

Plant Nomenclature and Taxonomy

An Horticultural and Agronomic Perspective

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I. INTRODUCTION

Now the whole world had one language and a common speech. Then they said, "Come, let us build ourselves a city, with a tower that reaches to the heavens, so that we may make a name for ourselves and not be scattered over the face of the whole earth." The Lord said, "Come, let us go down and confuse their language so they will not understand each other." So the Lord scattered them from there over all the earth, and they stopped building the city. That is why it was called Babel because there the Lord confused the language of the whole world.

(Genesis 11:1, 3, 4, 6-9; New International Bible)

Communication of taxonomists to agronomists and horticulturists can be hindered by specialized terminology that aids concise and effective communication of complex ideas among taxonomists, but may seem intractable and pedantic to agriculturalists. Our goals in this review are to provide agronomists and horticulturists basic conceptual tools of taxonomy: (1) to help understand the taxonomic classification in wild and cultivated plants; (2) to question whether the concept underlying this

taxonomy is appropriate; (3) to help understand why new data may require changes in nomenclature; and (4) place the taxonomy of crops in the context of legal requirements that depend on a taxonomic name. Different taxonomic concepts of wild plants and cultivated plants are reviewed because both classes are used in breeding and germplasm evaluation.

The goals and practices of two codes of plant nomenclature, the International Code of Botanical Nomenclature (ICBN) and the International Code of Nomenclature for Cultivated Plants (ICNCP) are compared, the former (Greuter et al. 2000) used primarily for wild plants, and the latter (Trehane et al. 1995) used exclusively for cultivated plants. The plethora of specialized terms used in this review is presented as a glossary in Table 1.1.

Table 1.1 Glossary of terms used highlighted in **bold italic** in the text.

artificial classification. Classification that may be based on any special-purpose criteria that users view as relevant to group plants, not based on evolutionary relationships (see **natural classification**).

basionym. The original name of a taxon, which may be changed in rank, say from variety to species. For example, when *Solanum jamesii* Bitter var. *brachistotrichium* Bitter was recognized as a species, its name became *Solanum brachistotrichium* (Bitter) Rydb., but the basionym remains *Solanum jamesii* Bitter var. *brachistotrichium* Bitter.

biological species concept. The concept of a species as a population or group of populations that freely interbreed but are reproductively isolated from other populations.

biosystematics. A term that originally referred to the use of breeding programs (by biosystematists) to infer evolutionary relationships among organisms; the term later became broadened to refer to a wide variety of experimental data gathering programs.

cenospecies. Assemblages of related ecospecies that when crossed produce highly to completely sterile hybrids.

cladogram. A branching phylogenetic tree of individuals or taxa, rooted on an outgroup(s) produced by a method that minimizes evolutionary changes (by parsimony, maximum likelihood, or other methods) of characters believed to be homologous among a group of organisms.

cladistic species concepts. A philosophy and set of methods that use cladistic criteria to determine the limits of species.

closed classification system. Hierarchical system where the categories at every rank are totally filled up by the sum of the categories at the next lower rank.

comparium. A group of related cenospecies that cannot be crossed with one another.

ecological species concepts. A philosophy that ecological factors are primary in forming and maintaining a species.

(continues)

Table 1.1 (continued)

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- compilospecies.** Genetically aggressive, highly polymorphic species, often of complex hybrid origin, often containing more than one ploidy level, often very weedy, and obscuring other species boundaries.
- conservation.** In order to avoid disadvantageous changes in the nomenclature of families, genera, and species entailed by the strict application of nomenclatural rules, and especially of the principle of priority, names may be retained as legitimate even though initially they may have been illegitimate, by petitioning in the journal *Taxon*, and later vote at the International Botanical Congress. Conservation operates only within the taxa in which they have been voted upon, and is not operative if the taxon is classified in another group.
- convariety (convar).** A group of cultivars. These can be roughly comparable to cultivar groups, but convarieties, unlike cultivar groups, do not necessarily contain named varieties, and convarieties are members of traditional “Linnaean” ranks. The ICNCP replaced this term with the term cultivar-group, and convarieties should not be used in modern cultivated plant taxonomy.
- crop.** The total of all cultivars/cultivar-groups that constitute an agricultural, horticultural, or silvicultural product; examples: potato, cabbage, or tulips.
- cytodemes.** Groups of plants characterized by having a constant chromosome number, with all accessions of the same cytodeme being fully interfertile, while those of different cytodemes are essentially cross-sterile.
- cultigen.** A taxon with only cultivated representatives; example: *Triticum aestivum*, the species name encompassing all hexaploid wheat varieties.
- cultivar.** A systematic group of cultivated plants that is clearly distinct, uniform, and stable in its characteristics and which, when propagated by appropriate means, retains these characteristics.
- cultivar-group.** A group of properly named cultivars, based on one or more criteria.
- cultivated plant.** One whose origin or selection is primarily due to the intentional activities of mankind. Such a plant may arise either by deliberate or, in cultivation, accidental hybridization, or by selection from existing cultivated stock, or may be a selection from minor variants within a wild population and maintained as a recognizable entity solely by deliberate and continuous propagation (Trehane et al. 1995).
- culton.** A systematic group of cultivated plants; there are two types of culta: the cultivar and the cultivar-group.
- cultonomy.** Cultonomy is the entire body of principles, philosophies, and methodologies leading to classifications of cultivated plants into culta, and following the rules of ICNCP.
- dendrogram.** A branching diagrammatic representation of a set of individuals or taxa, constructed from overall similarity of a set of characters among organisms, which generally is not provided any phylogenetic interpretation.
- denomination class.** Agreed upon systematic group (often a genus) within which a cultivar epithet may only be used once.

1. PLANT NOMENCLATURE AND TAXONOMY

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Table 1.1 (continued)

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- eclectic species concepts.** A philosophy that species are defined, formed, and maintained by a variety of biological factors, including morphological, interbreeding, ecological, and phylogenetic factors.
- ecospecies.** An assemblage of ecotypes and are separated by incomplete sterility barriers.
- ecotype.** All members of a species fitted to survive in a particular environment; different ecotypes within species have no interbreeding barriers.
- epithet.** Part of the full name of a species; a complete species name consists of the name of the genus to which the species belongs, plus the specific epithet, plus the author of the species.
- form.** The lowest rank in the taxonomic hierarchy (below variety), meant to convey minor variants in nature.
- gene pool classification.** A classification of cultivated plants focused on the crossability of species to an individual crop plant, with gene pool 1 being the crop and those species easily crossable to it, gene pool 2 being species crossable to the crop with some difficulty, and gene pool 3 being species crossable to the crop with extreme difficulty.
- homologous.** Characters that arise by common descent.
- ICBN.** International Code of Botanical Nomenclature (latest version is Greuter et al. 2000).
- ICNCP.** International Code of Nomenclature of Cultivated Plants (latest version is Treharne et al. 1995).
- ingroup.** A putatively monophyletic group that is the prime subject of a cladistic analysis.
- indigen.** Wild taxa in their natural habitat and distribution area.
- interbreeding species concepts.** A philosophy and set of methods that define species almost entirely on the ability of species to exchange genes naturally or artificially, as assessed by artificial crossing programs, studies of mechanisms to facilitate gene flow, and biological isolating mechanisms.
- landrace.** Cultivar that originated as a product of (the first stages of) mass selection (and not as a product of modern plant breeding), generally confined to a certain region.
- lumper.** Refers to a taxonomist who focuses more on similarities than differences, discounting the importance of minor variation among individuals, and tending to recognize fewer taxa (see **splitter**).
- maximum likelihood.** A set of methods used to construct cladograms based on certain evolutionary models of character state changes (compare to parsimony).
- monophyletic group.** A group that includes an ancestral species and all of its descendants.
- morphological species concepts.** A philosophy and set of methods that define species entirely on morphological or anatomical characters.
- natural classification.** Classification based on the evolutionary relationships between the entities to be classified.

(continues)

Table 1.1 (continued)

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- nomenclatural types.** Objects (usually a herbarium sheet) to which a name of a taxon is permanently attached. When a species is described, a type specimen is designated that serves as a reference point for others to compare their concept of names.
- nominalistic species concepts.** A philosophy that questions the very existence of species, and believes that individuals or interbreeding populations are the only population system with any objective reality.
- nothotaxon.** A taxon of hybrid origin (as notho species, nothogenus).
- open classification.** Nonhierarchical system of flexible groups that do not automatically need to be grouped together in larger groups, nor subdivided in smaller groups.
- orthologous.** Genetic characters that are homologous from a speciation event, that is, identical by descent.
- outgroup.** Any group used in a cladistic analysis that is not included in the taxon under study, which is used to root a phylogenetic tree.
- ordination plot.** A phenetic analysis (as principal components analyses, principal coordinates analyses, multidimensional scaling analyses), showing overall similarity of individuals or taxa on two- or three-dimensional plots.
- paralogous.** Characters that have arisen as a result of gene duplication.
- paraphyletic group.** A nonmonophyletic group containing some, but not all representatives of a taxon; said another way, an incomplete group of descendants from one common ancestor with one or more descendants missing.
- parsimony.** A set of methods that assumes that the simplest solution is the most likely one. It is used to construct cladograms, and assumes that minimizing the number of character state changes on a tree is the best approximation of phylogenetic history.
- plesiomorphy.** An ancestral character, not viewed as useful in cladistic analyses for defining monophyletic groups.
- pluralist species view.** The idea that species are formed and maintained by a variety of criteria including morphological, geographical, biological, and ecological criteria.
- polyphyletic group.** A nonmonophyletic group where the common ancestor is placed in another taxon; in other words, a group in which the members do not ultimately derive from one common ancestor, where the descendants of one or more other groups are included.
- priority.** A principle in the ICBN stating that the earliest validly published name is the proper name assigned to a species.
- sister group.** The most closely related monophyletic outgroup to the ingroup.
- splitter.** Refers to a taxonomist who focuses more on small differences among taxa, emphasizing minor variation among individuals, and who tends to recognize more taxa (see **lumper**).
- standard.** A specimen, seed sample, or illustration kept and maintained in a conserved place to illustrate the diagnostic characteristics of a cultivar (used in the ICNCP).

Table 1.1 (continued)

symplesiomorphy.	A set of shared primitive characters, viewed as useless in cladistic analyses for defining monophyletic groups.
synapomorphy.	A set of shared derived characters, viewed as useful in cladistic analyses for defining monophyletic groups; said another way, characters shared by two or more taxa as a result of their immediate common ancestry.
taxon.	A systematic group of plants in a hierarchical system.
total evidence analysis.	A philosophy that cladistic analyses should be constructed with many separate sets of data.
type (nomenclatural type).	That element to which the name of a taxon is permanently attached, whether as a correct name or as a synonym (used in the ICBN).
variety.	A “botanical” variety is a rank in the taxonomic hierarchy below the rank of species and subspecies and above the rank of form (form/variety/subspecies/species). Another meaning, as used in legal texts is synonymous with cultivar (see Section V.A., Ambiguity of the Term <i>Variety</i>).

A. Taxonomy and Systematics

A plant's name is the key to its literature.

Van Steenis (1957)

One of the greatest assets of a sound classification is its predictive value.

Mayr (1969)

Taxonomy is the theory and practice of describing, naming, and classifying organisms (Lincoln, Boxshall, and Clark 1998). *Systematics* is a related term, sometimes used synonymously, but involves a broader discipline of discovering phylogenetic relationships through modern experimental methods using comparative anatomy, cytogenetics, ecology, morphology, molecular data, or other data (Stuessy 1990). It also could be more generally defined as the science of developing methods and philosophies for the systematic grouping of organisms. Whatever term one chooses (we use taxonomy here for simplicity), taxonomists are basically involved with: (1) determining what is a species (or their subdivisions, as subspecies), (2) distinguishing these species from others through keys and descriptions and geographic boundaries and mapping their distributions, (3) investigating their interrelationships, and (4) determining proper names of species and higher order ranks (as

genera or families) using international rules of nomenclature. In addition, some taxonomists investigate processes of evolution that lead to the existing pattern of species and their interrelationships.

There are many rationales for biological taxonomy, including the need (1) to understand the world about us and to conceptualize and order this through classifications; (2) to have classifications for identification and communication; (3) for a convenient information retrieval system; (4) to use stable names that maintain continuity of the literature; (5) to construct a predictive classification; and (6) to construct a useful framework to understand phylogenetic relationships. Taxonomy has special use for conservators including (7) to provide a useful reference system for biodiversity conservation; (8) to aid gene bank managers to rationally organize collections; (9) to aid germplasm collectors to plan expeditions based on gaps in a genebank (Warburton 1967; Mayr 1982; Stuessy 1990; Judd et al. 1999; Woodland 2000).

For agriculturists and horticulturists, stability of names and prediction are major rationales, but the prediction rationale is controversial, as we shall discuss. The need for stable names is only amplified with crop plants where the frequency and need for information retrieval from the literature, through the convenient label of a species name, is much greater than for other plants. One reason for using Latin names or scientific names or Linnaean binomials for plants is to avoid the potential Babel of different common names for the same entity (synonyms). As we discuss, however, many factors are in conflict with this extremely practical goal of stability, leading to different scientific names for the same plant.

What factors conflict with a stable nomenclature?

1. Different classification philosophies have fundamental differences in primacy put on morphological, crossability, phylogenetic, ecological, molecular, or other data that may provide different names to taxa.
2. Powerful new technologies (molecular systematics and computer algorithms to analyze these data) are revising knowledge on species limits and species interrelationships.
3. Taxonomists are far from agreement between the often competing goals of stability of names and potentially improved predictivity of new classifications.
4. Revised phylogenetic data and emerging classification philosophies threaten to overturn long-held traditional classifications.

