



First International Phylogenetic Nomenclature Meeting

Paris, *Muséum National d'Histoire Naturelle*, July 6-9, 2004

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Abstracts



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Foreword

This booklet contains the abstracts of the proposed talks of the *First International Phylogenetic Nomenclature Meeting*, which is scheduled (as of this writing) to take place in the *Muséum National d'Histoire Naturelle* in Paris on July 6-9, 2004. Please note that since the *PhyloCode* is not yet implemented, the names and definitions included in this abstract volume should not be considered established. Furthermore, the names and definitions that will appear in the symposium volume may differ from those found below, so the contents of this abstract volume should be viewed as provisional.

I would like to thank the *Muséum National d'Histoire Naturelle* for giving us free use of its very nice amphitheater of the *Grande Galerie de l'Évolution*, the *Fondation Hugot du Collège de France* for giving us a grant to support parts of the cost of this event, the *CNRS* for providing us with some supplies, and the *Académie des Sciences de Paris* for agreeing to publicize this event as one of the scientific meetings that is held under its auspices. I also thank Louise Zylberberg for proof-reading two drafts of this booklet.

Timetable

Time	Day			
	Tuesday, July 6	Wednesday, July 7	Thursday, July 8	Friday, July 9
9-12	Registration	Second regular session	Third regular session	Fourth regular session
12-14	Lunch break	Lunch break	Lunch break	Lunch break
14-16	Opening ceremony and plenary lectures	Symposium on the Theory of Phylogenetic Nomenclature	Business meeting	Definition of some popular names
16-18	First regular session			Fifth regular session
18-21	Reception dinner			

Note: The business meeting will include the inauguration of the *International Society for Phylogenetic Nomenclature*, election of officers of the *ISPN*, and the formation of its committees.

Detailed schedule

Tuesday, July 6

- 9:00h-12:00h** **Registration**
- 12:00h-14:00h** **Lunch break**
- 14:00h-16:00h** **Opening ceremony (moderator: M. Laurin)**
14:00h-14:15h Laurin, M. Welcome speech
14:15h-14:55h de Ricqlès, A. Early French systematists and evolutionists
14:55h-15:15h Padian, K. Phylogeny, classification, and names: on the history of winning hearts and minds
15:15h-16:00h de Queiroz, K. A short history of Phylogenetic Nomenclature
- 16:00h-16:20h** **Coffee break**
- 16:20h-18:00h** **First regular session (moderator: B. D. Mishler)**
16:20h-16:40h Simpson, A. G. B. Highest-level taxa within eukaryotes
16:40h-17:00h Richardson, S. L. Phylogenetic definitions for *Foraminifera*, *Panforaminifera*, *Soritacea*, and *Soritida*
- 17:00h-17:20h** **Coffee break**
17:20h-17:40h Cantino, P. D. & M. J. Donoghue. Phylogenetic nomenclature of some major plant clades
17:40h-18:00h Fisher, K. M. & B. D. Mishler. Monography and the PhyloCode: a practical example from the moss clade *Leucophanella*
- 18:00h-19:00h** **End of first regular session, departure towards “Le Train Bleu”, for the reception dinner (included in your registration fees)**
- 19:00h-** **Reception dinner in “Le Train Bleu”**

Wednesday, July 7

- 9:00h-12:00h** **Second regular session (moderator: J. A. Gauthier)**
9:00h-9:20h **Cantino, P. D. & R. G. Olmstead.** Phylogenetic nomenclature of *Lamiaceae*
9:20h-9:40h **Olmstead, R. G. & P. D. Cantino.** Phylogenetic nomenclature of *Lamiales*
9:40h-10:00h **Souza-Chies, T.T. & L. Essi.** Phylogeny of the *Linearia* and *Notata* groups of *Paspalum* L. (*Poaceae*) and nomenclature proposed for some clades
10:00h-10:20h **Bakhshi Khaniki, G.** A phylogenetic nomenclature of *Rhinopetalum* (*Liliaceae*) based on nectary morphology and Giemsa C-banding studies
- 10:20h-10:40h** **Coffee break**
10:40h-11:00h **Nwosu, M.** Review of Nomenclature and Classification in *Carnarium* (*Burseraceae*)
11:00h-11:20h **Manuel, M. et al.** Phylogenetic nomenclature of sponge taxa
11:20h-11:40h **Artois, T. et al.** Nomenclature and conflicting hypotheses: phylogenetic definitions within (and outside) the flatworms
11:40h-12:00h **Discussion period for the regular talks**
- 12:00h-14:00h** **Lunch break**
- 14:00h-18:00h** **Symposium on the Theory of Phylogenetic Nomenclature (moderator: P. D. Cantino)**
14:00h-14:20h **Baum, D. A.** Reticulate genealogy and its bearing on the PhyloCode
14:20h-14:40h **Clarke, J.** Definitions of species names in a system of phylogenetic nomenclature: conclusions from a paleontological case study
14:40h-15:00h **Cellinese, N. & M. J. Donoghue.** The demise of the ranked system in the arrangement of herbaria : utopia or reality?
- 15:00h-15:20h** **Coffee break**
15:20h-15:40h **Dayrat, B.** Selecting a form of species names in the PhyloCode
15:40h-16:00h **Sereno, P. C.** Notation, definitional rationale, and recall in phylogenetic taxonomy
16:00h-16:20h **Marjanovic, D.** How to preserve historical usage in phylogenetic definitions? – Self-destructive definitions for names of grades
- 16:20h-16:40h** **Coffee break**
16:40h-17:00h **Mishler, B. D. & K. M. Fisher.** Terminating species: a rank-free approach to terminal taxa
17:00h-17:20h **de Queiroz, K. & J. Gauthier.** Toward an integrated system of phylogenetically defined names
17:20h-17:40h **Wagner, J. R.** The general case of phylogenetic definitions, alternate classes of definitions, and the phylogenetic definition of Life (with a capital L)
17:40h-18:00h **Discussion of the talks on the Theory of Phylogenetic Nomenclature**

Thursday, July 8

- 9:00h-12:00h** **Third regular session (moderator: R. R. Reisz)**
9:00h-9:20h **Schultze, H.-P. & G. Arratia.** A phylogenetic nomenclature of bony fishes (*Osteichthyes*)
9:20h-9:40h **Arratia, G. & H.-P. Schultze.** A phylogenetic nomenclature of advanced ray-finned fishes (*Actinopterygii*)
9:40h-10:00h **Laurin, M.** A phylogenetic nomenclature of early limbed vertebrates
10:00h-10:20h **Damiani, R., J. S. Steyer & A. M. Yates.** Phylogenetic nomenclature of Mesozoic temnospondyls
- 10:20h-10:40h** **Coffee break**
10:40h-11:00h **Anderson, J. S.** Phylogenetic taxonomy of *Lepospondyli*: “top-down” versus “bottom-up” approaches to nomenclature in uncertain topologies
11:00h-11:20h **Cannatella, D.** A Phylogenetic Nomenclature of *Anura*
11:20h-11:40h **Gauthier, J. A. et al.** A Phylogenetic Nomenclature for the major clades of *Amniota* Haeckel 1866, with emphasis on non-avian *Reptilia* Laurentus 1768
11:40h-12:00h **Discussion of the regular talks**

- 12:00h-14:00h** **Lunch break**
- 14:00h-18:00h** **Business meeting (moderator: M. J. Donoghue)**
- Friday, July 9**
- 9:00h-12:00h** **Fourth regular session (moderator: K. de Queiroz)**
- 9:00h-9:20h** **Reisz, R. R.** Early Amniote Phylogeny and Nomenclature
- 9:20h-9:40h** **Sereno, P. C.** Phylogenetic Nomenclature for stem crocodylians and birds, exclusive of *Pterosauria*
- 9:40h-10:00h** **Padian, K.** The nomenclature of *Pterosauria* (*Reptilia*, *Archosauria*)
- 10:00h-10:20h** **Wagner, J. R.** The Phylogenetic Nomenclature of ornithischian dinosaurs (*Vertebrata: Reptilia*) and a consideration of the difficulties in converting the names of extinct clades
- 10:20h-10:40h** **Coffee break**
- 10:40h-11:00h** **Brochu, C. A.** Phylogenetic Nomenclature for *Crocodylia*: a success story in the face of phylogenetic uncertainty
- 11:00h-11:20h** **Clarke, J. et al.** A Phylogenetic Nomenclature for the major clades of *Amniota* Haeckel 1866, with emphasis on *Aves* Linnaeus 1758
- 11:20h-11:40h** **Rowe, T. et al.** A Phylogenetic Nomenclature for the major clades of *Amniota* Haeckel 1866, with emphasis on *Mammalia* Linnaeus 1758
- 11:40h-12:00h** **Discussion of the regular talks**
- 12:00h-14:00h** **Lunch break**
- 14:00h-15:45h** **Session on the definition of some popular names and other controversies on the application of Phylogenetic Nomenclature (moderator: R. G. Olmstead)**
- 14:00h-14:05h** **Anderson, J. S.** Case for an apomorphy-based definition of the name *Tetrapoda*
- 14:05h-14:10h** **Laurin, M.** Case for a crown-clade definition of the name *Tetrapoda*
- 14:10h-14:30h** **Discussion of the name Tetrapoda**
- 14:30h-14:35h** **Marjanovic, D.** Case for a stem-based definition of the name *Aves*
- 14:35h-14:40h** **Gauthier, J. A.** Case for a crown-clade definition of the name *Aves*
- 14:40h-15:00h** **Discussion of the name Aves**
- 15:00h-15:45h** **Discussion of all other names**
- 15:45h-16:00h** **Coffee break**
- 16:00h-17:20h** **Fifth regular session (moderator: C. A. Brochu)**
- 16:00-16:20h** **Wolsan, M. & H. N. Bryant.** Phylogenetic nomenclature of carnivoran mammals
- 16:20h-16:40h** **Folinsbee, K.E. & D.R. Begun.** Phylogenetic Nomenclature of living and fossil catarrhines
- 16:40h-17:00h** **Bonde, N. & B. Westergaard.** New non-Linnaean, neo-cladistic nomenclature and classification conventions exemplified by recent and fossil hominids
- 17:00h-17:20h** **Discussion of the regular talks**
- 17:20h-18:00h** **Discussion on any topic pertaining to the meeting (moderator: M. Laurin)**
- 18:00h** **End of the *First International Phylogenetic Nomenclature Meeting***

