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On the Use of Taxonomic Concepts in Support of Biodiversity Research and Taxonomy

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Abstract

Future biodiversity research will make increased use of distributed data networks, scientific workflows, and powerful mechanisms for resolving a broad spectrum of primary data. This paper outlines the anatomy of an ecological niche modeling workflow and concomitant needs for taxonomic resolution. Contemporary Linnaean names and synonymy relationships are shown to be too imprecise too support these needs. Taxonomic concepts (i.e., the meanings of names as specified in a particular source) and a new vocabulary for expressing their semantic interrelationships are introduced as a more reliable long-term solution. The concept approach has so far been implemented with success in select taxonomic databases and regional floristic treatments. Quantitative analyses have added further weight to the claim that taxonomic concepts are suitable to overcome the problem of name/meaning disjunction inherent in conventional nomenclature. Therefore, full documentation of the taxonomic process will depend on a wider adoption of concept taxonomy. The concept approach will improve communication about nature without compromising any of the useful properties of the Linnaean system.

"Linnaean nomenclature is stable enough to say what we know, flexible enough to accommodate what we learn; independent of specific theory, yet reflective of known empirical data; compatible with phylogenetic theory, but not a slave to it; particular enough for precise communication, general enough to reflect refuted hypotheses" – Wheeler (2004: 577).

Introduction

The current system of nomenclature works well enough for many users and purposes. Linnaean names are both responsive to certain changes in taxonomic perspective and fairly stable. The former is necessary so that taxonomists can express what they learn about nature's entities and their relationships. The latter helps users such as ecologists understand each other's results – even if they are separated in space and time. Linnaean names have successfully played the role of a working compromise for 250 years.

New developments are beginning to challenge the view that the Linnaean system of nomenclature is able to satisfy the requirements of the scientific community. Future biodiversity research will become increasingly dependent upon distributed data networks, scientific workflows, and ontology-driven mechanisms for resolving a broad spectrum of primary data (Ludäscher et al., 2005a, 2005b). Biodiversity informatics must therefore provide an information technology infrastructure to support such complex tasks (Michener et al., 2005).

A prime use case for developers of biodiversity informatics technology is the ecological niche modeling (predicting of geographic ranges – past, present, and future) of a specific set of taxa based on museum specimen data (Soberón and Peterson, 2004). Taxonomic resolution is an important part of this use case, yet Linnaean names by themselves are often not precise enough to resolve data to the level required. In what context these issues occur, why they exist, how significant they are, and what ideas and tools are being developed to solve them – is the subject of this paper. Throughout, the "taxonomic concept" approach is presented as a solution not only to problems in biodiversity research, but for the long-term management of evolving perspectives in taxonomy proper.

The challenge of taxonomic resolution in a complex biodiversity analysis

Taxonomic resolution presents a significant challenge in a wide range of biodiversity studies. Consider for example the task of predicting the distributions of species of North American mammals using a workflow analysis. Two major sources of input are needed to run such an analysis. One is a list of individual specimens as recorded by museum databases and made accessible (e.g.) via the *Mammal Networked Information System.*[1] A user of the workflow infrastructure may thus call up approximately 1.5 million records, an estimated 10-20% of which have latitudinal/longitudinal data in decimal format. A typical record for the striped skunk would read "*Mephitis mephitis;* 42.456° N; -84.013° W". The other input source is a set of geo-referenced environmental variables such as topographic indices, historical climate measurements (precipitation, cloud cover, temperature, etc.), and vegetation type information. The entirety of these variables makes up the ecological niche that an individual taxon can presumably inhabit. Future distributions are then modeled using a generic algorithm for rule-set prediction under varying global climate scenarios (Peterson et al., 2002). The output is a color map with range predictions.

Like most biodiversity studies, the aforementioned mammal workflow has a critical taxonomic component. Suppose a researcher wants to predict the distributions for two different species of skunk. The process of importing the museum records must therefore produce all relevant distribution data for two separate biological entities – and nothing else. If the query fails to retrieve all data, the analysis loses power. If irrelevant records are included, or the delimitations of taxa are blurred, then the results might be false. Reliable niche predictions require precise taxonomic resolution.

When the researcher enters the names "*Mephitis mephitis*" and "*Spilogale purtorius*" to assemble all records for two kinds of skunk, he or she has to make several assumptions. The museum records might cover the entire North American region. Many date back to the 19th century. One assumption is that the specimens were identified correctly according to the then preferred reference works. Although the quality of identification can vary with the taxa under study (Meier and Dikow, 2004), this is not something one can rectify easily from a remote location.

Even if the identifications were carried out properly, a number of questions remain. For instance, is it safe to assume that data linked to different names belong to separate taxa? And vice-versa, is it safe to assume that data linked to the same name may be pooled into one list? Furthermore, is everything that used to be labeled "*Mephitis*" still part of *Mephitis* as recognized now? And will a query for "*Mephitis*" necessarily yield all records pertinent to the analysis? In each case the answer is likely negative, and so the researcher will have to take additional steps to resolve the names to meaningful biological entities. This task may include recognizing and correcting for variant name spellings (Chapman, 2005), adding records with names that are subordinate in the Linnaean hierarchy, and – most importantly – identifying and merging records labeled with synonyms. Although these resolution steps will greatly improve the analysis, two significant problems remain. First, any decision to rectify, separate, or merge data will be made in accordance with (at least) one authoritative taxonomic treatment. The latter may play the role of a "standard" now but will be outdated in a few years. The possibility to interpret and reutilize the data in the future will therefore decrease (see also Michener et al., 1997). Second, and for reasons that will be explained hereafter, the practice of merging or disjoining data on the basis of synonymy is inherently too imprecise to meet all resolution needs. In short, the conventional approach to taxonomic resolution via Linnaean names, hierarchy, and synonymy relationships is not an optimal long-term solution.

The relationship of Linnaean names and evolving taxonomic perspectives

Today's nomenclatural practice relies on methods such as the designation of type specimens and the Principle of Priority. Although sometimes under attack, these conventions have a long record of improving communication about nature. They are open to more than one theoretical interpretation (Farber, 1976; Stevens, 1984), thereby contributing to the trans-generational character of the Linnaean system. Nevertheless, because the rules of nomenclature were designed to strike a working balance, continuity and change in naming are not inextricably linked to the evolution of taxonomic perspectives. Not every new taxonomic judgment is labeled with a unique name, and not every name change reflects a revised view of taxonomic circumscription or relationship. This insight is old and might seem trivial, since all humans are accustomed to updating terms or revising their meanings from time to time. However, in the context of achieving precise taxonomic resolution, it is appropriate to examine the connection of nomenclature and taxonomy more closely.

Taxonomists and most other biologists are familiar with the particularities of naming versus delimiting taxa. For example, the senior author recently published an analysis of the weevil tribe Derelomini Lacordaire (Franz, 2006). The tribe now includes 11 genera that were placed elsewhere in the preceding weevil *Catalogue* (Alonso-Zarazaga and Lyal, 1999). It also excludes six genera that used to be part of the tribe. Only two of the 41 currently recognized genera, one of them now under a different name, were assigned to the Derelomini (then spelled *Dérélomides*) when the name was first defined in the mid 19th century. Future taxonomic updates such as revised diagnoses, additions, and subtractions of non-type elements will change the meaning of "Derelomini", but not the name itself. In such cases the name and its meaning evolve independently.

The partial disconnect of nomenclature and taxonomy may be illustrated with a contrived example (Figure 1; see also Kennedy et al., 2005). Suppose that in 1798 Fabricius named a new genus *Fantasia* F. and species *F. prima* F., based on a heterogeneous series of specimens.[2] One specimen was designated as the holotype. In 1903 Champion decided that parts of the series belong to two additional distinct species, named *F. secunda* Champion and *F. tertia* Champion. Two more holotypes were selected to represent the new entities. In 1948 Bondar reassigned the specimens "unevenly" to two of the three existing names. A heterotypic synonym *F. secunda* was created for *F. prima* which has priority. Also, a subset of the *F. secunda* specimens (according to Champion) was renamed *F. tertia*. Finally, in 2000 Afterall analyzed parts of the original 1798 material, as well as newly collected specimens with somewhat deviating features. The specimen circumscription of *F. prima* is now more inclusive in comparison to 1798 or 1903, and overlapping with 1948. The name *F. secunda* is resurrected to apply to Champion's holotype and several other specimens. The material named *F. tertia* by Champion is judged sufficiently distinctive to merit the creation of a new genus name *Realo* Afterall. The epithet for its type species is changed to *R. tertio* (Champion) to match the new gender.