Most users of taxonomy intuitively accept the putative predictive component of classifications (Mayr 1969). Claims of the predictive value of classifications can be found in Michener (1963), Rollins (1965), War-

burton (1967), Sokal (1985), and Stuessy (1990). For example, Warburton (1967) states:

[Prediction] means that one can describe a trait as characteristic of all members of a taxon before it has been verified for all. It also means that if organisms have been classified together as a taxon because they have all been found to share certain traits, they will later be found to share other traits as well.

For plant breeders, prediction would mean that germplasm could be chosen or avoided based on past positive or negative evaluations. Germplasm evaluations organized with species or higher ranks are common in the literature, for example, species-specific statements of breeding value of wild potato germplasm are found in Ross (1986), Hawkes (1990), and Ruiz de Galerreta et al. (1998). Clearly, not all accessions of a species share traits, but lacking prior evaluation data, taxonomy provides a useful guide to make inferences on unevaluated germplasm based on present knowledge.

While differences in classification philosophies provide fascinating debate among taxonomists and advances the field, the remaining biological community largely focuses on stability of names for purely practical considerations. Some see a failure of the stability goal as the failure of taxonomists to fulfill their service role. Many taxonomists, however, focus on improved phylogenetic classifications as primary.

B. Wild and Cultivated Plants

Botanists have generally neglected cultivated varieties as beneath their notice.

Darwin (1868)

Most modern taxonomists do next to nothing with cultivated plants; many deliberately avoid studying or even collecting them.

Anderson (1952)

Almost one-third [of Conley K. McMullen's *Flowering Plants of the Galapagos*, 1999] covers cultivated species. That seems to place a rather excessive emphasis on the least interesting plants, but undoubtedly tourists will appreciate the information.

Ulloa Ulloa (2001)

Cultivated plants have various definitions, but all focus on the activities of humans. De Wet (1981) simply considered a cultivated plant one that

is adapted to the man-made habitat. Schwanitz (1967) defined cultivated plants as:

the result of evolution processes, that were going on in prehistoric and historic times and are still going on nowadays, both under direct and indirect influence of mankind.

Trehane et al. (1995) defined a cultivated plant as:

one whose origin or selection is due to the activities of mankind. Such plants may arise either by deliberate or chance hybridization or by further selection from existing cultivated stock or they may be selected from a wild population and maintained as an entity by continuous cultivation.

Frequently, domestication is regarded as just a special form of evolution as it happens unconsciously and the same mechanisms of selection are at work (Hanelt 1986; Van Raamsdonk 1993; Van Raamsdonk and van der Maesen 1996; Zohary 1984).

Specialized terms (Table 1.1) are used to refer to cultivated plants that are important for effective communication and classification. A ***cultigen*** is defined as taxon with only cultivated representatives, such as *Triticum aestivum* L., the species name encompassing all hexaploid wheats. The term *taxon* for this definition is controversial, however, as we will discuss. This term is contrasted with an ***indigen***, that is, a wild taxon in its natural habitat and distribution area, that is, a noncultivated plant. A ***culton*** is a systematic group of cultivated plants, and the ICNCP recognizes two types of culta: the cultivar and the cultivar-group. A ***cultivar*** is a nomenclatural term referring to the most basal taxonomic unit of cultivated plants. A ***cultivar-group*** refers to an assemblage of similar named cultivars. A ***landrace*** is a cultivar that originated as a product of (the first stages of) mass selection (and not as a product of modern plant breeding), mostly confined to a certain region. It also had been referred to as an *indigenous cultivar* or a *primitive cultivar*.

Schwanitz (1967) outlined some special features of cultivated plants that can make for rapid divergence from their progenitors: (1) increase of number of desired plant parts; (2) increase of size of desired plant parts by allometric growth; (3) loss of undesired morphological or chemical traits; and (4) loss of defense mechanisms.

All of these traits may arise rapidly, make the cultivated plant quite different from its progenitor(s), obscuring the connection between them. In addition, the study of relationships of crops to progenitors can be hindered by hybridization with weeds producing "crop-weed complexes."

Crop-weed complexes have long been a subject of extensive systematic study and reviews (De Wet and Harlan 1975; Hanelt 1986; Harlan 1965, 1975; Pickersgill 1971, 1981, 1986; Van Raamsdonk and Van der Maesen 1996). Most of these studies point out the complex interaction among weeds, domesticates, and their wild relatives. Extensive hybridization makes the classification of crop-weed complexes especially difficult. Pickersgill (1981, 1986) suggested that weedy progenitors evolve to cultivated plants, but cultivated plants can also evolve back to weeds. Modern cultivars are produced by extensive artificial hybridization, and pedigree records are often incomplete or unavailable for proprietary reasons. For example, separate modern cultivars of potato have in total incorporated germplasm from 16 wild species in the pedigrees (Ross 1986; Plaisted and Hoopes 1989). Despite these separate pedigrees, all are classified as the single species *Solanum tuberosum* L.

II. SPECIES CONCEPTS IN WILD PLANTS

The discussion of species concepts has become a cottage industry. Not only does the number of pages and full-length books devoted to the topic continue to grow, but new concepts of species proliferate at an extraordinary rate.

Rieseberg and Burke (2001)

Species have a central place in taxonomy as they form the basic units of biological classification (Davis and Heywood 1963; Greuter et al. 2000), but there is no consensus on how to define species, and likely never will be. Why? New species concepts have changed considerably with the development of new data and theory, and are likely to continue to change. Each development has led to new species concepts, and Mayden (1997) lists a total of 22. Many concepts, however, are minor variations of others, and some are rarely applied. The following are six major classes of species concepts.

A. Morphological Species Concepts

Morphological species concepts define species entirely on morphological or anatomical characters. Because of their utility, they are frequently applied, especially historically when taxonomists worked in large herbaria and the form of the plant was the major data set available. This can operate effectively by a method referred to as *sheet shuffling*, whereby a collection of herbarium specimens is initially sorted into species based on a subjective impression of overall form. This can be followed by

microscopic examination to gain additional data to modify species delimitation. Cronquist (1978) defined this practical application of the morphological species concept as the *taxonomic morphological species concept*:

Species are the smallest groups that are consistently and persistently distinct, and distinguishable by ordinary means.

The characters leading to this subjective judgment are often unclear, sometimes even to the taxonomist applying them. Typically, characters of special value are weighted, for example more weight is given to reproductive than to vegetative characters. A potential problem with this is that because the methods of the taxonomist are not always evident, preference for one of several conflicting taxonomic treatments are often made based on a taxonomist's reputation, rather than on the inherent qualities of a classification.

The advent of computers allowed the practical application of multivariate techniques to taxonomic data. In practice, morphological, anatomical, chemical, or any character type was appropriate for analyses. The basic idea was that many characters were overlooked in defining species, and that species were best defined by an objective and equal treatment of all characters, reproductive and vegetative (Sneath and Sokal 1962). An added claim was that these methods opened up these classifications to scrutiny, as data and analytical techniques were open for evaluation by all and not hidden and inscrutable impressions of experts. In practice, a taxonomist scores quantitative or qualitative characters and enters them on rectangular data matrices (data entry cells with characters versus individuals). Various algorithms then transform this matrix into a triangular similarity (or dissimilarity) matrix of individuals by individuals. Different individual data reduction techniques then convert a similarity matrix to a graphical display of phenetic trees (phenograms or *dendrograms*), *ordination plots* (as principal components analyses, principal coordinates analyses, or multidimensional scaling analyses). Decisions are made on species limits based on clustering of individuals, but there is no universally accepted objective criterion to determine the degree of clustering to define species or higher taxonomic levels. Sokal and Crovello (1970) defined this *phenetic morphological species concept* as "dense regions of hyperdimensional space" (referring to clustering of individuals in ordination analyses). This concept can provide misleading results of species boundaries in certain crops however where only a few genes have remarkable mor-

phological effects as in the case of *Brassica oleracea* where the same species has been selected for forms as divergent as broccoli, brussels sprouts, cabbage, cauliflower, kale, and kohlrabi.

B. Interbreeding Species Concepts

The *interbreeding species concepts* focus almost entirely on the ability of species to exchange genes naturally or artificially, as assessed by artificial crossing programs, studies of mechanisms to facilitate gene flow, and biological isolating mechanisms. Mayr (1942) advanced the *biological species concept* as "Species are groups of interbreeding natural populations that are reproductively isolated from other such groups." This concept matches that held in the minds of the general public and is intuitively appealing, but many practical and theoretical problems were raised. Procedurally, it is almost impossible to apply to a group of any size because replicated pair-wise crosses are needed in most interspecific combinations to be confidently interpreted (Sokal and Crovello 1970). As well, data from greenhouse situations are not always applicable to the field, and varying degrees of crossing success are not easily interpreted. Also, the concept is inapplicable to species reproducing apomictically. The lifetime of crossing studies by Rick (1963, 1979) in tomato is a notable application, but this depth of study is exceptional and rarely has been applied to other groups. Such crossing studies were common in the 1940s to 1960s and the term *biosystematics* originally referred to the use of breeding programs (by biosystematists) to infer evolutionary relationships among organisms. The term later became broadened to refer to a wide variety of experimental data gathering programs. Because of the broad definition of the term the need for this term has lessened (Stuessy 1990).

The difficulty to define differing degrees of intercrossability led to qualifier terms. Harlan and de Wet (1963), working in grasses, recognized *compilospecies* as genetically aggressive, highly polymorphic species, often of complex hybrid origin, often containing more than one ploidy level, often very weedy, and obscuring other species boundaries. They suggested that such species were typical progenitors of crops. Grant (1981) referred to *semispecies* as populations of plants on the way to becoming species but yet without sufficient reproductive isolation, and used Lotsy's (1925) term *syngameon* to refer to a broadly sympatric set of semispecies.

Some biosystematic terms were placed in a hierarchy of relationships (Clausen et al. 1945; Clausen 1951; Grant, 1981), from ecotype (lowest)

to ecospecies, cenospecies, and comparium. An **ecotype** consists of all members of a species that are fitted to survive in a particular environment, and different ecotypes within species have no interbreeding barriers. An **ecospecies** is an assemblage of ecotypes and are separated by incomplete sterility barriers. **Cenospecies** are assemblages of related ecospecies that when crossed produce highly to completely sterile hybrids. A **comparium** is a group of related cenospecies that cannot be crossed with one another.

Patterson (1985) advanced a variant of the biological species concept termed the *recognition species concept*. Mayr's (1942) biological species concept suggested that biological isolating mechanisms were an accidental by-product of genetic reconstruction during speciation. Patterson, on the other hand, suggested that specific forces were responsible for such reconstruction, and viewed biological isolating mechanisms as an active, positive force in speciation. His concept stimulated the search for adaptations that assist the process of meiosis and fertilization, but he realized that isolation and recognition are just two components of the same process.

C. Ecological Species Concepts

Van Valen (1976) was confounded by the perplexing array of variation in oaks. Oaks have broadly sympatric sets of very similar species, often hybridizing among each other, which he termed **multispecies**. These were similar to the compilospecies of Harlan and de Wet (1963, described earlier). He noted that despite many hybrids, species maintained their integrity in specific habitats. For example, *Quercus bicolor* Willd. (swamp white oak) was broadly sympatric with *Quercus macrocarpa* Michx. (burr oak) in the Great Lakes and Ohio River basins, and they frequently hybridized. The former, however, grew in wet bottomlands, streamsides and swamps, and the latter in mesic habitats of rich woods and fertile slopes. Van Valen stated, The control of evolution is largely by ecology and the constraints of individual development. He outlined the **ecological species concept** as:

A species is a lineage (or a closely related set of lineages) which occupies an adaptive zone minimally different from that of any other lineage in its range and which evolves separately from other lineages outside its range.

He contended that reproductive isolation of allopatric populations is of minor evolutionary importance, and that ecological factors are more closely related to genetic differences than reproductive isolation.

D. Cladistic Species Concepts

The most recent, conceptually difficult, and terminology-laden set of species concepts are grouped here under **cladistic species concepts**. They arose out of the ideas of Hennig (1950, 1966) who used phylogenetic history as the sole criterion for grouping taxa, irrespective of morphology, interbreeding behavior, or ecological considerations, except as they may be used to help reconstruct phylogenetic history. He never used cladistics to help define species, but his concepts have been applied this way as will be discussed.

Basic cladistic terms are briefly explained; the reader is directed to Wiley et al. (1991) for more detailed explanations. Cladistics refers both to a set of methods for inferring phylogeny and a philosophy of systematics in which only monophyletic groups are accepted. Not everyone who uses cladistic methods, however, accepts a cladistic philosophy of classification, and some do not consider cladistics to be appropriate to recognize species. A **monophyletic group** encompasses an ancestor and all of its descendants, as determined by a cladistic analysis that produces phylogenetic branching trees (**cladogram**). The basic procedure to construct cladograms is to try to begin with a putatively monophyletic group, referred to as an **ingroup**, such as “species A” or “tuber-bearing solanums,” or “the sunflower family.” Evolutionary relationships within the ingroup are determined by the use of an **outgroup(s)** that are analyzed for the same characters and are used to construct the tree. A **sister group** is the most closely related monophyletic outgroup to the ingroup, and further outgroups also can be used for a multiple outgroup analysis (Maddison et al. 1984). (See Fig. 1.1.)

