therefore, the intension of *Pseudoxiphophorus* will be the set of apomorphies {1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16};
- (ii) In order to maintain the 'subgenus' *Heterandria*, monotypic, we have to consider it as the unitary set of the intensional set of its sole species, that is, the 'subgenus' *Heterandria* will be the set

$$\{1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16\}$$
  
 $\cap \{\{1, 2, 3, 4, 5, 28, 29, 30, 31, 32, 33\}\} = \emptyset.$ 

This means that *there is no* 'genus' *Heterandria* - as it should be the *non-empty* intersection of the intensional set '*Pseudoxiphophorus*' with the intensional set 'subgenus *Heterandrid*'. Those two subgenera are, necessarily, disjunct sets!

To avoid this absurd, two solutions may be employed:

- (i) We synonymize the names of the 'subgenera' (the *praenomina Pseudoxiphophorus* Bleeker, 1860 and *Heterandria* Agassiz, 1853; and then we work normally with the method naming all the ancestral taxa (Figure 11.3) and thus obtaining the classification shown in Table 11.2.
- (ii) We maintain the *praenomina*, then obtaining the result shown in Figure 11.4 and the classification presented in Table 11.3. We are only keeping *names*, not concepts of 'subgenera'.

The decision whether to synonymize or not the names belongs to the first revisor, that is, the author who first establishes the phylogeny of the group.

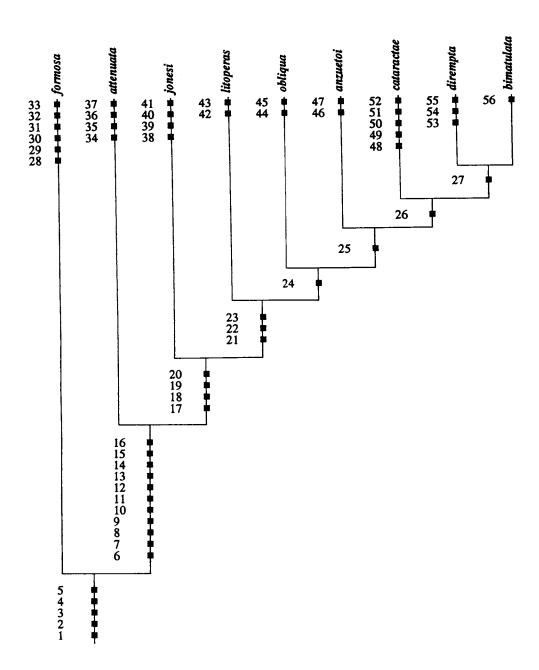


Figure 11.2. Phylogeny of the species of Heterandria (adapted from Rosen, 1979).

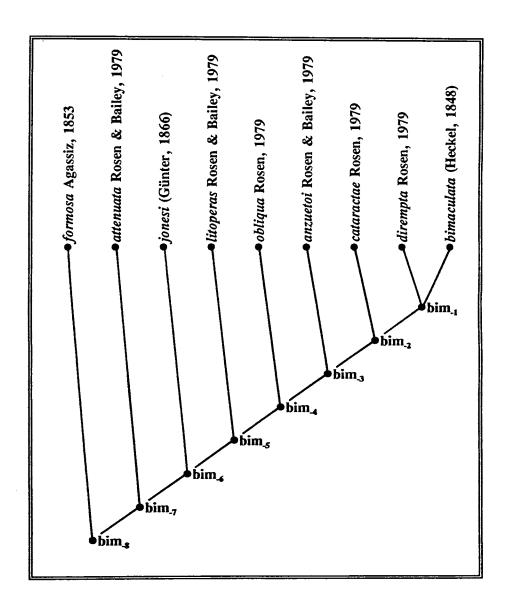


Figure 11.3. Phylogeny of the species of *Heterandria*, using the synonymy of the 'subgenera' *Heterandria* and *Pseudoxiphophorus*.

- TABLE 11.2 Classification of P-Heterandria Agassiz, 1853, with *Pseudoxiphophorus* as junior synonym of *Heterandria*
- 1) H. bimaculata, (Heckel, 1848)
- 2) H. bimaculata, (Heckel, 1848): H. formosa Agassiz, 1853
- 3) H. bimaculata<sub>6</sub> (Heckel, 1848): H. attenuata Rosen & Bailey, 1979
- 4) H. bimaculata<sub>.s</sub> (Heckel, 1848): H. jonesi (Günther, 1866)
- 5) H. bimaculata (Heckel, 1848): H. litoperas Rosen & Bailey, 1979
- 6) H. bimaculata, (Heckel, 1848): H. obliqua Rosen, 1979
- 7) H. bimaculata<sub>.2</sub> (Heckel, 1848): *H. anzuetoi* Rosen, 1979
- 8) H. bimaculata<sub>1</sub> (Heckel, 1848): H. cataractae Rosen, 1979
- 9) H. bimaculata (Heckel, 1848): H. dirempta Rosen, 1979
- TABLE 11.3. Classification of P-Heterandria Agassiz, 1853, maintaining the name of the 'subgenus' *Pseudoxiphophorus*.
- 1) Heterandria, Agassiz, 1853
- 2) Heterandria formosa Agassiz, 1853:

- Pseudoxiphophorus Bleeker, 1860 (= P. bimaculatus., (Heckel, 1848))
- 3) P. bimaculatus<sub>6</sub> (Heckel, 1848): *P. attenuatus* (Rosen & Bailey, 1979)
- 4) P. bimaculatus, (Heckel, 1848): P. jonesi (Günther, 1866)
- P. bimaculatus<sub>4</sub> (Heckel, 1848) : P. litoperas (Rosen & Bailey, 1979)
- 6) P. bimaculatus, (Heckel, 1848): P. obliquus (Rosen, 1979)
- 7) P. bimaculatus<sub>2</sub> (Heckel, 1848): *P. anzuetoi* (Rosen & Bailey, 1979)
- 8) P. bimaculatus<sub>.1</sub> (Heckel, 1848): *P. cataractae* (Rosen, 1979)
- 9) P. bimaculatus (Heckel, 1848): P. diremptus (Rosen, 1979)

### 11.3. 'Subgenera' that are P-gene

Let's finally consider the hypothetical case of Figure 11.5. Let's suppose it represents the phylogeny of the species of a 'genus' M-us, divided into three 'subgenera': (i) M-us sensu stricto, with the species m-us, n-us, o-us, p-us and q-us; (ii) N-us, with the species r-us and s-us; (iii) O-us, with the species t-us, u-us, v-us and x-us.

As each one of those 'subgenera' constitutes a monophyletic P-genos, we keep the *praenomina* and work with the system as seen, naming the ancestral taxa. The result is shown in Figure 11.5.

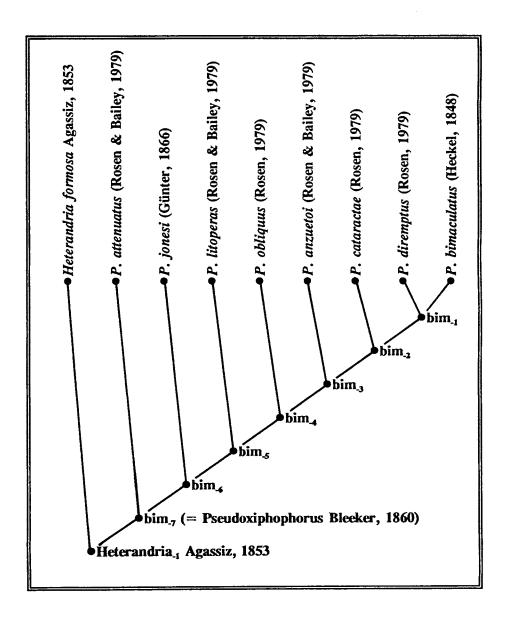


Figure 11.4. Phylogeny of the species of *Heterandria*, without the synonymy of the 'subgenera' *Heterandria* and *Pseudoxiphophorus*.

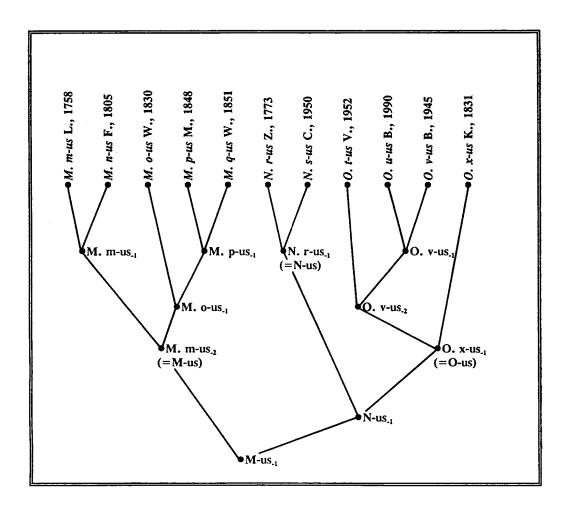


Figure 11.5. Conventions used for phylogenies with 'subgenera' that are P-gene.

# 12. ON THE STABILITY OF NOMENCLATURE, OR, WHAT HAPPENS WHEN A PHYLOGENY CHANGES?

A few preliminary considerations are necessary in order to discuss what happens, within our new system of nomenclature, when different phylogenies are proposed for the "same" P-genos.

Let's begin by defining what should be understood by 'stability of (biological) nomenclature'. If we denote by T the set of all species (including eidophoronts) and by N the set of 'scientific' names, let be a function  $f_c: T \to N$  such that  $f_c$  is a bijective function (i.e., both injective and surjective). The function  $f_c$  is what is commonly called 'the

stability of nomenclature'. In other words, each species must have only one name, and each name must denote only one species (a one-to-one correspondence). This means that, given two different species (or eidophoronts), each must have a different name; conversely, we should never apply two or more different names to the same (and only one) concept (species or eidophoront).

In second place, let's consider what happens when we take species from the old (traditional) taxonomy and transform them into Hennigian species. We are actually reinterpreting the whole thing, as the underlying ontologies (of the traditional taxonomy and of Phylogenetic Systematics) are different. *Musca domestica* was one thing to Linnaeus in 1758, and is

an entirely different concept when we (let's suppose) do the phylogeny of the 'species of the genus Musca'. Linnaeus was employing unchangeable 'essences' to define what he called 'Musca domestica'; we are employing apomorphies. Rigorously, phylogeneticists should employ a different name for their new concept of 'Musca domestica'. We traditionally baptize, however, with the same name, an essencialist class and an evolutionary species! In this case, we are giving the same ontological value to 'essences' and 'apomorphies', which is (one more) absurd. But let's accept that as a fatality of the historical development of taxonomy.