The example clarifies the effect of the method of types and nomenclatural priority. For instance, there are at least three different perspectives on what the name *F. prima* means. They share the same holotype, yet the non-type elements can vary greatly in their circumscription. On the other hand, Champion's *F. tertia* and Afterall's *R. tertio* are different names with the same meaning. But this does not mean that synonymy, which is essentially a two-point comparison, can always provide the required level of taxonomic resolution. The relationships of names and meanings become still more difficult to trace if strictly nomenclatural errors are considered (spelling, availability, validity, etc.).

With the important exceptions of the genus/species link and ranks, Linnaean names change in response to new taxonomic judgments only to the extent that the uniqueness and priority of primary types is affected. Whatever "surrounds" these types and otherwise lacks priority may undergo rearrangement without triggering additional naming acts. And therein lies the inherent imprecision of Linnaean names. A researcher aiming for accurate niche modeling results must understand which circumscription of *F. prima* was used to label the museum records of interest. Was it that of 1798, 1903, or 1948? The identification label "*F. prima* F." is likely not enough to retrieve a taxonomically congruent set of records. Reliable inferences of future distributions will have to depend upon more precise semantics than offered by Linnaean names and synonymy alone.

Introducing taxonomic concepts

The solution to the above challenge is to specify the author and publication where the meaning of *F. prima* was defined or redefined. This solution is called the "taxonomic concept" approach. It is already implemented in select taxonomic databases.[3] A taxonomic concept is the underlying meaning, or referential extension, of a scientific name as stated by a particular author in a particular publication. It represents the author's full-blown view of how the name is supposed to reach out to objects in nature.[4] It is a direct reflection of what has been written, illustrated, and deposited by a taxonomist, regardless of his or her theoretical orientation.

In order to label the different usages of a name, Berendsohn (1995) proposed the term "sec." from the Latin *secundum*, or "according to". The "sec." is preceded by the full Linnaean name and followed by the specific author and publication. Two examples are *F. prima* F. sec. Fabricius (1798; the original concept) and *F. prima* F. sec. Afterall (2000; the most recent concept). Thus the concept approach allows one to address the various published meanings of the name *F. prima* F. It is now possible to trace their evolution through time.

An emerging language for concept relationships

As soon as the multiple usages of a name are assigned to their source, each of them may be reconnected in ways that are more precise than type-based definitions and synonymy relationships.[5] Five basic symbols and meanings derived from set-theory are used for comparing two concepts A and B (Figure 2): B is congruent with A, B is more inclusive than A, B is less inclusive than A, B overlaps with A, and B excludes A. The meanings should be viewed as mutually exclusive in order to maximize their usefulness (Koperski et al., 2000). Hence "overlap" means that each concept has some unique (non-shared) elements in addition to shared ones. A relationship assessment may take everything into consideration that is tied to the respective concepts, including sets of specimens, subordinate concepts, and character circumscriptions. Explanatory comments can complement the assessments, especially in the case of incongruence.

Several additional terms have proven useful for expressing concept relationships. Their meanings and applications are summarized in Table 1. Most high quality concepts will have both a diagnosis (intensional component) and a list of included subelements (ostensive component). These two aspects tend to complement each other, although the message they send need not be the same. Diagnoses reach out to as of yet unexamined objects; specimens are sometimes mislabeled, etc. Assessing concept relationships is a non-trivial task left for taxonomic experts.

Returning to the case above (Figure 1), one can now specify the taxonomic changes within *Fantasia* F. using the concept approach. For instance, *F. prima* F. sec. Fabricius (1798) is more inclusive (>) than *F. prima* F. sec. Champion (1903). Champion's other two concepts must be added to obtain congruence: *F. prima* F. sec. Fabricius (1798) is congruent (==) with the sum of *F. prima* F. sec. Champion (1903) plus (+) *F. secunda* Champion sec. Champion (1903) plus (+) *F. tertia* Champion sec. Champion (1903). In another comparison, *F. secunda* Champion sec. Champion (1903) overlaps (><) with *F. tertia* Champion sec. Bondar (1948). The two concepts share some non-type elements. Finally, *F. prima* F. sec. Champion (1903) is intensionally congruent (== INT) with *F. prima* F. sec. Afterall (2000), and also, *F. prima* F. sec. Champion (1903) is less inclusive ostensively (< OST) than *F. prima* F. sec. Afterall (2000). The latter author listed more elements, albeit of the same kind as Champion's. The intensional/ostensive distinction is useful in particular at higher taxonomic levels.

Long-term taxonomic resolution using the concept approach

The imperfect connection of nomenclatural and taxonomic adjustments over time mandates that long-term taxonomic resolution for biodiversity research be based not just on type-driven name definitions, but on the more powerful concept relationships. The vision for implementing such a service is as follows. The future storage and integration of ecological data will be made possible via a comprehensive metadata approach (Michener and Brunt, 2000). An integral part of this approach is the linking of primary observations to taxonomic concepts. This means that biodiversity researchers, when submitting their data to a networked database, will be required to *identify* these observations to sets of well specified concepts. As an example, the conventional entry "*Mephitis mephitis* Schreber" would be submitted as "*Mephitis mephitis* Schreber sec. Wilson and Reeder (1993)", if the latter were the reference consulted in the identification process. Researchers may equip their identifications with an assessment of certainty. Eventually the authoritative concepts will need to receive unique identifiers, such as those of the *Digital Object Identifier* system (Paskin, 2005).

In a separate process, taxonomic concepts must be related to each other using the above language for concept relationships (e.g. *Mephitis mephitis* sec. Wilson and Reader [1993] is more inclusive [>] than *Mephitis major* sec. Howell [1901]). The integration and dissociation of data is then based upon the relationships, with some flexibility to match the resolution needs of each analysis. The primary biodiversity data will remain resolvable for the long term, so long as the originally referenced concepts are well specified and connectable to elements in succeeding classifications.

Biodiversity studies that pay attention to the dynamics of taxonomy often yield astonishing results. For instance, Peterson and Navarro-Sigüenza (1999) analyzed avian endemism in Mexico using two alternative taxonomies. Under the biological species concept, 101 endemic species were obtained, with most endemics concentrated in the southern and western montane areas. Application of the phylogenetic species concept, in turn, produced 249 endemic species, a majority of which occurs in the western lowlands and mountains. Selecting one classification over the other therefore greatly affects conservation priorities. The concept approach is well suited to expose such critical interdependencies. Analyses similar to those of Peterson and

Navarro-Sigüenza (1999) present a powerful way to convince the ecological user community of its utility.

The taxonomic concept approach put in practice

In order to benefit biodiversity research, the concept approach must above all make practical sense for taxonomists. The implementation of concept taxonomy in two otherwise traditional treatments indicates that this is so. The particularities of each treatment will be reviewed briefly.

The *Checklist of German Mosses* (Koperski et al., 2000) is a pioneering effort in concept taxonomy. According to the authors' perspective, 1,548 names and concepts are accepted at the generic and lower levels (see Geoffroy and Berendsohn, 2003). An additional 6,996 invalid names, i.e. homotypic and heterotypic synonyms, are listed. The names and synonyms are derived from an analysis of 11 major taxonomic reference works for Central European mosses, the oldest dating back to 1927. The authors combine the 8,544 names and 12 references for a total of 24,390 cited taxonomic concepts. They established 7,891 concept relationships connecting each member in the accepted pool of concepts to one or more suitable predecessors. In short, the *Checklist* provides insight into the evolution of German moss classifications over a time span of 73 years.

The format adopted by Koperski et al. (2000) places conventional information about nomenclature alongside the new concept relationships (Figure 3A). For each entry of an accepted concept the authors provide the complete original citation. They also list the existing synonyms, either homotypic or heterotypic, as well as other invalid or unavailable names ("auct."). The entry is then completed with a series of concept relationships (typically less than ten) connecting the accepted concept to its congruent or (partly) incongruent predecessors. Often notes are added to explain particular judgments and kinds of incongruence. At the end of a genus-level entry, all unaccepted names are assigned to their valid counterparts (Figure 3A). These assignments are necessary due to the fact that there may be many-to-many relationships between invalid and valid names. In summary, the German moss *Checklist* offers its users more nomenclatural and taxonomic information than any traditional work of this scope.

The *Flora of the Carolinas* project (Weakley, 2006) is another powerful example of concept taxonomy put in practice. This treatment considers approximately 6,300 names and concepts as valid. The latter are connected to taxonomic elements of up to ten earlier reference works published between 1933 and 2005. More than 40,000 concept relationships connect the accepted concepts to their predecessors (Figure 3B). The format for displaying the relationships dovetails neatly with the remaining content and greatly enhances the taxonomic value of this publication.

Several additional implementations of the concept approach are currently underway (see also footnote 3). For instance, the major repository for prokaryote nomenclature and taxonomy is adopting concepts in combination with unique identifiers (Garrity and Lyons, 2003). North American vascular plant databases are also preparing for this transition. Smaller-scale projects such as a concept-based database of angelfishes (R.L. Pyle, personal communication) are emerging at various locations. These efforts underscore the general practicality of the concept approach.

