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Peter R. Crane  
*The Field Museum*

Paul Kenrick  
*Swedish Museum of Natural History*

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## PROBLEMS IN CLADISTIC CLASSIFICATION: HIGHER-LEVEL RELATIONSHIPS IN LAND PLANTS

PETER R. CRANE

*Department of Geology, The Field Museum,  
Roosevelt Road at Lake Shore Drive, Chicago, Illinois, 60605-2496, USA*

AND

PAUL KENRICK

*Department of Palaeobotany, Swedish Museum of Natural History,  
Box 50007, S-104 05, Stockholm, Sweden*

### ABSTRACT

Recent cladistic analyses of green plants recognize an extensive hierarchical series of relatively well-supported monophyletic groups. Translating this hierarchical pattern of relationships into a usable and informative written classification is important for purposes of scientific communication, research and teaching. However, in the context of the "Linnean" hierarchy, as manifested in the current International code of Botanical Nomenclature (ICBN), effecting this translation confronts substantial practical difficulties—especially the proliferation of hierarchical levels. These problems are exacerbated by the current emphasis of the ICBN on a hierarchy in which different ranks have different formal rank-based endings. These difficulties could be ameliorated by de-emphasizing the importance of ranks in the ICBN and relaxing the constraints on how they are treated, especially at the higher taxonomic levels. Modifications are needed that permit a more straightforward integration of systematic knowledge and botanical nomenclature, and at the same time foster increased stability in the association between names and the groups of organisms that they designate.

**Key Words:** botanical code, classification, fossils, ICBN, land plants, nomenclature.

"The *Code* is a living and adapting body of law, and as long as it keeps evolving in tune with changing needs and new challenges, it will keep its authority and strength."

International Code of Botanical Nomenclature (ICBN 1994, Preface)

### INTRODUCTION

Systematics—the science of biological diversity—fulfills three fundamentally important and interconnected roles in modern biology. First, systematics has the primary responsibility for synthesizing knowledge about organisms and for integrating information from all other areas of biology into a single internally consistent and coherent understanding of the diversity of life. Second, by developing a classification that reflects patterns of evolutionary interrelationships, systematics provides a maximally predictive framework for comparative biology, and the foundation for evolutionary studies of all kinds. Third, systematics has the responsibility to develop an explicit, universal, and stable system of names that allows precise communication about the diversity of living things.

Through synthesis and analysis, systematics seeks to build new knowledge about how organisms are interrelated, and strives to improve the conceptual framework for comparative studies. But at the same time, through biological nomenclature, systematics is

concerned with communicating current knowledge in a way that is effective for a great diversity of users. These two basic goals are, to some extent, in conflict. Acquiring and synthesizing new data results in improved knowledge of relationships, which should be reflected in improved, and ultimately more stable, classifications. But changes in formal classifications inevitably introduce ambiguity, and are antithetic to the notion of stability. These contrasting goals generate tension and raise basic questions about why we do systematics and how we can best contribute to the advancement of science. On the one hand, in order to sustain itself as a scientific discipline and develop maximally predictive classifications, systematics must view patterns of relationships as hypotheses, which are subject to testing and open to falsification. But on the other hand the service function of systematics places great emphasis on stability—even tradition—as the most effective way to meet the communication needs of users in biology and other disciplines.

In this paper we explore the tension between stability and change in plant systematics, particularly as it relates to the higher-level classification of land plants. First, we provide an example where improved and more comprehensive attempts at synthesis—particularly the integration of neobotanical and paleobo-

tanical data—have resulted in a new understanding of relationships among major groups of land plants. Based on this new understanding of relationships we present a revised classification of land plants, focusing particularly on the “higher” categories. Second, we use this case study to briefly consider some of the broader issues involved in accurately translating current knowledge of relationships into written classifications, and especially in attempting to reconcile advances in systematic knowledge at higher taxonomic levels with clarity and stability of communication. In particular, this example raises the question of whether the current system of formal “Linnean” ranks embodied in the International Code of Botanical Nomenclature (ICBN 1994) eases the tension between incorporating new knowledge and nomenclatural stability, or exacerbates the problem. We conclude, that as currently formulated, some aspects of the Code do not contribute positively to its primary aims—“the provision of a stable method of naming taxonomic groups, avoiding and rejecting the use of names which may cause error or ambiguity or throw science into confusion,” and “the avoidance of the useless creation of names” (ICBN 1994, Preamble 1).

#### PATTERNS OF RELATIONSHIP

Over the last 20 years there has been rapid progress toward developing detailed hypotheses of relationships among green plants that include both extant and extinct taxa. The basis for this progress has been the development of explicit methods of phylogenetic analysis (cladistics) and the use of the principle of parsimony to test and discriminate among competing phylogenetic hypotheses. Progress has also been greatly facilitated by: i) new investigative techniques (e.g., molecular systematics) that have made available many new characters of great phylogenetic utility; ii) detailed comparative studies and increased integration and systematization of the relevant neobotanical and paleobotanical data; and, iii) the widespread availability of new computer-assisted analytical techniques that have increased the speed and accuracy with which large datasets can be analyzed and competing hypotheses can be compared.

Based on a cladistic approach the major features of green-plant classification can be summarized in terms of a simple model that includes five progressively less inclusive groups: green plants (chlorobionts), land plants (embryophytes), vascular plants (tracheophytes), seed plants (spermatophytes) and flowering plants (angiosperms) (Crane 1985). Under this model the “green algae,” “bryophytes,” “pteridophytes” and “gymnosperms,” as traditionally circumscribed, are paraphyletic and cannot be defined by derived features that they alone possess. In effect, “green algae”

Table 1. Selected cladistic studies of relationships among major groups of land plants that provide the basis for the patterns of relationships summarized in Fig. 1.

Chlorobionts	Mishler et al. (1994)
Streptobionts	Graham et al. (1991), McCourt et al. (1996)
Embryobionts	Mishler and Churchill (1985a,b) Kenrick and Crane (1991, 1997)
Marchantiomorphs (hepatics)	Mishler and Churchill (1985a,b)
Anthocerotomorphs (hornworts)	Mishler and Churchill (1985a,b)
Bryomorphs (mosses)	Mishler and Churchill (1985a,b)
Polysporangiomorphs (polysporangiophytes)	Kenrick and Crane (1991, 1997)
Tracheophytes	Kenrick and Crane (1991, 1997)
Lycophytes	Crane (1990), Kenrick and Crane (1991, 1997)
Euphyllophytes	Kenrick and Crane (1991, 1997)
Moniliforms	Kenrick and Crane (1991, 1997)
Filicopsids	Pryer et al. (1995)
Radiates	Kenrick and Crane (1991, 1997)
Spermatophytes	Crane (1985), Doyle and Donoghue (1986), Nixon et al. (1994), Rothwell and Serbet (1994)
Angiosperms	Chase et al. (1993), Doyle et al. (1994), Drinnan et al. (1994)

are the “residue” of green plants after the land plants have been removed. Similarly, “bryophytes” are merely nonvascular land plants, “pteridophytes” are those vascular plants that are not seed plants, and “gymnosperms” are the “residue” of seed plants after angiosperms are excluded.

Using this model as the framework, and utilizing other studies that provide more detailed treatments of extinct and extant plants (Table 1), it is now possible to develop a classificatory scheme that recognizes and defines a large number of nested groups. These groups describe the relationships among living and fossil land plants in greater detail than has previously been possible, and the resulting scheme provides a useful basis for comparative studies in the plant sciences. The pattern of relationships for part of this hierarchy (land plants up to but not including seed plants) is summarized in the form of a cladogram in Fig. 1.