Let's consider next the situation within Phylogenetic Systematics. If two morphospecies exist (and then they are non-comparable, intensionally speaking), they should of course receive two different names. If two eidophoronts exist (and then one of them will be, intensionally speaking, a proper part of the other), this indicates that one precedes the other in time (is the 'ancestor' of the other) and, also in this case, should receive different names.

One more consideration: when we take a name (a binomen), for intance, *Musca domestica* Linnaeus, 1758, defined in an essencialist way, and reinterpret it at the light of Phylogenetic

Systematics, we end up with an entirely new concept. To avoid the absurdity of considering as equivalent 'essences' and 'apomorphies', we should use the following device: using, for instance, the formula Musca domestica Linnaeus, 1758 sensu X., 1980 (or, abbreviately, Musca domestica Linnaeus, 1758 s. X., 1980), where 'X., 1980' refers to the author (and his paper) who reinterpreted Linnaeus' essencialist concept at the light of Phylogenetic Systematics. It goes without saying that two different authors may reinterpret the same traditional concept in different ways (as different sets of apomorphies which, notwithstanding, will have a non-empty intersection). In this case, we could have, for instance, Musca domestica Linnaeus, 1758 s. X., 1980, and Musca domestica Linnaeus, 1758 s. Y., 1985.

In the sequence we will demonstrate that our new system of nomenclature, using the above devices, insures, in a very rigorous way, the desideratum of 'the stability of nomenclature'.

Let's illustrate this by an example. Let's consider the phylogeny of P-Heterandria Agassiz, 1853 (*sensu* Rosen, 1979), as shown in our Figure 11.2. The intensions of all the elements (species and eidophoronts) of this P-genos is given in Table 12.1:

TABLE 12.1. Intensions of the species and eidophoronts of P-Heterandria Agassiz, 1853 (according to Rosen, 1979)

```
1) H. bimaculata-, (Heckel, 1848) s. Rosen, 1979 = {1, 2, 3, 4, 5}
2) H. formosa Agassiz, 1853 s. Rosen, 1979 = {1, 2, 3, 4, 5, 28, 29, 30, 31, 32, 33}
3) H. bimaculata-, (Heckel, 1848) s. Rosen, 1979 = {1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16}
4) H. attenuata Rosen & "Bailey, 1979 = {1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 34, 35, 36, 37}
5) H. bimaculata-, (Heckel, 1848) s. Rosen, 1979 = {1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20}
6) H. jonesi (Günther, 1866) s. Rosen, 1979 = {1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 38, 39, 40, 41}
7) H. bimaculata-, (Heckel, 1848) s. Rosen, 1979 = {1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21, 22, 23}
8) H. litoperas Rosen & Bailey, 1979 = {1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21, 22, 23, 42, 43}
9) H. bimaculata-, (Heckel, 1848) s. Rosen, 1979 = {1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21, 22, 23, 24}
10) H. obliqua Rosen, 1979 = {1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21, 22, 23, 24, 44, 45}
11) H. bimaculata-3 (Heckel, 1848) s. Rosen, 1979 = {1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21, 22, 23, 24, 25}
12) H. anzuetoi Rosen, 1979 = {1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21, 22, 23, 24, 25, 46, 47}
14) H. cataractae Rosen, 1979 = {1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21, 22, 23, 24, 25, 26, 48, 49, 50, 51, 52}
15) H. bimaculata-1 (Heckel, 1848) s. Rosen, 1979 = {1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21, 22, 23, 24, 25, 26, 27}
16) H. dirempta Rosen, 1979 = {1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21, 22, 23, 24, 25, 26, 27, 53, 54, 55}
17) H. bimaculata (Heckel, 1848) s. Rosen, 1979 = {1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21, 22, 23, 24, 25, 26, 27, 56}
```

There is a one-to-one correspondence between taxa (be them morphospecies or eidophoronts) and names.

The classification results as shown in Table 12.2:

### **TABLE 12.2**

Classification of P-Heterandria Agassiz, 1853 sensu Rosen, 1979

- 1) H. bimaculata, (Heckel, 1848) s. Rosen, 1979
- 2) H. bimaculata, (Heckel, 1848) s. Rosen, 1979: H. formosa Agassiz, 1853 s. Rosen 1979
- 3) H. bimaculata (Heckel, 1848) s. Rosen, 1979: H. attenuata Rosen & Bailey, 1979
- 4) H. bimacualta (Heckel, 1848) s. Rosen, 1979: H. jonesi (Günther, 1866) s. Rosen, 1979

- 5) H. bimaculata (Heckel, 1848) s. Rosen, 1979: H litoperas Rosen & Bailey, 1979
- 6) H. bimaculata, (Heckel, 1848) s. Rosen, 1979: H. obliqua Rosen, 1979
- 7) H. bimaculata, (Heckel, 1848) s. Rosen, 1979: H. anzuetoi Rosen, 1979
- 8) H. bimaculata, (Heckel, 1848) s. Rosen, 1979: H. cataractae Rosen 1979
- 9) H. bimaculata (Heckel, 1848) s. Rosen, 1979: H. dirempta Rosen, 1979

Let's suppose now that the author G, in 1993, introduces two new species in this group, and proposes the phylogeny shown in Figure 12.1 Let's suppose that the intensions of the species and eidophoronts of this P-genos are as shown in Table 12.3:

TABLE 12.3. Intensions of the species and eidophoronts of P-Heterandria Agassiz, 1853 (according to G., 1993)

- 1) H. bimaculata-10 (Heckel, 1848) s. G., 1993 = {1, 2, 3, 4, 5}
- 2) H. formosa Agassiz, 1853 s. Rosen, 1979 = {1, 2, 3, 4, 5, 28, 29, 30, 31, 32, 33}
- 3) H. bimaculata-<sub>9</sub> (Heckel, 1848) s. G., 1993 = {1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16}
- 4) H. x-ana G., 1993 = {1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 57}
- 5) H. bimaculata-, (Heckel, 1848) s. G., 1993 = {1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 58}
- 6) H. attenuata Rosen & Bailey, 1979 s. G., 1993 = {1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 34, 35, 36, 37, 58}
- 7) H. bimaculata-, (Heckel, 1848) s. G., 1993 = {1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 58}
- 8) H. jonesi (Günther, 1866) s. G., 1993 = {1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 38, 39, 40, 41, 58}
- 9) H. bimaculata-, (Heckel, 1848) s. G., 1993 = {1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21, 22, 23, 58}
- 10) H. litoperas Rosen & Bailey, 1979 s. G., 1993 = {1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21, 22, 23, 42, 43, 58}
- 11) H. bimaculata-, (Heckel, 1848) s. G., 1993 = {1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21, 22, 23, 24, 58}
- 12) H. obliqua Rosen, 1979 s. G., 1993 = {1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21, 22, 23, 24, 44, 45, 58}
- 13) H. bimaculata-, Rosen, 1979 s. G., 1993 = {1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21, 22, 23, 24, 25, 58}
- $14) \ H. \ anzuetoi \ Rosen, 1979 \ s. \ G., 1993 = \{1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21, 22, 23, 24, 25, 46, 47, 58\}$
- 15) H. bimaculata-, (Heckel, 1848) s. G., 1993 = {1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21, 22, 23, 24, 25, 58, 59}
- 16) H. y-ana G., 1993 = {1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21, 22, 23, 24, 25, 58, 59, 60}
- 17) H. bimaculata-2 (Heckel, 1848) s. G., 1993 = {1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21, 22, 23, 24, 25, 26, 58, 59, 60}
- 18) H. cataractae Rosen, 1979 s. G., 1993 = {1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21, 22, 23, 24, 25, 26, 48, 49, 50, 51, 52, 58, 59, 60}
- 19) H. bimaculata-, (Heckel, 1848) s. G., 1993 = {1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21, 22, 23, 24, 25, 26, 27, 58, 59, 60}
- 20) H. dirempta Rosen, 1979 s. G., 1993 = {1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21, 22, 23, 24, 25, 26, 27, 53, 54, 55, 58, 59, 60}
- 21) H. bimaculata (Heckel, 1858) s. G., 1993 = {1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21, 22, 23, 24, 25, 26, 27, 56, 58, 59, 60}

Comparing Tables 12.1 and 12.3 we notice that:

- H. bimaculata<sub>.8</sub> (Heckel, 1848) s. Rosen, 1979 and H. bimaculata<sub>.10</sub> (Heckel, 1848) s. G., 1993 are synonyms. The valid name will be H. bimaculata<sub>.10</sub> (Heckel, 1848) s. G., 1993, if G.'s hypothesis is accepted.
- H. formosa Agassiz s. Rosen, 1979 and H. formosa Agassiz s. G., 1993 are synonyms (as they have the same intension). In this case, in G.'s system (1993) we indicate this by writing: H. formosa Agassiz, 1853 s. Rosen, 1979 and G., 1993.
- 3. H. bimaculata, (Heckel, 1848) s. Rosen, 1979 and H. bimaculata, (Heckel, 1848) s. G., 1993 are synonyms. The valid name will be H. bimaculata, (Heckel, 1848) s. G., 1993 (= H. bimaculata, (Heckel, 1848) s. Rosen, 1979).
- H. attenuata Rosen & Bailey, 1979 is not a synonym of H. attenuata Rosen & Bailey, 1979 s. G., 1993. Notice that the former is an eidophoront in relation to the latter (intensionally, it is a proper part of the latter).
- H. bimaculata<sub>.6</sub> (Heckel, 1848) s. Rosen, 1979 is an eidophoront in relation to H. bimaculata<sub>.7</sub> (Heckel, 1848) s. G., 1993 (and therefore not a synonym).
- 6. H. jonesi (Günther, 1866) s. Rosen, 1979 is an eidophoront in relation to H. jonesi (Günther, 1866) s. G., 1993 (and, therefore not a synonym).
- H. bimaculata<sub>s</sub> (Heckel, 1848) s. Rosen, 1979 is an eidophoront in relation to H. bimaculata<sub>s</sub> (Heckel, 1848) s. G., 1993.
- H. litoperas Rosen & Bailey, 1979 is an eidophoront in relation of H. litoperas Rosen & Bailey, 1979 s. G., 1993.
- H. bimaculata, (Heckel, 1848) s. Rosen 1979, is an eidophoront in relation to H. bimaculata, (Heckel, 1848) s. G., 1993.