Characters are scored for all ingroup and outgroup taxa, just as in phenetic studies. Any character type can potentially be used, including

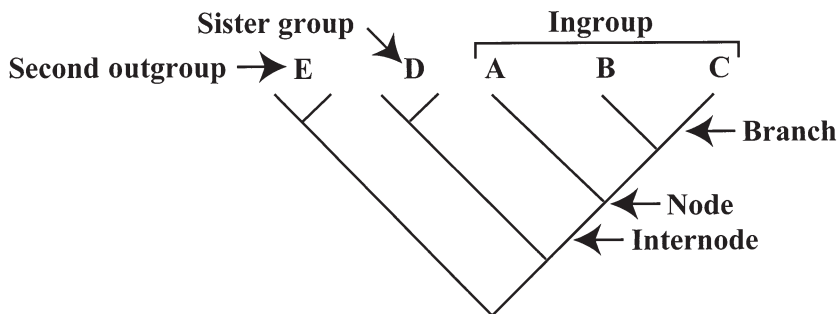


Fig. 1.1. Terms relative to cladograms.

morphological or molecular characters (as DNA base pairs or restriction endonuclease sites). Most analyses score these characters qualitatively, as presence or absence (0-1), or as a range of discrete character states (0-1-2-n). Great care is taken to score only **homologous** characters arising from common ancestry, avoiding characters that may look similar but actually arise in parallel from different ancestors. **Orthologous** characters are homologous by a speciation event, meaning that they trace their ancestry to a common progenitor, and are taken as the only useful type of homologous character. Molecular taxonomists are searching for single-copy nuclear genes for phylogeny construction, and doing everything possible to avoid **paralogous** characters that have arisen from gene duplication. Such duplicated genes can evolve separately in the same lineage, may falsely appear to be homologous, but can provide misleading phylogenetic information.

Cladograms are then constructed from these data by various methods, but a common method is to use the **parsimony** criterion, that invokes the minimum number of evolutionary changes to construct the tree. Other techniques also are used, such as **maximum likelihood** (Felsenstein 1981; Swofford et al. 1996) that searches for trees that may be longer but that represent character changes based on certain evolutionary models. The tree is rooted based on characters of the outgroup(s), and in this method monophyletic groups are supported only by **synapomorphies** (shared derived characters) relative to the **plesiomorphies** (ancestral or primitive characters) of the outgroup(s). Cladograms may look like phenetic trees (dendrograms), but phenetic analyses are based on overall similarity and dendrograms are constructed by an average of all characters, not individual characters on each branch as in cladograms. Pheneticists infer only overall similarity of organisms from their phenograms, not phylogeny, and most cladists interpret cladograms phylogenetically. Monophyletic groups are then determined from the cladogram that trace to a single internode (all of which are supported by synapomorphies). Cladists avoid recognizing all nonmonophyletic groups, including **paraphyletic groups** (groups containing some, but not all descendants of the most recent common ancestor), and **polyphyletic groups** (groups where the common ancestor is placed in another taxon). Paraphyletic species have been recognized, however, as described in Figure 1.2.

There is a wide diversity of opinion on application and interpretation of these concepts, providing further problems. For example, phylogenetic results of the same organisms obtained from different data sources are frequently in conflict (Wendel and Doyle 1998). Some advocate analyzing data separately to discover datasets providing misleading results,

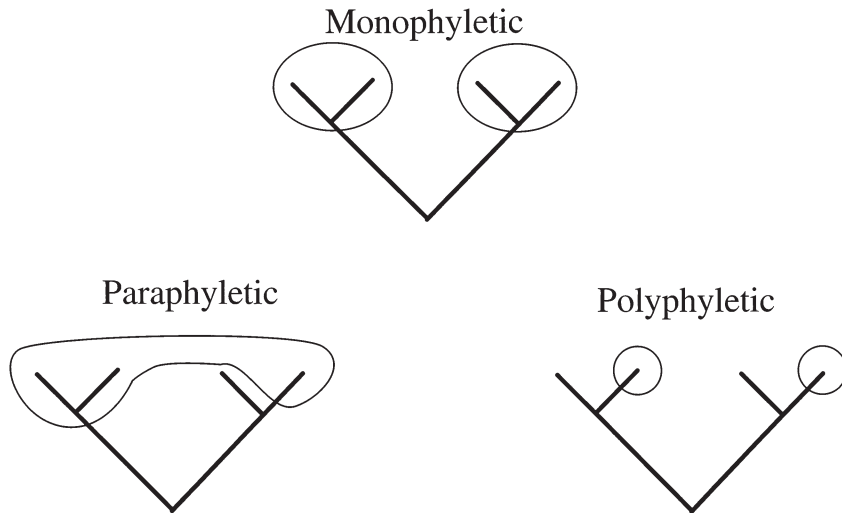


Fig. 1.2. Cladistic relationships relative to cladograms.

while others advocate combining all data into a single matrix for a **total evidence analysis** (e.g., Eernisse and Kluge 1993). Cladistic results also can be affected by poor choice of outgroups, by analysis of unrecognized nonorthologous characters, by different choice of cladistic algorithms to construct trees, by insufficient ingroup or outgroup sampling, and by different methods to handle missing data. There is also debate among cladists whether cladograms truly reflect recency of common ancestry (*process cladists*), or whether they need to be theory neutral and only show patterns decoupled from assumptions of ancestry (*pattern cladists* or *transformed cladists*) (Ereshefsky 2001). Perhaps the greatest source of debate is the use of cladistics at all at the species level. This is because cladistic procedures assume divergent taxa, yet individuals within species often (generally) hybridize, leading some to consider cladistics to be an inappropriate method to define species (Templeton 1989).

Another complication is the differences in opinion in cladistic species concepts. The most strict interpretation of the cladistic species concept was advanced by the process cladists Mishler and Brandon (1987) as the *autapomorphic species concept*:

A species is the least inclusive taxon recognized in a classification, into which organisms are grouped because of evidence of monophyly . . . that is ranked as a species because it is the smallest “important” lineage deemed worthy of formal recognition.

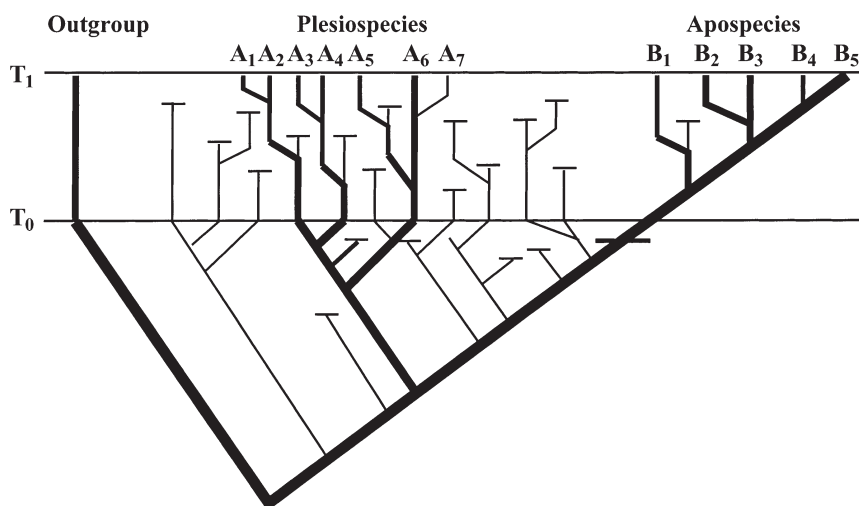


Fig. 1.3. Apospecies and plesiospecies as depicted by Olmstead (1995). Under this evolutionary model, a set of populations is shown at initial time T_0 when a speciation event occurs, as depicted by the thick horizontal line designating a synapomorphy forming the species. At initial time T_0 , the new apospecies leaves a remnant set of populations that are now paraphyletic (plesiospecies). Later (at time T_1) extinction of populations leads to monophyly of both species. Bold lines designate populations surviving to time T_1 . This shows the theoretical need to withdraw the strict criterion for monophyly in cladistic species concepts.

The criterion for “important lineage” necessary to define a species can vary from ecological, reproductive, or developmental criteria.

Recently, Rieseberg and Brouillet (1994) and Olmstead (1995) have argued that geographically localized models of speciation typically produce a monophyletic daughter species and remnant paraphyletic progenitor species, and argue that a strict concept for monophyly fails for many species. Olmstead (1995) termed the former *apospecies* and the latter *plesiospecies*. He traced a hypothetical set of populations over time T_0 (initial species divergence) and T_1 (later time with full development of apospecies) that showed the necessity of recognition of paraphyletic species if apospecies are to be recognized at all (Fig. 1.3).

Cracraft (1989) has a tendency to lean in the direction of pattern cladistics and advanced the *phylogenetic species concept* as:

A species is an irreducible (basal) cluster of organisms, diagnosably distinct from other such clusters, and within which there is a parental pattern of ancestry and descent.

This definition emphasizes smallest diagnosable units by a practical set of diagnostic characters, as discovered by cladistic procedures, but makes no inference that these are monophyletic.

E. Eclectic Species Concepts

The former species concepts highlight single processes as definitive for species. ***Eclectic species concepts***, in contrast, take a pluralistic view that species are formed and maintained by a variety of criteria. For example, Doyden and Slobobchikoff (1974) constructed a flow chart detailing a variety of morphological, geographical, biological, and ecological criteria to define species. Mayr (1982) modified his biological species concept to include an ecological component: *A species is a reproductive community of populations that occupies a specific niche in nature*. Stuessy (1990) concluded his discussion of species concepts with a basic agreement with Crum (1985):

Although subjectivity is involved with decision making, a species is only as good as the knowledge and insights used in its delimitation. Certain methodologies help. So do good sense and good judgment based on meaningful experiences, and the more the better.

Templeton (1989) outlined the *cohesion species concept* as:

The most inclusive group of organisms having the potential for phenotypic cohesion through intrinsic cohesion mechanisms through genetic and or demographic exchangeability.

He attempted to define specific mechanisms that drive the evolutionary process to speciation. He considered that his concept

attempts to utilize the strengths of [biological, evolutionary, and recognition species concepts] while avoiding their weaknesses with respect to the goal of defining species in a way that is compatible with a mechanistic population genetics framework.

Ereshefsky (2000) outlined several classes of species concepts, and advanced a ***pluralist species view*** that no single correct definition of species exists and that a number of alternative concepts may be legitimate.

F. Nominalistic Species Concepts

Some question the very existence of species, and believe that individuals or interbreeding populations are the only population system with any

objective reality. This concept arose out of the philosophy of nominalism, arguing that only individuals are real and that classes of any kind (as species, genera, or families) are artificial constructs. For example, Burma (1954) stated: *species are highly abstract fictions*. Levin (2000) likewise argued that only the local population is the unit of evolution, and species are artificial.

Some evidence supported ***nominalistic concepts***. Ehrlich and Raven (1969) documented many cases of reduced gene flow in both plants and animals that would preclude any cohesive force to maintain species. They contended:

Selection alone is both the primary cohesive and disruptive force in evolution . . . for sexual organisms it is the local interbreeding population and not the species that is clearly the evolutionary unit of importance.

Rieseberg and Burke (2001) countered this view, arguing that prior studies grossly underestimated levels of gene flow, and that only very low rates of gene flow are actually needed for the diffusion of strongly advantageous alleles needed to maintain species integrity.

III. CLASSIFICATION PHILOSOPHIES IN WILD AND CULTIVATED PLANTS

A. Wild Plants

The previous section reviewed a variety of types of data and analytical and philosophical methods used to define species, and similar criteria are used to group species into higher ranks (as genera, families, and orders). The early classifications were based on intuitive interpretations of morphological data, and in many cases, they defined groups that have continued to be maintained. For example, the grass family, sunflower family, and many other traditional taxa are clearly natural as determined by molecular data.

The intuitive, interbreeding, phenetic, cladistic, and eclectic classification philosophies mentioned in the previous section for species also are used to group species within genera, and all but the interbreeding classification philosophies have been used to classify above the genus level (reviewed in Stuessy 1990; Judd et al. 1999). Many botanists today examine cladistic relationships, but major disagreement rests on how to translate cladistic results into a classification. Some argue (e.g., Stuessy 1990), that cladistic data are only one component of phylogenetic relationships, other components being chronistic (time of divergence of

clades), patristic (amount of character divergence within lineages), and phenetic (overall similarity). There are no algorithms to incorporate all of these data types into a classification, however, unlike classifications based on phenetics or cladistics, and intuitive judgments are still used by many to construct these eclectic classifications.

B. Cultivated Plants

The inconsistencies and lack of agreement of taxonomists dealing with the same materials are remarkable, to say the least, and are even more striking when the treatment of differing crops are compared.

Harlan and de Wet (1971)

The major goals of taxonomy reviewed suggest that for agronomists and horticulturists, stability and predictivity would be very important. The philosophies and practices to define wild species and to group them into genera and higher-level ranks are wide and diverse. The question remains—what would happen if different taxonomists were to work on the same group of plants and produced different classifications? Would one be “better,” and by what criteria could we judge one classification to be “better”?

These questions can be explored by comparing such different classifications, and we give examples from tomato, potato, *Brassica*, lettuce, *Prunus*, and wheat. One of the major reasons for discrepancies among taxonomic treatments is that the taxonomy of plants is often complicated by the occurrence of outcrossing, selfing, apomixis, clonal propagation, or polyploidization, producing different variation patterns that can be difficult to subdivide into easily recognizable units. The taxonomy of cultivated plants has the extra complication of the influence of the domestication process on variation patterns, with domestication having major and rapid effects on morphological characters used for classifications.