#### TOWARD A PHYLOGENETIC CLASSIFICATION

Cronquist et al. (1966, p.129) pointed out that the “general system of plants and the nomenclature of higher taxa at the level of divisions and classes are now unstable and in a state of confusion.” They went on to point out (p.129) “there is now a bewildering plethora of systems and partial systems, each of which may lay some claim to being the best representation of the similarities, differences and evolutionary relationships within all or some part of the plant kingdom.” These words are as true today as they were 30

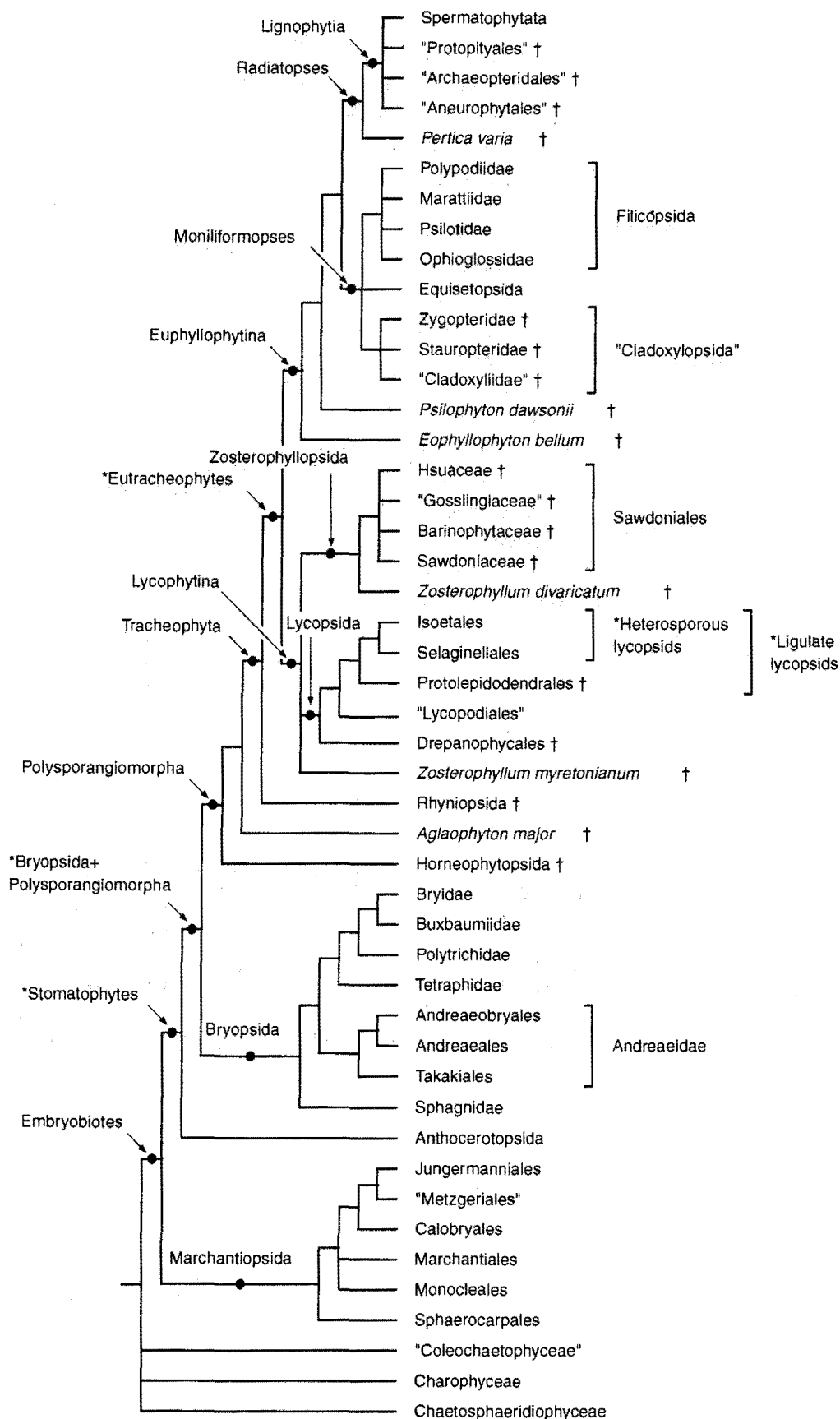


Fig. 1. Cladogram showing hypothesized relationships for all major taxa between Charophyceae and seed plants for comparison with the classifications in Tables 5-7. Fossil taxa indicated †; \* indicates clades not named in formal classification.

Table 2. Classification of the higher taxa of embryophytes (Cronquist et al. 1966).

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Division Rhyniophyta
Class Rhyniatae
Division Bryophyta
Class Anthocerotae
Class Marchantiatae
Class Bryatae
Division Psilotophyta
Class Psilotatae
Division Lycopodiophyta
Class Lycopodiatae
Class Isoetatae
Division Equisetophyta
Class Hyeniatæ
Class Sphenophyllatae
Class Equisetatae
Division Polypodiophyta
Class Polypodiatae
Subclass Protopteridiidae
Subclass Archaeopteridiidae
Subclass Ophioglossidae
Subclass Noeggerathiidae
Subclass Marattiidae
Subclass Polypodiidae
Subclass Marsileidae
Subclass Salviniidae
Division Pinophyta
Subdivision Cycadicae
Class Lyginopteridiatae
Class Cycadatae
Class Bennettitatae
Subdivision Pinicae
Class Ginkgoatae
Class Pinatae
Subclass Cordaitidae
Subclass Pinidae
Subdivision Gnéticæ
Class Gnetatae
Subclass Ephedriidae
Subclass Welwitschiidae
Subclass Gnétidae
Division Magnoliophyta
Class Magnoliatae
Class Liliatae

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years ago. Cronquist et al. (1966) presented a new classification based on their combined experience with botanical phylogeny (Table 2), but the availability now of a refined, more explicit and relatively well-supported understanding of the relationships among major groups of land plants (Kenrick and Crane 1997) offers a new opportunity to develop a revised classification. The objective of this new classificatory scheme is to reflect accurately patterns of relationships—in the same way that Cronquist et al. believed (1966, p.129-130) “that any proper taxonomic classification must be consistent with phylogeny.”

Bremer (1985) and Bremer et al. (1987) were among the first to attempt a comprehensive “higher”-level classification of land plants based on early stud-

Table 3. Cladistic classification of green plants from Bremer (1985). Paraphyletic taxa or taxa of uncertain monophyly are indicated in quotes.

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Subkingdom Chlorobionta, green plants
Division Chlorophyta
Class “Ulvophyceae”
Class Pleuroastrophyceae
Class Chlorophyceae
Division Streptophyta
Subdivision Chlorokybophytina
Class Chlorokybophyceae
Subdivision “Zygophytina”
Class Zygothryceae
Class “Klebsormidiophyceae”
Subdivision Chaetosphaeridiophytina
Class Chaetosphaeridiophyceae
Subdivision Charophytina
Class Charophyceae
Subdivision “Coleochaetophytina”
Class “Coleochaetophyceae”
Subdivision Embryophytina
Superclass Marchantiatae
Class Marchantiopsida
Superclass Anthocerotatae
Class Anthocerotopsida
Superclass Bryatae
Class Bryopsida
Superclass Tracheidatae
Class Psilotopsida
Class Lycopodiopsida
Class Equisetopsida
Class “Polypodiopsida”
Subclass Ophioglossidae
Subclass Marattiidae
Subclass Polypodiidae
Class Spermatopsida

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ies of cladistic relationships among major plant groups (Table 3). The approach adopted by Bremer et al. (1987), as well as that advocated by most of the cladistic literature (e.g., Wiley 1981), is based on two axioms. First, all groups recognized must be monophyletic (see Brummitt 1996, for a contrasting view and Table 4 for a list of selected paraphyletic or otherwise problematic groups of land plants). Second, the pattern of relationships should be directly retrievable from the formal classification. To follow this second axiom, but to avoid excessively proliferating the number of hierarchical levels in their classifications, Bremer et al. (1987), Wiley (1981) and others have adhered to several formal conventions in constructing their classificatory schemes. We have followed these axioms and similar conventions in attempting to translate Fig. 1 into a written classification, but because the extent of phylogenetic resolution has resulted in numerous hierarchical levels, the process confronts a variety of practical difficulties.

Several of the problems in converting cladistic patterns of relationships into formal classifications were addressed in a classic paper by Patterson and Rosen

Table 4. Commonly used paraphyletic or otherwise problematic groups.