What concept relationships say about the precision and reliability of Linnaean names

The applications of concept taxonomy offer new and quantitative insights into the performance of Linnaean names. Specifically, evaluations of the relative abundance of congruent versus incongruent relationships reflect on the precision and reliability of names over a given time span. Such assessments may be carried out as a series of two-point comparisons (i.e., reaching out repeatedly from a current set of concepts to multiple preceding sets), or through examination of entire "concept lineages" in chronological order. The results are then contrasted with parallel analyses of stability and change in naming alone.

Geoffroy and Berendsohn (2003) analyzed the moss data published by Koperski et al. (2000) along these lines. Taking the 1,548 therein recognized concepts as the accepted standard, they calculated that 1,509 concepts (97.5%) had at least one congruent predecessor. Many concepts had additional incongruent predecessors (Table 2). At a finer level of resolution, 550 concepts (35.5%) were likely taxonomically stable from 1927 to 2000, citing only homotypic synonyms and congruent relationships to previously established concepts. As many as 310 concepts (20.0%) were potentially unstable due to heterotypic synonyms or misapplied names. And no less than 688 concepts (44.5%) were explicitly unstable, citing one or more incongruent relationships. Within the latter group of unstable concepts, 530 concepts (77.0%) referenced a single kind of incongruence, 122 concepts (17.7%) mentioned two kinds, 35 concepts (5.1%) cited three kinds (see also Figure 3A), and one concept (0.1%) had all four kinds. In what is perhaps the most telling statistic from this analysis, the authors concluded that only 207 concepts

(13.3%) out of a total of 1,548 concepts have remained the same in name *and* taxonomic meaning throughout the past 73 years (Figure 4). This value is low, especially if one considers how well this particular flora was studied by 1927. Biodiversity researchers who need to integrate data across the analyzed time period may trust a name roughly one out of eight times.

Weakley (2006) carried out similar analyses with relationships originating from the *Flora of the Carolinas* project. The two-point concept comparisons between the *Flora's* perspective and eight relevant predecessors yielded 77% to 94% congruence (Table 3). Not surprisingly, the percentage of incongruent concepts increases with time. The overwhelming majority of incongruent relationships were of the ">" or "<" kind. The author also provided data on stability in name *and* taxonomic meaning, which ranged from 55% to 88% in the eight comparisons. These numbers seem more reassuring than the results for German mosses. Yet this impression will change when entire concept lineages are analyzed. An example of concept evolution in *Andropogon* L. sec. Weakley (2006) shows how poorly the names and taxonomic perspectives match among succeeding treatments (Figure 5). Using the concept approach is required to discover such discrepancies in the first place and to properly realign them.

Name/concept disjunction in five higher-level classifications of weevils

The above studies demonstrate that both the status and the meaning of Linnaean names continue to evolve from one authoritative revision to the next. What they cannot show very clearly, however, is the extent to which the transformations in naming and meaning become *disjunct* over time. For this purpose, and also to complement the picture with a zoological example, five higher-level classifications of weevils (Coleoptera: Curculionoidea) were analyzed.

The classifications were authored by Crowson (1981), Thompson (1992), Kuschel (1995), Alonso-Zarazaga and Lyal (1999), and Marvaldi and Morrone (2000). Kuschel (1995) published the first matrix-based phylogeny for weevils, which was subsequently expanded and reanalyzed by Marvaldi and Morrone (2000). The other three classifications are traditional, i.e. not cladistic. Alonso-Zarazaga and Lyal's (1999) *Catalogue* is the most recent comprehensive perspective on weevil taxonomy. The extent of topological variation among these perspectives is readily apparent (Figures 6 and 7).

A total of 172 names and 267 concepts were derived from the five taxonomies, and 1,088 concept relationships were established among their constituent elements. The entire vocabulary for expressing relationships (Table 1) was used in order to maximize the amount of congruence between classifications. Comparisons that were labeled with a ">" or "<" simply because one system did not reach down to the same hierarchical level (i.e. inclusions per rank) were excluded from the analysis. The results are therefore as favorable towards the Linnaean system as possible with this data set and approach.

The two-point comparisons between the five perspectives yielded only 18% to 54% congruence among related concepts (Table 4). The numbers were expectedly lower when stability in naming *and* meaning was assessed, ranging from 6% to 29%. In other words, each new treatment has made at least half of the preceding names and concepts unstable.

In all, 171 relationships were established between concepts carrying the same Linnaean name, and 597 relationships were made between concepts with different names (Table 5). These two sets of relationships are best suited to uncover the name/meaning disjunction inherent in the five taxonomies. Specifically, only 89 of the 171 nomenclaturally identical relationships (52.0%) were also taxonomically congruent. The other 82 relationships (48.0%) were either more or less inclusive, or overlapping. In each of these 82 cases the Linnaean names were unable to signal the changes in meaning. Overlap is typically the most complex kind of relationship; it means that the two classifications cannot be reconciled unless certain groups of subelements are added or subtracted from at least one side of the equation. The fact that there are no "|" relationships in the identical-name set is due to the method of types.

Within the other set where the compared names are not the same, 177 relationships (29.6%) are nevertheless taxonomically congruent (Table 5). Synonymy accounts for 13 of these comparisons (2.2%), whereas changes in rank – and thus in spelling – make up 30 additional cases (5.0%). The remaining 134 congruent relationships (22.4%) often represent very different nomenclatural perspectives, as illustrated in two examples of concept lineages for Brentidae and Curculionidae (Figure 8). Linnaean names are not capable of signaling the congruence in meaning in these cases. Among the 420 non-congruent relationships, the 47 assessments of overlap are also a sign of taxonomic complications (see above).

Not included in the analysis are variations in naming with purely nomenclatural origins. For instance, according to information from the *Catalogue* (Alonso-Zarazaga and Lyal, 1999; see also Figure 7), the 85 valid names are associated with 283 homotypic synonyms, 107 heterotypic synonyms, and 155 names with incorrect spelling ("lapsus").[6] At least the homotypic synonyms and the misspelled names could in principle have come into existence without reexamining specimens or new taxonomic judgments. They might further promote the name/meaning disjunction.

In summary, quantitative analyses of concept evolution in German mosses, North American vascular plants, and weevils do not support the impression that Linnaean names are sufficiently precise to accommodate what researchers have learned throughout the decades about the relationships among these taxa. Instead, the numbers demonstrate that the scenario described for the hypothetical taxon *Fantasia* (Figure 1) has abundant real-life parallels. Nomenclatural emendations and changes in taxonomic circumscription often evolve independently. Concept relationships provide the necessary resolution.

Authoritative taxonomic databases – a prime application for the concept approach

A more widespread adoption of the concept approach requires an efficient strategy for implementation. One area of application is the development and upkeep of authoritative taxonomic databases (see also Berendsohn et al., 2003; Garrity and Lyons, 2003; Kennedy et al., 2005).[7] These databases are rapidly diversifying and have become indispensable tools for research. Examples are the *USDA PLANTS Database* (http://plants.usda.gov/), the *BioSystematic Database of World Diptera* (http://www.sel.barc.usda.gov/Diptera/biosys.htm), the *Catalog of Fishes On-Line* (http://www.calacademy.org/research/ichthyology/catalog/), and the *Mammal*

Species of the World (www.nmnh.si.edu/msw/). The latter is based on a book with the same title published more than a decade ago (Wilson and Reeder, 1993). The therein proposed names and classification are routinely cited in mammal research.

Wilson and Reeder (personal communication) now have a completely revised version of the 1993 treatment. The new perspective contains significant changes in nomenclature and taxonomy; many are of the sort that cannot be expressed with names or synonymy relationships alone. In a name-based database, this all-to-common situation creates two almost equally undesirable options. The first option is to fully replace the old system with the new one. This would mean that the concepts advocated in 1993 are no longer available on-line. Consequently, other works in which these concepts were cited will lose their semantic underpinning. Users who assume that the older and newer names are taxonomically congruent incur the aforementioned risks of imprecision. The second option is to leave the database in its original state. But this amounts to a failure to adjust to latest and most supported perspective. In other words, a name-based database system is unable to fully document its own taxonomic development.

The concept approach is well suited to overcome these challenges. Using the "sec." annotation, the 1993 and 2005 perspectives can both be displayed. Precise concept relationships would connect the elements contained in each taxonomy. Users can access this information to understand the proposed changes in meaning. The concept approach is also useful for occasional "local" updates of particular taxa that have undergone revision after the latest comprehensive update went into print. Any attempt to capture the evolution of taxonomic perspectives in an on-line environment will in some form depend on this approach.