- 10. H. obliqua Rosen, 1979 is an eidophoront in relation to H. obliqua Rosen, 1979 s. G., 1993.
- 11. H. bimaculata, (Heckel, 1848) s. Rosen, 1979 is an eidophoront in relation to H. bimaculata, (Heckel, 1848) s. G., 1993.
- 12. *H. anzuetoi* Rosen, 1979 is an eidophoront in relation to *H. anzuetoi* Rosen, 1979 s. G., 1993.
- H. bimaculata<sub>2</sub> (Heckel, 1848) s. Rosen, 1970 is an eidophoront in relation to H. bimaculata<sub>2</sub> (Heckel, 1848) s. G., 1993. Notice that, although both names have the same negative subindex, they refer to different concepts.
- H. cataractae Rosen, 1979 is an eidophoront in relation to H. cataractae Rosen, 1979 s. G., 1993.
- 15. H. bimaculata (Hecekl, 1848) s. Rosen, 1979 is an *eidophoront* in relation to H. bimaculata (Heckel, 1848) s. G., 1993. The same remark made above (13) applies to this case.
- H. dirempta Rosen, 1979 is an eidophoront in relation to H. dirempta Rosen, 1979 s. G., 1993.
- 17. H. bimaculata (Heckel, 1848) s. Rosen, 1979 is an eidophoront in relation to H. bimaculata (Heckel, 1848) s. G., 1993.

Therefore, in this (hypothetical) case of alteration in a phylogeny, only two cases of synonymy occur. Each of the other names apply univocally to a different taxon.

Notice that in G.'s phylogeny we can include Rosen's phylogeny, since it is a proper subsystem of the first. Our new method of nomenclature presents also this advantage: in certain cases, from one (more recent) phylogeny, we may retrieve another (previous) phylogeny. Figure 12.3 illustrates how this can be done, and the resulting classification is given in Table 12.4.

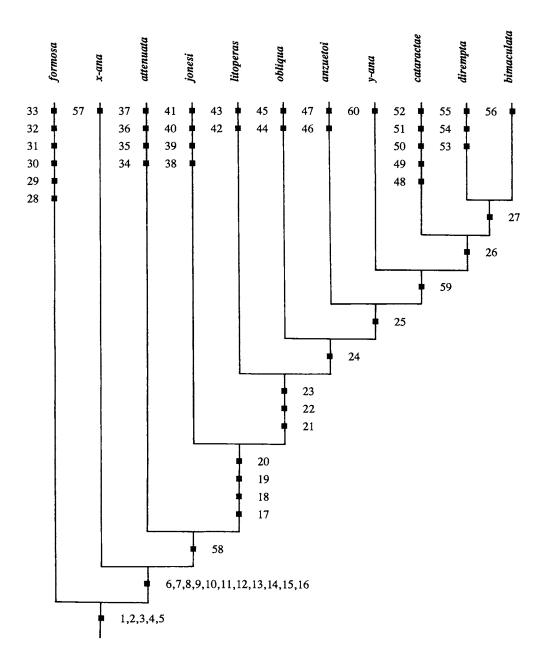


Figure 12.1. Hypothetical phylogeny of the species of Heterandria, according to a ficticious author G., 1993.

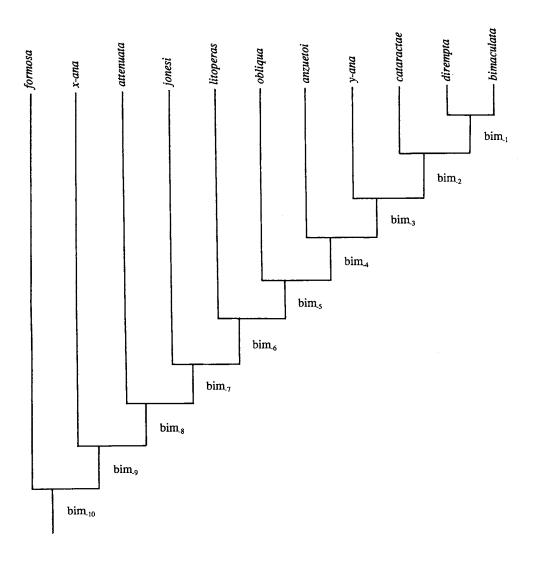


Figure 12.2. Phylogeny of the species of Heterandria according to G., 1993, with all the ancestral eidophoronts named.

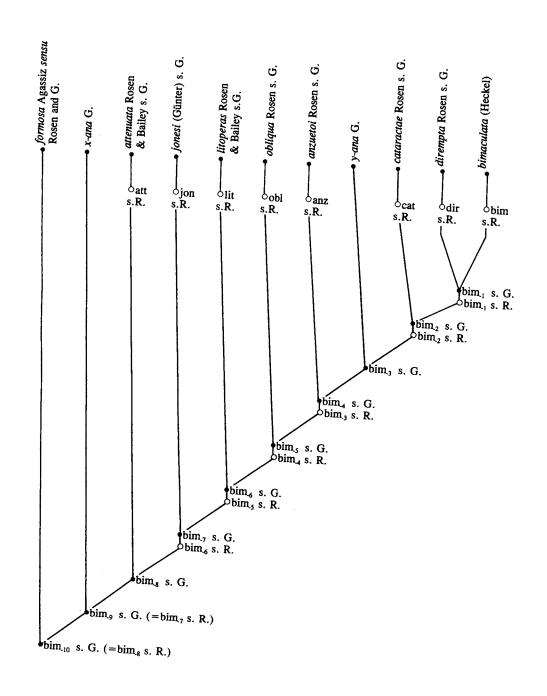


Figure 12.3. Rosen's (1979) phylogeny of the species of *Heterandria* included in G's (1993) phylogeny of the same group with two additional species.