"Green algae"	Paraphyletic with respect to land plants (embryophytes). Comprises green plants that are not embryophytes.
"Charophycean algae"	Paraphyletic with respect to land plants (embryophytes). Comprises embryophyte stem-group taxa such as Chlorokybophyceae, Zygnemophyceae, Klebsormidiophyceae, Chaetosphaeridiophyceae, Charophyceae, Coleochaetophyceae.
"Bryophytes"	Probably paraphyletic with respect to vascular plants (tracheophytes). Comprises three monophyletic groups: liverworts (Marchantiopsida), hornworts (Anthocerotopsida), and mosses (Bryopsida).
"Protracheophytes"	Paraphyletic with respect to tracheophytes. Comprises extinct, nonvascular polysporangiophytes such as <i>Aglaophyton major</i> and <i>Horneophyton lignieri</i> and some nonvascular <i>Cooksonia</i> -like fossils.
"Rhyniophytina" <i>sensu</i> Banks ("rhyniophytes")	Paraphyletic (possibly polyphyletic) with respect to eutracheophytes. Much disagreement over scope and definition.
"Zosterophyllophytina" <i>sensu</i> Banks ("zosterophylls")	Paraphyletic with respect to Lycopsidea. Comprises extinct zosterophylls and basal lycophytes.
"Trimerophytina" <i>sensu</i> Banks ("trimerophytes")	Paraphyletic with respect to Moniliformopses and Radiatopses. Comprises taxa such as <i>Psilophyton</i> and <i>Pertica</i> .
"Pteridophytes"	Paraphyletic with respect to seed plants (Spermatophytata). Comprises nonseed plant tracheophytes.
"Progymnosperms"	Paraphyletic with respect to seed plants (spermatophytes). Comprises woody seed plant stem-group taxa such as <i>Tetraxylopteris</i> and <i>Archaeopteris</i> .
"Pteridosperms"	Paraphyletic or polyphyletic assemblage of extinct basal seed plants (spermatophytes). Comprises taxa in the seed plant stem-group, such as hydraspermans and medullosans, as well as taxa that are more closely related to extant seed plants, such as <i>Callistophyton</i> , <i>Caytonia</i> , glossopterids, etc.
"Gymnosperms"	Paraphyletic with respect to angiosperms. Comprises all non-angiosperm seed plants.

(1977) at an early stage in the development of cladistics. These authors were particularly concerned with difficulties that arise from incorporating fossils into classifications based on extant taxa. They noted (Patterson and Rosen 1977, p.155) "If we accord equal

rank to sister-taxa, even a single paleospecies will have to be accorded a rank equal to its recent sister group, and the two sister-groups together a still higher inclusive rank. The addition of fossils to the classificatory system, while according them taxonomic rank on an equal basis with Recent organisms, can only further compound the growing problem of nomenclatorially representing phylogenetic hypotheses."

In response to this difficulty Patterson and Rosen (1977), Wiley (1981) and others, have advocated classifying fossils with Recent organisms, but treating them in a different way. This approach also persists in more recent cladistic discussions (e.g., de Queiroz and Gauthier 1992, Appendix). Patterson and Rosen (1977) proposed that fossils should be designated as "plesions," and in doing so suggested that "it should no longer be necessary to rank fossils formally" (Patterson and Rosen 1977, p.160). Plesions may be inserted at any level in a classification without altering the rank or name of any other group. This convention does not go as far as Crowson (1970) and Hughes (1976, 1994) in advocating completely separate classifications of extant and fossil organisms, but it does treat fossils differently from extant taxa. In particular, it circumvents the need to assign new higher formal ranks to fossils and thereby conserves levels in the hierarchy, and the formal name endings associated with them. Used in conjunction with the sequencing convention (Nelson 1974)—in which consecutive taxa of the same rank and indentation are the sister group of all those succeeding them—the plesion convention minimizes the contributions of fossils to the proliferation of formally recognizing hierarchical levels.

In considering how to translate our current understanding of land plant relationships (Fig. 1) into a meaningful classification (Table 5) we have gone further than Nelson (1974) and Patterson and Rosen (1977) in applying the sequencing convention not only to fossils but also to extant taxa. We have also followed Wiley (1981) in using two annotations to indicate uncertainty in the pattern of systematic relationships. Use of *sedis mutabilis* indicates that the taxa which follow at the next level of the hierarchy are of uncertain relationship (i.e., form a polychotomy). The use of *incertae sedis* indicates that the taxon to which this epithet is attached is of uncertain relationship. Groups for which monophyly is equivocal are marked with quotes (e.g., "Aneurophytales").

In constructing our classification (Table 5) we have attempted to preserve, as far as possible, the groups recognized in the early cladistic classification of Bremer et al. (1987). We have also sought to conserve common usage, particularly at the level of angiosperms, by not using hierarchical categories at the ordinal level or below for "higher" groups of seed plants. We have followed the ICBN (1994) with re-

Table 5. Cladistic classification of green plants from Kenrick and Crane (1997) using a modified "Linnean" hierarchy (indented at the level of categories and incorporating the sequencing convention for both fossil and extinct taxa: plesion convention also used for fossils which are indicated †). At the level of Class the two alternative standardized endings given in the ICBN for classes of algae (-ophyceae) and "higher" green plants (-opsida) are shown throughout to emphasize their application to the same level of the hierarchy. Taxa that are of questionable monophyly, or that are only weakly supported in the cladistic analysis are marked with quotes. *Sedis mutabilis* indicates that the taxa which follow at the next level of the hierarchy are of uncertain relationship (i.e., form a polytomy). *Incertae sedis* indicates that the taxon to which this epithet is attached is of uncertain relationship. This classification is identical to that presented by Kenrick and Crane (1997 Table 7.1).

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Superkingdom Eukaryota (Domain Eucarya)
Kingdom Chlorobiota (Metaphytae, Plantae)
Subkingdom "Micromonadobionta" <i>incertae sedis</i>
Division "Micromonadophyta"
Class "Micromonadophyceae" ("Micromonadophytopsida")
Subkingdom Ulvobionta
Division Ulvophyta
Class "Ulvophyceae" ("Ulvophytopsida")
Class Pleurastrorphyceae (Pleurastrorphytopsida)
Class Chlorophyceae (Chlorophytopsida)
Subkingdom Streptobionta
Infrakingdom Chlorokybiotes
Division Chlorokybophyta
Class Chlorokybophyceae (Chlorokybophytopsida)
Infrakingdom "Klebsormidiobiontes"
Division "Klebsormidiophyta"
Class "Klebsormidiophyceae" ("Klebsormidiophytopsida")
Infrakingdom Zygnemobiontes
Division Zygnemophyta
Class Zygnemophyceae (Zygnemophytopsida)
Infrakingdom Charobiontes <i>incertae sedis</i>
Division Charophyta
Class Charophyceae (Charophytopsida)
Infrakingdom Chaetosphaeridiobiontes <i>incertae sedis</i>
Division Chaetosphaeridiophyta
Class Chaetosphaeridiophyceae (Chaetosphaeridiophytopsida)
Infrakingdom "Coleochaetobiontes" <i>incertae sedis</i>
Division "Coleochaetophyta"
Class "Coleochaetophyceae" ("Coleochaetophytopsida")
Infrakingdom Embryobiontes
Superdivision Marchantiomorpha
Division Marchantiophyta
Class Marchantiopsida (Marchantiophyceae)
Order Sphaerocarpaceae
Order Monocleales <i>incertae sedis</i>
Order Marchantiales <i>incertae sedis</i>
Order Calobryales
Order "Metzgeriales"
Order Jungermanniales
Superdivision Anthocerotomorpha
Division Anthocerotophyta
Class Anthocerotopsida (Anthocerotophyceae)
Superdivision Bryomorpha
Division Bryophyta
Class Bryopsida (Bryophyceae)
Subclass Sphagnidae
Subclass Andreaeidae
Order Takakiales
Order Andreaeales
Order Andreaebryales
Subclass Tetraphidae
Subclass Polytrichidae
Subclass Buxbaumiidae
Subclass Bryidae
Superdivision Polysporangiomorpha
Plesion Horneophytopsida†

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Table 5. Continued.