Schemas and tools in support of concept taxonomy

A "taxonomic concept schema" has been created to promote the transition towards concept taxonomy (Hyam, 2005; Kennedy et al., 2005). The schema was written in XML and is based on an inclusive model for the representation and transfer of nomenclatural and taxonomic data. It accommodates a range of information stored in different formats without data distortion. The schema has been developed in close collaboration with the *Taxonomic Databases Working Group* community and was ratified as a standard for data transfer at the 2005 Annual Meeting in Saint Petersburg, Russia.[8] For providers interested in transforming their current holdings into concepts, the taxonomic concept schema will become an essential tool. In addition there are numerous tools available that allow taxonomic experts to visualize two or more classifications, and to infer or establish new concept relationships between their constituent elements (Graham et al., 2002; Güntsch et al., 2003; Munzner et al., 2003; Parr et al., 2004; Wang and Goguen, 2004; Liu et al., 2006). Such "concept relationship tools" will combine the most powerful solutions for visualizing hierarchies with a full-scale implementation of concept taxonomy.

Conclusions – promise and practical challenges for the concept approach

This paper started out by describing the taxonomic resolution needs in a specific biodiversity research workflow. Linnaean names were shown to be too imprecise too support these needs, and taxonomic concepts and relationships were introduced as a more reliable long-term solution. This approach has so far been implemented with success in select taxonomic databases and regional floristic treatments. Quantitative analyses have added further weight to the claim that taxonomic concepts are suitable to overcome the problem of name/meaning disjunction. A full on-line documentation of the taxonomic process will therefore depend on a wider adoption of concept taxonomy. New tools are emerging towards this goal.

The concept approach improves communication about nature without compromising any of the useful properties of the Linnaean system. It does not aim to alter the method of types, the Principle of Priority, ranks, or other nomenclatural rules and conventions – all of which play a critical role in making Linnaean names more precise and reliable.

It is worth reiterating that the added semantic granularity of concepts is not required in all contexts. In many everyday cases Linnaean names are precise enough or a considerable amount of vagueness is acceptable. In other situations human cognitive abilities come to assistance. Researchers who have been exposed to similar academic environments have amazing and often intractable capabilities to understand each other's uses of language. For instance, no living weevil taxonomist would think of the meaning of "Derelomini" in the original mid 19th century sense of the term. Instead, he or she will have in mind a list of the approximately 40 genera cited in the *Catalogue* (Alonso-Zarazaga and Lyal, 1999), complemented by mental images of examined specimens, and perhaps also an influential tribal definition for "Petalochilinae" published by Kuschel (1952). A small group of experts will "understand" that there are several unpublished problems with the position taken in the *Catalogue.* They may even have exchanged views about necessary changes, and so on. In other words, competent speakers are highly accustomed to using Linnaean names in reference to a specific published or unpublished context. Naturally, this is an implicit use of the concept approach. The challenge is to uncover this kind of implied precision and make it available to a wider audience.

The concept approach is furthermore an adequate response to the discussion about "unitary taxonomy" (Scoble, 2004). Vane-Wright (2003) showed that it is almost impossible to arrive at a universally accepted classification for a particular taxonomic group. Working taxonomists tend to disagree not only with others but with their *own* previous views. It could not be any other way if new evidence is supposed to count towards the meanings of scientific terms. Instead of forcing research (however authoritative) to a standstill, a more desirable bench-mark for taxonomists is to precisely understand and document the *nature* of their disagreements. What they and other biodiversity researchers need first and foremost is the ability to *reconcile* the different views; and this is what concept relationships will provide. Whether everybody uses exactly the same "correct" taxonomy is neither as critical nor realistic. In a close match with actual practice, the concept approach allows multiple competing taxonomic perspectives to coexist and gradually undergo refinement. It was invented by people with real-life data management and integration needs.

Lastly, a more widespread adoption of the concept approach will pose several challenges. The greatest among them is to minimize unnecessary "concept inflation", or the proliferation of vaguely specified and potentially redundant concepts (Berendsohn, 1995). Indeed, in a world where the semantics of names are not fully defined unless their source is mentioned as well, every usage of a name must signal what its taxonomic source is. From a standpoint of effective communication, the ideal situation includes a pool of high quality concepts that is only as large as necessary to accommodate all taxonomically diverging perspectives. The elements in the pool are connected to their closest matches via concept relationships. Users routinely cite these concepts in their publications. Taxonomic experts take a conservative approach towards authoring new concepts, preferring instead to credit a preexisting source whose perspective they accept (if such a match is available). In short, a successful implementation of the concept approach will require experts, providers, and users of taxonomic information to be very explicit about their speaker roles. What is the switch point going from authorship to citation of a concept? It will take time and intellectual as well as sociopolitical effort to adjust to this requirement in practice.

Another challenge is the integration of phylogenetic insights and traditional classifications. This challenge is not unique to the concept approach, however, the latter carries the highest promise of resolution (Franz, 2005). In modern systematics an increasing number of phylogenetic analyses are no longer translated into classifications, even though the precise transmission of phylogenetic insights depends on the frequent revision of Linnaean names. For those phylogeneticists who are typically not interested in classifying, the threshold will be lowered to author new concepts, without also having to author new names. They can therefore reach a wider audience with their products. But the realization of this prospect depends on a better physical and semantic integration of phylogenetic and taxonomic databases (see also Page, 2004).

To conclude, the taxonomic concept approach promises immense benefits for data integration in taxonomy, phylogenetics, and biodiversity research. The challenges related to implementation are considerable, yet in light of a community-wide motivation to ready taxonomy for the *Semantic Web* (Berners-Lee et al., 2001), it appears that time is on its side.

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Endnotes

[1] See http://elib.cs.berkeley.edu/manis/

[2] The example could be modified to apply to higher-level taxa such as families and genera, or to characters, instead of specimens.

[3] The *Australian Plant Name Index* (http://www.anbg.gov.au/apni/) and the *Euro+Med PlantBase* (http://www.euromed.org.uk/) are two examples.

[4] Note that the term "concept" is not used here in the same sense as "species concepts". Species concepts are theories about what species are, how they arise, and how to recognize them (see Wheeler and Meier, 2000).

[5] The possibility remains to connect taxonomic concepts via traditional nomenclatural relationships (homonymy, synonymy, etc.).

[6] For quantitative analyses of rates of synonymization in a range of taxa see Olson (1987), Gaston and Mound (1993), Solow et al. (1995), Bouchet (1997), and Alroy (2002).

[7] In the present context "authoritative" means that the provided information was created according to standards that are very close to those established for a traditional publication in taxonomy.

[8] See http://www.tdwg.org/

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Tables

Table 1. Additional terms to express concept relationships (see also Figure 2).

Symbol or term	Meaning	Example
is parent of	A concept is superordinate to another within the same hierarchy.	A is a parent of B
is child of	A concept is subordinate to another within the same hierarchy.	C is a child of D
+ (plus)	The extensions of two concepts are added together.	A + B == C
– (minus)	The extension of a concept is subtracted from another.	B == C – D
AND	Permits the concatenation of multiple valid assertions.	A == (INT) B AND A > (OST) B
OR	Permits the expression of uncertainty via alternative assertions.	A == B OR A > B
INT (intensional)	The relationship is based only on diagnostic properties.	A == (INT) B
OST (ostensive)	The relationship is based only on constituent subelements.	A > (OST) B

Table 2. Distribution of five kinds of relationship linking the 1,548 accepted concepts in Koperski et al. (2000) to their respective predecessors (see Geoffroy and Berendsohn, 2003).

Relationship	# of concepts	% of concepts
==	1,509	97.5
>	267	17.2
<	515	33.3
><	90	5.8
|	11	0.7

Table 3. Quantitative analysis of relationships linking accepted concepts in Weakley (2006) to predecessors in eight pertinent *Floras* (complete references in Weakley, 2006).

Relationship comparison	**Relationship (%)**					**Nom./tax. stable[1]**	
Weakley (2006) *with*…	==	>	<	><	|	%	totals
Kartesz (1999)	92.9	2.5	4.6	0.0	0.0	86.4	4,064 / 4,705
Flora of North America (1993)	93.9	0.5	5.6	0.0	0.0	87.5	1,737 / 1,985
Gleason and Cronquist (1991)	87.3	2.5	10.1	0.1	0.0	75.9	2,385 / 3,144
Godfrey and Wooten (1979, 1981)	82.4	1.1	16.4	0.0	0.0	72.8	975 / 1,339
Radford et al. (1968)	81.1	2.6	16.3	0.0	0.0	68.7	1,884 / 2,742
Gleason (1952)	81.9	8.0	10.0	0.1	0.0	67.8	1,866 / 2,751
Fernald (1950)	77.1	16.4	6.2	0.3	0.0	63.5	1,951 / 3,073
Small (1933)	78.2	10.5	11.0	0.3	0.0	54.9	1,571 / 2,859

[1] Nomenclature *and* taxonomy stable.