Theory of Phylogenetic Nomenclature

Reticulate genealogy and its bearing on the PhyloCode

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The development of the PhyloCode was guided, in part, by the assumption that life has evolved along a single, strictly divergent tree. However, it is clear that evolution has not been purely divergent due to phenomena such as hybrid speciation, introgression, horizontal gene transfer, and endosymbiosis. This is acknowledged in Chapter 1, Article 2 of the PhyloCode, which points out that it is impossible to build a strictly hierarchical systematization in the face of certain kinds of reticulation, such as hybrid speciation. In this presentation I will further explore reticulation and show that it is much more pervasive than acknowledged in the PhyloCode because lineage sorting, a ubiquitous phenomena in rapid or recent radiations, is properly considered a type of reticulate genealogy. I will suggest that the PhyloCode needs to provide clearer guidelines as to how to accommodate such reticulation in the naming of clades. Specifically, I will suggest a clear biological criterion be provided to distinguish dominant from minority histories and that the former by the implicit context of phylogenetic definitions. I will also explore some alternative conventions that might be used to track minor histories or, in cases such as hybrid speciation, to track codominant histories. One implication of this analysis of reticulation is that the current, clade-only version of the PhyloCode can deal effectively with taxa traditionally treated at the species “rank” without the need for a separate set of rules governing species names.

Definitions of species names in a system of phylogenetic nomenclature: conclusions from a paleontological case study

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Among an array of issues surrounding species names in a system of phylogenetic nomenclature, the possible generalized form for their definitions has been comparatively little debated, especially compared to the possible form of converted species names. In a paleontological case study, the implementation of one possible form for the definitions of species names is explored. These definitions take the form: the name for the species that includes the specifier (specimen “X”). It uses a single internal specifier that for converted species would in most cases be the valid holotype specimen. The form of the definition of species names employed is close to that in current rank-based systems (e.g., the ICZN) but the term species used in the definition and the species so named are not ranked taxonomic units. An individual is assumed to be part of only one species, however problematic it may be to determine what other individuals are part of this species.

In this particular case study, the term species was specified explicitly to refer to species under the general lineage concept de Queiroz (1998, 1999). However, the definition used is intentionally agnostic with respect to species concept, except that as named taxa they are not required to be monophyletic; as already noted, this property of species appears necessary to justify the inclusion of species as a distinct taxonomic unit in a system of phylogenetic nomenclature (i.e., that they be at least potentially distinct from clades). The definition of species names investigated is also agnostic on the criteria by which individuals may be identified as part of a species (e.g., by autapomorphy; potentially interbreeding).

Whatever is ultimately decided with respect to the definitions of species names, it is clear that they are faced with unique issues with the form of clade name definitions already outlined under a system of phylogenetic nomenclature (i.e., node-, stem-, and apomorphy-based and “modified” variants thereof). Finally, it is also concluded that although the term ‘typification’ may conjure too much of the pre-evolutionary world view of a rank-based system, explicitly tying a species name to a single specifier makes good taxonomic sense.

The demise of the ranked system in the arrangement of herbaria : utopia or reality?

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Herbaria have been arranged according to a variety of both phylogenetic and non-phylogenetic rank-based classification systems. Curators and Collection Managers have never reached a consensus on the best arrangement system to implement, leaving each institution to adopt its own approach, which often depends on the history and size of the collection. One view is that the arrangement of a collection does not have to reflect evolutionary relationships. This is taken to the extreme when collections are alphabetically arranged by family.

The view has been expressed that any arrangement reflecting a modern phylogenetic system will be unstable. It is worth remembering how confusing the various current systems are, especially to younger systematists who need to recall outdated classifications and family circumscriptions in order to locate what they need. Because institutions generally provide search tools only at family level, this task can become daunting when searching for lower level taxa. When the herbarium is used as a teaching tool, outdated systems positively defeat the usual purpose of comparing closely related taxa.

The Phylocode offers the opportunity to apply a nomenclaturally more stable system to the arrangement of natural history collections. The Yale University Herbarium provides an example of how a rank-free classification is highly applicable to the arrangement of herbaria. Specimens are arranged into clades and various named clades are tagged inside and outside of the cabinets; cabinet rows represent major nodes in the phylogenetic tree. An alphabetical index of higher level taxa is displayed to provide the location (row and cabinet numbers) where specimens are located. In addition, a database of clade names has been designed to allow searches for clade names at any level in the tree, and to retrieve classification and specimen location details. Because names do not change, only specimens are relocated when necessary, most often to neighboring shelves or cabinets. In contrast, improved knowledge of phylogenetic relationships may require both the movement of specimens and various nomenclatural adjustments in rank-based arrangements

Our reorganization of the Yale University Herbarium demonstrates that natural history collections can be arranged and easily maintained using rank-free phylogenetic nomenclature, and that this has benefits over rank-based systems.

Selecting a form of species names in the PhyloCode

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A method for naming species in the PhyloCode is needed, not only because the current draft does not provide any method, but also because a convincing form of species names is going to be critical to incite taxonomists and users of species names as well to adopt the PhyloCode. Notice that rules for governing 'species' names are needed regardless of one's opinion on 'species' (i.e., whether one should talk about 'species' or 'least-inclusive units').

The main issue with which we must deal is the uniqueness of species names. Unfortunately, the uninominal uniqueness of clade names does not work with species names because too many species have the same epithet. There are two main approaches for converting the uniqueness of Linnaean species names to a rank-free system. These approaches were first proposed in the mid 1960s by authors whose goal was not to reject ranks but rather that species names could be both stable and unique. First, Michener (1964, *Syst. Zool.*) suggested that uniqueness be guaranteed by permanently fixing the combination between the two parts of a Linnaean *binomen*: the name of the sea slug *Anisodoris nobilis* would be converted to *Anisodoris-nobilis*. Second, Lanham (1965, *Syst. Zool.*) suggested that uniqueness be guaranteed by the association between the species epithet, the author's name, the date of publication, and the page number where the name first appeared: *Anisodoris nobilis* would then be converted to *nobilis* MacFarland, 1905:38. All the methods proposed to guarantee uniqueness of species names in a rank-free system, such as the methods by Cantino and co-authors (1999, *Syst. Biol.*), are variants of these two main approaches: 1) Linnaean binomials are permanently fixed; 2) species names are epithet-based and uniqueness is guaranteed by an additional tag attached to the epithet.

I shall compare Lanham's method to all the methods proposed so far for naming species in a rank-free system and explain why Lanham's method, which surprisingly has been overlooked since its publication (Cantino and co-authors did not consider it), provides the best result. I shall address several concerns about Lanham's proposal by modifying it slightly. Uniqueness could be addressed in three levels of complexity: 1) a page number would not be required, e.g., *nobilis* MacFarland, 1905 (this form is equivalent to what Schander and Thollesson [1995, *Zool. Scr.*] proposed); 2) a page number is added when an author gave the same epithet to different species in a single year, e.g., *mauritiana* Bergh, 1889:815 and *mauritiana* Bergh, 1889:818; 3) a letter could be added after the page number when an author gave the same epithet to different species on the same page. For communication purposes, I suggest that in addition to 'official names' (i.e., Lanham's epithet-based names, with the slight modifications proposed for uniqueness), we use 'common names' that could include additional taxon names in front of epithets: e.g., *Discodorididae nobilis* MacFarland, 1905, or simply *Discodorididae nobilis*. Continuity with Linnaean binomials could possibly be addressed by using those binomials as 'common names,' although they may convey incorrect phylogenetic information (e.g., *Anisodoris nobilis* is inaccurate because we only know that *nobilis* MacFarland, 1905 belongs to the clade Discodorididae). However, I personally favor the use of meaningful clade names instead of meaningless old generic names in front of species epithets in 'common names.' Overall, Lanham's method guarantees continuity with the current taxonomic literature; it helps taxonomists handle absence of resolution in phylogenetic relationships (through the use of names such as *Discodorididae nobilis* instead of *Anisodoris nobilis*); more broadly, it would solve the problem of recognition of taxonomic work by requiring people to cite original species descriptions.

Notation, definitional rationale, and recall in phylogenetic taxonomy

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Phylogenetic taxonomy broke from Linnean tradition by distinguishing taxonomic definition from diagnosis and by formalizing an unranked taxonomy based solely on the branching pattern of phylogeny. Nevertheless, two aspects of phylogenetic taxonomy (as codified in the draft PhyloCode) bear the hallmarks of Linnean tradition: (1) recourse to a phylogenetic tree, rather than a cladogram, for graphical representation and terminological definitions and (2) the continued use of morphology, along with phylogenetic geometry, in clade recognition. Both practices have brought unnecessary complexity and confusion to graphical representation, symbolic notation or definitional abbreviation, operational terminology, and definitional rationale in phylogenetic taxonomy.