## TABLE 12.4. Classification of P-Heterandria Agassiz, 1853 sensu G., 1993 (⊃ sensu Rosen, 1979)

- 1) H. bimaculata, (Heckel, 1848) s. G., 1993 (= H. bimaculata, (Heckel, 1848) s. Rosen 1979)
- H. bimaculata, (Heckel, 1848) s. G., 1993 (= H. bimaculata, (Heckel, 1848) s. Rosen, 1979): H. formosa Agassiz, 1853 sensu Rosen, 1979 and G., 1993
- 3) H. bimaculata, (Heckel, 1848) s. G., 1993: H. x-ana G., 1993
- H. bimaculata, (Heckel, 1848) s. G., 1993 (

   — H. bimaculata, (Heckel, 1848) s. Rosen, 1979): H. attenuata Rosen & Bailey, 1979 s. G., 1993 (

   — H. attenuata Rosen & Bailey, 1979).
- H. bimaculata, (Heckel, 1848) s. G., 1993 (

  H. bimaculata, (Heckel, 1848) s. Rosen, 1979): H. jonesi (Günther, 1866) s. G., 1993 (

  H. jonesi (Günther, 1866) s. Rosen 1979)
- H. bimaculata, (Heckel, 1848) s. G., 1993 (

   — H. bimaculata, (Heckel, 1848) s. Rosen, 1979): H. litoperas Rosen & Bailey, 1979 s. G., 1993 (

   — H. litoperas Rosen & Bailey, 1979)
- H. bimaculata, (Heckel, 1848) s. G., 1993 (
   H. bimaculata, (Heckel, 1848) s. Rosen, 1979): H. obliqua Rosen, 1979 s. G., 1993 (
   H. obliqua Rosen, 1979)
- 8) H. bimaculata, (Heckel, 1848) s. G., 1993: H. anzuetoi Rosen, 1979 s. G., 1993 (

  H. anzuetoi Rosen, 1979)
- 9) H. bimaculata, (Heckel, 1848) s. G., 1993 (

  H. bimaculata (Heckel, 1848) s. Rosen, 1979): H. y-ana G., 1993
- H. bimaculata, (Heckel, 1848) s. G., 1993 (

   — H. bimaculata (Heckel, 1848) s. Rosen, 1979): H. cataractae Rosen, 1979 s. G., 1993 (

   — H. cataractae Rosen, 1979)
- 11) H. bimaculata (Heckel, 1848) s. G., 1993 (

  H. bimaculata (Heckel, 1848) s. Rosen, 1979): H. dirempta Rosen, 1979 s. G., 1993 (

  H. dirempta Rosen, 1979).

Let's now consider some other cases.

A. Two or more different phylogenies for the same C-genos, occasioned by the occurrence of homoplasies

Let's imagine that W., 1980, found two possible phylogenies for the same C-genos, as illustrated in Figure 12.4:

 $C_{.1}$  L., 1758 s. W., 1980 (version 1) is neither a synonym nor a homonym of  $C_{.1}$  L., 1758 s. W., 1980 (version 2).  $C_{.1}$  L., 1859 s. W., 1980 (version 2) = {3, 4}, whereas  $C_{.1}$  L., 1758 s. W., 1980 (version 1) = {9, 10, 11, 12, 13, 14, 15}. Different taxa must have different names (version 1 is different from version 2).

On the other hand, C<sub>.2</sub> L., 1758 s. W., 1980 (version 1) is a synonym of C<sub>.2</sub> L., 1758 s. W., 1980 (version 2) and should be synonymized. We could write, for instance, C<sub>.2</sub> L., 1758 s. W., 1980 (version 1 = version 2).

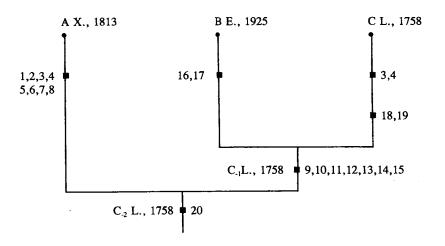
### B. Resolution of a polytomy

Let's imagine that X (1978) published the following phylogeny (Figure 12.5):

Then S. (1985) restudied the group and resolved the polytomy, with the discovery of new apomorphies, presenting the following phylogeny (Figure 12.6):

It is obvious that A<sub>1</sub> s. S., 1985 differs from A<sub>2</sub> s. X., 1978; A<sub>2</sub> s. S., 1985 is different from A<sub>2</sub> s. X., 1978; A<sub>3</sub> s. S., 1985 is a synonym of A<sub>4</sub> s. X., 1978; A<sub>4</sub> s. S., 1985 is a synonym of A<sub>2</sub> s. X., 1978. If S., 1985's hypothesis is valid then X.'s 1978 classification can also be included in S.'s 1985 classification, as was done above in the case of *Heterandria*. The classification of this group will be:

- 1) A<sub>4</sub> s. S., 1985 (= A<sub>.</sub>, s. X., 1978)
- 2) A<sub>.3</sub> s. S., 1985 (= A<sub>.1</sub> s. X., 1978) : E s. X., 1978 and S., 1985
- 3) A, s. S., 1985 : B s. X., 1978 and S., 1985
- 4) A<sub>1</sub> s. S., 1985 : C s. S., 1985 (⊃ C s. X., 1978)
- 5) A s. S., 1985 (⊃ A s. X., 1978) : D s. S., 1985 (⊃ D s. X., 1978).



version 1

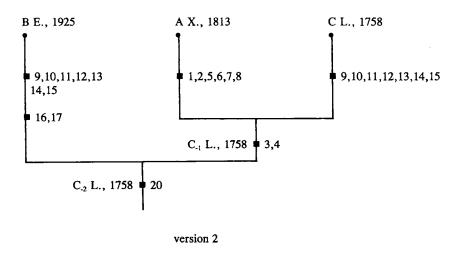


Figure 12.4. Two possible phylogenies of the same group, due to the presence of homoplasies.

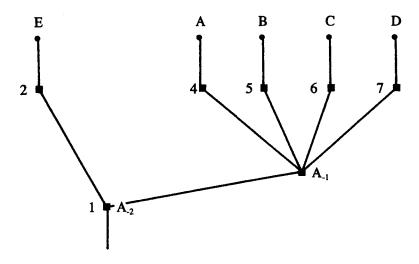


Figure 12.5. Hypothetical phylogeny of the group A-us published by X (1978).

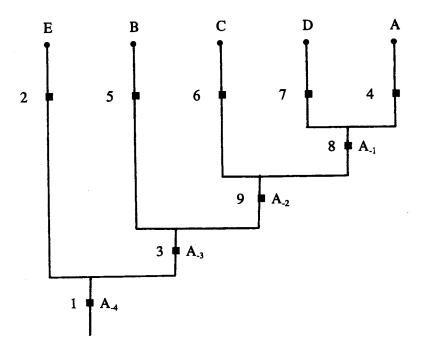


Figure 12.6. Hypothetical phylogeny of the group A-us published by S. (1985).

### APPENDIX I

### LIST OF THE ZOOLOGICAL LINNAEAN PRAENOMINA BY ORDER OF PRIORITY (LINNAEUS, 1758. SYST. NAT. ED. X)

Psophia: 154a Otis: 154b

(Mammalia)	Falco: 88			
(	Strix: 92			
Homo: 20	Lanius: 93			
Simia: 25	Psittacus: 96			
Lemur: 29	Ramphastos: 103			
Vespertilio: 31	Buceros: 104			
Elephas: 33	Crotophaga: 105a			
Trichechus: 34a	Corvus: 105b			
Bradypus: 34b	Coracias: 107			
Myrmecophaga: 35	Gracula: 108			
Manis: 36	Paradisaea: 110a			
Phoca: 37	Cuculus: 110b			
Canis: 38	<i>Jynx</i> : 112a			
Felis: 41	Picus: 112b			
Viverra: 43	Sitta: 115a			
Mustela: 45	Alcedo: 115b			
Ursus: 47	Merops: 117a			
Sus: 49	<i>Upupa</i> : 117b			
Dasypus: 50	Certha: 118			
Erinaceus: 52a	Trochilus: 119			
Talpa: 52b	Anas: 122			
Sorex: 53	Mergus: 129			
Didelphis: 54	Alca: 130			
Rhinoceros: 56a	Procellaria: 131			
Hystrix: 56b	Diomedea: 132a			
Lepus: 57	Pelecanus: 132b			
Castor: 58	Phaeton: 134			
Mus: 59 Colymbus: 135				
Sciurus: 63	<i>Larus</i> : 136			
Camelus: 65	Sterna: 137			
Moschus: 66a	Ryncops: 138			
Cervus: 66b	Phoenicopterus: 139a			
Capra: 68	Platalea: 139b			
Ovis: 70	Mycteria: 140a			
Bos: 71	Tantalus: 140b			
Equus: 73 Ardea: 141				
Hippopotamus: 74	Scolopax: 145			
Monodon: 75a	Tringa: 148			
Balaena: 75b	Charadrius: 150			
Physeter: 76	Recurvirostra: 151			
Delphinus: 77	Haematopotus: 152a			
-	Fulica: 152b			
(Aves)	Rallus: 153			
` '	Psophia: 154a			

Vultur: 86

Struthio: 155 Pavo: 156a Meleagris: 156b Crax: 157 Phasianus: 158 Tetrao: 159 Columba: 162 Alauda: 165 Sternus: 167 Turdus: 168 Loxia: 171 Emberiza: 176 Fringilla: 179 Motacilla: 184 Parus: 189 Hirundo: 191 Caprimulgus: 193

### (Reptilia)

Testudo: 197

Draco: 199 Lacerta: 200 Rana: 210 Crotalus: 214 Coluber: 216 Anguis: 227 Amphisbaena: 229a Caecilia: 229b

### (Pisces)

Petromyzon: 230 Raja: 231 Squalus: 233 Chimaera: 236a Lophius: 236b Acipenser: 237 Muraena: 244 Gymnotus: 246a Trichiurus: 246b Anarhichas: 247 Ammodytes: 247 Stromateus: 248a Xiphias: 248b Callionymus: 249 Uranoscopus: 250a Trachinus: 250b Gadus: 251 Blennius: 256