Table 4. Quantitative analysis of relationships linking accepted concepts in five succeeding weevil classifications to each other, part I: percent values.

Relationship comparison[1]	**Relationship (%)**					**Nom./tax. stable[2]**	
Succeeding *with* preceding classification	==	>	<	><	|	%	totals
M. and M. (2000) *with* A.-Z. and L. (1999)	38.7	24.0	18.7	4.0	14.7	6.7	5 / 75
M. and M. (2000) *with* Kuschel (1995)	26.8	25.0	26.8	21.4	0.0	12.5	7 / 56
M. and M. (2000) *with* Thompson (1992)	41.3	33.3	20.6	4.8	0.0	7.9	5 /63
M. and M. (2000) *with* Crowson (1981)	18.2	34.5	34.5	12.7	0.0	10.9	6 / 55
A.-Z. and L. (1999) *with* Kuschel (1995)	33.7	9.9	44.6	4.0	7.9	12.9	13 / 101
A.-Z. and L. (1999) *with* Thompson (1992)	41.3	31.2	18.1	2.2	7.2	18.1	25 / 138
A.-Z. and L. (1999) *with* Crowson (1981)	30.8	9.6	40.4	5.8	13.5	5.8	3 / 52
Kuschel (1995) *with* Thompson (1992)	29.7	56.5	8.0	5.8	0.0	7.2	10 / 138
Kuschel (1995) *with* Crowson (1981)	37.1	25.8	22.6	14.5	0.0	11.3	7 / 62
Thompson (1992) *with* Crowson (1981)	53.6	14.3	32.1	0.0	0.0	28.6	8 / 28

[1] M. and M. (2000) = Marvaldi and Morrone (2000); A.-Z. and L. (1999) = Alonso-Zarazaga and Lyal (1999).
[2] Nomenclature *and* taxonomy stable.

Table 5. Quantitative analysis of relationships linking accepted concepts in five succeeding weevil classifications to each other, part II: absolute values and name/meaning disjunction (marked in the totals with "!"; see text for further details).

Relationship comparison[1]	**Relationship**					**Total**
Nomenclature *stable* in comparison	==	>	<	><	|	
M. and M. (2000) *with* A.-Z. and L. (1999)	5	7	2	0	0	14
M. and M. (2000) *with* Kuschel (1995)	7	0	4	0	0	11
M. and M. (2000) *with* Thompson (1992)	5	4	0	1	0	10
M. and M. (2000) *with* Crowson (1981)	6	0	1	1	0	8
A.-Z. and L. (1999) *with* Kuschel (1995)	13	4	10	0	0	27
A.-Z. and L. (1999) *with* Thompson (1992)	25	11	8	0	0	44
A.-Z. and L. (1999) *with* Crowson (1981)	3	3	6	0	0	12
Kuschel (1995) *with* Thompson (1992)	10	11	1	2	0	24
Kuschel (1995) *with* Crowson (1981)	7	0	1	1	0	9
Thompson (1992) *with* Crowson (1981)	8	1	3	0	0	12
Total	**89**	**41!**	**36!**	**5!**	**0!**	**171**
Nomenclature *unstable* in comparison	==	>	<	><	|	**Total**
M. and M. (2000) *with* A.-Z. and L. (1999)	24	11	12	3	11	61
M. and M. (2000) *with* Kuschel (1995)	8	14	11	12	0	45
M. and M. (2000) *with* Thompson (1992)	21	17	13	2	0	53
M. and M. (2000) *with* Crowson (1981)	4	19	18	6	0	47
A.-Z. and L. (1999) *with* Kuschel (1995)	21	6	35	4	8	74
A.-Z. and L. (1999) *with* Thompson (1992)	32	32	17	3	10	94
A.-Z. and L. (1999) *with* Crowson (1981)	13	2	15	3	7	40
Kuschel (1995) *with* Thompson (1992)	31	67	10	6	0	114
Kuschel (1995) *with* Crowson (1981)	16	16	13	8	0	53
Thompson (1992) *with* Crowson (1981)	7	3	6	0	0	16
Total	**177!**	**187**	**150**	**47**	**36**	**597**

[1] M. and M. (2000) = Marvaldi and Morrone (2000); A.-Z. and L. (1999) = Alonso-Zarazaga and Lyal (1999).

Figure captions

Figure 1. Sequence of four treatments of the hypothetical taxon *Fantasia* F., authored by (A) Fabricius (1798); (B) Champion (1903); (C) Bondar (1948); and (D) Afterall (2000). Individual specimens are represented with the symbols □, △, ○, etc. The relevant nomenclatural types for species and higher-level taxa are shown as ■, ▲, and ●. See text for further details.

Figure 2. Schematic representation of the five basic kinds of concept relationships. The referential extension of concept A is indicated by the white rectangle, whereas that of concept B is indicated by the shaded rectangle. (A) congruence; (B) B is more inclusive than a; (C) B is less inclusive than A; (D) B overlaps with A; and (E) B excludes A.

Figure 3. Exemplary representational conventions for implementing concept taxonomy in practice (slightly modified). (A) Entry for the concept of *Dicranum fuscescens* Sm. sec. Koperski et al. (2000), including eight (partially) annotated concept relationships and three exemplary assignments of invalid to valid names. (B) Entry for the concept of *Aureolaria flava* (Linnaeus) Farwell var. *flava* sec. Weakley (2006). Data on bionomics are followed by ten concept relationships displayed in square brackets []. "C, G, K, RAB, W" etc. are abbreviations for preceding reference works, and "--" is used instead of "sec."

Figure 4. Pie diagram showing the percent distribution of nomenclaturally and/or taxonomically stable and unstable concepts analyzed in Koperski et al.'s (2000) *Checklist* (N = 1,548 accepted concepts; data from Geoffroy and Berendsohn, 2003).

Figure 5. Concept evolution in the grass genus *Andropogon* L. according to eight succeeding treatments (data from A.S. Weakley). Each column contains a coherent perspective, and

each row represents a congruent concept – irrespective of the names used to label the individual cells. Taxonomic concepts whose circumscriptions are shared among multiple authors are colored with unique patterns of shading, whereas concepts unique to a single source are white.

Figure 6. Phylogenetic classification of Curculionoidea sec. Kuschel (1995). Each concept is labeled with a unique number (see also Figure 8). Non-ranked concepts were assigned informal names, e.g. concept 155 was named Platypodinae-Scolytinae sec. Kuschel (1995). The author introduced one new name (Carinae) in this system.

Figure 7. Classification of Curculionoidea (excepting Platypodidae and Scolytidae) sec. Alonso-Zarazaga and Lyal (1999), to the level of subfamily. Seven new names were proposed. To illustrate a concept relationship to Kuschel's (1995) system (Figure 7): Brentidae **+** Eurhynchidae **–** Cyladinae sec. Alonso-Zaraza & Lyal (1999) **==** Brentinae sec. Kuschel (1995). Note that only concept relationships are able to convey the inverse nestedness of elements this example (i.e. a subfamily including a family).

Figure 8. Two taxonomically congruent concept lineages including the names (A) Brentidae and (B) Curculionidae, as defined in five weevil classifications (Platypodidae and Scolytidae are not explicitly treated in Alonso-Zarazaga and Lyal [1999], thus in [INT] annotation). Two examples with single names are: Brentidae sec. Alonso-Zarazaga and Lyal (1999) **><** Brenthidae sec. Crowson (1981); and Curculionidae *s.s.* sec. Marvaldi and Morrone (2000) **>** Curculionidae sec. Thompson (1992).