Four *graphical styles* have been used to depict phylogenetic definitions using either a phylogenetic tree, cladogram, or combination cladogram/tree. A cladogram using dots and arrows is here recommended, given that phylogenetic taxonomy is grounded on reproduceable phylogenetic analysis routinely presented on cladograms. Current notation and shorthand abbreviation of phylogenetic definitions do not distinguish universal versus optional components or accurately capture other definitional components. A modified scheme is presented that distinguishes *symbolic notation* (which captures all of the functional components of a phylogenetic definition or set of definitions) from *shorthand* and *longhand* versions (which replace most or all symbols, respectively, with specific operands or phrases). In this way, fundamental patterns in phylogenetic definitions are clarified and can be mapped directly to their longhand versions.

One result is the realization that there are only two fundamental patterns for phylogenetic definitions, node and stem. Apomorphies, which have long been regarded as equivalent to taxonomic specifiers (species, specimens), are attributes, not phylogenetic entities. They occupy positions in character space that usually are not unique, permanent or necessarily known in phylogenetic entities under consideration. Apomorphies are dependant clauses in phylogenetic definitions. Like time and geographic range, apomorphies operate as *qualifiers*, setting conditions on clade membership.

Formulation of phylogenetic definitions should involve three heuristic criteria: stability, simplicity, and prior usage. Time-honored phylogenetic dichotomies are stabilized with node-stem triplets. Likewise, multiple internal/external specifiers and taxon qualifiers stabilize and restrict taxonomic content, respectively. Definitional revision is divided into “first” and “second-order” changes to better recognize prior usage, and a searchable database, *TaxonSearch*, allows rapid recall of historical and definitional information.

How to preserve historical usage in phylogenetic definitions? – Self-destructive definitions for names of grades

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Recently several names which have traditionally been expressedly used for paraphyletic or even polyphyletic grades have received definitions that turn them into names of clades. In many cases the results have been huge changes in content. For example, *Reptilia*, so far used as a grade, now includes birds but excludes the long and diverse mammalian stem, contrary to all previous usages; *Sauria*, so far used for the paraphyletic lizards excluding snakes (and sometimes amphisbaenids), now includes snakes, crocodiles and birds, among many others; *Stegocephali*, so far restricted to the basalmost tetrapods, now includes the entire crown group of *Tetrapoda* and several of its outgroups; *Cotylosauria*, formerly an assemblage of the putatively basalmost amniotes, now includes all amniotes and their sistergroup *Diadectomorpha*. Moreover, some of these former grade names have been exhumed after having been largely or completely out of use among cladists (and sometimes precladists as well), like *Stegocephali* or *Reptiliomorpha*. (The latter seems to have been used practically not at all in the last 5 or more decades; a Google search turns up one certain [in Russia] and one possible usage [in Slovakia] of Reptiliomorpha in the original paraphyletic sense, of about 50 in total.)

In the general interested public*, as well as important parts of the systematist community, these phenomena commonly produce deep confusion or even frustration – which would likely seriously damage the acceptance of phylogenetic nomenclature as a whole. It has already become a common perception that many names that were used for grades have been abolished by “cladistics” because their contents are “unsaveably” para-/polyphyletic. Stegocephali/-a/-ia and Cotylosauria are examples. (Indeed, for most such names no attempt has, to my knowledge, ever been made to give them phylogenetic definitions: Sporophyta, Coelenterata, Protista, Prokaryo(n)ta, Pelycosauria despite the existence of *Eupelycosauria*...) To reintroduce them with radically altered contents would be counterproductive, and would not accord to the spirit of Recommendation 11A.

Therefore I introduce the idea to give certain such names self-destructive definitions (e. g. stem-based ones with several internal specifiers) which will preserve their contents should they ever be applicable to real clades. For example, *Reptilia* could be given a node-based definition with a crocodile, a lepidosaur (or more), a turtle, and perhaps a “pelycosaur” (= non-therapsidan therapsid) as internal and a bird and a mammal as external specifiers. This would ensure that, should the internal specifiers ever be found to form a clade to the exclusion of the external ones, this clade would be called *Reptilia*, and it would ensure that, under phylogenies currently deemed credible, the name *Reptilia* would not apply to any clade and could not be used. It would “self-destruct”.

Which names should be given self-destructive definitions, however, would have to be decided on a case-by-case basis; this is unavoidable because of the subjective nature of historical usage.

* I mention the general public because the PhyloCode will necessitate to rewrite stupendous amounts of secondary and tertiary literature all the way down to biology schoolbooks and perhaps even etiquettes on sales packages of balcony flower seeds. It cannot be overemphasized what a huge undertaking the invention of a whole new biological nomenclature is – and that this size should not be a cause for failure!

Terminating species: a rank-free approach to terminal taxa

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The species problem is a special case of the taxon problem. Once a decision is made about what taxa in general are to represent, then species in particular should simply be the least inclusive taxon of that type. Thus if we favor a rank-free phylogenetic basis for taxonomy, then we should apply that basis to species (and infraspecific) taxa as well. In this paper we advocate the application of rank-free phylogenetic taxonomy to the terminal level. In brief the argument is: (1) Because of the many documented problems with instability and lack of comparability of ranks in the formal Linnaean system, we need to move to a rank-free phylogenetic classification system at all levels; (2) In such a system, not all hypothesized monophyletic groups need be named, but those that are named formally should be given unranked (but hierarchically nested) uninomials; (3) The least inclusive taxon, formally known as "species," should be treated in the same unranked manner. Finally, we explore the practical implications of eliminating the rank of species for such areas as education, ecology, evolution, and conservation, and conclude that these purposes are better served by this move.

Many authors have made a firm distinction, in their particular theories of systematics, between species and higher taxa. The idea is that somehow species are units directly participating in the evolutionary process, while higher taxa are at most lineages resulting from past evolutionary events. However appealing this distinction is in theory, these arguments have resulted more from wishful thinking than from empirical observations. When anyone has searched for an empirical criterion to uniquely and universally distinguish the species rank from all others, the attempt has failed. Current entities ranked as species are not comparable in age, internal genetic diversity, ecology, the amount of morphospace they occupy, the size of the phenetic "moat" around them, or the amount of interbreeding within them (or lack thereof between them), nor can they be made to be comparable through any massive realignment of current usage. To summarize, there is no criterion for distinguishing species from other ranks in the Linnaean hierarchy. This is not to say that particular species taxa are unreal; they *are* real, but their reality is no different than that of phylogenetic taxa at any other level. Species are not special.

Curiously, many advocates of rank-free phylogenetic classification have wanted to retain the species rank as a special case, probably because the species concept is so ingrained and comfortable in current thinking. However, all the arguments that can be massed against Linnaean ranked classification can be brought to bear against the species rank as well. As difficult as it is to overthrow ingrained habits of thinking, logical consistency demands that all levels in the classification should be treated alike. The species rank must go the way of all others. We must end the endless bickering over how this rank should be applied, and instead get rid of the rank itself.

Biological classification should be a set of nested, named groups for interested clades at all levels. Not all clades need be named, but those that are should be named on the basis of evidence for monophyly. We stop naming groups at some point approaching the tips of the phylogeny because we don't have solid evidence for monophyly at the present stage of knowledge. This *may* be due to rampant reticulation going on below some point, or simply lack of appropriate markers for distinguishing finer clades. We shouldn't pretend that the smallest clades named at a particular time are ontologically different from other, more inclusive named clades.

The PhyloCode is still incomplete; it must not be implemented until the species rank is dealt with, and hopefully terminated!

Toward an integrated system of phylogenetically defined names

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Up to the present time, phylogenetic nomenclature has emphasized methods for associating names with clades (phylogenetic definitions) and rules for determining nomenclatural precedence (priority, conservatism) in cases involving nomenclatural redundancy (synonymy) and ambiguity (homonymy). Although a few rules deal with the relationships between names (e.g., Art. 11.8, which deals with converted genus names and names based on the same word stems), by and large, names are independent of one another. The publication of a volume that will serve as a starting point for phylogenetic nomenclature presents an opportunity for practitioners of phylogenetic nomenclature to develop an integrated system of phylogenetically defined names. We describe a proposal for such an integrated system based on three categories of clades, the importance of which has long been recognized: crown clades, stem clades, and apomorphy-based clades (e.g., Hennig 1966 *Annual Review of Entomology* 10:97-116). In this system, crown clades are given the most widely known names commonly associated with those clades (or with slightly more inclusive clades). Their names are defined using node-based definitions (including stem-modified and apomorphy-modified variants). Names derived from the classical Greek or Latin vernacular names for particular kinds of organisms (e.g., *Aves*, *Arachnida*, *Plantae*) or from proper names (e.g., *Lachesis*, *Nereidae*, *Iridaceae*) are particularly well suited for crown clades, as are names that describe characters that are rarely preserved in fossils (e.g., *Mammalia*, *Deuterostomia*, *Embryophyta*). Names that describe characters that are commonly preserved in fossils (e.g., *Tetrapoda*, *Arthropoda*, *Spermatophyta*) may also be appropriate for crown clades if those names are much better known than the alternatives. Names in the last two categories are best defined using apomorphy-modified node-based definitions. Stem clades (total clades, pan-monophyla) are given names formed by combining the names of their corresponding crowns with the prefix *Pan-* (e.g., *Panaves*, *Pandueterostomia*, *Panspermatophyta*), derived from the term “pan-monophylum” (Lauterbach 1989 *Zoologischer Anzeiger* 223:139-156). The names of stem-clades are defined using branch-based definitions. Because several distinctive apomorphies may arise between a stem and its crown, forming the names of apomorphy-based clades by adding a single prefix or suffix to the name of the corresponding crown clade is not feasible. Therefore, apomorphy-based clades are given names that describe the apomorphies upon which they are based (e.g., *Synapsida*, *Xiphosura*, *Polysporangiomorpha*), provided that the names are not sufficiently well known to be applied to crown clades. If a name that describes an apomorphy has been used for a crown clade, then the clade stemming from the ancestor in which that apomorphy originated may be given a name formed by combining the name of the crown clade with a prefix or suffix that suggests possession of the relevant apomorphy (e.g., *Tetrapodomorpha*, *Arthropodiformes*, *Spermatophytomorpha*). The names of apomorphy-based clades are defined using apomorphy-based definitions. An integrated system of phylogenetically defined names has significant advantages in terms of cognitive efficiency over one in which there is no necessary relationship between the names of crown clades and those of their corresponding stem clades. In particular, knowing the name of a crown automatically means knowing the name of its corresponding stem. This situation effectively reduces the number of names that must be memorized by the number of named crowns, and it greatly facilitates communication among biologists who study distantly related taxa. Although the adoption of an integrated system will require many practitioners of phylogenetic nomenclature to make concessions regarding the definitions of particular names (and the names of particular clades), it would be most unfortunate if personal attachments and investments were allowed to interfere with the development of a system of phylogenetically defined names that has greater utility for the community of biologists as a whole.