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Plesion <i>Aglaophyton major</i> †
Division Tracheophyta
Plesion Rhyniopsida†
Subdivision Lycophytina
Plesion <i>Zosterophyllum myretonianum incertae sedis</i> †
Class Lycopsidea (Lycophyceae)
Plesion Drepanophycales†
Order "Lycopodiales"
Plesion Protolepidodendrales†
Order Selaginellales
Order Isoetales
Plesion Zosterophyllopsida (Zosterophyllophyceae)†
Plesion <i>Zosterophyllum divaricatum</i> †
Plesion Sawdoniales (families <i>sedis mutabilis</i> )†
Plesion Sawdoniaceae†
Plesion Barinophytaceae†
Plesion "Gosslingiaceae"†
Plesion Hsuaceae†
Subdivision Euphylllophytina
Plesion <i>Eophyllophyton bellum</i> †
Plesion <i>Psilophyton dawsonii</i> †
Infradivision Monilliformopses (classes <i>sedis mutabilis</i> )
Plesion "Cladoxylopsida" ("Cladoxylophyceae") (subclasses <i>sedis mutabilis</i> )†
Plesion "Cladoxyliidae"†
Plesion Stauropteridae†
Plesion Zygopteridae†
Class Equisetopsida (Equisetophyceae)
Class Filicopsida (Filicophyceae) (subclasses <i>sedis mutabilis</i> )
Subclass Ophioglossidae
Subclass Psilotidae
Subclass Marattiidae
Subclass Polypodiidae
Infradivision Radiatopses
Plesion <i>Pertica varia</i> †
Supercohort Lignophytia (cohorts <i>sedis mutabilis</i> )
Plesion "Aneurophytales"†
Plesion "Archaeopteridales"†
Plesion "Protopityales"†
Cohort Spermatophytata
Plesion "Calamopityaceae" <i>incertae sedis</i> †
Plesion "Hydraspermaceae"†
Plesion "Lyginopteridaceae"†
Plesion Medullosaceae†
Subcohort Euspermatocoides (infracohorts <i>sedis mutabilis</i> )
Infracohort Cycadatae
Plesion Callisotphytaceae†
Infracohort Coniferophytatae
Plesion Cordaitida†
Superclass Coniferidra (Pinidra)
Plesion Glossopteridaceae†
Plesion Czekanowskiaceae†
Infracohort Ginkgoatae
Plesion "Peltaspermaceae"†
Plesion "Corystospermaceae" ("Umkomasiaceae")†
Plesion Caytoniaceae†
Infracohort Anthophytatae (superclasses <i>sedis mutabilis</i> )
Plesion Pentoxylales†
Plesion Bennettitales†
Superclass Gnetidra
Superclass Magnolidra
Class "Magnoliopsida" (Magnoliophyceae)
Class Liliopsida (Liliophyceae)
Class Hamamelidopsida (Hamamelidophyceae)

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Table 5. Continued.

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Subclass Ranunculidae
Subclass Hamamelididae (infraclasses <i>sedis mutabilis</i> )
Infraclass Caryophyllidna
Infraclass "Rosidna"
Infraclass "Dilleniidna"
Infraclass Lamiidna
Infraclass Asteridna

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spect to the five principal ranks (excluding genera and species) and their hierarchical order (Art. 3.1) and we have also used the prefix "sub" to designate additional levels (Art. 4.2). Because there is an insufficient number of ranks in the Code to accommodate the number of hierarchical levels in our classification, we have introduced the rank Cohort between Division and Class. This is permissible under the ICBN, but differs from usage in some zoological classifications in which Cohort is often used as equivalent to Class. The ICBN provides that "Further ranks may also be intercalated or added, provided that confusion or error is not thereby introduced" (Art. 4.3). Therefore, to create further hierarchical levels we have also used the prefix "infra" to designate ranks immediately below the levels Subkingdom, Subclass and Subdivision; and used the prefix "super" in conjunction with Division, Cohort and Class. We considered using the prefix "intra" to create an additional hierarchical level—Intradivision—between Division and Subdivision (e.g., for eutracheophytes, Fig. 1) but for the time being we have not utilized this level in our classification.

The resulting classification (Table 5), constructed within the framework provided by the ICBN, incorporates 16 different ranks as follows: Superkingdom, Kingdom, Subkingdom, Infrakingdom, Superdivision, Division, Subdivision, Intradivision, Supercohort, Cohort, Subcohort, Infracohort, Superclass, Class, Subclass and Infraclass. To avoid the need for further ranks between Kingdom and Division we differ from Bremer (1985) in recognizing green plants as a Kingdom rather than a Subkingdom. Eukaryotes are considered a Superkingdom and embryophytes are considered an Infrakingdom. Angiosperms are treated as a Superclass with monocots and eudicots treated as Classes.

#### PROBLEMS AND ALTERNATIVE APPROACHES

It is self-evident that as sampling of botanical diversity increases based on new knowledge of living and fossils plants, as relationships become better understood, and as phylogenetic resolution improves, the hierarchy of cladistic relationships that needs to be expressed as a classification will become steadily more complex and will obviously require an increasingly large number of hierarchical levels (Fig. 1, Table 5).

As suggested by previous authors, the number of hierarchical levels needed can be reduced by applying the sequencing and plesion conventions. However, from Fig. 1 and Table 5, it is clear that these approaches fail to solve the fundamental problem of the proliferation of ranks. Also, these approaches have their own limitations. In the context of evolutionary biology, the plesion convention makes an arbitrary distinction between living and fossil organisms, while the sequencing convention will ultimately fail because it precludes the naming of potentially important clades. For example, in Table 5, to reduce the proliferation of ranks, the eutracheophytes (Lycophytina plus Euphyllophytina) of Kenrick and Crane (1991) are not named.

It is also clear that, the sequencing convention will become less and less effective in "conserving" hierarchical levels as cladograms become more highly branched and less pectinate. In addition, while previous authors have highlighted fossils as major contributors to the problem of proliferation of ranks (e.g., Patterson and Rosen 1977), exactly the same difficulties arise in dealing with any diverse group of extant organisms—single species can be the sister group to larger clades. For example, continuing to apply the approach adopted here within angiosperms would require establishing many more hierarchical levels between Infraclass and Order, and between Order and Family. Even moderate resolution of relationships in the Orchidaceae, Asteraceae or Fabaceae would also undoubtedly require many more ranks between family and genus than the three mentioned in the Code (Art. 4.2). Additional ranks become necessary because resolution of relationships within a group with a large number of members—whether extant, extinct or a mixture of the two—inevitably results in a hierarchy with many levels.

While the ICBN can, in theory, accommodate an unlimited number of additional ranks (Art. 4.3), in practice this is very problematic. As is clear from Table 5, devising numerous new categories—each with new endings—is tedious, unwieldy and provides enormous potential for confusion. While it would be possible to further elaborate the Code to ensure that a vast number of new ranks are used consistently, with the same endings, and in exactly the same order, it is self evident that the proliferation of rank-based endings

would be a major practical inconvenience to researchers and a serious barrier to students and other users. It is also clear that the associated problems would multiply rapidly as different systematists used the same name and rank for slightly different groups—or arbitrarily used different names and ranks for the same groups. Both of these problems are already especially prevalent at the higher levels of plant classification where they are a major cause of confusion and ambiguity. Compare, for example, the very different circumscriptions of angiosperm families by different authors, the very different concepts of Magnoliidae adopted by Cronquist (1981) and Takhtajan (1987), or the variety of different rank-based names that have been used for the clubmoss clade that contains *Lycopodium* s.l., *Selaginella*, and *Isoetes*.

In our view the proliferation of formal hierarchical levels that is permitted under the Code, and previous attempts to sidestep the problem (e.g., sequencing convention, plesions), do not provide a satisfactory methodology for developing modern higher-level classifications based on phylogenetic results. They undermine the main objective of equivalency between phylogenetic hierarchies and formal written classifications, and have serious practical limitations. As knowledge of relationships increases, as the number of ranks proliferates, and as the ranks and their formal endings are used more frequently with conventions such as sequencing, plesions, *sedis mutabilis* and *incertae sedis*, it will inevitably become increasingly difficult to readily retrieve the pattern of relationships from a written classification. Also, from the standpoint of evolutionary biology, it is clear that equivalency in rank between sister groups is lost by use of the sequencing convention. For example, within mosses, the Sphagnidae and Bryidae are not equivalent units, and of course there is no equivalence between taxa assigned to the same rank in different parts of the classification. Sphagnidae and Ranunculidae, for example, are not equivalent evolutionary units—even though that is implied by their equivalent rank-based endings.