Fig. 1

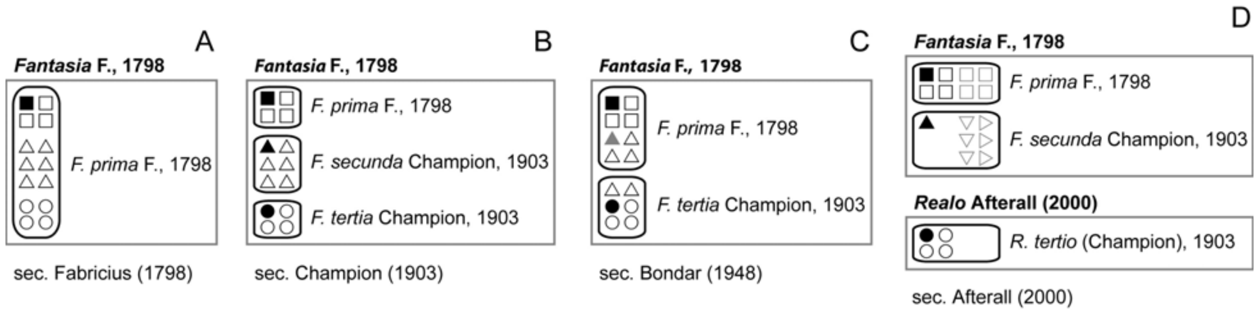

A
Fantasia F., 1798
F. prima F., 1798
sec. Fabricius (1798)
B
Fantasia F., 1798
F. prima F., 1798
F. secunda Champion, 1903
F. tertia Champion, 1903
sec. Champion (1903)
C
Fantasia F., 1798
F. prima F., 1798
F. tertia Champion, 1903
sec. Bondar (1948)
D
Fantasia F., 1798
F. prima F., 1798
F. secunda Champion, 1903
Realo Afterall (2000)
R. tertio (Champion), 1903
sec. Afterall (2000)

Fig. 2

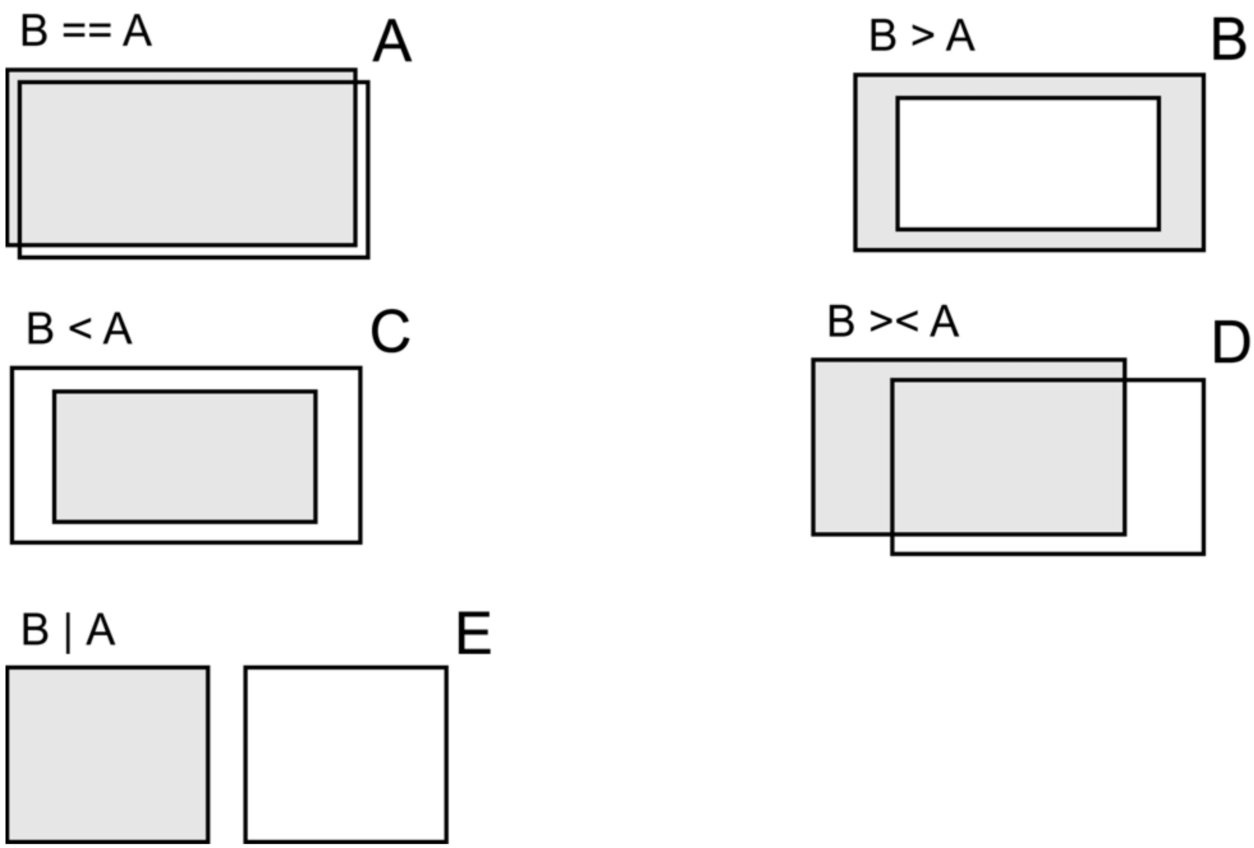


Fig. 3

A

Dicranum fuscescens Sm. [sec. Koperski et al., 2000]

Flora Britannica, 1804: 27 [nomenclatural source]

= *Dicranum congestum* Brid. [heterotypic synonym]

==	*Dicranum fuscescens* Sm.	sec. Corley et al. (1981, 1991)
==	*Dicranum fuscescens* Sm.	sec. Ludwig et al. (1996)
	Ludwig et al. (see there) refer to the concept of Corley et al.	
==	*Dicranum fuscescens* var. *eu-fuscescens* Mönk.	sec. Mönkemeyer (1927)
<	*Dicranum fuscescens* Turner	sec. Frahm and Frey (1992)
	Includes *D. flexicaule* (see comments there).	
<	*Dicranum fuscescens* Turner	sec. Mönkemeyer (1927)
	Includes *D. flexicaule* (see comments there).	
<	*Dicranum fuscescens* Sm.	sec. Smith (1980)
	Includes *D. flexicaule* in the type variety (cf. morphological account).	
>	*Dicranum fuscescens* var. *congestum* (Brid.) Husn.	sec. Smith (1980)
	This taxon is evidently a montane growth form of *D. fuscescens.*	
><	*Dicranum fuscescens* var. *fuscescens*	sec. Smith (1980)

Dicranum congestum Brid. → *Dicranum fuscescens* Sm.
Dicranum enerve Hedw. → *Paraleucobryum enerve* (Hedw.) Schimp.
Dicranum palustre Bruch & Schimp. → *Dicranum bonjeanii* De Not.
...

B

Aureolaria flava (Linnaeus) Farwell var. ***flava,*** Estearn Smooth Oak-leach. Pd, Mt, Cp (GA, NC, SC, VA): oak forests and woodlands; common. August-September; September-October. ME west to MN, south to GA, FL, and AL. Var. *reticulata* (Rafinesque) Pennell, of the southeastern Coastal Plain, needs additional study. It is alleged to differ in its lower leaves entire, dentate, or divided less than 1/2 way to the midrib (vs. deeply pinnatifid-divided).
[**==** C, G, K; ***< A. flava*** -- RAB, W; ***> Gerardia flava*** Linnaeus *var.* ***flava*** -- F; ***> A. flava*** ssp. ***typica*** -- P; ***>< flava*** ssp. ***flava*** -- S; ***> A. flava*** spp. ***reticulata*** (Rafinesque) Pennell -- P, S]

Fig. 4

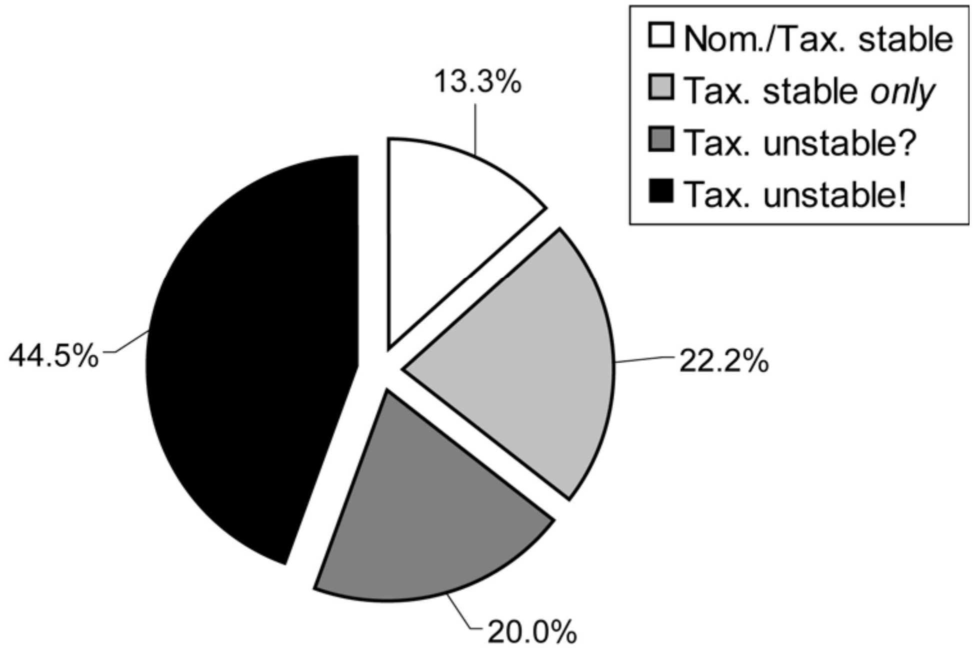

Nom./Tax. stable
Tax. stable *only*
Tax. unstable?
Tax. unstable!
13.3%
22.2%
20.0%
44.5%