The general case of phylogenetic definitions, alternate classes of definitions, and the phylogenetic definition of Life (with a capital L)

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Can a stable phylogenetic definition of Life be formulated? Exhaustive enumeration of living species in a node-based definition is impossible. Use of a restricted set of specifiers dooms the definition to interminable emendation with changing phylogenetic hypotheses. Discovery of new outgroups to life as currently known would foil either strategy. The logical impossibility of an external specifier for Life precludes a stem-based definition, and lack of a universally accepted, unambiguous definition of life (the process) precludes its use as a specifier in an apomorphy-based definition. Our best hope lies in a new definitional format.

Phylogenetic definitions are formulae for finding the nominal ancestor of the clade. These formulae consist of two elements: “operations,” such as tracing ancestry or descent, determine a set of possible ancestors; “criteria,” including position at the intersection of lineages, first (oldest), last (youngest), presence of features, *etc.*, are used to select members of this set. The “node-based” and “stem-based” definitional formats invoke a single operation: tracing the ancestries of specifiers to their intersection. The nominal ancestor is the entity at that intersection (node-based), or its first descendant on the lineage of the internal specifier (stem-based). In an “apomorphy-based” definition, the lineage of the specifying entity is searched for the oldest ancestor that exhibits the specifying apomorphy. The “stem-modified, node-based” format, proposed by Wyss and Meng in 1996, invokes multiple operations: the ancestries of the specifiers are traced to intersection, and the first descendant of their last common ancestor on the lineage of the internal specifier is the ancestor of an intermediate set; a subset of this set is then recognized on the presence of a criterion, survival to the recent, and the ancestries of known members of the subset are traced to their coincidence at the nominal ancestor. This definitional format is only “node-based” in that it specifies an ancestor and only “modified” in that it requires more than a single operation; it is a unique format, which should be called the Wyss and Meng Crown Clade Definition.

How can new classes of definition be constructed? First, other operations can be used; these may be especially useful in defining entities other than clades. De Queiroz has described the phylogenetic definition of species using the “width” of a lineage, *e.g.*, “the most inclusive population” containing the type specimen. Populations within a species (including “metapopulations” or subspecies) might then be defined as “the second most inclusive population” containing the type. It is also possible to name populations indirectly, *e.g.*, “the most inclusive population containing the last organism ancestral to all living *Homo sapiens*.” Second, criteria other than apomorphies or extancy may be employed, *e.g.*, “the first *Homo sapiens* to leave Africa, and all of its descendants,” “the first ancestor of *Bos taurus* to live entirely in the Pliocene,” or “the last common ancestor of all North American species closer to *Panthera leo* than to *Canis lupus*, and all of its descendants.” Lineages can be named by invoking a descendant and all of its ancestors. Third, old criteria may also be applied in new ways: *e.g.*, “the last species ancestral to *Homo sapiens*,” “the last ancestor of *Homo sapiens* and all of its descendants.” Combinations of the above allow even more flexibility, *e.g.*, a hybrid clade could be defined as the first ancestor of a particular species that arose from two independent species lineages and all of its descendants.

Given this perspective, I offer the following definitions of Life, but only provisionally, as they are extremely heterodox.

NAMES PROVISIONALLY DEFINED:

Panbiota: “the first ancestor of *Homo sapiens* and all of its descendants.”

Biota: “the most recent common ancestor of all extant descendants of the first ancestor of *Homo sapiens*, and all of its descendants.”

Eukaryota

Highest-level taxa within Eukaryotes

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The highest-level eukaryote clades are particularly difficult to accommodate under existing codes of nomenclature. The jurisdictional boundaries of botanical and zoological codes are unclear, cannot possibly have a simple phylogenetic basis, and in practice, substantially overlap. Further, modern phylogenetic studies confirm that adequately informative, monophyletic systems would require the creation of numerous new ranks above the kingdom level and/or massive changes to the ranks of many familiar taxa.

I will provide phylogenetic definitions for the names of some of the most inclusive clades within eukaryotes. Wherever possible, these definitions are abstracted from the original intentions behind the names, and are harmonized with the rank-less, hierarchical classification for 'protistan' eukaryotes currently being compiled by a committee from the Society of Protozoologists. For historical reasons, including an expectation that relevant fossil data will remain extremely sparse, most definitions are apomorphy-based.

The most inclusive names below *Eukaryota* include: *Opisthokonta*, *Amoebozoa*, *Cercozoa*, *Excavata*, *Chromalveolata*, *Plastida*, and *Unikonta*. *Opisthokonta* contains both animals and fungi plus some 'protistan' organisms. *Amoebozoa*, *Cercozoa* and *Excavata* are exclusively protistan, and predominantly contain organisms traditionally considered to be 'protozoa'. *Plastida* is proposed for the primary algae/plants (with plastids derived from an endosymbiotic photosynthetic prokaryote) – green algae, land plants, red algae and glaucophytes. This assemblage is equated with 'plantae' by some, although this name is assigned to clades nested within it by others. *Chromalveolata* contains most of the secondary algae (with plastids derived from an endosymbiotic photosynthetic eukaryote), in addition to several major clades of protozoan organisms (e.g. ciliates, apicomplexa). *Unikonta* is the minimal clade including *Opisthokonta* and *Amoebozoa* - there is now strong evidence that these two major taxa are related to the exclusion of the others mentioned above. Otherwise the relationships amongst these higher clades are currently too poorly understood to merit nomenclatural action. Names and definitions will be provided for some important less inclusive clades.

The taxa covered above probably include the bulk of extant eukaryote phylogenetic diversity, but it is also likely that some protistan eukaryotes fall outside these major clades. Organisms that are problematic at present include foraminifera and most radiolaria (both of which are closely related to, but not necessarily members of, *Cercozoa*), centrohelid heliozoa, and several groups of heterotrophic flagellates.

SELECTED NAMES TO BE DEFINED:

Eukaryota: Clade (cell nucleus in *Magnolia virginiana* L. 1753).

Opisthokonta: Clade (posterior flagellar insertion in [spermatozoa of] *Homo sapiens* L. 1758).

Amoebozoa: Clade (lobose pseudopodia in *Chaos chaos* [L. 1758] L. 1767).

Cercozoa: Clade (*Cercomonas longicauda* Dujardin 1841 and *Plasmodiophora brassicae* Woronin 1878).

Excavata: Clade (Suspension feeding groove in *Jakoba libera* [Ruinen 1938] Patterson, 1990).

Plastida: Clade (Plastids of primary [direct prokaryote] origin in *Magnolia virginiana* Linnaeus 1753).

Chromalveolata: Clade (plastids of secondary origin, in *Fucus vesiculosus* L. 1753).

Unikonta: Clade (*Homo sapiens* L. 1758 and *Chaos chaos* [L. 1758] L. 1767).

Phylogenetic definitions for *Foraminifera*, *Panforaminifera*, *Soritacea*, and *Soritida*

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Traditionally, the name *Foraminifera* has been applied to a group of single-celled, marine eukaryotes, the most diagnostic features of which include the presence of an external test, or shell, that may be single-chambered or multichambered, and the possession of granuloreticulate pseudopodia (=granuloreticulopodia). Living foraminiferans are ubiquitous in the marine realm, inhabiting the surface waters of the world's oceans, dwelling within the sediments of near-shore salt marsh and mangrove swamps, and living attached to seagrasses and coral reefs. Many species are found in extreme environments, such as sediments of the Antarctic benthos and deep-sea hydrothermal vents. Foraminiferans have a long and well-documented fossil record reaching back to the Early Cambrian, and the group is considered by paleontologists to have one of the best fossil records of any organism. The fossilized tests of foraminiferans are widely used as tools in biostratigraphy, paleoceanography, and paleoclimatology. A phylogenetic definition of *Foraminifera*, therefore, must reflect both the neontological and paleontological utility of the group, as well as traditional usage of the name.