1. Tomato. Spooner, Anderson, and Jansen (1993) examined outgroup relationships of tomato (many recognize as the genus *Lycopersicon* Mill.) to potato and other members of the *Solanaceae* L. (Fig. 1.4). The results convincingly showed tomato to be firmly interrelated in the genus *Solanum* L. Based on these results, Spooner et al. (1993) followed a cladistic classification to assign tomato to the genus *Solanum*, matching the original treatment of Linnaeus (1753), and a minority of other taxonomists who foresaw this generic relationship based on morphological data. Subsequent molecular studies unequivocally supported the cladistic placement of tomato in *Solanum* (Olmstead and Palmer 1992, 1997;

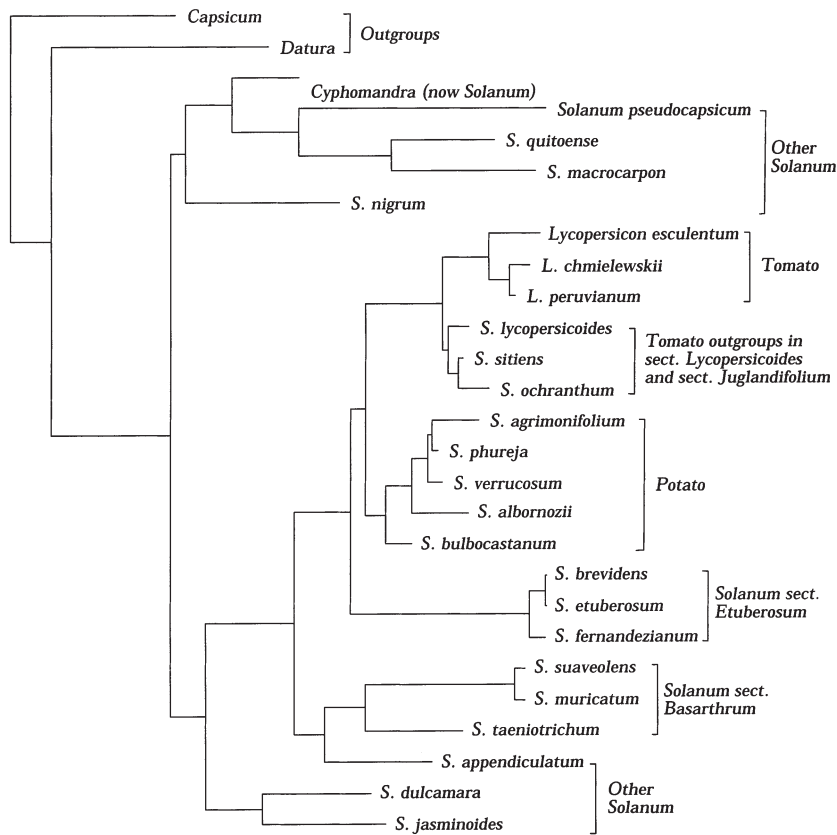


Fig. 1.4. One of two-most parsimonious cladograms (as a phylogram) of chloroplast DNA restriction site data examining wild tomatoes (here labeled *Lycopersicon*), their sister groups (*Solanum* sect. *Lycopersicoides*, sect. *Juglandifolium*), wild potatoes (*Solanum* sect. *Petota*), and further outgroups in *Solanum* sect. *Etuberosum*, sect. *Basarthrum*, and other *Solanum* (modified from Spooner et al., 1993).

Bohs and Olmstead 1997, 1999; Peralta and Spooner 2001). These unequivocal cladistic results are stimulating many taxonomists to place tomato in *Solanum*, but many agronomists and horticulturists have not accepted the name (but see Van der Heuvel et al. 2001). Most users of *Lycopersicon* clearly base their reluctance entirely on a desire to maintain nomenclatural stability rather than adherence to any particular classification philosophy.

Ingroup relationships within tomato have varied greatly. Müller (1940), Luckwill (1943), and Child (1990) treated tomato based on tax-

1. PLANT NOMENCLATURE AND TAXONOMY

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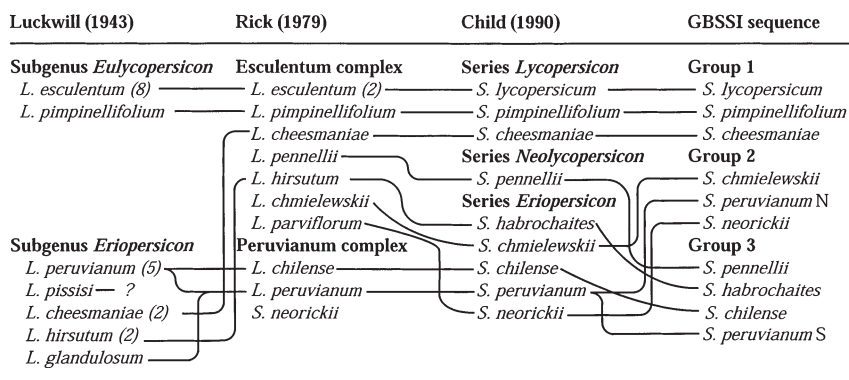


Fig. 1.5. A comparison of taxonomic treatments of wild tomatoes from Luckwill (1943; a taxonomic morphological species concept), Rick et al. (1979; a biological species concept), Child (1990; taxonomic morphological species concept), and a possible cladistic interpretation of a GBSSI DNA sequence cladogram of Peralta and Spooner (2001; Fig. 1.6).

onomic morphological species concepts. The treatments of Rick (1963, 1979) and Rick, Laterrot, and Philouze (1990) grouped the species completely differently based on interbreeding concepts (Fig. 1.5). Peralta and Spooner (2001) produced a phylogeny of tomato based on DNA sequences of the single-copy GBSSI (waxy) gene (Fig. 1.6 on page 24). It could be interpreted to distinguish three groups. One of the species, the highly polymorphic *Solanum (Lycopersicon) peruvianum* L. would be placed into two groups, one consisting of populations from northern Peru, and another of populations from central to southern Peru (Fig. 1.5). A phenetic morphological study by Peralta and Spooner (in press) supported all species, including a north and south *Solanum peruvianum* species. A taxonomic monograph of tomato is in preparation by Iris Peralta, Sandra Knapp, and David Spooner.

2. Potato. Ingroup relationships within potato have differed even more than within tomato. Harlan and de Wet (1971) advanced the gene pool concept (a variant on the biological species concept) based on their frustration with traditional taxonomy to provide consistent answers to relationships of crops and their wild relatives. They initially tried to use taxonomic treatments of crops to give insight into materials to use in their breeding programs. They noted, however, such great discordance between taxonomic treatments of potato, maize, wheat, and sorghum that they rejected traditional treatments and constructed the **gene pool classification**. They compared the taxonomic treatments of potato of

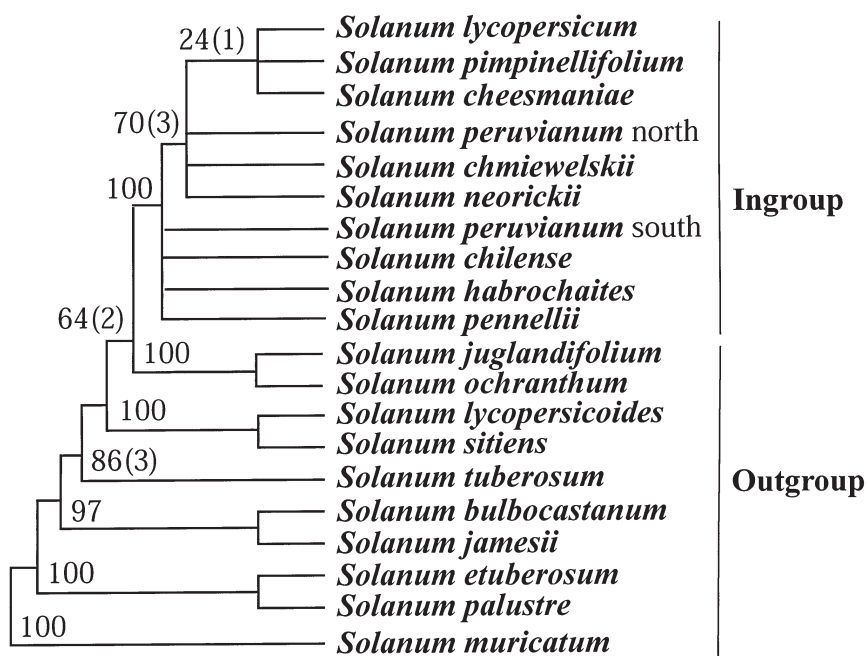


Fig. 1.6. Abstracted results of a GBSSI (waxy) gene phylogeny of wild tomatoes and outgroups (Peralta and Spooner 2001).

Bukasov (1933) and Bukasov and Kameraz (1959) to Hawkes (1963), and noted that Hawkes (1963) recognized about one-half as many species, and grouped these species very differently into series.

Their classification starts from the *crop* itself. Crossability is represented in a graph with three genepools, with the primary genepool 1 being the crop and wild species easily crossable to it, and the second and third being the rest of the plant kingdom, according to degree of crossability to the crop (genepool 2 crossable with some difficulty, genepool 3 crossable with great difficulty). Genepool 1 is based on the biological species concept and is then to be subdivided in two subspecies, one with spontaneous populations, the other containing the cultivated “races” (their “race” not being equivalent with cultivar of cultivated plant classification).

This system is a very special purpose classification and not an alternative to any form of taxonomy in general. Why? Every primary genepool chosen results in a separate classification based entirely on the choice of each crop used for comparison. This could lead to as many dif-

ferent classifications of plants as there are primary genepools for comparison. This is unacceptable, since genepools 2 and 3 contain close and less close relatives of the primary genepool "species" and do in fact thus represent the entire rest of plant kingdom (genepool 4?). The relationships of the genepools with the rest of the plant kingdom remain unresolved. Another objection is that the category of subspecies is misused for convenience to contain either wild plants or cultivated material. This last option creates an unfortunate hybrid between the taxonomy of wild plants (the category itself) and of cultivated plants (the actual content of the category). Similar problems exist in the biological species concept. The system proposed by Harlan and De Wet has already led to many "infraspecific" classifications of crops, using Latin binomials for cultivated plant groups that as we argue should be avoided.

Spooner and van den Berg (1992) followed up on the Harlan and de Wet (1971) comparison of potato with an examination of later taxonomic treatments of Bukasov (1978) and Hawkes (1990), and added Correll (1962) and Gorbatenko (1989) (Fig. 1.7). All four of these authors apparently applied a taxonomic morphological species concept, but Hawkes (1990) also took intercrossability data into account. The treatments differ in the number of series recognized, the number of species in each series, and the different affiliation of species to these series. Likewise, Spooner and van den Berg (1992) also compared the near-simultaneous independent publication of the potatoes of Bolivia by Hawkes and Hjerting (1989) and Ochoa (1990). Their treatments differed in the number of species recognized, their affiliation to series, the taxonomic rank used to recognize divisions of species (botanical varieties or subspecies), and in their hypotheses on which of these species are of hybrid origin and whether they form introgressant populations with other species.

3. Lettuce. The influence of domestication on taxonomic classification is shown very clearly in cases where through the domestication process the morphology of the plants are changed, and species are described based on these morphological characters. In the case of lettuce, the obvious differences between cultivated and wild material led to the distinction of the species *Lactuca sativa* L. as separate from its presumed wild ancestor *L. serriola* L. Cultivated material lacks the prickles on the midrib of the lower side of the leaves, and shows prominent heads. De Vries and van Raamsdonk (1994) reiterated this separation in a numerical morphological analysis. However, it is highly questionable whether botanical species should be recognized using characters that are clearly the results of human selection. An alternative classification would be to consider wild and

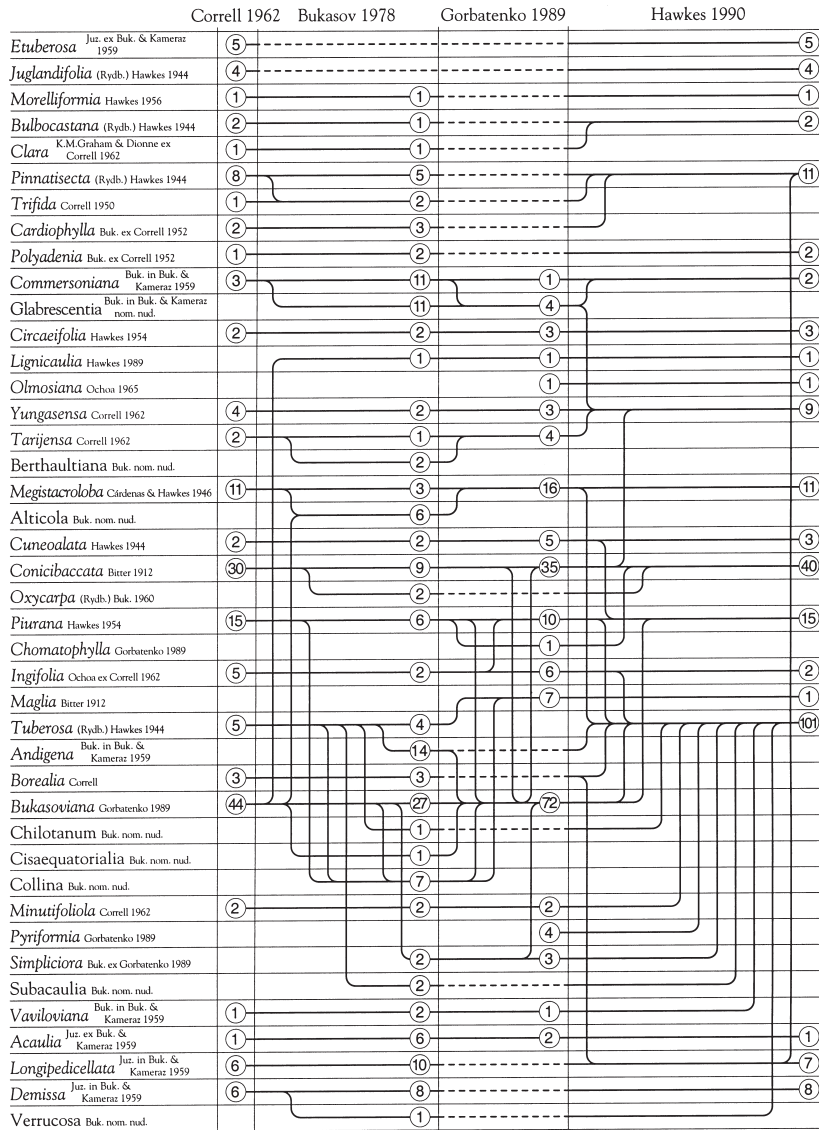


Fig. 1.7. A chronological history of hypotheses of placement of wild potato species into series by Correll (1962), Bukasov (1978), Gorbatenko (1989), and Hawkes (1990). The nonitalicized series names of Bukasov were treated as series but not validly published. Solid lines connecting series indicate the maintenance or transfer of species between series. Dotted lines indicate that an author did not treat these series. The numbers in circles are the number of species accepted for the series. (From Spooner and van den Berg 1992).

cultivated lettuce as the same species, that would, unfortunately, have to be called *L. sativa*, this being the earlier name. Different nomenclatural solutions can be proposed. The name *Lactuca serriola* could be considered a synonym of *L. sativa*. Alternatively, Frietema de Vries (1996) recognized two subspecies: subsp. *sativa* encompassing the groups of cultivated lettuce and subsp. *serriola* (L.) Frietema de Vries for the wild material.