Fig. 5

sec. Hackel (1889)	sec. Small (1933)	sec. Blomquist (1948)	sec. Hitchcock & C. (1950)	sec. RAD (1968)	sec. Godfrey and W. (1979)	sec. Campbell (1983)	sec. Weakley (2005)
A. virginicus var. *glaucus* subvar. *glaucus*	*A. capillipes*	*A. capillipes*	*A. capillipes*	*A. virginicus*	*A. capillipes*	*A. virginicus* var. *glaucus* "drylands variant"	*A. capillipes* var. *capillipes*
A. virginicus var. *glaucus* subvar. *dealbatus*	*A. capillipes*	*A. capillipes*	*A. capillipes*	*A. virginicus*	*A. capillipes*	*A. virginicus* var. *glaucus* "wetlands variant"	*A. capillipes* var. *dealbatus*
A. virginicus var. *viridis* subvar. genuinus	*A. virginicus*	*A. virginicus* var. *virginicus*	*A. virginicus* var. *virginicus*	*A. virginicus*	*A. virginicus* var. *virginicus*	*A. virginicus* var. *virginicus* "old-field variant"	*A. virginicus* var. *virginicus*
A. virginicus var. *viridis* subvar. *genuinus*	*A. virginicus*	*A. virginicus* var. *virginicus*	*A. virginicus* var. *virginicus*	*A. virginicus*	*A. virginicus* var. *virginicus*	*A. virginicus* var. *virginicus* "smooth variant"	*A. virginicus* var. *virginicus*
A. virginicus var. *viridis* subvar. *genuinus*	*A. virginicus*	*A. virginicus* var. *virginicus*	*A. virginicus* var. *virginicus*	*A. virginicus*	*A. virginicus* var. *virginicus*	*A. virginicus* var. *decipiens*	*A. virginicus* var. *decipiens*
A. macrourus var. *glaucopsis*	*A. glomeratus*	*A. virginicus* var. *glaucopsis*	*A. virginicus* var. *glaucopsis*	*A. virginicus*	*A. glaucopsis*	*A. glomeratus* var. *glaucopsis*	*A. glaucopsis*
A. macrourus var. *hirsutior*	*A. glomeratus*	?	*A. virginicus* var. *hirsutior*	*A. virginicus*	*A. virginicus* var. *abbreviatus*	*A. glomeratus* var. *hirsutior*	*A. glomeratus* var. *hirsutior*
A. macrourus var. *abbreviatus*	*A. glomeratus*	*A. glomeratus*	*A. glomeratus*	*A. virginicus*	*A. virginicus* var. *abbreviatus*	*A. glomeratus* var. glomeratus	*A. glomeratus* var. *glomeratus*
A. macrourus var. *genuinus*	*A. glomeratus*	*A. virginicus* var. *tenuispatheus*	*A. glomeratus*	*A. virginicus*	*A. virginicus* var. *abbreviatus*	*A. glomeratus* var. *pumilus*	*A. tenuispatheus*

Fig. 6

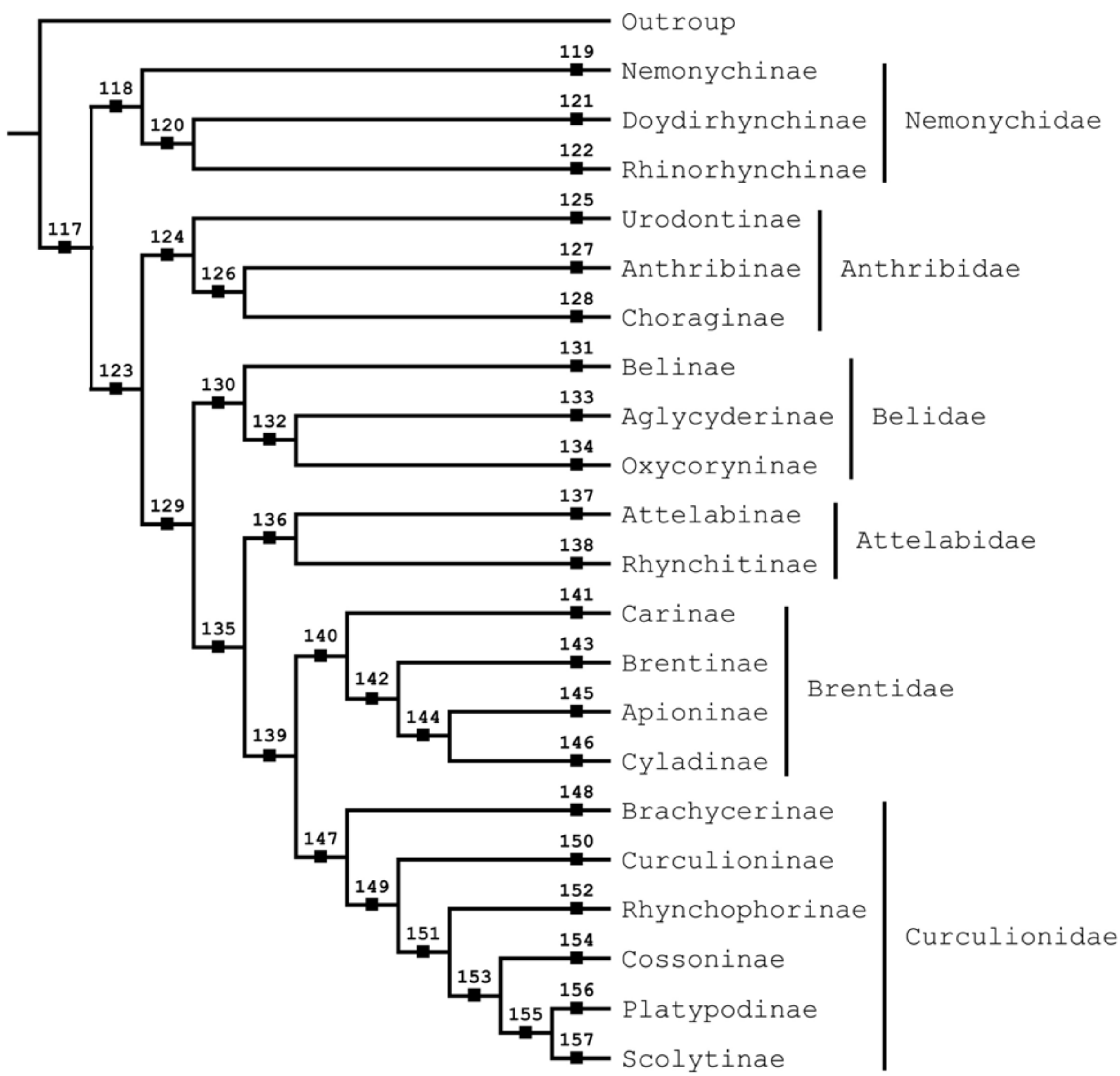

Outroup
119
Nemonychinae
118
121
120
Doydirhynchinae
Nemonychidae
122
Rhinorhynchinae
125
Urodontinae
117
124
127
126
Anthribinae
Anthribidae
128
Choraginae
131
Belinae
123
130
133
132
Aglycyderinae
Belidae
134
Oxycoryninae
137
129
136
Attelabinae
Attelabidae
138
Rhynchitinae
141
Carinae
135
140
143
Brentinae
142
145
Brentidae
144
Apioninae
146
139
Cyladinae
148
Brachycerinae
150
147
Curculioninae
149
152
Rhynchophorinae
151
154
Curculionidae
153
Cossoninae
156
155
Platypodinae
157
Scolytinae