Thus, I propose to define the name *Foraminifera* d'Orbigny 1826 (converted clade name) for the clade stemming from the most recent common ancestor of the following extant species: *Allogromia laticollaris*, *Astrammia rara*, *Reticulomyxa filosa*, *Saccammina sphaerica*, *Syringammia corbicula*, *Ammodiscus incertus*, *Patellina corrugata*, *Quinqueloculina seminulum*, *Peneroplis planatus*, *Trochammia hadai*, *Cibicides refulgens*, *Rosalina vilardeboana*, *Globigerina bulloides*, *Elphidium excavatum*, and *Nummulites venosus*. Most known fossil foraminiferans are encompassed by this definition, as well as all extant taxa currently recognized as foraminiferans. Most of the taxa originally included by d'Orbigny (1826) in his *Ordre Foraminifères* (Class Cephalopodes) fall within the clade *Foraminifera* as defined above. The monophyly of the clade *Foraminifera* has been demonstrated by numerous recent molecular phylogenetic studies. I also propose to define the name *Panforaminifera* for the more inclusive clade containing *Foraminifera* and all extinct taxa that are closer to *Foraminifera* than to any other extant taxon.

I propose to define the name *Soritacea* Gudmundsson 1994 (converted clade name) for the clade stemming from the most recent common ancestor of the following foraminiferal species: *Peneroplis planatus* (extant), *Dendritina arbuscula* (fossil), *Coscinospira pertusus* (extant), *Spirolina cylindracea* (fossil), *Puteolina protea* (extant), *Cyclorbiculina compressa* (extant), *Archaias angulatus* (extant), *Parasorites orbitolitoideus* (extant), *Sorites orbiculus* (extant), *Amphisorus hemprichii* (extant), *Orbitolites complanatus* (fossil), and *Marginopora vertebralis* (extant). *Soritacea* is a clade of subtropical to tropical, reef-dwelling foraminiferans, extant members of which possess endosymbiotic photosynthetic single-celled eukaryotes (rhodophytes, chlorophytes, or dinoflagellates). The monophyly of the clade *Soritacea* has been demonstrated by recent morphological and molecular phylogenetic studies. I propose to define the name *Soritida* Schultze 1854 (converted clade name) for the clade stemming from the most recent common ancestor of the following foraminiferal species: *Parasorites orbitolitoideus* (extant), *Sorites orbiculus* (extant), *Amphisorus hemprichii* (extant), *Orbitolites complanatus* (fossil), and *Marginopora vertebralis* (extant). The monophyly of the clade *Soritida* has also been demonstrated by recent morphological and molecular phylogenetic studies.

DEFINED NAMES:

Foraminifera: Clade (*Allogromia laticollaris* and *Nummulites venosus*)

Panforaminifera: Clade (*Allogromia laticollaris* and *Nummulites venosus*, not *Gromia oviformis*)

Soritacea: Clade (*Peneroplis planatus* and *Marginopora vertebralis*)

Soritida: Clade (*Parasorites orbitolitoideus* and *Marginopora vertebralis*)

Plantae

Phylogenetic nomenclature of some major plant clades

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We propose tentative phylogenetic definitions for the names of a number of major plant clades but anticipate that discussion with colleagues may result in some changes before these names and definitions are published. Although the name *Plantae* has been used for a variety of groups in the past, it is now applied in almost equal frequency to two clades: 1) land plants and 2) the clade comprising green algae and land plants. We prefer to apply *Plantae* to clade 2 because clade 1 has another widely used name (*Embryophyta*), while none of the alternative names for clade 2 (e.g., *Chlorobionta*, *Viridiaeplantae*) are as widely used.

In selecting and defining names for well supported deep clades within *Plantae*, we adopt the following procedures: 1) Widely used names are applied to crown clades. 2) For each crown, the corresponding total group ("panstem") is named PanX, where X is the crown clade name, using a standard definition adapted from Joyce et al.: "the panstem of crown X". 3) Character-based names (e.g., *Spermatophyta*, *Monocotyledonae*) are given an apomorphy-based or apomorphy-modified node-based definition unless the apomorphy is ambiguous. 4) Apomorphy-based definitions are used in only a few cases in which the apomorphy is commonly fossilized and there is likely to be a need to refer to the clade (e.g., *Lignophyta*). 5) When a clade that has traditionally been classified as a suprageneric taxon is represented by only one extant genus (e.g., *Equisetum* and *Equisetophyta*), the genus name is applied to the crown clade for consistency with species names.

SELECTED NAMES TO BE DEFINED:

Plantae: crown clade (*Magnolia virginiana* L. 1753 and [organisms containing chloroplasts with chlorophyll b in *Magnolia virginiana*, excluding organisms in which the chloroplast is an endosymbiotic eukaryote]).

Streptophyta: crown clade (*Magnolia virginiana* L. 1753 and [*Magnolia virginiana* not *Chlamydomonas pulvisculus* (O. F. Müll.) Ehrenb. 1834]).

Embryophyta: crown clade (*Pinus sylvestris* L. 1753 and [embryo in *Pinus sylvestris*]).

Embryo: young sporophyte retained on the gametophyte or in the seed.

Tracheophyta: crown clade (*Pinus sylvestris* L. 1753 and [tracheids in *Pinus sylvestris*]).

Tracheids: elongate water-conducting cells with differentially thickened walls.

Lycophyta: crown clade (*Lycopodium clavatum* L. 1753 and [*Lycopodium clavatum* not *Equisetum arvense* L. 1753, *Pteris longifolia* L. 1753, *Psilotum nudum* (L.) P. Beauv. 1805, and *Magnolia virginiana* L. 1753]).

Pterophyta: clade (*Pteris longifolia* L. 1753, *Marattia alata* Sw. 1788, and *Ophioglossum vulgatum* L. 1753).

Equisetum: crown clade (*Equisetum arvense* L. 1753 and [*Equisetum arvense* L. not *Pteris longifolia* L. 1753, *Psilotum nudum* (L.) P. Beauv. 1805, *Marattia alata* Sw. 1788, *Ophioglossum vulgatum* L. 1753, *Lycopodium clavatum* L. 1753, and *Magnolia virginiana* L. 1753]).

Lignophyta: clade (bifacial vascular cambium in *Pinus sylvestris* L. 1753). Bifacial

vascular cambium: a meristematic layer of cells producing secondary xylem and secondary phloem.

Spermatophyta: crown clade (*Pinus sylvestris* L. 1753 and [ovule in *Pinus sylvestris*]).

Ovule: an indehiscent megasporangium that abscises after fertilization.

Holospermatophyta: clade (ovule in *Pinus sylvestris*). Ovule: an indehiscent megasporangium that abscises after fertilization.

Coniferophyta: clade (*Pinus sylvestris* L. 1753, *Podocarpus elongatus* (Aiton) Pers. 1807, *Taxus baccata* L. 1753, *Cupressus sempervirens* L. 1753, and *Sciadopitys verticillata* (Thunb.) Siebold & Zucc. 1842).

Angiospermae: crown clade (*Magnolia virginiana* L. 1753 and [carpel in *Magnolia virginiana*]).

Monocotyledonae: the most inclusive crown clade that exhibits a single cotyledon as inherited by *Lilium candidum* L. 1753 and excludes *Ceratophyllum demersum* L. 1753 and *Nymphaea alba* L. 1753.

Tricolpatae: crown clade (*Dicentra spectabilis* Lem. 1847 and [tricolpate pollen in *Dicentra spectabilis*]).

The following total groups are defined with reference to their crown clades using a standard format (e.g., *Panplantae* is the panstem of crown *Plantae*): *Panplantae*, *Panstreptophyta*, *Panembryophyta*, *Pantracheophyta*, *Panlycophyta*, *Panpterophyta*, *Panequisetum*, *Panspermatophyta*, *Panconiferophyta*, *Panangiospermae*, *Panmonocotyledonae*, and *Pantricolpatae*.

Monography and the PhyloCode: a practical example from the moss clade *Leucophanella*

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To date, the treatment of terminal taxa (the “species” rank) remains a pivotal yet unresolved and contentious obstacle in the drafting of the PhyloCode. One possible means of coping with terminal taxa would be to preserve the rank of species, including the Latin binomial, and simply omit any guidelines for their treatment from the PhyloCode. An alternative approach advocates a PhyloCode that retains a consistent methodology for the naming of all taxa, regardless of their position in the phylogeny. While many possibilities exist for dealing with terminal taxa (e.g. Cantino et al 1999, Mishler 1999, Pleijel and Rouse 2000), few practical attempts have been made to apply phylogenetic nomenclature at the terminal taxonomic level.

Here we present a cladistically based monograph of *Leucophanella*, a complex of closely-related lineages in the moss clade *Syrrhopodon*. Monographs remain a critical and indispensable component of systematics; however, traditional monographic practices require some revisions if modern monographs are to truly reflect and incorporate phylogenetic understanding. We will summarize the methods we used to address issues relating to sampling and the formation of OTUs for this monograph, and emphasize the importance of carefully considering the incorporation of terminal lineages from the earliest stages of a cladistic monograph.

Leucophanella has been subjected to successive bouts of fervent taxonomic splitting and lumping, chronicled in the proliferation of species names synonymized under *S. involutus* by Mohamed and Reese (1985). This monographic treatment recognizes five distinct lineages in the *Leucophanella* clade: *Banksii*, *Borneensis*, *Involutus*, *Rufescens*, and *Revolutus*. Following the PhyloCode recommendations for the designation and naming of more inclusive taxa, we have named terminal taxa with an italicized uninomial, and have provided stem-based definitions with two internal and one external specifier. The internal specifiers for the stem-based phylogenetic definitions of taxa are chosen to maximize geographic breadth, and whenever possible current type specimens are designated as specifiers. The rank-free treatment of terminal taxa provides a logically consistent and truly practical taxonomy for all purposes, including biodiversity inventories and conservation.