In the face of these difficulties, and other problems with current approaches to nomenclature, several authors (e.g., de Quieroz and Gauthier 1992, 1994) have proposed an alternative approach to hierarchical classification that rejects many aspects of the current (“Linnean”) system, and especially the emphasis placed on taxonomic rank by current approaches to nomenclature. These authors suggest that *ad hoc* modifications of the “Linnean” system by the use of sequencing, plesions and other conventions do not accomplish their stated objectives of retrievability of phylogenetic information. Instead they propose a more radical approach to revising nomenclatural methods that would render such *ad hoc* solutions unnecessary. The aim of the approach they propose is to create a

“phylogenetic system of taxonomy” that provides a system of names for taxa that is “stable, universal and unambiguous. . . with regard to what they signify about common ancestry.” This approach seeks to replace the “Linnean” categories with the principle of descent as the basis for taxonomic convention (de Quieroz and Gauthier 1992). If fully implemented such a radical system would remove the need for the formal categories (ranks) currently recognized by the ICBN, define taxon names in terms of common ancestry, and change the way that binomials are employed. Under such a system taxon names would only be synonymous if they referred to the same clade, and priority would be based not on “first use of a name in association with a particular Linnean category, but on first use of a name in association with a particular clade” (de Quieroz and Gauthier 1992, p. 465). Formal ranks with formalized Latin endings would be discarded in favor of a simple indented system. Abandoning these formal ranks would also have the incidental advantage of reducing the inappropriate use of supraspecific categories as the units of comparison in evolutionary studies.

While these proposals may seem excessively radical, with the potential to cause nomenclatural chaos, the issues that have been raised are substantive and deserve careful consideration. There is also an interesting convergence between some of the phylogenetic (de Quieroz and Gauthier 1992, 1994) and more conventional criticisms (e.g., Bisby and Hawksworth 1991) of current nomenclatural practices. It is therefore important that phylogenetic systematics be part of the debate on the future of botanical nomenclature and discussions of how well the current Code is serving science and meeting its objectives of universality, clarity and stability in communication.

#### ALTERNATIVE CLASSIFICATIONS OF LAND PLANTS

As a case study, to inform discussions about constructing cladistic classifications of plants at the “higher” taxonomic levels, we developed three different classifications that provide contrasting representations of the same pattern of phylogenetic relationships (Fig. 1, Tables 5-7). All three classifications seek to recognize only monophyletic groups. Taxa that are of questionable monophyly, or that are only weakly supported in the cladistic analysis, are marked with quotes. The structure of the original cladogram (Fig. 1) has been fully retained in all three classifications through the application of various conventions relating to the layout on the printed page.

As discussed above, Table 5 is a classification based on a modified “Linnean” hierarchy that follows the relative rank order convention (ICBN 1994, Arts 3, 4, 5). In order to name additional important clades ad-

ditional ranks were required. These were created in accordance with Articles 4.2 and 4.3 of the ICBN (1994). Relationships among taxa are represented using the indentation and sequencing conventions recommended by Wiley (1981) and thus not all clades are named. Naming additional clades would have required the use of additional "Linnean" categories. For example, following the sequencing convention, subclasses in Bryopsida have a pectinate relationship (e.g., Sphagnidae is sister group to an unnamed clade comprising all other subclasses) that is retrievable from their layout on the page, but not from their "Linnean" ranks. This relationship could also be represented by inserting further "Linnean" categories and changing subclass names to names of successively lower rank. Table 5 also makes use of the terms *sedis mutabilis* and *incertae sedis* to override the sequencing convention and to indicate polytomies among taxa of the same rank and same indentation (e.g., the four plesions within Sawdoniales form a polytomy). The plesion convention is used for extinct taxa (Wiley 1981), which are marked "+".

We regard the classification in Table 5 as problematic for several reasons. First, in terms of written classification, the formal endings associated with the various "Linnean" ranks communicate no additional information (i.e., are redundant) because the topology of the cladogram is entirely represented by indentation and sequencing. Second, in order to name additional clades (e.g., Eutracheophyta—named in Table 6 and 7, but not in Table 5) the creation of further "Linnean" categories would be necessary. This would result in a potentially very large number of additional ranks in some groups, for example within angiosperms. Most of these would be redundant in other less species rich groups, although under the Code these ranks need not be filled. Third, there are several categories that are required by the Code (ICBN 1994, Art. 3.1) but that are redundant under certain circumstances (e.g., Class Marchantiopsida and Division Marchantiophytata within the Superdivision Marchantiomorpha). Fourth, certain rank endings are not used consistently (e.g., the class and subclass endings in "green algae" and land plants are not identical (ICBN 1994, Recommendation 16A.3). Fifth, the different treatment of fossil and living taxa (use of the plesion convention) results in a potentially confusing juxtaposition of rank-based endings. For example, the plesion Rhyniopsida has a class level ending but is used at the subdivisional rank.

In our view however, the most unsatisfactory element of the classification in Table 5 is that it requires arbitrary decisions as to the rank at which particular clades should be recognized. It is appropriate that the ICBN should not seek to restrict the freedom of plant scientists to make necessary taxonomic modifications to classifications that result from new knowledge. But,

it is more questionable whether the Code should create the conditions under which purely arbitrary decisions are effectively encouraged by the formal requirement to use rank-based endings for order, suborder, family, subfamily and tribe (ICBN 1994, Arts 17-19).

The classification in Table 6 represents relationships among taxa using the indentation and sequencing conventions recommended by Wiley (1981). The main difference from the classification in Table 5 is that commonly used taxonomic names have been conserved and the relative rank order convention has *not* been followed (*contra* ICBN 1994, Arts 3, 4, 5). In Table 6 "Linnean" ranks are not recognized and the latinized name endings formerly associated with specific ranks have no meaning. In this classification taxonomic names have a unique purpose—they are simply a means of referring to a taxon (a clade)—instead of the dual purpose stated in the ICBN—a means of referring to a taxon *and* a means of indicating rank. New taxonomic names would be simple Latinized adjectival or substantive terms appropriate to the group. The endings of such terms would not be indicative of a particular rank. As in the classification in Table 5, that in Table 6 also makes use of the terms *sedis mutabilis* and *incertae sedis* to override the sequencing convention and to indicate polytomies among taxa of the same indentation.

One consequence of the approach taken in Table 6 is that traditional Linnean taxonomic rank-based endings become mixed into an unfamiliar order, and this may be confusing unless it is clearly recognized that under the approach adopted here such endings have no meaning. For example, in this classification the "division/phylum" Embryophyta contains other taxa of the same rank such as Tracheophyta and Spermatophyta. Similarly, the "order" Euspermatales contains the "class" Angiospermopsida (c.f. examples in de Queiroz and Gauthier 1994). The main advantage of the classification in Table 6 is that commonly used names are conserved at all levels in the hierarchy and that "stability" is achieved by ignoring the strict hierarchy of ranks specified in the Code. Furthermore, with this approach, the recognition of additional taxa (fossil or extant) does not require the creation of additional Linnean ranks and does not result in nomenclatural changes that are merely the consequence of the relative rank order convention.

The classification in Table 7 represents relationships among taxa using a fully indented format. The main difference from the classification in Table 6 is that the sequencing convention (Wiley 1981) is not used, because with full indentation it is redundant. Taxa which do not have an existing name are labeled "unnamed clade," which could be Latinized if desired or ultimately replaced by formal names. The terms *sedis mutabilis* and *incertae sedis* are also redundant because

Table 6. Indented and sequenced cladistic classification of green plants using commonly applied names for individual units without regard to their rank or hierarchical ordering of ranks and rank-based endings. Fossil taxa are indicated †. Taxa that are of questionable monophyly, or are only weakly supported in the cladistic analysis are marked with quotes. *Sedis mutabilis* indicates that the taxa which follows at the next level of the hierarchy are of uncertain relationship (i.e., form a polychotomy). *Incertae sedis* indicates that the taxon to which this epithet is attached is of uncertain relationship.