4. *Brassica*. The taxonomy of cabbage (*Brassica* L. spp.) is extremely complex. Even the delimitation of genera in this part of the family Brassicaceae can be questioned. *Raphanus* L. and *Sinapis* L., the genera including radish and mustards, are closely related to the genus *Brassica*. Viable hybrids have been produced from *Brassica* × *Raphanus* crosses (described in the nothogenera × *Brassicoraphanus* Sagerent or × *Raphanobrassica* Karpechenko, depending from which taxon the female parent originated). Within the genus *Brassica*, a number of species form a closely-knit network. Cytogenetic studies of U (1935) showed that three primary species (*B. oleracea* L., *B. rapa* L., and *B. juncea* (L.) Czern.) formed amphidiploid species, resulting in the “triangle of U.” Molecular work confirmed these findings and established the male and female contributions of each primary species, using chloroplast DNA restriction site data (Palmer et al. 1983) and nuclear restriction site polymorphism data (Song and Osborn 1992). *Brassica oleracea* displays an extreme variability, where through different directional selection a large number of crops was produced, each targeting a different organ of the plant (leaves surrounding the terminal bud: cabbage and kale; enlarged axillary buds: Brussels sprouts; inflorescence: cauliflower and broccoli; swollen bulblike stem: kohlrabi). All of these variants were classified in botanical varieties, which in modern cultonomic terms would be cultivar-groups.

A number of wild taxa associated with *Brassica oleracea* have been described but their exact number and delimitation have remained a matter of debate. Harberd (1972) proposed the concept of **cytodemes**: groups characterized by having a constant chromosome number, all accessions of the same cytodeme being fully interfertile while those of different cytodemes are essentially cross-sterile. He listed 11 species as members of the *Brassica oleracea* ($2n=18$) cytodeme that nearly all have been regarded as subspecies of *Brassica oleracea* at some time. Snogerup (1979, 1980) recognized only seven wild taxa, reducing some species to a *B. rupestris-incana* complex, which itself contains eight species names. Hanelt (2001) listed ten species in a *Brassica oleracea* group, and followed Helm (1963) for the infraspecific classification of the cultivated forms within *B. oleracea*, using subspecies, convarieties and varieties.

5. *Prunus*. Cherries, plums, peaches, apricots, and almonds all are classified as species within the genus *Prunus* L., besides many other wild species and species that are in use as ornamentals. Rehder (1960) discussed 77 cultivated species out of the nearly 200 species. Other sources mentioned up to 430 species within the genus (Royal Horticultural Society, 1992). A major difference is found in the infrageneric classification. This treatment subdivides *Prunus* into a number of subgenera and these in sections. Plums (*Prunus domestica* L.) and apricots (*P. armeniaca* L.) are accommodated in different sections of subgenus *Prunophora* (Neck.) Focke ex Engl. and Prantl. Almond (*Prunus dulcis* [Mill.] D. A. Webb) and peach (*P. persica* Batsch) are placed together in subgen. *Amygdalus* (L.) Benth. and Hook. f., and sour and sweet cherries (*P. cerasus* L. and *P. avium* L.) in subgen. *Cerasus* Pers. The flora of the USSR (Shishkin and Yuzepczuk 1971) and Hanelt (2001), however, recognized several genera within a subfamily *Prunoideae* Focke. Not only is the taxonomic level of many groups changed from subgenus to genus, but also the affinities between the different crops is interpreted differently, with sour and sweet cherries still together in one genus *Cerasus*, but almonds and peaches now placed in the separate genera *Amygdalus* L. and *Persica* Mill., respectively.

6. *Wheat*. Hybridization and polyploidization have played an important role in the origin of bread wheat (Zohary and Feldman 1962). At the diploid level crosses between the wild species *Triticum boeoticum* Boiss. (wild einkorn) and a species from a different grass genus, *Aegilops speltoides* Tausch, produced tetraploid material (wild and cultivated emmer). The process was repeated on the tetraploid level with another species from the genus *Aegilops* L., *A. squarrosa*, resulting in hexaploid *Triticum tauschii* (Cosson) (= *T. aestivum* auct. Mult. non L.) with a genome formula AABBDD reflecting the contributions of at least three species with different genomes. The apparent crossability of *Aegilops* and *Triticum* L. led Stebbins (1956) to propose the unification of these two genera, which was supported by Bowden (1959). MacKey (1981) suggested that one might even lump the whole tribe Triticeae Dumort. based on the criterion of crossability. He favored a separation of the genera because of the discontinuity developing in this complex, with *Aegilops* evolving towards weediness, and *Triticum*, under the influence of human selection, following a completely different trend in ear construction.

The number of species within the genus *Triticum* varies dramatically among treatments. Thellung (1918) recognized only three wheat species (*T. monococcum* L., *T. turgidum* L., and *T. aestivum*). MacKey (1966,

1968) recognized six biological species within the genus *Triticum*, and MacKey (1981) criticized the detailed hierarchical subdivision of the genus by Dorofeev and Korovina (1979), who used the categories subgenera, sections, species, subspecies, convarieties, subconvarieties, varieties, and forms. Dorofeev and Korovina (1979) recognized 27 different species, subdivided in no less than 1031 varieties. Hanelt (2001) listed eight species divided into various subspecies.

These comparisons illustrate that the very wide differences in taxonomic interpretations of the same group persist, continuing to present agronomists and horticulturists with a confusing decision as to which one to use. Different taxonomists continue to provide alternative taxonomic treatments of the same group of organisms, as was so effectively shown by Harlan and de Wet (1971). These treatments are sometimes vastly different based on different classification philosophies. A purpose of this chapter is to explain these different philosophies and show why the treatments of crops differ, and why names are being changed. Adherents to different philosophies will strongly argue that their classification is "better" in the sense of being more predictive. However, we are aware of *no objective test* of this claim of predictivity in *any* crop plant, and such tests are needed to test predictivity of alternative classifications. There is no taxonomic consensus emerging on classification philosophies, and different treatments of both wild and cultivated plants are likely to persist.

IV. BRIEF HISTORY OF NOMENCLATURE AND CODES

One of the most remarkable features of the human species is our ability to use a highly developed system of speech to communicate. There are unique words to identify unique objects but also many words to identify collections of items. These collective terms are the result of our innate need to classify objects into groups, and groups of groups. Such collective terms represent not only the group itself but also the way in which humans have decided to classify the objects. Needless to say, different cultures may use different criteria to group a set of objects, resulting in different classifications for that same set. Interestingly, the very term *classification* dates back to the Greek botanist Theophrastus in the third century BCE.

If terms are not made distinct between different groups in classifications, confusion will eventually arise. For biological classifications that have universal applicability, a standardized system of nomenclature would eventually be necessary. Scholarly texts by early botanists (e.g. herbalists) identified groups of plants by using long Latin (the academic

language at the time) phrases enumerating characters of those plants. This cumbersome method cried out for a simplification.

The first successful attempt to standardize names to classify all known plants was from Linnaeus (1753). His classification was based on similarities and differences among groups of plants. Those showing “relevant” similarities were grouped together. Linnaeus’ most fundamental object in his classification was the species. He used the species in its oldest definition, being an immutable entity (the typological species, an outdated morphological species concept that allows little to no variation within species). The next higher level of grouping of species was the genus. Linnaeus used a combination of two Latin terms (one for the genus and one for the specific *epithet*) to singularly identify and name a species. Thus binary nomenclature was born, which we still use today (Stafleu 1971). A full species name consists of three elements: (1) a genus name, (2) a species epithet, and (3) a taxonomic author (e.g., *Solanum tuberosum* L.). Sometimes two authors follow a plant name, as in the wild potato name *Solanum brachistotrichium* (Bitter) Rydb. Friedrich Bitter described the plant as a variety, and Per Alex Rydberg transferred it to the species level. This originally published name is the *basionym*, or the original name later transferred in rank (here from variety to species). This use of two authors is not meant to serve as a credit device, but rather as a very useful way to trace the nomenclatural history of names.

Brummitt and Powell (1992) provide a reference of taxonomic author abbreviations that is listed in many standard instructions to authors of scientific journals. This is useful because of many variants on abbreviations that introduce confusion in citations. Heiser and Janick (2000) point out that authors of many crops are improperly listed in standard references of names (e.g., Liberty Hyde Bailey Hortorium 1976), and may be unnecessary. New references (e.g., Wiersma and León 1999; Hanelt 2001) are properly listing species names of crops to help alleviate this problem, and bolster Heiser and Janick’s argument to eliminate taxonomic authors in journals.

Standard ranks in the taxonomic hierarchy from lowest to highest are form, variety, subspecies, species, series, section, genus, tribe, family, order, class, division, and kingdom. If more ranks are needed, a potentially infinite number can be created for all ranks by using qualifier terms such as *sub* or *super*, for example to create subgenus or supergenus. Families have standard endings of *-aceae* (e.g., Rosaceae), orders *-ales* (Rosales). Eight economically important angiosperm families have alternative family names of long usage not ending in *-aceae* that are maintained to keep links to the older literature. These are: Apiaceae

(Umbelliferae), Arecaceae (Palmae), Asteraceae (Compositae), Brassicaceae (Cruciferae), Clusiaceae (Guttiferae), Lamiaceae (Labiatae), Fabaceae (Leguminosae), and Poaceae (Gramineae).

Most ranks currently used were developed in the eighteenth century, and are mental constructs that are *not* comparable across all plants. There are *no objective criteria* or set of characters to indicate what taxonomic level is a genus, family, and order. As such, families or any rank are not comparable regarding age or diversity. Put in a phylogenetic context, traditional ranks are not necessarily equivalent in that they do not designate sister clades. Ranks only have meaning in a relative (not absolute) sense in that a genus is less inclusive than a family, and a family is less inclusive than an order (Stevens 1998).

Because there are no universally accepted definitions of what constitutes a genus, species, or other rank, they are interpreted differently by different taxonomists. **Lumpers** are taxonomists who focus more on similarities than differences, discount the importance of minor variation among individuals, and tend to recognize fewer taxa. **Splitters**, on the other hand, focus on small differences among individuals and recognize more taxa. Both of these terms have negative connotations as they refer to extremes of taxonomic interpretation, but in reality they are relative terms and are best applied when independent taxonomists treat the same group in different ways.

Botanists agreed that nomenclature should be as stable as possible and not change drastically with new classifications. De Candolle (1867) devised a set of nomenclatural rules, which finally led to the first edition of the *Regles de la Nomenclature Botanique*, later editions being published as the ICBN. The ICBN is amended every six years, based on votes at the International Botanical Congress. The last Congress was held in St. Louis, Missouri, in 1999, resulting in the latest edition of the ICBN (Greuter et al. 2000).

The ICBN has six main principles. The first three enter into our discussion of how plants get their names, and how new names may be assigned to species that previously had another name.

Principle I. *Botanical nomenclature is independent of zoological and bacteriological [and viral] nomenclature.* As discussed in Section VII.A., however, some suggest a unified code (BioCode) should be sought.

Principle II. *The application of names of taxonomic groups is determined by means of **nomenclatural types**.* A nomenclatural type is that element (usually a herbarium sheet) to which the name of a taxon is permanently attached. What this means is that

when a species is described, a type specimen needs to be designated that serves as a reference point for others to compare to their concept of names.

Principle III. *The nomenclature of a taxonomic group is based upon **priority** of publication.* This means that the earliest validly published name is the proper name assigned to a taxon.