Ophidion: 259 Cyclopterus: 260a Echeneis: 260b Coryphaena: 261 Gobius: 262 Cottus: 264 Scorpaena: 266a Zeus: 266b Pleuronectes: 268 Chaetodon: 272 Sparus: 277 Labrus: 282 Sciaena: 288 Perca: 289 Gasterosteus: 295 Scomber: 297 Mullus: 299 Trigla: 300 Cobitis: 303 Silurus: 304 Loricaria: 307 Salmo: 308 Fistularia: 312 Esox: 313 Argentina: 315a Atherina: 315b

Mugil: 316a
Exocoetus: 316b
Polynemus: 317a
Clupea: 317b
Cyprinus: 320
Mormyrus: 327a
Balistes: 327b
Ostracion: 330
Tetraodon: 332
Diodon: 334
Centriscus: 336a
Syngnathus: 336b

### (Insecta)

Pegasus: 338

Scarabaeus: 345 Dermestes: 354 Hister: 358 Silpha: 359 Cassida: 362 Coccinella: 364 Chrysomela: 368 Curculio: 377 Attelabus: 387 Cerambyx: 388 Leptura: 397 Cantharis: 400 Elater: 404 Cicindela: 407 Buprestis: 408 Dytiscus: 411

Carabus: 413 Tenebrio: 417 Meloe: 419 Mordella: 420 Necydalis: 421a Staphylinus: 421b Forficula: 423 Blatta: 424 Gryllus: 425a Mantis: 425b Acrida: 427a Bulla: 427b Acheta: 428 Tettigonia: 429 Locusta: 431 Cicada: 434 Notonecta: 439 Nepa: 440 Cimex: 441 Aphis: 451 Chermes:453 Coccus: 455 Thrips: 457 Papilio: 458 Sphinx: 489 Phalaena: 495 Libellula: 543 Ephemera: 546 Phryganea: 547 Hemerobius: 549 Panorpa: 551 Raphidia: 552 Cynips: 553 Tenthredo: 555 Ichneumon: 560 Sphex: 569 Vespa: 572 Apis: 574 Formica: 579 Mutilla: 582 Oestrus: 584 Tipula: 585 Musca: 589 Tabanus: 601 Culex: 602 Empis: 603 Conops: 604 Asilus: 605 Bombylius: 606 Hippóbosca: 607 Lepisma: 608a Podura: 608b Termes: 609 Pediculus: 610 Pulex: 614 Acarus: 615 Phalangium: 618 Aranea: 619 Scorpio: 624 Cancer: 625

Monoculus: 634

Oniscus: 636 Scolopendra: 637 Julus: 639

### (Vermes)

Gordius: 647a Furia: 647b Lumbricus: 647c Ascaris: 648a Fasciola: 648b Hirudo: 649 Myxine: 650 Teredo: 651 Limax: 652 Doris: 653a Tethys: 653b Nereis: 654 Aphrodita: 655a Lernaea: 655b Priapus: 656a Scyllaea: 656b Holothuria: 657 Triton: 658a Sepia: 658b Medusa: 659 Asterias: 661 Echinus: 663 Chiton: 667a Lepas: 667b Pholas: 669 Mya: 670 Solen: 672 Tellina: 674 Cardium: 678 Donax: 682 Venus: 684 Spondylus: 690 Chama: 691 Arca: 693 Ostrea: 696 Anomia: 700 Mytilus: 704 Pinna: 707 Argonauta: 708 Nautilus: 709 Conus: 712 Cypraea: 718 Bula: 725 Voluta: 729 Buccinum: 734 Strombus: 742 Murex: 746 Trochus: 756 Turbo: 761 Helix: 768 Nerita: 776 Haliotis: 779 Patella: 780 Dentalium: 785 Serpula: 786

Tubipora: 789 Millepora: 790 Madrepora: 793 Isis: 799 Gorgonia: 800 Alcyonium: 803a Tubularia: 803b Eschara: 804 Corallina: 805 Sertullaria: 807 Hydra: 816 Pennatula: 818 Taenia: 819 Volvox: 820

### APPENDIX II.

LIST OF THE ZOOLOGICAL LINNAEAN *PRAENOMINA* ALPHABETICALLY ARRANGED (LINNAEUS, 1758. SYST. NAT. ED. X).

Acarus: 615

Acheta: 428

Acipenser: 237

Acrida: 427a

Alauda: 165

Buceros: 104

Bula: 725

Bulla: 427b

Buprestis: 408

Alca: 130

Alca: 130

Alcado: 115b

Alcyonium: 803a

Ammodytes: 247

Amphisbaena: 229a

Anarhichas: 247

Caecilia: 229b

Callionymus: 249

Camelus: 65

Cancer: 625

Canis: 38

Cantharis: 400

 Anas: 122
 Capra: 68

 Anguis: 227
 Caprimulgus: 193

 Anomia: 700
 Carabus: 413

 Aphis: 451
 Cardium: 678

 Aphrodita: 655a
 Cassida: 362

 Apis: 574
 Castor: 58

 Aranea: 619
 Centriscus: 336a

 Aranea. 619
 Centricus. 336a

 Arca: 693
 Cerambyx: 388

 Ardea: 141
 Certha: 118

 Argentina: 315a
 Cervus: 66b

 Argonauta: 708
 Chaetodon: 272

 Ascaris: 648a
 Chama: 691

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