## Eukaryota

## Chlorophyta

"Micromonadophyceae" *incertae sedis*

## Ulvoophyta

"Ulvoophyceae"

Pleurostrophyceae

Chlorophyceae

## Streptophyta

Chlorokybophyceae

"Klebsormidiophyceae"

Zygnemophyceae

Charophyceae *incertae sedis*

Chaetosphaeridiophyceae *incertae sedis*

"Coleochaetophyceae" *incertae sedis*

## Embryophyta

## Marchantiopsida

Sphaerocarpaceae

Monocleales *incertae sedis*

Marchantiales *incertae sedis*

Calobryales

"Metzgeriales"

Jungermanniales

## Anthocerotopsida

## Bryopsida

Sphagnales

Andreaeopsida

Takakiales

Andreaeales

Andreaebryales

Tetraphidales

Polytrichales

Buxbaumiales

Bryales

## Polysporangiophyta

Horneophytids†

*Aglaophyton major*†

Tracheophyta

Rhyniopsids†

Lycophytina

*Zosterophyllum myretonianum* *incertae sedis*†

Lycopsidea

Drepanophycales†

"Lycopodiaceae"

Protolpidodendrales†

Selaginellaceae

Isoetales

Zosterophyllopsids†

*Zosterophyllum divaricatum*†

Sawdoniales (taxa *sedis mutabilis*)†

Sawdoniaceae†

Barinophytaceae†

"Gosslingiaceae"†

*Hsua robusta*†

Euphyllphytina

*Eophyllophyton bellum*†

Table 6. Continued.

*Eophyllophyton bellum*†

*Psilophyton dawsonii*†

Moniliformophyta (taxa *sedis mutabilis*)

"Cladoxylopsida" (taxa *sedis mutabilis*)†

"Cladoxylales"†

Stauropteridales†

Zygopteridales†

Equisetopsida

Filicopsida (taxa *sedis mutabilis*)

Ophioglossales

Psilotales

Marattiales

Polypodiales

Radiatophyta

*Pertica varia*†

Lignophyta (taxa *sedis mutabilis*)

"Aneurophytales"†

"Archaeopteridales"†

"Protopytales"†

Spermatophyta

"Calamophytales" *incertae sedis*†

"Hydraspermales"†

"Lyginopteridales"†

Medullosales†

Euspermatales (taxa *sedis mutabilis*)

Cycadales

Callisotphytales†

Coniferophytales

Cordaitales†

Coniferales (Pinales)

Glossopteridales†

Czekanowskiales†

Ginkgoales

"Peltaspermales"†

Corytospermales" ("Umkomastales")†

Caytoniales†

Anthophytales (taxa *sedis mutabilis*)

Pentoxylales†

Bennettitales†

Gnetales

Angiospermopsida

"Magnoliopsida"

Liliopsida

Hamamelidopsida

Ranunculales

Hamamelidales (taxa *sedis mutabilis*)

Caryophyllales

"Rosales"

"Dilleniales"

Lamidna

Asterales

polytomies are represented by three or more consecutive taxa of the same indentation. Widely spaced groups of the same indentation are flagged with superscript numbers to aid identification of sister group pairs and polytomies. This also allows the degree of indentation to be reset at the beginning of each page. As in Table 6, commonly used taxonomic names have been conserved, the relative rank order convention has *not* been followed, rank-based endings have no meaning and are not necessary to express relationships. As

Table 7. Fully indented cladistic classification of green plants. Consecutive or numbered (superscript) taxa of similar indentation are either sister groups or unresolved polytomies. Fossil taxa are indicated †. Taxa that are of questionable monophyly, or are only weakly supported in the cladistic analysis are marked with quotes. Superscripts indicate widely separated taxa recognized at the same rank.

---

Eukaryota
Chlorophyta
<sup>1</sup> "Micromonadophyceae"
<sup>1</sup> Ulvophyta
"Ulvophyceae"
unnamed clade
Pleuroastrophyceae
Chlorophyceae
<sup>1</sup> Streptophyta
Chlorokybophyceae
unnamed clade
"Klebsormidiophyceae"
unnamed clade
Zygnemophyceae
unnamed clade
Charophyceae
Chaetosphaeridiophyceae
"Coleochaetophyceae"
Embryophyta
<sup>2</sup> Marchantiopsida
Sphaerocarpaceae
unnamed clade
Monocleales
Marchantiales
Jungermanniidae
Calobryales
unnamed clade
"Metzgeriales"
Jungermanniales
<sup>2</sup> Stomatophyta
Anthocerotopsida
unnamed clade
<sup>3</sup> Bryopsida
Sphagnales
unnamed clade
<sup>4</sup> Andreaeopsida
Takakiales
unnamed clade
Andreaeales
Andreaebryales
<sup>4</sup> unnamed clade
Tetraphidales
unnamed clade
Polytrichales
unnamed clade
Buxbaumiales
Bryales
<sup>3</sup> Polysporangiophyta
Horneophytids†
unnamed clade
<i>Aglaophyton major</i> †
Tracheophyta
Rhyniopsids†
Eutracheophyta
<sup>5</sup> Lycophytina
<sup>6</sup> <i>Zosterophyllum myretonianum</i> †

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Table 7. Continued.

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<sup>6</sup> <i>Zosterophyllum myretonianum</i> †
<sup>6</sup> Lycopsidea
Drepanophycales†
unnamed clade
"Lycopodiaceae"
Ligulateae
Protolpidodendrales†
Heterosporales
Selaginellaceae
Isoetales
<sup>6</sup> Zosterophyllopsida†
<i>Zosterophyllum divaricatum</i> †
Sawdoniales†
Sawdoniaceae†
Barinophytaceae†
"Gosslingiaceae"†
<i>Hsua robusta</i> †
<sup>5</sup> Euphylllophytina
<i>Eophyllophyton bellum</i> †
unnamed clade
<i>Psilophyton dawsonii</i> †
unnamed clade
<sup>7</sup> Moniliformophyta
<sup>8</sup> "Cladoxylopsida"†
"Cladoxylales"†
Stauropteridales†
Zygopteridales†
Equisetopsida
<sup>8</sup> Filicopsida
Ophioglossales
Psilotales
Marattiales
Polypodiales
<sup>7</sup> Radiatophyta
<i>Pertica varia</i> †
Lignophyta
"Aneurophytales"†
"Archaeopteridales"†
"Protopytales"†
Spermatophyta
"Calamopityales"†
unnamed clade
"Hydraspermales"†
unnamed clade
"Lyginopteridales"†
unnamed clade
Medullosales†
Euspermatales
Cycadales
Callistophytales†
Coniferophytales
Cordaitales†
Coniferales (Pinales)
Glossopteridales†
Czekanowskiales†
Ginkgoales
"Peltaspermales"†
"Corystospermales"
("Umkomasiales")
Caytoniales†
Anthophytales
Pentoxylales†
Bennettitales†

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Table 7. Continued.

	Bennettitales†
	Gnetales
	Angiospermopsida
	“Magnoliopsida”
	unnamed clade
	Liliopsida
	Hamamelidopsida
	Ranunculales
	Hamamelidales
	Caryophyllales
	“Rosales”
	“Dilleniales”
	Lamidna
	Asterales

in Table 6, commonly used names are conserved at all levels in the hierarchy and the recognition of additional taxa does not require the creation of additional Linnean ranks or the associated nomenclatural adjustments. The main advantage over the classification in

Table 6 is that the underlying phylogeny is represented with a single consistent convention (full indentation) rather than a combination of two conventions (indentation and sequencing). A full comparison of the three cladistic classifications in Tables 5–7 is given in Table 8. Definitions of the major groups recognized are given in Table 9.

CONCLUSIONS

The conflict between stability and change in the particular taxonomic treatments of organisms finds an interesting parallel in the discussion over the future of the Linnean hierarchy. On the one hand the concepts of orders, families, and other categories are deeply embedded in the history of biology. On the other hand, the system is clearly not working well, particularly at the “higher” taxonomic levels that are so important for the rational design of comparative studies of all kinds, as well as research and teaching in evolutionary biology. At the same time that the botanical commu-

Table 8. Comparison of the three cladistic classifications in Tables 5–7.