In order to provide an “out” to the strict application of these rules for well-known and frequently used plant names (as economic plants), the ICBN provides a way to avoid name changes based on principles II and III called **conservation** of names of families, genera, and species. This is done by petitioning for a name to be conserved (*nomina conservanda*). Anyone can petition to have names conserved by a published proposal in the journal *Taxon*. This proposal is voted on at the general assembly of the International Botanical Congress, and if a majority accepts the proposal the name is added to a list of conserved names in the ICBN that are valid despite having violated rules of the Code. For example, it was discovered that the proper name for the cultivated tomato within the genus *Lycopersicon* was not the well-known name *Lycopersicon esculentum* Mill., but rather *L. lycopersicum* (L.) H. Karst. A petition was made and later voted on by a majority at a Congress to conserve the name *L. esculentum*. Conservation is valid however, only within the genus *Lycopersicon*. If a later taxonomist decided that tomato was better classified in the genus *Solanum*, the conservation has no validity outside of the genus *Lycopersicon*. This point is frequently misunderstood by those who think that conservation is meant to preserve classifications (e.g., Merrick 2000). Conservation is only a nomenclatural device that operates within the taxa in which they have been voted upon, and is not operative if the taxon is classified in another group.

What does it take to validly publish a new species or other taxon name? Not much. There is no license needed, nor do you need to have an academic degree, or be a botanist, or to be part of any professional organization. Anyone can validly publish a new taxon if they: (1) provide a description or diagnosis (a short statement of how the new taxon differs from something similar) in Latin; (2) designate a type specimen (generally a single herbarium specimen affixing the name to the new taxon); (3) follow rules outlined in the ICBN such as using the proper form of a name regarding spelling and not using names that have been validly published before; (4) effectively publish the new name. Effective publication typically is through peer-reviewed scientific taxonomy journals, but it is stipulated in the ICBN only as “distribution of printed matter (through sale, exchange, or gift) to the general public or at least to botanical institutions with libraries accessible to botanists generally.”

Botanists keep track of most new taxon names through indexing services such as the *Gray Card Index* (Gray Herbarium, Harvard University, Cambridge, Massachusetts) or the *Index Kewensis* (Royal Botanic Gardens, Kew, UK), or the International Plant Name Index (<http://www.ipni.org/>), maintained by these two organizations and the Australian National Herbarium.

We've described the basics of nomenclatural principles and rules inherent in the ICBN. This system is commonly referred to as "Linnaean nomenclature" or "traditional nomenclature." The term *Linnaean nomenclature* is actually a misnomer, however, because some key features of the ICBN postdate Linnaeus, such as the principle of priority, the reliance on type specimens, or even the use of families. Therefore we use the term *traditional nomenclature* here.

Although many early botanical texts dealt with cultivated plants, their role in the development of plant nomenclature was very limited (Hettterscheid et al. 1996). Focus was directed mainly toward plants in the wild, untouched by humans. Cultivated forms were to get "fancy-names" (as Rosa 'Splendor') but these names would have to be linked to botanical Latin names of the species, subspecies, or botanical varieties from which the cultivated plants were derived. As such, the nomenclature of cultivated plants became a mere appendix of the nomenclature of wild plants.

Cultivated plants have many differences from wild plants, however, and the linking of their nomenclature to the ICBN became untenable. In 1952, a proposal was published (Lanjouw et al. 1952) for an independent set of nomenclature rules for cultivated plants, and in 1953 resulted in the first edition of the International Code of Nomenclature for Cultivated Plants (ICNCP; Stearn 1953). Other changes to the Code are discussed in three separate Proceedings of the International Symposia on Taxonomy of Cultivated Plants: (1) *Acta Horticulturae* 182(1), 1985; (2) *Acta Horticulturae* 413(2), 1994; (3) Taxonomy of Cultivated Plants, Proceedings of 3rd International Symposium, Royal Botanic Gardens, Kew, 1999. The reason for divorcing both codes was hardly fundamental but more of a practical nature. Most botanists dealing with the ICBN did not want to discuss cultivated plant nomenclature at length, and were glad to dispose of these rules to a different nomenclatural body.

V. FUNDAMENTAL DIFFERENCES IN THE CLASSIFICATION AND NOMENCLATURE OF CULTIVATED AND WILD PLANTS

In the interest of nomenclatural stability it may at first glance seem wise to standardize the nomenclature of biological objects once and for all. This would not allow, however, for changes to accommodate new

theories of evolution and classification. For example, Linnaeus's very useful development of binomial nomenclature predated modern ideas of evolution espoused by Darwin (1859). If traditional nomenclature was "frozen" since the time of Linnaeus we would be burdened with an archaic system with little biological relevance. Hence, classification rules change along with new data and needs (every six years for the ICBN, irregularly for the ICNCP). We outline major emerging new proposals for classification changes for the ICNCP.

A. Ambiguity of the Term *Variety*

The term *variety* has caused much confusion. One meaning, as used by the ICBN (the "botanical variety"), is a particular rank in the taxonomic hierarchy below the rank of species and subspecies and above the rank of form (form/variety/subspecies/species). Another meaning, as used in the ICNCP (the "cultivated variety" or "cultivar"), refers to cultivated variants originating through human influence.

Regarding the use of variety in the ICBN, species variation has been subdivided through infraspecific classifications. The relationships of the infraspecific categories allowed in the ICBN are strictly hierarchical, and as such they are differentiated by their degree of uniqueness: subspecies within a species should differ less among themselves than separate species, varieties should differ less among themselves than subspecies, and forms less than varieties. In practice, however, different taxonomists treat variation patterns differently. For example, sometimes a species is subdivided in subspecies and these in varieties, but in other cases a species is subdivided directly into varieties and the subspecies rank is not used at all (Hamilton and Reichard 1992). Some taxonomists feel that recognizing subspecies indicates a geographical component, with subspecies being mostly allopatric, while varieties may be sympatric. This is not a formal or universally held distinction between these ranks, however.

The term becomes especially confusing with the wish to assign cultivated plants to the species from which they originate, resulting in the application of the term to cultivated plants in a form that appears as a botanical variety. The use of the rank variety for cultivated plants goes back to Linnaeus (1753). In many cases Linnaeus started his treatment of a species with the wild plant, mentioning cultivated varieties at the end (Wijnands 1986). Linnaeus clearly considered varieties as minor variants due to the influence of climate or soil, or in the case of cultivated varieties, of human influence. He later stated that the grouping of cultivated plants should be the task of beginners in botany, while qual-

ified botanists should study species and higher taxonomic levels (Linnaeus 1764). Many later workers on the taxonomy of cultivated plants continued the practice of applying variety names for cultivated plants, burdening nomenclature with formal names with all the inherent problems of typification and priority that these entail. In these systems (e.g. Helm, 1957, 1963) the varieties are often grouped in artificial higher categories like **convariety** (or **convar**). Convarieties can be roughly comparable to cultivar groups, but convarieties, unlike cultivar groups, do not necessarily contain named varieties, and convarieties are members of traditional “Linnaean” ranks. The ICNCP replaced this term with the term *cultivar-group*, and convarieties should not be used in modern cultivated plant taxonomy (Trehane et al., 1995). Some modern influential works, however (e.g., Hanelt 2001), ignore rules of the ICNCP and continue to use the term *convar* (convariety).

The term *cultivated variety* (cultivar) in the ICNCP, in contrast, is used in a very different way. The botanical variety has its fixed position in the taxonomic hierarchy. The cultivated variety stands outside this hierarchy because it could have resulted from many different processes as selection or a complex series of interspecific hybridizations, making it impossible to assign it a position in the hierarchy. Because of this, the nomenclature of the cultivated variety follows the ICNCP, dispensing with Latin epithets used in hierarchical ranks in the ICBN. Presently, however, names originally published as botanical varieties still refer to cultivated material. These entities can be reclassified as cultivars, or if a botanical variety was described to encompass many cultivated morphotypes (as is the case in the classification of *Brassica oleracea*) they can be reclassified as cultivar-groups (van den Berg 1999). Thus, the botanical variety *Brassica oleracea* var. *gemmifera* can be reclassified as *Brassica oleracea* Gemmifera Group, encompassing the many cultivars of brussels sprouts. However, the term variety for cultivar is still in wide use in legal documents all over the world. ICNCP deals with this in stating that the term *variety* as used in such texts is fully equivalent to *cultivar* (ICNCP, art. 2, note 2; art. 2.4).

Legally, *variety* can have additional definitions. For example, the U.S. Plant Variety Protection Act (PVPA) uses the term “cultivar” in a manner similar to the botanical “variety,” but with the additional stipulation that “development” must take place from wild stock, as through breeding or genetic engineering. That is, discovery of unique variants alone does not make a cultivar eligible for protection under the PVPA. In addition, PVPA protection of varieties is granted with the additional requirements that it is “new,” “distinct” from other cultivars, “uniform,” and “stable.”

The botanical rank *form* has also been used extensively to describe minor variants of cultivated plants. Its use in the classification of wild plants is generally discouraged because the entities that could be described as forms are usually such minor morphological variations that it is arguable whether their distinction is useful. For cultivated plants these forms may easily be reclassified as cultivars. The same goes for the many informal and often ill-defined terms like *strain*, *sport*, *type*, and so on. If any such entity is worthy of recognition and description, it will be best to employ the general term *cultivar* for all of these.

B. Culton Versus Taxon

A fundamental difference between the ICNCP and ICBN is their respective approach toward classification. Groups of plants used in the ICBN to classify and name are collectively designated as taxa (singular: *taxon*). The ICNCP uses the terms **cultivar** and **cultivar-group** for cultivated plants. Although it claims that they are taxa, these terms do not fit the definition of taxa for several reasons. This may become clear by the definition in the ICNCP of the term *cultivated plant*:

A cultivated plant is one whose origin or selection is primarily due to the intentional activities of mankind. Such a plant may arise by deliberate or, in cultivation, accidental hybridization, or by selection from existing cultivated stock, or may be a selection from minor variants within a wild population and maintained as a recognizable entity solely by deliberate and continuous propagation.

A key point is the influence of humans on the origin of cultivated plants, disrupting natural evolutionary and environmental factors and constraints. Plants in the wild are subject to natural selection, whereas cultivated plants are subject to conscious or unconscious human selection.

Hetterscheid, van den Berg, and Brandenburg (1996) have argued that classifications of cultivated plants and wild plants have different goals. Whereas wild plants are classified in a system that seeks to clarify evolutionary relationships, cultivated plants are (or should be) classified according to special purpose user-defined criteria, with stability of names as primary, requiring a totally different classification philosophy. Practitioners of the taxonomy of cultivated plants have not yet completely accepted this (Hetterscheid and van den Berg 1996). Since the term *taxon* is used as a basis for evolutionary classifications, it seems illogical to use the same term for very different kinds of classifications. The most important consequence of this is the substitution of the concept of “culton” for “taxon” for systematic groups of cultivated plants

(Hettterscheid and Brandenburg 1995a, 1995b), but this term has not yet been included in ICNCP rules to the full extent. The definition reads:

A culton is a systematic group of cultivated plants based on one or more user-criteria. A culton must have a name according to the rules of the International Code of Nomenclature for Cultivated Plants.

This definition emphasizes the essential role of human activity, in using the term “user-criteria” as the sole basis for the creation of systematic groups of cultivated plants (*cultra*). This does not preclude studies of the origin of cultivated plants from existing natural populations. The point here is to divorce the *nomenclature* of cultivated plants from closed classifications that imply relationships, because artificial selection and hybrid origins often render this system nonsensical and nomenclaturally unstable.

C. Open Versus Closed Classifications

Classifying plants involves putting sets of individual plants in boxes, where the boxes are the ranks in the taxonomic hierarchy (e.g., species, genus, family, order). On the basis of classification criteria, a number of individuals are put in a box. This system of boxing has one important principle: every box belongs in a higher, more inclusive (larger) box and, vice versa, every box contains one or more boxes itself, with the largest box being “life.” In classification terms, this equates to: one or more species add up to form a genus, one or more genera add up to form a family, all the way through the taxonomic hierarchy.

When we supplant the term *box* with *taxon* we have described the classification system of the ICBN and which is called a ***closed classification system***. The ICBN says that there are an infinite number of levels (ranks) that can be constructed and named. Some ranks are specifically mentioned (e.g., the ranks called subspecies, species, genus, family, order) but their number may be increased infinitely. This is the nature of the hierarchy of levels typical in traditional nomenclature.

Another mechanism typical for closed classifications is that when the individuals in a certain box (taxon) are going to be put in smaller boxes, *all* those individuals must be in smaller boxes and not one may be left on its own in the larger box. For that one leftover, a separate box *has* to be created and even named.

The content of the boxes (taxa) is determined for a particular group of individuals by a taxonomist studying that group. Currently, evolutionary relationship is the primary criterion for grouping plants in taxa.

Such classifications are called *natural classifications* because they describe relationships that taxonomists think are “real” in nature (see “Culton Versus Taxon”). Typical for such classifications is the use of as many characters as possible to gain a solid evolutionary basis. This frequently is contrasted to *artificial classifications* that are based on nonevolutionary special-purpose criteria.

Whereas taxonomists of wild plants follow this closed classification system, taxonomists of cultivated plants have good reason *not* to use it (Hettterscheid, van den Berg, and Brandenburg 1996). Cultivated plants are created according to the whim of individuals. They arise by considerable hybridization and rapid selection for extreme forms. Classifying cultivated plants is directed by needs of individual groups of users, completely unlike the reason for classifying wild plants. Whereas one group may want to classify certain cultivated plants based on resistance against pests, another group may want to classify those same plants based on ornamental value. As such, the classification criteria for a certain group of cultivated plants may vary considerably, leading to the need of several coexisting special purpose classifications. Typically such classifications use few criteria and are sometimes called “artificial” classifications.