DEFINED NAMES (stem-based definitions):

Leucophanella: nomen cladi conversum (internal specifier: Type: *S. banksii* Müll. Hal., *Botanische Zeitung. Berlin* 16: 162. 1858. TAHITI; internal specifier: Type: *S. involutus* Schwägr., *Species Muscorum Frondosorum, Supplementum Secundum* 1(2): 117. pl. 132. 1824. MOLUCCAS; external specifier: Type: *S. trachyphyllus* Mont. *Sylloge Generum Specierumque Cryptogamarum* 47. 1856. SINGAPORE)

Banksii: (internal specifier: Type: *S. banksii* Müll. Hal., *Botanische Zeitung. Berlin* 16: 162. 1858. TAHITI; internal specifier: *W.R. Sykes 16464*. NIUE; external specifier: Type: *Trachymitrium bornense* Hampe, *Nuovo Giornale Botanico Italiano* 4: 280. 1872. BORNEO)

Borneensis: (internal specifier: Type: *Trachymitrium bornense* Hampe, *Nuovo Giornale Botanico Italiano* 4: 280. 1872. BORNEO; internal specifier: Type: *Syrrhopodon rotundatus* Broth., *Oefversigt af Förhandlingar, Finska Vetenskaps-Societeten* 35: 40. 1893. PAPUA NEW GUINEA; external specifier: Type: *Syrrhopodon revolutus* Dozy & Molk., *Annales des Sciences Naturelles; Botanique, sér. 3* 2: 315. 1844. JAVA)

Involutus: (internal specifier: Type: *S. involutus* Schwägr., *Species Muscorum Frondosorum, Supplementum Secundum* 1(2): 117. pl. 132. 1824. MOLUCCAS; internal specifier: Type: *Syrrhopodon asperrimus* Broth., *Oefversigt af Förhandlingar, Finska Vetenskaps-Societeten* 37: 157. 1895. MIOKO; external specifier: Type: *S. trachyphyllus* Mont. *Sylloge Generum Specierumque Cryptogamarum* 47. 1856. SINGAPORE)

Rufescens: (internal specifier: Type: *Syrrhopodon rufescens* Hook. & Grev., *Edinburgh Journal of Science* 3: 227. 1826. SINGAPORE; internal specifier: Type: *Syrrhopodon ridleyi* Broth. ex Dix., *Bulletin of the Torrey Botanical Club* 51: 229. 3 f. 7. 1924. SINGAPORE; external specifier: Type: *S. trachyphyllus* Mont. *Sylloge Generum Specierumque Cryptogamarum* 47. 1856. SINGAPORE)

Revolutus: (internal specifier: Type: *Syrrhopodon revolutus* Dozy & Molk., *Annales des Sciences Naturelles; Botanique, sér. 3* 2: 315. 1844. JAVA; internal specifier: Type: *Syrrhopodon microbolax* Müll. Hal., *Annales des Sciences Naturelles; Botanique, sér. 6, 9*: 348. 1880. MADAGASCAR; external specifier: Type: *Syrrhopodon involutus* Schwägr., *Species Muscorum Frondosorum, Supplementum Secundum* 1(2): 117. pl. 132. 1824. MOLUCCAS)

Phylogenetic nomenclature of Lamiaceae

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Prior to 1992, the name Lamiaceae was almost universally applied to what is now known to be a polyphyletic group. Through a broadening of membership, "Lamiaceae" is now widely applied to a clade. This latter usage is captured with a node-based definition with 10 specifiers. Because basal resolution within *Lamiaceae* is poor, many internal specifiers are used to reduce the likelihood of attaching the name to a less inclusive clade than intended. The following widely used names for well supported crown clades within *Lamiaceae* are defined below: *Viticina*, *Ajugoideae*, *Lamioideae*, *Scutellarioideae*, *Prostantheroideae*, *Nepetoideae*, *Elsholtzieae*, *Mentheae*, and *Ocimeae*. Definitions are also provided for several other well supported crown clades of Lamiaceae. Where apomorphy-modified or stem-modified node-based definitions are used, "crown clade" implies that both basal branches have members that are extant as of 2004, unless otherwise noted. In the case of *Scutellarioideae*, "extant as of 1936" is specified in order to include *Wenchengia*, a monotypic genus that has not been collected since 1936 and is now probably extinct. In many cases, stem-modified or apomorphy-modified definitions are used to reduce the likelihood of future content instability where there is poor resolution within a well supported clade. The name *Lamioideae* has been applied to several different groups in the past 20 years. It is applied here to the same clade as in a monograph of *Lamiaceae* by R. Harley (in press) which is likely to stabilize the application of this name in rank-based nomenclature.

DEFINED NAMES:

Lamiaceae: clade (*Lamium purpureum* L. 1753, *Callicarpa dichotoma* (Lour.) K. Koch 1872, *Congea tomentosa* Roxb. 1820, *Glechoma hederacea* L. 1753, *Petraeovitex multiflora* (Sm.) Merr. 1917, *Premna microphylla* Turcz. 1863, *Prostanthera rotundifolia* R. Br. 1810, *Tectona grandis* L.f. 1782, *Ajuga reptans* L. 1753, and *Vitex agnus-castus* L. 1753).

Symphorematina: crown clade (*Symphorema involucreatum* Roxb. 1805 and [paniculiform inflorescence composed of cymes that are surrounded by an involucre of winglike bracts in *Symphorema involucreatum*]).

Viticina: crown clade (*Vitex agnus-castus* L. 1753 and [*Vitex agnus-castus* not *Callicarpa dichotoma* (Lour.) K. Koch 1872, *Congea tomentosa* Roxb. 1820, *Glechoma hederacea* L. 1753, *Lamium purpureum* L. 1753, *Petraeovitex multiflora* (Sm.) Merr. 1917, *Prostanthera rotundifolia* R. Br. 1810, *Tectona grandis* L.f. 1782, and *Ajuga reptans* L. 1753]).

Ajugoideae: clade (*Ajuga reptans* L. 1753, *Rotheca myricoides* (Hochst.) Steane and Mabberley 1998, *Karomia speciosa* (Hutch. and Corbish.) R.B. Fernandes 1988, and *Glossocarya coriacea* Munir 1990).

Lamiina: clade (*Lamium purpureum* L. 1753 and *Scutellaria galericulata* L. 1753).

Lamioideae: crown clade (*Lamium purpureum* L. 1753 and [*Lamium purpureum* not *Scutellaria galericulata* L. 1753]).

Scutellarioideae: crown clade (*Scutellaria galericulata* L. 1753 and extant as of 1936 [*Scutellaria galericulata* not *Lamium purpureum* L. 1753]).

Prostantheroideae: clade (*Prostanthera lasianthos* Labill. 1806 and *Chloanthes stoechadis* R. Br. 1810).

Chloantheae: crown clade (*Chloanthes stoechadis* R. Br. 1810 and [*Chloanthes stoechadis* not *Prostanthera lasianthos* Labill. 1806]).

Prostanthereae: crown clade (*Prostanthera lasianthos* Labill. 1806 and [*Prostanthera lasianthos* not *Chloanthes stoechadis* R. Br. 1810]).

Nepetoideae: crown clade (*Nepeta cataria* L. 1753 and [hexacolpate pollen in *Nepeta cataria*]).

Mentheae: clade (*Mentha spicata* L. 1753, *Nepeta cataria* L. 1753, *Salvia officinalis* L. 1753, *Hyssopus officinalis* L. 1753, and *Lycopus europaeus* L. 1753).

Nepetinae: crown clade (*Nepeta cataria* L. 1753 and [posterior stamens longer than the anterior stamens in *Nepeta cataria*.]).

Ocimeae crown clade (*Ocimum basilicum* L. 1753, *Tetradenia riparia* (Hochst.) L. E. Codd 1983, and [declinate stamens in *Ocimum basilicum*]).

Elsholtzieae: crown clade (*Elsholtzia cristata* Willd. 1790 and [*Elsholtzia cristata* not *Nepeta cataria* L. 1753, *Ocimum basilicum* L. 1753, *Melissa officinalis* L. 1753, *Salvia officinalis* L. 1753, and *Lavandula multifida* L. 1753]).

Phylogenetic nomenclature of Lamiales

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The name Lamiales generally was applied to a group of plants in the clade Asteridae that was characterized by a reduced ovule number to two per carpel and the presence of a dividing tissue ('false septum') separating each carpel into two uniovulate locules. Molecular phylogenetic studies have shown this circumscription to be artificial, with several lineages derived independently from multiovulate ancestors. A monophyletic group encompassing most of these taxa and related groups has been identified and accepted in recent classifications as Lamiales. Several well-supported clades have been identified within Lamiales, but relationships among them are weakly supported or remain unresolved, including some deep nodes, and no clear sister group has been identified. Thus, a node-based definition for Lamiales requires several specifiers to assure that the name is applied as intended. For the same reason, node-based definitions are preferred for most of the included clades, because no clear sister groups can be identified. Several smaller clades are not sufficiently well characterized to merit naming at this time. The following previously used names for well supported crown clades within Lamiales are defined.