	Table 5	Table 6	Table 7	Comments
Subordination by Linnean category	yes	no	no	In Tables 6 and 7 widely used “Linnean” names are retained as labels for clades, but subordination and rank is not implied by the name ending.
Subordination by indentation	partial	partial	full	In Table 7 ambiguity in recognizing equivalent levels in the fully indented scheme is reduced through flagging with superscript numbers.
Nelson sequencing convention for extant and fossil taxa	yes	yes	no	In Tables 5 and 6 consecutive taxa of the same rank are either a sister group pair, or three or more progressively less inclusive clades along a pectinate branch.
“Linnean” ranks listed	yes	irrelevant	irrelevant	In Tables 6 and 7 ranks such as “Order” or “Class” are irrelevant.
“Linnean” rank endings for fossils	not enforced	not relevant	not relevant	In Table 5 “Linnean” rank endings are not enforced for fossils according to the plesion convention.
Extinct taxon designation	Plesion†	†	†	In Table 5 the plesion convention for fossil taxa is enforced.
Polytomy recognition	explicit	explicit	implicit	In Table 7 three or more taxa at the same level of indentation are a polytomy. In Tables 5 and 6 polytomies are flagged using <i>incertae sedis</i> or <i>sedis mutabilis</i> .
Unnamed clades listed	no	no	yes	In Table 7 all nodes are explicitly recognized, but only nodes that require discussion have a unique name. In Tables 5 and 6 unnamed clades are obscured by the Nelson sequencing convention and not listed.
Monophyletic groups recognized	yes	yes	yes	Only monophyletic groups are recognized in all three Tables.
Paraphyletic or polyphyletic groups recognized.	no	no	no	Paraphyletic or polyphyletic groups are not recognized in any of the Tables.
Groups of doubtful monophyletic status	quotes	quotes	quotes	Taxa of doubtful monophyletic status are marked with quotes (“ ”).

Table 9. Node-based definitions and characters for selected higher taxa recognized in the classification given in Table 7, based on the recommendations of de Queiroz and Gauthier (1994). Synapomorphy-based definitions are derived from cladistic analysis. Stability in the relationship between names and the taxa that they designate is addressed by associating names (irrespective of their latinized ending) with two specific taxa (in this cases species). For example, Embryophyta can be defined as the clade that contains the liverwort *Marchantia polymorpha* and the angiosperm *Nymphaea odorata*. These two taxa provide a fixed reference point for the name Embryophyta. The effect of this approach is to conserve the names of groups that are subsequently shown to be paraphyletic or polyphyletic by allowing the group name to be applied at a more inclusive level in the hierarchy of relationships. In other words, the name remains the same but its level of generality may be adjusted as knowledge of relationships changes. Groups defined in this way are always monophyletic. For further details see de Queiroz and Gauthier (1992, 1994).

Clade	Node-based definition: the common ancestor of the following two species and all of its descendants (fossils indicated †):		Characteristics of group that could be used to form synapomorphy-based definitions
	Species 1	Species 2	
Embryophyta	<i>Marchantia polymorpha</i>	<i>Nymphaea odorata</i>	i) multicellular sporophytes, ii) cuticle, iii) archegonia, iv) antheridia, and v) sporangium (Graham 1993, Kenrick and Crane 1997, Mishler and Churchill 1985a,b). Other synapomorphies include, vi) details of spermatozoid ultrastructure (Garbary et al. 1993, Graham and Repavich 1989, Mishler et al. 1994), vii) details of cell division (Brown and Lemmon 1990), and viii) sporopollenin in the spore wall (Graham 1990). Molecular studies summarized in Manhart (1994, 1995), Mishler et al. (1994), McCourt (1995), McCourt et al. (1996) and Kranz et al. (1995).
Marchantiopsida	<i>Marchantia polymorpha</i>	<i>Porella pinnata</i>	i) oil bodies, ii) spermatozoid ultrastructure, and possibly iii) presence of lunularic acid (Garbary, Renzaglia, and Duckett 1993, Mishler et al. 1994). Molecular studies summarized in Manhart (1994, 1995), Mishler et al. (1994), and Bopp and Capesius (1996).
Stomatophyta	<i>Phaeoceros laevis</i>	<i>Nymphaea odorata</i>	i) stomates, and possibly ii) columellate sporangium, and iii) D-methionine (Kenrick and Crane 1997, Mishler and Churchill 1985a,b).
Anthocerotopsida	<i>Phaeoceros laevis</i>	<i>Notothylas breutellii</i>	i) apical cell shape, ii) pyrenoid in chloroplast, iii) mucilage cells in thallus, iv) cavities in thallus, v) endogenous antheridia. Other putative synapomorphies include, vi) sunken archegonium, vii) vertical division of zygote, and viii) meristem at base of sporangium (Graham 1993, Hässel de Menéndez 1988, Kenrick and Crane 1997, Mishler and Churchill 1985a,b), and vi) spermatozoid ultrastructure (Garbary et al. 1993, Mishler et al. 1994).
Bryopsida	<i>Andreaea rupestris</i>	<i>Dicranum scoparium</i>	i) multicellular gametophytic rhizoids, ii) gametophytic leaves, and iii) spermatozoid ultrastructure (Garbary et al. 1993, Mishler et al. 1994).
Polysporangiophyta	<i>Horneophyton lignieri</i> †	<i>Nymphaea odorata</i>	i) multiple sporangia (sporophyte branching), ii) independent alternation of generations, and possibly iii) sunken archegonia (Kenrick and Crane 1991, 1997).
Horneophytidsida	<i>Horneophyton lignieri</i> †	<i>Caia langii</i> †	i) branched sporangia, ii) small, multicellular protuberances from the sporangium surface, and possibly iii) dehiscence through an apical slit or pore (Kenrick and Crane 1991, 1997).
Tracheophyta	<i>Rhynia gwynne-vughanii</i> †	<i>Nymphaea odorata</i>	i) annular/helical thickenings in tracheids, and possibly ii) lignin deposition on the inner surface of the tracheid cell wall (Kenrick and Crane 1991, 1997).
Rhyniopsida†	<i>Rhynia gwynne-vughanii</i> †	<i>Huvenia kluei</i> †	i) distinctive adventitious branching ( <i>Rhynia</i> -type), ii) abscission or isolation layer at base of sporangium, and iii) sporangia attached to a "pad of tissue" (Kenrick and Crane 1991, 1997).

Table 9. Continued.

Clade	Node-based definition: the common ancestor of the following two species and all of its descendants (fossils indicated †):		Characteristics of group that could be used to form synapomorphy-based definitions
	Species 1	Species 2	
Eutracheophyta	<i>Huperzia selago</i>	<i>Nymphaea odorata</i>	i) thick, lignified wall layer in tracheid, ii) pitlets between thickenings or within pits in tracheid and iii) sterome (peripheral zone of decay resistant cells in stem) (Kenrick and Crane 1991, 1997).
Lycopytina	<i>Zosterophyllum myretonianum</i> †	<i>Huperzia selago</i>	i) more or less reniform sporangia, ii) marked sporangial dorsiventrality, iii) isovalvate dehiscence, iv) conspicuous cellular thickening of the dehiscence line, v) sporangia on short, laterally inserted stalks, and vi) exarch xylem differentiation (DiMichele and Bateman 1996, Hueber 1992, Kenrick and Crane 1997).
Lycopsidea	<i>Huperzia selago</i>	<i>Isoetes engelmannii</i>	i) microphylls, ii) stellate xylem strand, iii) the close developmental association of sporangium and microphyll, iv) pitted tracheids, and v) loss of sporangium vasculature (DiMichele and Bateman 1996, Kenrick and Crane 1997).
Drepanophycales†	<i>Drepanophycus qujingensis</i> †	<i>Asteroxylon mackiei</i> †	i) bulbils or small lateral buds—a parallelism with extant Lycopodiaceae in the <i>Huperzia selago</i> group (Kenrick and Crane 1997).
Lycopodiaceae	<i>Huperzia selago</i>	<i>Lycopodium clavatum</i>	i) foveolate-fossulate microspore wall morphology (DiMichele and Bateman 1996, Kenrick and Crane 1997).
Ligulateae	<i>Leclercqia complexa</i> †	<i>Isoetes engelmannii</i>	i) ligule, ii) terete, ribbed stele, and iii) possibly radial extension of sporangium (reversed in Selaginellaceae) (DiMichele and Bateman 1996, Kenrick and Crane 1997).
Protolpidodendrales†	<i>Leclercqia complexa</i> †	<i>Minarodendron cathayensis</i> †	i) forked microphylls, and possibly ii) anisotomous branching, iii) nonsinuate sporangial epidermal cells, and iv) radial dehiscence of sporangium (Kenrick and Crane 1997).
Heterosporales	<i>Selaginella selaginoides</i>	<i>Isoetes engelmannii</i>	i) heterospory, ii) strobili, and possibly iii) reduction of gametophyte, iv) endosporic microgametophyte, and v) free nuclear cell divisions in early stages of megagametophyte (DiMichele and Bateman 1996, Kenrick and Crane 1997).
Selaginellaceae	<i>Selaginella selaginoides</i>	<i>Selaginella martensii</i>	i) more or less spherical microsporangia, and possibly ii) distal dehiscence (reversal to plesiomorphic condition from radial dehiscence), iii) 4 megaspores per sporangium, iv) suspension of stele in cavity by trabeculate endodermal cells, and v) echinate microspores (Kenrick and Crane 1997).
Isoetales	<i>Paralycopodites pulcherrima</i>	<i>Isoetes engelmannii</i>	i) cambium, ii) pseudobipolar growth involving rhizomorphic root system, and iii) monarch xylem strand in root (Bateman et al. 1992, DiMichele and Bateman 1996).
Zosterophyllopsida†	<i>Zosterophyllum divaricatum</i> †	<i>Gosslingia breconensis</i> †	i) circinate growth, ii) two-rowed sporangial arrangement, and possibly iii) elliptical xylem strand (Hueber 1992, Kenrick and Crane 1997).
Sawdoniales†	<i>Sawdonia ornata</i> †	<i>Gosslingia breconensis</i> †	i) pseudomonopodial branching, ii) planated branching system, and iii) a unique form of subordinate axillary branching (Kenrick and Crane 1997).
Sawdoniaceae†	<i>Sawdonia ornata</i> †	<i>Anisophyton gothanii</i> †	i) multicellular spines (Kenrick and Crane 1997).
Barinophytaceae†	<i>Protobarinophyton obrutsch-evii</i> †	<i>Barinophyton citrulliforme</i> †	i) unique form of heterospory (megaspores and microspores in same sporangium), ii) compact, unbranched strobilus, iii) a unique form of “clasping” sporangial orientation, and possibly iv) loss of well-defined sporangial dehiscence (Kenrick and Crane 1997).