In the philosophy of *open classification* (Brandenburg, Oost, and van de Vooren 1982; Brandenburg, 1986) special purpose classifications are allowed. In this system, the only boxes created are those needed for utility to users. That is, cultivated plants not possessing the characters of interest are left out of that particular classification. This is quite logical, because if we would include this last group, it would have to be based on *not* having a number of characters, which is contrary to the goal of the classification in the first place. For instance, in a classification of a crop the attribute of leaf shape may have led to the recognition of a box called the Laced-leaf Group and a box called the Dentate-leaf Group. The mere existence of these two boxes does not mean that all plants of that crop *not* having laced or dentate leaves automatically define a third box because this would have to be defined as “plants not having dentate or laced leaves,” which is quite the opposite of the original classification intent. That particular “left-over” group would contain a very heterogeneous assemblage of cultivars, which is diametrically opposite the whole idea of user-criteria driven classification (for examples see Hettterscheid and van den Berg 1996; Hoffman 1996; Hettterscheid et al. 1999).

Another simplifying attribute of open classifications compared to closed ones is the avoidance of complex hierarchies and hierarchy names. Currently, classifying cultivated plants in an open classification system only requires two categories, the cultivar and the cultivar-group

(van den Berg 1999). Fewer names means greater stability of names (Hettterscheid 1999) and this is further aided by the fact that the ICNCP provides substantially fewer nomenclatural mechanisms compared to the ICBN.

VI. A COMPARISON OF THE ICBN AND ICNCP

The essential differences between codes of nomenclature for wild plants (ICBN) and cultivated plants (ICNCP) are shown in Table 1.2.

A. Nomenclatural Types and Standards

In the ICBN it is mandatory to designate a conserved specimen (the type specimen) to which a new species name is permanently linked. This specimen is an exclusively nomenclatural device and is designated during a new species description. Type specimens are important in revisionary studies when a taxonomist reconsiders species boundaries. For

Table 1.2 Major differences between the ICBN and the ICNCP.

International Code of Botanical Nomenclature (ICBN)	International Code of Nomenclature for Cultivated Plants (ICNCP)
Nomenclature rules for taxa (groups proposed on the basis of evolutionary classification criteria)	Nomenclature rules for culta (man-made entities)
Exclusively devised for objects classified in a closed classification system	Exclusively devised for objects classified in an open classification system
A potentially infinite number of categories	A limited number of categories, presently the cultivar and cultivar-group
Categories are not defined	The cultivar is defined
No basal rank	The cultivar is the basal unit and cannot be subdivided
Names are fixed to types	A cultivar's name and circumscription are fixed to standards
Basic binomial consists of a genus name plus a species epithet	Basic binomial consists of a (notho-)genus name plus a cultivar epithet
No nomenclature devised apart from the ranked categories	The denomination class as an extra nomenclature device
Reuse of names forbidden (homonymy)	Reuse of names allowed in certain cases

example, if a taxonomist considers two species to really be only one, type specimens determine the proper application of competing names. In such a case two or more names compete for the final choice of a name, and the ICBN provides rules to determine what is the proper name and what is the synonymized name. Generally the older name must be used (the principle of priority). In other cases, even in the absence of combining two species, existing names may be found to be incorrect because nomenclatural rules were never applied properly from the beginning.

In the ICNCP, however, cultivars are essentially not subject to revision. They are static units and once they are defined by a set of characters they are immutable, with fixed boundaries. To accomplish this, the ICNCP presents an alternative mechanism to fix both a cultivar *name* and its *description* (ICNCP Art. 32) at the same time with nomenclatural standards that are analogous to type specimens in the ICBN. These standards are specimens or collections of specimens and/or documentation designated by the author, and are deposited in public herbaria. Thus a standard is not exclusively a nomenclatural tool but also an immutable cultivar-defining device.

B. Denomination Classes and the Reuse of Epithets

A ***denomination class*** is a nomenclatural device found only in the ICNCP. It is defined (ICNCP Arts. 6.1, 17.2) as a taxon, or a designated subdivision of a taxon, or a particular cultivar-group, within which cultivar epithets must be unique. The botanical genus is the most often and widely used denomination class, but it can be any taxon as described below. A cultivar epithet must only exist once in every genus because the very nature of cultivars often defies assignment to botanical species, whereas at the level of genus (or hybrid genus) cultivars can be assigned. That is to say that attributing a cultivar to a genus is a relatively simple task and seems to work fine, whereas assigning it to a species is difficult or impossible because there are so many interspecific hybrids (sometimes of multiple hybrid origins) and sometimes companies keep pedigrees a secret. Therefore, a species epithet is not a mandatory part of a full cultivar name, but a (notho)genus is. Thus it would not be allowed to have two ornamental fig cultivars named 'Beauty' because within the genus *Ficus* only one such name would be allowed. The situation *Ficus elastica* 'Beauty' and *Ficus altissima* 'Beauty' would thus not be allowed because both could be *Ficus* 'Beauty,' and *Ficus* is a denomination class (the species is not mandatory for nomenclature of the ICNCP).

In the ICBN, however, a species epithet must *never* be used twice in the same genus. This would create two homonyms (the same name for different entities). In contrast, Article 26 of the ICNCP allows reuse of cultivar epithets in two cases. The first case allows reuse of epithets only among, but not within, a denomination class as explained with *Ficus* (ICNCP Art. 26.1). The second case allows reuse of epithets within the same genus, species or other denomination class, subject to various conditions (ICNCP Art. 26.2). For various reasons (mostly in crops with numerous cultivars and long and ongoing breeding histories) a genus may be subdivided in smaller denomination classes. In this case, a particular cultivar epithet may be used in every one of the designated denomination classes in that one genus. Thus that particular cultivar epithet is allowed to exist more than once in combination with a particular genus name. A well-known example is the three denomination classes within the Brassicaceae: (1) *Brassica campestris* + *B. juncea* + *B. napus* + *B. nigra* + *B. rapa* + *Sinapsis*, (2) *B. oleracea*, (3) the rest of *Brassica*. The same cultivar epithet could be applied in all three denomination classes, indicating different cultivars, the names of which would be indistinguishable if they would be combined only with the genus name. Another example is the situation in beets where two denomination classes are present within the species *Beta vulgaris*, making the use of the cultivar-group names necessary. Often these denomination classes are in fact perfectly useful cultivar-groups even though they may still bear cumbersome ICBN based names (ICNCP appendix IV provides a list of denomination classes at other levels than botanical genus).

Sometimes one or more botanical species are used as denomination classes (e.g., in tobacco the species *Nicotiana rustica* and *N. tabacum* together form one denomination class). Quite often genera are taken together to form a denomination class or a mixture of genera and species (e.g., in the melon family, a denomination class is established for the genus *Citrullus* + the genus *Cucurbita* + the species *Cucumis melo*). Such supra-generic or mixed denomination classes are often established because the botanically established limits between the taxa in the class are narrow and the breeding history of their cultivars easily transcends these limits. Such a breeding history makes it difficult to impossible to establish the taxon to which one could assign such cultivars. This classification uncertainty would be especially vulnerable to the destabilizing effects when cultivars are shifted from one taxon to another, with a later discovery that a cultivar epithet already exists in that other taxon, thus leading to a mandatory change of the epithet. In short,

denomination classes enhance cultivar name stability by creating a nomenclatural framework that is less sensitive to taxonomic change.

Despite this mechanism influencing the extent of reuse of cultivar epithets, reuse may also occur *within* a denomination class. The conditions for this are laid down in Article 26.2 of the ICNCP. It allows reuse of an epithet when the original cultivar bearing that epithet is no longer in existence. This decision is to be taken with great caution.

C. Botanical Hybrid (Species) Names

The ICBN contains a fairly extensive section solely describing special rules for the naming of hybrids, called the Hybrid Appendix. A **nothotaxon** is a taxon of hybrid origin and designated by the prefix notho- (as nothospecies, nothogenus). The tie between the ICNCP and the Hybrid Appendix of the ICBN is clear from ICBN Art. 28.1 Notes 1 and 3 that read:

Note 1: Hybrids, including those arising in cultivation, may receive names as provided in App. I (*App. I is the Hybrid Appendix*).

Note 3: Nothing precludes the use, for cultivated plants, of names published in accordance with the requirements of the botanical Code.

These unfortunate notes still remain in the latest edition of the ICBN (Greuter et al. 2000), as does the unaltered Hybrid Appendix. A proposal to deconstruct the Hybrid Appendix and omit Notes 1 and 3 did not make the voting floor of the latest International Botanical Congress in St. Louis in 1999.

Why do we consider the tie of the ICNCB to the Hybrid Appendix of the ICBN unfortunate? Hybrid nomenclature as described in the ICBN Hybrid Appendix is a typical set of rules based on a concept of cultivars as taxa rather than culta. It contains rules that we consider superfluous for the nomenclature and classification of cultivated plants because of the complexities of determining their relationships. They complicate matters considerably. The ICNCP specifically discourages the use of the Hybrid Appendix in circumstances of cultivated plant breeding (Recommendation 16A). Use of the Hybrid Appendix from the ICBN for describing cultivars also will increase nomenclatural instability in cultivar names because these are taxa, not tied to the ICNCP, and they have less stability as names than those in the ICNCP where stable names are part of this code's rules.

Under current nomenclatural rules, when a breeder creates a new cultivar using hybridization techniques, they may use either the ICNCP or the ICBN to create a name for it. When they use the ICBN, especially

the Hybrid Appendix, the result is a so-called Latin hybrid binomen (a genus name and specific epithet with a multiplication (\times) between the genus name and hybrid species epithet, for example *Begonia* \times *svalbardensis*). The multiplication sign indicates that plants with such a name are part of the progeny of a hybridization event. When they use the ICNCP, the result will be a cultivar name (e.g., *Begonia* 'Darling'). Under this system, two names designate the same cultivar. Since the cultivar category is especially founded to accommodate the results of all sorts of breeding techniques (including hybridization under nonnatural circumstances, ICNCP Art. 2), we consider it logical that only the ICNCP be used to name cultivars of hybrid origin, and to reserve the Hybrid Appendix for the naming of hybrids originating under natural conditions and the formation of hybrid generic names (so called notho-genera). This automatically implies that Notes 1 and 3 of ICBN Art. 28 can be deleted in future editions of the Code.

D. The Species Category in Cultivated Plant Taxonomy (Cultonomy)

The use of species epithets in the full name of a cultivar would be taxonomically superfluous because the combination of a genus name (or other denomination class) and a cultivar epithet to form the full cultivar name is sufficient to create a unique name. This is essentially the same mechanism that creates unique species names as seen in the ICBN. Nomenclatural rules for cultivated plants must establish that such a combination must be unique and then provide means to maintain that uniqueness. The development of cultivars is a process where species and generic boundaries either combine germplasm of different taxa or involve processes of selection where determining origins is very difficult. Therefore, the species category cannot be used a priori in a universal way as part of the full cultivar name.

The species category may be used when a cultivar is known to be directly selected from stock to which the species binomen is still applicable (e.g., selection of introduced ornamentals from a natural population). On the other hand, most successful ornamental crops have pedigrees of extensive hybridization that have blurred species boundaries almost entirely (e.g., *Gerbera*, *Lilium*, *Dianthus*, *Chrysanthemum*). Most agricultural crops have pedigrees of complex cultigenetic gene pools (e.g., *Brassica*, *Beta*, *Zea*).

The use of species epithets in a full cultivar name also introduces nomenclatural instability because the species epithets are subject to change by taxonomic revisions of species boundaries. With the use of only the genus name as part of the full name of a cultivar, possibilities

of name changes are reduced. This is often not yet fully recognized in statutory circumstances, where outdated classifications of crops at the level of botanical species and infraspecific levels are still in use (see Hettterscheid et al. 1999 for such a case in *Allium* and its “cultonomic” solution). Where people may object that species names are useful as classificatory devices, the ICNCP provides a better alternative with the cultivar-group. That is the primary category for grouping cultivars without having to resort to an ICBN category.

E. The (Notho-)Genus Category in Cultivated Plant Taxonomy (Cultonomy)

The botanical genus name is the only really *necessary* ICBN-based item in cultivated plant nomenclature and taxonomy. The generic identity of cultivars is usually still apparent even after a prolonged history of breeding. Therefore, a cultivar classification may be covered by a genus name as an umbrella. The combination of genus name and cultivar name becomes the necessary and sufficient basis for all cultivated plant nomenclature. The rules of the ICNCP are essentially based on this concept.

The matter may seem to be complicated by breeding efforts that transcend the limits of established plant genera. In such cases the ICBN Hybrid Appendix provides a relatively simple mechanism to create artificial genera (nothogenera) and their names to expand the possibilities of the genus level as a nomenclatural device for cultivated plants. There is a possibility that entirely unnatural nothogeneric names (only containing culta) should be lifted from the ICBN and transferred to the ICNCP to act as purely nomenclatural devices. Examples are many artificial orchid nothogenera, representatives of which will never be found in nature but only in cultivation. Thus the genus as a nomenclatural device remains as the sole useful category common to both the ICBN and ICNCP, although for different purposes.

F. Ties Between the ICBN and ICNCP

At present not all ties between the ICBN and ICNCP are severed, nor do they have to be. The remaining ties are:

1. The use of the term *taxon* in the ICNCP (hopefully to be severed).
The reasons for deleting the ICBN term *taxon* from the ICNCP were discussed earlier. The word *culton* must replace *taxon*.
2. The use of botanical hybrid (species) names in the ICNCP (hopefully to be severed).
3. The use of the species category in the ICNCP (to be limited).

4. The use of the (notho-)genus category in the ICNCP (to be maintained).

VII. POSSIBLE NEW CODES

Two vigorously debated proposals for changes in the ICBN have emerged that if adopted could affect the ICNCP as well. One of these, termed the BioCode, concerns a debate about producing a unified code for the nomenclature of all life. The other, termed the PhyloCode, has arisen out of new phylogenetic discoveries and cladistic classification theory.