DEFINED NAMES:

Lamiales: Clade (*Lamium purpureum* L. 1753, *Plocosperma buxifolium* Benth. 1876 [If Salinas 8050 (MEXU) should turn out not to belong to *Plocosperma*, *Plocosperma buxifolium* shall be removed from the list of internal specifiers.], *Tetrachondra hamiltonii* Petrie 1892, *Peltanthera floribunda* Benth. 1876, and *Olea europaea* L. 1753).

Oleaceae: Clade (*Olea europaea* L. 1753, *Fontanesia fortunei* Carr. 1859, *Nyctanthes arbor-tristis* L. 1753, *Jasminum officinale* L. 1753, and *Forsythia suspensa* (Thunberg) Vahl 1804).

Tetrachondraceae: Clade (*Tetrachondra hamiltonii* Petrie 1892 and *Polyprenum procumbens* L. 1753).

Calceolariaceae: Clade (*Calceolaria pinnata* L. 1770 and extant [*Calceolaria pinnata* not *Lamium purpureum* L. 1753, *Veronica officinalis* L. 1753, *Gesneria humilis* L. 1753, *Carlemmania griffithii* Benth. 1853, *Scrophularia nodosa* L. 1753, and *Stilbe vestita* L. 1767]).

Gesneriaceae: Clade (*Gesneria humilis* L. 1753, *Peltanthera floribunda* Benth. 1876, and *Sanango durum* Bunting & Duke 1961).

Veronicaceae: Clade (*Veronica officinalis* L. 1753, *Gratiola pilosa* Michx. 1803, *Angelonia pubescens* Benth. 1836, *Ourisia poeppigii* Benth. 1846, *Tetranema mexicanum* Benth. 1843, and *Chelone obliqua* L. 1768).

Scrophulariaceae: Clade (*Scrophularia nodosa* L. 1753, *Myoporum mauritianum* A. DC. 1847, *Hemimeris sabulosa* L.f. 1782, *Alonsoa unilabiata* Ruiz & Pav. Ex Steud. 1821, *Colpias mollis* E. Mey. 1836, *Anticharis glandulosa* Aschers. 1866, and *Nemesia strumosa* Benth. 1836).

Stilbaceae: Clade (*Stilbe vestita* L. 1767, *Halleria lucida* L. 1753, and *Charadrophila capensis* Marloth 1899).

Verbenaceae: Clade (*Verbena officinalis* L. 1753, *Duranta erecta* L. 1753, *Citharexylum ligustrinum* van Houtte 1887, and *Petrea volubilis* L. 1753).

Bignoniaceae: Clade (*Bignonia capreolata* L. 1753, *Jacaranda arborea* Urb. 1912, *Tourrettia lappacea* (L'Hérit.) Willd. 1800, *Argyria bustillosii* Phil. 1857, *Delostoma lobbii* Seem. 1862, *Catalpa bignonioides* T. Walter 1788, *Oroxylum indicum* (L.) Kurz 1877, *Tabebuia lepidota* Britton 1915, *Spathodea campanulata* Beauv. 1805, and *Tecoma stans* (L.) Kunth in H. B. & K. 1819).

Acanthaceae: Clade (*Acanthus mollis* L. 1753, *Thunbergia alata* Sims 1825, and *Elytraria crenata* Leonard 1938).

Orobanchaceae: Clade (*Orobanche major* L. 1753, *Lindenbergia philippinensis* Benth. in DC 1846, *Buchnera floridana* Gand. 1919, *Bartsia alpina* L. 1753, *Castilleja linariifolia* Pennell 1938, and *Brandisia hancei* Hook. 1884).

Phylogeny of the *Linearia* and *Notata* groups of *Paspalum* L. (Poaceae) and nomenclature proposed for some clades

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The genus *Paspalum* L., with about 400 species in the world and 220 in Brazil, is of ecological and agronomical importance. In 1929, Agnes Chase divided the genus into 25 informal groups which are traditionally used by taxonomists. This classification into groups is artificial and do not reflect the phylogeny. The “*Linearia*” and “*Notata*” groups were independently revised using morphological characters, in both cases the group’s circumscription was ambiguous. Some species were placed in both groups, whose monophyly was questioned by some authors. A phylogenetic analysis of these two groups and allied species is presented here using an evolutionary approach with molecular characters. The topology is: {(*P. minus*, *P. subciliatum*, (*P. nummularium*, *P. pumilum*), (*P. conduplicatum*, *P. notatum*)}, [*P. filifolium*, (*P. equitans*, *P. ramboi*)]} The two main clades in the produced trees have a very good bootstrap support and constancy among the several performed analyses. These clades are given node-based definitions and can receive a formal taxonomic name based on morphological affinities and their phylogenetic relationships. Taxon *Notata* is defined as (*P. minus*, *P. subciliatum*, *P. nummularium*, *P. pumilum*, *P. conduplicatum* and *P. notatum*). These species form a very homogeneous group, but represent only a small part of the informal *Notata* group. Taxon *Filifolia* includes (*P. filifolium*, *P. equitans* and *P. ramboi*); it has high support in the trees. Nevertheless, for many taxonomists, these species belong to different informal groups (respectively: *Linearia*, *Ovalia* and *Notata*). We can also emphasize a taxon formed by two accessions of *P. ellipticum* Doell: each of them represents a biotype of this species, but is accepted by some authors as valid species (*P. ellipticum* and *P. proximum* Mez). The close relationships of these accessions, which form a constant and supported clade in major trees, corroborates the synonymization of *P. proximum* and *P. ellipticum*. This synonymization was previous proposed by morphological analysis (Oliveira & Valls, 2002). This work intends to name the groups that are supported by the molecular phylogenetic analysis. We also propose that the application of preexisting names, like the groups of *Paspalum* that are not clades or apomorphy-based, should be discouraged.

DEFINED NAMES:

Taxon *Notata*: Clade (*P. minus*, *P. subciliatum*, *P. nummularium*, *P. pumilum*, *P. conduplicatum* and *P. notatum*)

Taxon *Filifolia*: Clade (*P. filifolium*, *P. equitans* and *P. ramboi*)

A phylogenetic nomenclature of *Rhinopetalum* (*Liliaceae*) based on nectary morphology and Giemsa C-banding studies

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C-band patterns and nectary morphology are described for Old World *Rhinopetalum* species. All species have a similar basic karyotype ($n=12$), consisting of large symmetric (m, sm) and smaller asymmetric (t, st) chromosomes, but C-bands differ between them. The bands are rather few, located at intercalary, telomeric, centromeric and rarely secondary constriction regions. The genus *Rhinopetalum* is comparatively richer in heterochromatin. The patterns are characterized by the occurrence of thick telomeric/subtelomeric heteromorphic bands in the second pair of m-chromosomes. Presence of a distinct centromeric band in the short arms of these m-chromosomes in *Rh. bucharicum* discriminate it from the two allied species (synapomorphy). A certain level of banding heteromorphy was observed mostly in term of band size. It is obvious from this study that diversity exists between individual species studied both in the dispersion and quantity of detectable heterochromatin and chromosome morphology, i.e. asymmetric karyotype, which are evolutionary and derived characters. Nectary morphology in *Rhinopetalum* showed that they are deeply impressed, and the slit-like nectary orifice is bordered by two lobes, at least in the lower part densely hairy. In *Rh. stenanthum* and *Rh. bucharicum*, nectaries are equally impressed in all tepals and the nectary orifice is bordered by narrow, unfringed ridges. In *Rh. gibbosa*, *Rh. karelinii* and *Rh. ariana*, the flowers are \pm zygomorphic as the nectary on the upper tepal is more deeply depressed than the others, and the nectary lobes are rather broad and fringed. It seems that karyological studies confirm morphological studies of nectaries concerning dividing of *Rhinopetalum* nomenclaturely into two informal subgroups named *Bucharicum* and *Gibbosum*. The nectaries characteristics and Giemsa C-banding approaches in *Rhinopetalum* are also advanced and synapomorphic characters compare with allied genera in *Liliaceae*, for instance *Fritillaria*.

DEFINED NAMES

Fritillaria: Clade (*Fritillaria bucharica*, *Fritillaria stenantha*, *Fritillaria gibbosa*, *Fritillaria ariana*).

Rhinopetalum: Clade (*Rhinopetalum arianum*, *Rhinopetalum gibbosum*, *Rhinopetalum karelinii*, *Rhinopetalum buchaicum*, *Rhinopetalum stenanthum*)

Metazoa

Phylogenetic nomenclature of sponge taxa

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Although the phylogeny of sponges is still in its infancy, several important issues have been recently resolved, owing to the use of molecular data (mostly sequences of the small and large ribosomal units). There is high support for the monophyly of four main sponge clades: *Hexactinellida*, *Demospongiae*, *Homoscleromorpha* and *Calcispongia*, for which we provide phylogenetic definitions. Node-based definitions are used for *Demospongiae* and *Calcispongia* because there is substantial resolution of internal relationships for these two taxa; while for the two remaining names we use stem-based definitions. These converted names are defined in order to keep their traditional meaning. However, for demosponges, we adopt a compromise by defining *Demospongiae* in a restricted sense which excludes the *Homoscleromorpha*, due to uncertain position of the latter with respect to other sponge lineage and to non-sponge metazoans (*Eumetazoa*). The use of the name *Demospongiae* in this restricted meaning avoids the creation of a new name for the clade comprising demosponges in the classical sense without the homoscleromorphs.

We provide no higher-level definition of taxa because the phylogenetic relations between the four main clades are currently not resolved. For instance, the name *Porifera* is not used because there is debate about the monophyly or paraphyly of sponges. Nor do we use the name *Silicispongia*, because there is no compelling evidence for a clade grouping all sponges with siliceous spicules (*Hexactinellida*, *Demospongiae* and *Homoscleromorpha*).