Fig. 7

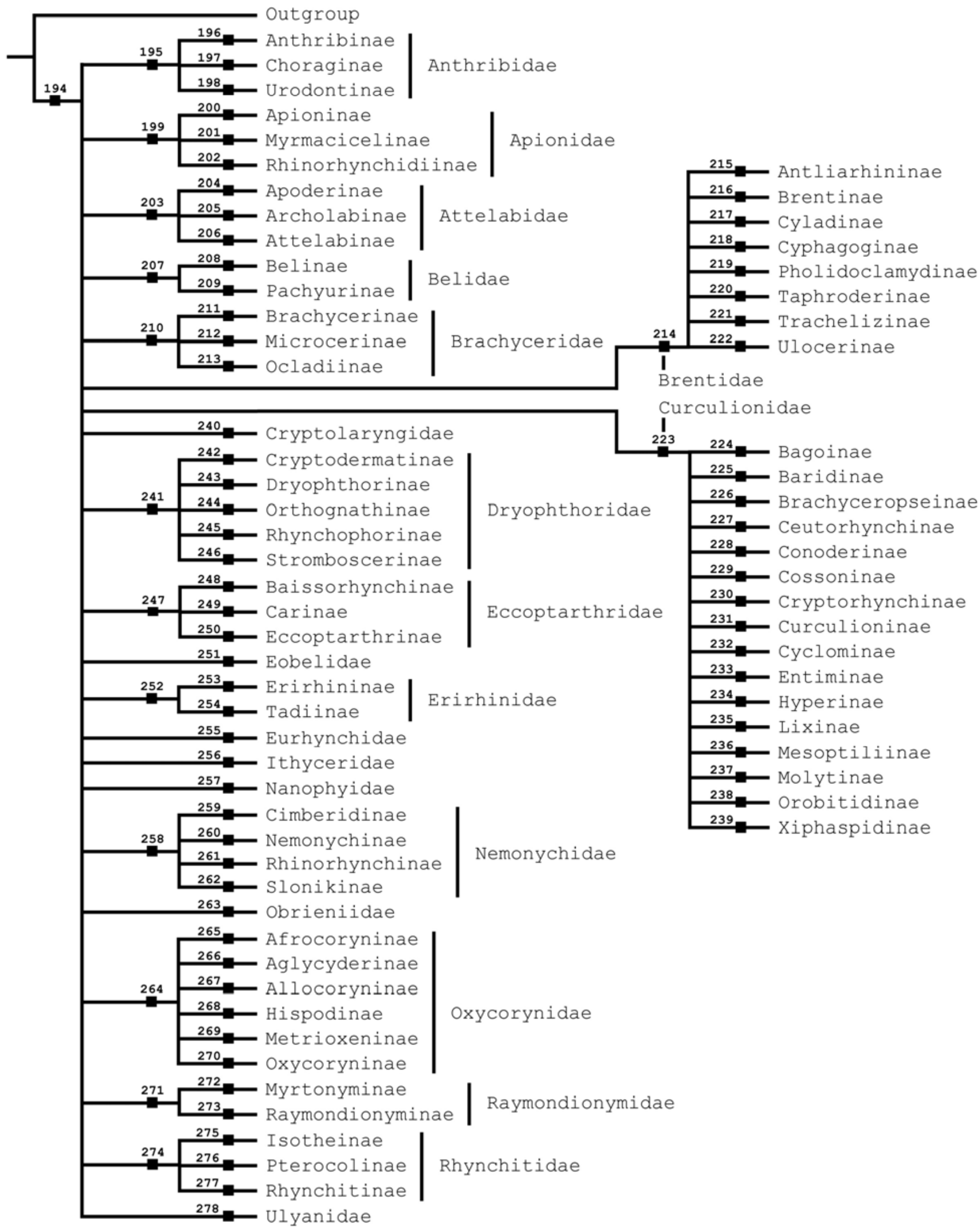
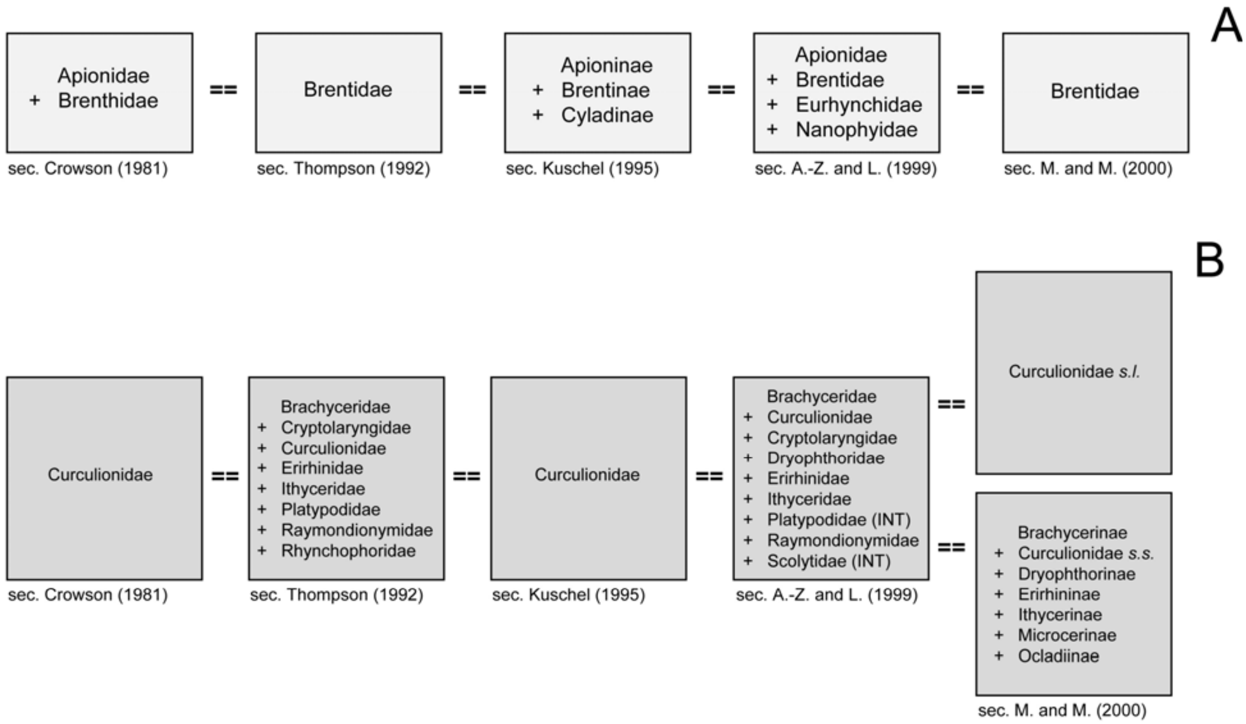

Outgroup
Anthribinae
Choraginae
Urodontinae
Anthribidae
Apioninae
Myrmacicelinae
Rhinorhynchidiinae
Apionidae
Apoderinae
Archolabinae
Attelabinae
Attelabidae
Belinae
Pachyurinae
Belidae
Brachycerinae
Microcerinae
Ocladiinae
Brachyceridae
Antliarhininae
Brentinae
Cyladinae
Cyphagoginae
Pholidoclamydinae
Taphroderinae
Trachelizinae
Ulocerinae
Brentidae
Curculionidae
Bagoinae
Baridinae
Brachyceropseinae
Ceutorhynchinae
Conoderinae
Cossoninae
Cryptorhynchinae
Curculioninae
Cyclominae
Entiminae
Hyperinae
Lixinae
Mesoptiliinae
Molytinae
Orobitidinae
Xiphaspidinae
Cryptolaryngidae
Cryptodermatinae
Dryophthorinae
Orthognathinae
Rhynchophorinae
Stromboscerinae
Dryophthoridae
Baissorhynchinae
Carinae
Eccoptarthrinae
Eccoptarthridae
Eobelidae
Erirhininae
Tadiinae
Erirhinidae
Eurhynchidae
Ithyceridae
Nanophyidae
Cimberidinae
Nemonychinae
Rhinorhynchinae
Slonikinae
Nemonychidae
Obrieniidae
Afrocoryninae
Aglycyderinae
Allocoryninae
Hispodinae
Metrioxeninae
Oxycoryninae
Oxycorynidae
Myrtonyminae
Raymondionyminae
Raymondionymidae
Isotheinae
Pterocolinae
Rhynchitinae
Rhynchitidae
Ulyanidae

Fig. 8


A
Apionidae
+ Brenthidae
==
Brentidae
==
Apioninae
+ Brentinae
+ Cyladinae
==
Apionidae
+ Brentidae
+ Eurhynchidae
+ Nanophyidae
==
Brentidae
sec. Crowson (1981)
sec. Thompson (1992)
sec. Kuschel (1995)
sec. A.-Z. and L. (1999)
sec. M. and M. (2000)
B
Curculionidae
==
Brachyceridae
+ Cryptolaryngidae
+ Curculionidae
+ Erirhinidae
+ Ithyceridae
+ Platypodidae
+ Raymondionymidae
+ Rhynchophoridae
==
Curculionidae
==
Brachyceridae
+ Curculionidae
+ Cryptolaryngidae
+ Dryophthoridae
+ Erirhinidae
+ Ithyceridae
+ Platypodidae (INT)
+ Raymondionymidae
+ Scolytidae (INT)
==
Curculionidae s.l.
==
Brachycerinae
+ Curculionidae s.s.
+ Dryophthorinae
+ Erirhininae
+ Ithycerinae
+ Microcerinae
+ Ocladiinae
sec. Crowson (1981)
sec. Thompson (1992)
sec. Kuschel (1995)
sec. A.-Z. and L. (1999)
sec. M. and M. (2000)