A. BioCode

At present there are five nomenclature codes for organisms. The first two of these are for plants and have been discussed in this chapter:

1. International Code of Botanical Nomenclature (ICBN; Greuter et al. 2000);
2. International Code of Nomenclature for Cultivated Plants (ICNCP; Trehane et al. 1995);
3. International Code of Zoological Nomenclature (ICZN; Ride et al. 1999);
4. International Code of Nomenclature of Bacteria: Bacteriological Code (BC; Lapage et al. 1992);
5. International Code of Virus Classification and Nomenclature (VC; Van Regenmortel et al. 2000).

All of these codes have different rules, creating a degree of confusion in nomenclature across disciplines. During the last decade, zoologists and botanists have discussed the possible merits of a unified code for the nomenclature of the above first four codes (not viruses). This initiative, called the BioCode (Greuter et al. 1996, 1997), has not yet been adopted, but may again be proposed at the next International Botanical Congress. The potential advantages would be for biologists working with a wide range of organisms, as ecologists and conservationists, to have a unified code of nomenclature. Others, however, argue that the BioCode would increase nomenclatural instability and generate confusion by the use of new rules and name changes (Brummitt 1996). The BioCode would not cater to the classification and nomenclature of cultivated plants in a direct sense. The discrepancy between taxa and culta will prohibit this. The BioCode would contribute only partly to the stability of names of cultivated plants inasmuch as a part of their names may still be dependent on that code (notably at the plant genus level).

For our purposes, Art. 35 of the fourth draft of the BioCode (Greuter et al. 1997) would be relevant. It stipulates the separate status of cultivars and their nomenclature and that the ICNCP would remain independent from the BioCode:

35.1. Distinguishable groups of cultivated plants and fungi, whose origin or selection is primarily due to the intentional actions of mankind (e.g., cultivars and cultivar-groups), are not covered by this Code, but are denominated under the provisions of the International Code of Nomenclature for Cultivated Plants.

B. PhyloCode

Knowledge of phylogenetic relationships of all life is being changed very rapidly by the explosion of new data arising from molecular systematics, and the development of computers and computer algorithms able to handle these data. Many long-accepted taxa, from species to division, are being shown to be paraphyletic or polyphyletic. New knowledge of life's kingdoms arose from DNA sequence data from the small subunit of ribosomal RNA (SSU rRNA). These phylogenies showed three "domains" (Archaea, Bacteria, Eukarya) with subordinate kingdoms within them, and showed lateral transfer of genomes through endosymbiotic events (Doolittle 1999). A recently deduced amino acid sequence dataset (from DNA sequence data) of four protein genes (α -tubulin, β -tubulin, actin, and elongation factor 1-alpha) tested relationships within the Eukarya domain. The results showed a number of striking differences to the SSU rRNA phylogeny. New relationships among angiosperms were demonstrated by DNA sequences of chloroplast and ribosomal genes (APG 1998; Chase et al. 2000; Savolainen et al. 2000; and Soltis et al. 2000). Many of these changes are summarized in the Tree of Life Project (Maddison and Maddison 1998), a Web-based searchable database useful for locating phylogenetic information about a particular group of organisms. It is intended eventually to treat all groups of organisms, and is organized by a nested set of phylogenetic trees (cladograms).

Traditional nomenclature as outlined in the ICBN encounters problems when naming these newly discovered clades. The problem relates to the reliance on a system of ranked hierarchical categories (the closed classification system described earlier) to try to name clades. Under the ICBN, every species is by definition part of a genus, all genera are part of families, all the way up the taxonomic hierarchy, and every rank needs to be named. Traditional rank-based nomenclature and PhyloCode

nomenclature both attempt to have a name apply to only one taxonomic group and for each group to have only one name. In the ICBN, priority dictates that the correct name is (generally) the earliest name provided *within a rank*. As a consequence, if a clade is reclassified at a different rank, its name is usually changed. Under the PhyloCode, however, priority operates independent of rank; the earliest phylogenetically defined (Fig. 1.8) name for a clade has priority over later-defined names for the same clade. Problems in ICBN-based nomenclature to name clades are manifested in various ways as a result of this rank-based nomenclatural system. For example, it is difficult to name clades, one at a time as they are discovered, without having to change the names of other clades. It becomes difficult to name the clades one wants to name without giving formal names to groups of uncertain cladistic support (Cantino 2000).

De Queiroz and Gauthier (1992, 1994) proposed that a new nomenclatural system was needed to name clades, in which the use of ranked categories such as the genus and family is not mandatory, and these categories (if used) have no bearing on names. In their system, called phylogenetic nomenclature, names are to be applied to clades by any one of three criteria: (1) node-based clade names; (2) stem-based clade names; and (3) apomorphy-based clade names (Fig. 1.8). Cantino and de Queiroz (2000) wrote a draft version of the PhyloCode that is advanced for discussion and modification. Like the BioCode, it is constructed to be applicable to all organisms, not just plants. Approachable discussions of the PhyloCode and its ramifications can be found in Milius (1999), Withgott (2000), and Cantino (2001).

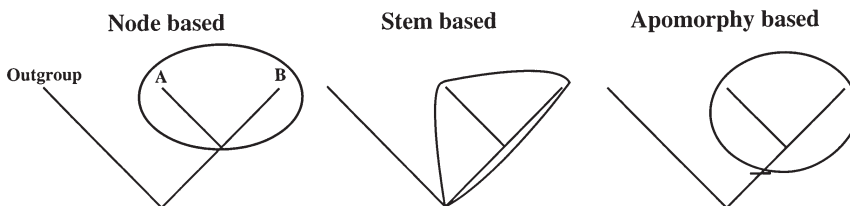


Fig. 1.8. Three classes of phylogenetic definitions (modified and redrawn from De Queiroz and Gauthier [1994]). These three trees represent a cladogram rooted on an outgroup, A and B can represent species or entire clades, and the horizontal bar under Apomorphy based represents a shared derived character (synapomorphy) delimiting a clade. Those advocating the PhyloCode propose to name clades based only on cladistic relationships and to remove the role of ranks in the application of names. *Node-based* names are defined as a clade stemming from the most recent common ancestor of species A and B. *Stem-based* clades comprise all organisms that share a more recent common ancestor with species A than with species B. An *apomorphy-based* name is defined as the clade stemming from the first species to possess a particular trait.

Needless to say, a proposal for such radical changes in nomenclature has attracted its critics (e.g., Brummitt 1996). The PhyloCode produces a more logical system for naming clades, which avoids the rank-related problems of the ICBN. However, it would drastically change a nomenclatural system that has served as a standard reference system since its inception in 1753, and critics claim that it could disrupt ties of names of all ranks, even species binomials, to the biological literature. De Queiroz (1996) and Cantino (2000) addressed these concerns. They claim that (1) many familiar names will continue to be used as they are now because these names already refer to clades (although not by explicit definition); (2) the PhyloCode does not have to supplant other codes but rather can coexist with it; (3) the abandonment of species binomials does not have to be so drastic in that species names can maintain a form that resembles existing binomials but with some qualifying label to distinguish them as PhyloCode names. We cannot predict the future of the PhyloCode, but it addresses critical concerns about nomenclature and is sure to be discussed and experimented with for some time.

VIII. CULTIVATED PLANT NOMENCLATURE AND THE LAW

National and international laws and treaties governing trade, intellectual property, breeding, and germplasm exchange of cultivars outline the economic importance of cultivated plants. Most of those using these laws are passive users of existing nomenclature of cultivars in the sense that they do not describe new names. In such laws cultivar and crop names are merely used to define the objects of the laws. Such laws may be influenced, knowingly or unknowingly, by changes in plant taxonomy. In order to keep such changes to a minimum, systems are in existence that stabilize cultivar and crop names by declaring certain names or classifications impervious to nomenclatural changes. A prominent example is the List of Stabilized Plant names as issued by the International Seed Testing Association (ISTA, see Websites). This list stabilizes names of economically important crops and may be incorporated in national or international laws. The ISTA nomenclature committee maintains the list.

Plant names have greater impact in the International Union for the Protection of New Varieties of Plants (UPOV) convention. This international treaty was developed under the aegis of UPOV (see Websites), based in Geneva. The convention lays down a system of legal protection of newly bred cultivars of plants. Breeders in countries that have signed reciprocal agreements to this convention may acquire legal ownership

of the cultivars they have developed. Breeders are given the opportunity to release cultivars under restricted circumstances and receive a profit on their investments. All the above has no direct effect on naming cultivars. However, the same convention issues a document called the "UPOV Recommendations on Variety Denominations." This document contains some imprecise recommendations on how cultivar names (the word *variety* in English-written legal texts is equivalent to the international term *cultivar*) could be established. The main purpose of this document is to ensure that, as far as possible, protected cultivars are given the same name in all member states.

The recommendations are clearly related to articles in the ICNCP but they are unfortunately not as precise, and provide much opportunity for diverse interpretations. The result is that nomenclature of cultivars differs from one member state to the other. This situation automatically leads to the establishment of cultivar epithets under legal ("statutory") circumstances that would not be allowed using the ICNCP. However, since the ICNCP has no legal status, such deviating epithets are nonetheless to be accepted (ICNCP Principle 7).

IX. CULTIVAR EPITHETS AND TRADEMARKS

Trademarks used in the trade of cultivated plants are an increasing source of nomenclatural confusion. Some breeders try to get ownership of the name of a cultivar as well as ownership of the cultivar itself. The UPOV convention and the U.S. Patent Act (see Websites) expressly prohibit this. A cultivar epithet may not be a protected trademark at the same time. This is a very logical consequence of the main purpose of a cultivar epithet: a label to be used worldwide to designate a particular cultivar in communication. A trademark may *not* be used worldwide and basically only at the discretion of the trademark owner. Obviously those two purposes are entirely different. The trademark serves to identify the products of a certain grower or company and may be used to enhance the focus of the public to the quality of the products of that particular grower or company. It is a typical commercial trading tool. However, all the individual products sold under the use of a trademark must still have generically usable individual names for purposes of communication and reference, and this is where the cultivar epithet comes in.

Unfortunately, practice is less strict. Currently, trademarks for the sale of cultivars are often made to look like cultivar epithets, which is quite often illegal but usually goes unnoticed. The actual cultivar epithet is suppressed entirely, or printed in small letters. Usually cultivar epithets in such cases are constructed to be unspeakable "words" or

numerals, thus focusing attention of the public to the commercially well-sounding trademark. For example, in 1988, UK Plant Breeders' Rights Grant No. 3743 was issued for a rose with the cultivar epithet 'Korlanum.' The cultivar is marketed under the trade designations Surrey, Sommerwind, and Vente D'Été in different countries (ICNCP Art. 11, Ex. 2). The ICNCP contains an article that enhances clarity in this matter (Art. 17.7) by stating that a cultivar epithet should be identified in a full name by demarcation marks (single quotation marks).

X. RECOMMENDATIONS FOR A UNIVERSALLY STABLE CROP NOMENCLATURE THROUGH CHANGES AND USE OF THE ICNCP

One may be daunted by all the apparent conflicts between the taxonomy of wild and cultivated plants, and if the important goal of stability of names is attainable at all. The following discussion focuses on recommendations for cultivated plant taxonomy. We support the sole use of the ICNCP for classification of cultivated plants. Attempts to merge the two have been tried ever since Linnaeus, notably at the infraspecific level. Hetterscheid and van den Berg (1996) introduced the term **cul-tonomy** for the taxonomy of cultivated plants. Although not totally accepted, here are the essential characters of the system that will enhance crop nomenclature stability:

1. Switching of emphasis in cultivated plant taxonomy from a plant-centered focus to a human-centered focus.
2. Acceptance of the culton as the fundamental systematic concept for the taxonomy of cultivated plants and simultaneous rejection of the taxon for that role.
3. Acceptance of the open classification philosophy for culta and simultaneously rejecting the use of closed systems of classification with extensive hierarchies.
4. Acceptance of the primacy of the ICNCP for nomenclatural purposes in cultivated plant taxonomy and using the ICBN only in a secondary capacity in governing names of taxa to which a classification of a crop may be linked.
5. Reducing the Hybrid Appendix of the ICBN so as to exclude rules solely based on phenomena exclusively apparent in cultivated plants. The Hybrid Appendix thus needs to be brought back to serve only nomenclatural purposes for wild plants. Consequently, hybrids of cultivated origin must not be named according to

- Hybrid Appendix rules (no further creation of hybrid species names for such plants) but exclusively using the ICNCP and its categories.
6. Avoidance, where possible, of using ICBN-based species epithets in full names of cultivars and in cultonomic classifications.
 7. Creating interest groups of users of crops that are in need of classification and evaluate their input in terms of characters to be used in the classification proposal.
 8. Promoting the use of ICNCP-based nomenclature in national and international law to obtain a worldwide standardization and stabilization of cultivar nomenclature for all circumstances where cultivar names are part of legal documents.

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- Biosys. <http://www.biosis.org/>. Provides access to information relevant to the life sciences in general.
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- Food and Agricultural Organization of the United Nations (FAO). www.fao.org/. Provides basic information on crop plants statistics. This organization has a Commission on Registration and Nomenclature, coordinating and guiding the International Cultivar Registration Authorities (ICRAs). There are ICRAs for genera of horticultural interest. An updated list will be found on this Website.
- Gardenweb. www.gardenweb.com/. Provides horticultural information and provides a glossary of horticultural and botanical terms.
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