Table 9. Continued.

Clade	Node-based definition: the common ancestor of the following two species and all of its descendants (fossils indicated †):		Characteristics of group that could be used to form synapomorphy-based definitions
	Species 1	Species 2	
"Gosslingiaceae"†	<i>Gosslingia breconensis</i> †	<i>Oricilla bilinearis</i> †	i) unique "auricular" sporangial orientation (Kenrick and Crane 1997).
Euphyllophytina	<i>Eophyllophyton bellum</i> †	<i>Nymphaea odorata</i>	i) pseudomonopodial or monopodial branching, ii) helical arrangement of branches, iii) small, "pin-nulelike" vegetative branches (nonplanated in basal taxa), iv) "recurvation" of branch apices, v) tracheids with scalariform bordered pits, vi) sporangia in pairs grouped into terminal trusses, vii) sporangial dehiscence along one side through a single slit, viii) radially aligned xylem in larger axes, and possibly ix) multiflagellate spermatozooids (convergent in <i>Isoetes engelmannii</i> ) (Bremer et al. 1987, Kenrick and Crane 1997, Stein et al. 1984). Molecular data summarized in (Albert et al. 1994, Kranz and Huss 1996, Raubeson and Jansen 1992).
Moniliformophyta	<i>Equisetum arvense</i>	<i>Thelypteris dentata</i>	i) mesarch protoxylem confined to lobes of xylem strand (Beck and Stein 1993, Kenrick and Crane 1997, Stein 1993).
Equisetopsida	<i>Equisetum arvense</i>	<i>Protocalamites longii</i> †	i) whorled appendages, ii) sporangiophore morphology, iii) stelar morphology, iv) regular alternation of appendages at successive nodes, v) microphyllous "leaves", vi) possibly cambium (lost in Equisetaceae), and vii) the presence of a perispore (possibly more general) (Stein et al. 1984). Additional characters noted by Bateman (1991) include: i) a medullated stele, ii) operculate strobili, and iii) columnar wall thickenings on sporangial epidermis. Characters supporting a close relationship between the early fossil <i>Ibyka</i> and sphenopsids include i) whorled branching (Stein et al. 1984), and ii) protoxylem disintegration to form lacunae (Kenrick and Crane 1997, Skog and Banks 1973).
Polypodiales	<i>Cephalomanes thysanostomum</i>	<i>Thelypteris dentata</i>	Leptosporangiate ferns (including Osmundaceae) i) distinctive annulate dehiscence of sporangium, ii) superficial antheridia, iii) operculate cell in antheridium, iv) "C" shaped leaf trace (Bierhorst 1971), and v) possibly siphono-dictyostelic anatomy (see also Pryer et al. 1995).
Radiatophyta	<i>Pertica varia</i> †	<i>Nymphaea odorata</i>	i) tetrastichous branching, and ii) a distinctive form of protoxylem ontogeny with multiple strands occurring along the mid-planes of the primary xylem ribs (Beck and Stein 1993, Kenrick and Crane 1997, Stein 1993).
Lignophyta	<i>Rellimia thompsonii</i> †	<i>Nymphaea odorata</i>	i) bifacial cambium producing secondary xylem, phloem and wood rays (Crane 1985, Crane 1990, Doyle and Donoghue 1986). Certain aspects of cambial activity convergent with Isoetales, sphenopsids, and some early clepsidropsids (Kenrick and Crane 1997).
Spermatophyta	<i>Elkinsia polymorpha</i> †	<i>Nymphaea odorata</i>	i) single megaspore per megasporangium and ii) integument. The medullosan plus platysperm clade is further defined on i) loss of lagenostome, ii) presence of pollen chamber, and iii) possibly also bilaterally symmetrical pollen (Crane 1985, Crane 1990, Doyle and Donoghue 1986, Rothwell and Serbet 1994).

nity is emphasizing the importance of nomenclatural clarity and stability (Hawsworth 1991, see also ICBN 1994, Preface), the current ICBN allows us to use the same names for different taxonomic units and encourages us to use different word endings for the same rank in closely related organisms (e.g., -phyceae and -opsida as class endings in "green algae" and land plants).

Even more frustrating, however, is the situation whereby different names—differing only in their Latinized ending—are used for the same taxonomic unit (e.g., Lycopodiales, Lycopodiopsida). This nomenclatural confusion has arisen because of arbitrary differences in the rank at which different authors recognize the same clade. While such differences arise because of differences of taxonomic opinion—which are properly outside the jurisdiction of the Code—they are encouraged by the emphasis on formal ranks in the ICBN. Thus, while a primary goal of the Code is to avoid "the useless creation of names" (ICBN 1994, Preamble 1) the emphasis that is placed on formal ranks creates a situation in which the useless creation of names is encouraged. It is also important to note that this situation has arisen even though most current classifications of land plants are "flat,"—that is, they attempt to convey relatively little hierarchical information—and are essentially agnostic on questions of relationships. Problems will only increase as these areas become the focus of more active research.

In this context the question that has to be asked is what function do these different ranks serve? The preamble to the Code (ICBN 1994, Preamble 1) states "The purpose of giving a name to a taxonomic group is . . . to supply a means of referring to it and to indicate its taxonomic rank." The first objective is straightforward and has broad support. However, the need to indicate rank is less obvious and more controversial. Why do we need to build an expression of formal rank into the uninomials of taxa above the level of genus? Based on the examples given here this practice contributes substantially to the complexity of nomenclatural rules. It also introduces confusion and instability because it requires that names must change with either arbitrary, or relationship-based, decisions on ranks. In an era in which the botanical community is increasingly concerned with the stability of names (see ICBN 1994, Preface) we think that most botanists—whether they support a phylogenetic approach or not—should feel uncomfortable with a Code that requires name changes for "purely nomenclatural reasons"—as opposed to "changes resulting from changing taxonomic concepts that hopefully reflect the progress of our science" (ICBN 1994, Preface). The Preamble to the current Code states "Name changes made purely for nomenclatural reasons . . . are to be avoided." In our experience, the formal system of ranks (order, suborder,

family, subfamily, tribe) and the associated system of nomenclatural rules currently recognized by the ICBN encourages just such changes. It also mandates the creation of useless names and encourages the proliferation of different names for the same taxonomic units. While it may not be necessary or desirable to formally name all clades, it seems to us that some of these difficulties could be ameliorated by de-emphasizing the importance of ranks in the ICBN and relaxing the constraints on how they are treated.

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