Within *Demospongiae* and *Calcispongia*, we provide a few definitions of taxon names, only for those clades that are well-supported in molecular phylogenies. Current classification (as used for example in the reference work *Systema Porifera* Hooper & Van Soest 2002) dividing *Demospongiae* between *Tetractinomorpha* and *Ceractinomorpha* is not phylogenetic, both of these groups being polyphyletic. The name *Keratosa* is converted from Bowerbank (1964) but used in a more restricted sense compared to the original meaning. The name *Myxospongia* is converted from Zittel (1878), with an emended composition (by adding *Verongida* to the original meaning). The name *Tetractinellida* is converted from Marshall (1876) and used in consistence with the original sense.

Within *Calcispongia*, molecular phylogenies have confirmed the existence of two monophyletic sister-groups, *Calcinea* and *Calcaronea* (both converted names). We provide two more definitions: *Baeriida* (converted name from Borojevic et al. 2000) is used in the original meaning with the addition of *Petrobiona*, which was previously classified in *Lithonida*. *Lithonida* includes *Calcaronea* with a reinforced skeleton made of fused spicules. All definitions within *Calcispongia* are stem-based.

DEFINED NAMES:

Hexactinellida (*nomen cladi conversum ex* Schmidt, 1870): clade (*Oopsacas minuta* not *Spongia officinalis*, *Chondrosia reniformis*, *Haliclona mediterranea*, *Oscarella lobularis* and *Grantia compressa*)

Homoscleromorpha (*nomen cladi conversum ex* Lévi, 1973): clade (*Oscarella lobularis* not *Geodia cydonium*, *Leucosolenia variabilis*, *Oopsacas minuta*, *Hydra viridis* and *Beroe ovata*)

Demospongiae (*nomen cladi conversum ex* Sollas, 1885): clade (*Haliclona mediterranea*, *Geodia cydonium*, *Spongia officinalis* and *Chondrosia reniformis*)

Keratosa (*nomen cladi conversum ex* Bowerbank, 1864): clade (*Spongia officinalis* not *Aplysina cavernicola*, *Haliclona mediterranea* and *Geodia cydonium*)

Myxospongiae (*nomen cladi conversum ex* Zittel, 1878): clade (*Aplysina cavernicola*, *Hexadella racovitzai*, *Chondrosia reniformis*, and *Thymosia guernei*)

Tetractinellida (*nomen cladi conversum ex* Marshall, 1876): clade (*Geodia cydonium*, not *Axinella polypoides*, *Suberites ficus*, *Microciona prolifera*, *Spongilla lacustris*, *Haliclona mediterranea*, *Spongia officinalis*, and *Aplysina cavernicola*)

Calcispongia (*nomen cladi conversum ex* Blainville, 1830 *emend.* Haeckel, 1872): clade (*Clathrina clathrus* and *Grantia compressa*)

Calcinea (*nomen cladi conversum ex* Bidder, 1898): clade (*Clathrina clathrus* not *Grantia compressa*)

Calcaronea (*nomen cladi conversum ex* Bidder, 1898): clade (*Grantia compressa* not *Clathrina clathrus*)

Baeriida (*nomen cladi conversum ex* Borojevic et al., 2000): clade (*Leuconia nivea* not *Plectroninia halli*, *Leucosolenia variabilis* and *Grantia compressa*)

Lithonida (*nomen cladi conversum ex* Vacelet, 1981): clade (*Plectroninia halli* not *Leuconia nivea*, *Leucosolenia variabilis* and *Grantia compressa*)

Nomenclature and conflicting hypotheses: phylogenetic definitions within (and outside) the flatworms

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In recent years, phylogenetic research on flatworms (*Platyhelminthes*) has gained interest for two reasons. First of all, some molecular studies suggested that the *Platyhelminthes* are not-monophyletic, with one (*Acoela*) or two (*Acoela* and *Nemertodermatida*) taxa at the base of the *Bilateria* and the rest of the *Platyhelminthes* part of a large clade also containing the *Deuterostomia*, *Lophotrochozoa* and *Ecdysozoa*. Secondly, research has focused on parasitic flatworms (*Neodermata*), trying to assess their monophyly and sister group. Both research points were approached from both a morphological and a molecular point of view, and the analyses included many free-living flatworms, often revealing surprising and controversial relationships.

Because of this state of flux, old names should be converted and new names defined with great care, trying to keep their original meaning in order to keep them universally applicable. Because of the heavy debate about the possible polyphyletic state of the *Platyhelminthes*, we decided to refrain from converting this name. Morphological as well as molecular evidence however show that the four main subclades within the *Platyhelminthes* are monophyletic and therefore their names can be defined phylogenetically: *Acoela*, *Nemertodermatida*, *Catenulida* and *Rhabditophora*. Because of uncertain sister group relationships of these clades, no higher-level taxa are defined (e.g. a definition for the *Acoelomorpha* is not provided). Within the *Rhabditophora*, recent molecular and morphological studies confirm the monophyletic state of many of the subtaxa, the names of which will be converted: *Neodermata*, *Rhabdocoela*, *Kalyptorhynchia*, *Eukalyptorhynchia*, *Schizorhynchia*, *Tricladida*, *Fecampiida*, *Prolecitophora*, *Unguiphora*, *Lithophora* and *Polycladida*. Of these, the *Fecampiida* will be defined sensu Norén & Jondelius (2002). The *Adiaphanida* was already defined phylogenetically with a node-based definition by Norén & Jondelius (2001), but the phrasing will be changed in order to be conform to the new PhyloCode. Well-known taxa that are not defined are: *Proseriata* (poly- or paraphyletic in some analyses, monophyletic but weakly supported in others), *Lithophora* (monophyletic in only some recent analyses, and even then weakly supported) *Neophora* (some analyses suggest they are not monophyletic), *Seriata*, *Typhloplanoida*, *Dalyellioida*, *Macrostomida*, *Revertospermata* and *Mediofusata* (all six probably not monophyletic) and *Lecithoepitheliata* (only *Geocentrophora* species included in recent analyses, the relationships with the marine *Lecithoepitheliata* since long considered uncertain).

All definitions are node-based. Stem-based definitions were mostly not possible because of the often uncertain sister group relationships between these taxa.

We decided only to name high-level taxa. Cladistical analyses are lacking for most of the lower level taxa and we think the respective specialist are better placed to judge how to define taxa that are now considered to be of the family or genus level.

DEFINED NAMES:

Acoela Uljanin, 1870 n.c.c.: Clade (*Anthroposthia unipora*, *Antigonaria arenaria*, *Convoluta convoluta*, *Diopisthoporus longitubus*, *Hallangia proporoides*, *Hofstenia atroviridis*, *Myopea crassula*, *Nadina pulchella*, *Paratomella unichaeta* & *Proporus venenosus*)

Catenulida Graff, 1905 n.c.c.: Clade (*Catenula lemnae*, *Chordarium leucanthium*, *Retronectes sterreri* & *Stenostomum leucops*)

Nemertodermatida Steinböck, 1931: Clade (*Ascoparia neglecta*, *Flagellophora appelti*, *Meara stichopi* & *Nemertoderma westbladi*).

Neodermata Ehlers, 1984 n.c.c.: Clade (*Austramphilina elongata*, *Calicotyle affinis*, *Echinococcus granulatus*, *Gyrocotyle urna*, *Multicotyle purvisi*, *Polystomoides malayi* & *Schistosoma mansoni*)

Rhabditophora Ehlers, 1984 n.c.c.: Clade (*Cirrifera dumosa*, *Fecampia bathycola*, *Geocentrophora sphyrocephala*, *Gnosonesima brattstroemi*, *Gyatrix hermaphroditus*, *Haplopharynx rostratus*, *Macrostomum tuba*, *Microstomum lineare*, *Nematoplana corsicana*, *Plagiostomum ochroleucum*, *Polycelis tenuis*, *Pseudostomum klostermanni* & *Schistosoma mansoni*).

References:

Jondelius U., Ruiz-Trillo I., Baguña J. & Riutort M. (2002). The Nemertodermatida are basal bilaterians and not members of the Platyhelminthes. *Zoologica Scripta* 31: 201-215.

Norén M. & Jondelius U. (2002). The phylogenetic position of the Prolecitophora (Rhabditophora, 'Platyhelminthes'). *Zoologica Scripta* 31: 403-414.

Vertebrata

A phylogenetic nomenclature of bony fishes (Osteichthyes)

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The vernacular name bony fishes has been used for advanced actinopterygians (clade *Teleostei* = bony fishes in a narrow sense) and for a taxon including actinopterygians and sarcopterygians. For the latter taxon the term *Osteichthyes* Huxley 1880 is commonly used, even though *Euteleostomi* and *Osteognathostomata* have been suggested by J.S. Nelson 1994 and W. Hennig 1983, respectively. *Osteognathostomata* and *Euteleostomi* were proposed to replace the precladistic paraphyletic taxon *Osteichthyes* which excluded tetrapods because of the aversion to connect the term fish (ichthys Greek = fish) with tetrapods, which form part of the clade *Osteichthyes*. The two terms have not found wide acceptance. We propose, therefore, to use the old term *Osteichthyes* for a clade including *Actinopterygii* Cope 1887 and *Sarcopterygii* Romer 1956 excluding *Acanthodii* Owen 1846, as done, e.g., by Rosen et al. (1980) and Janvier (1996). *Acanthodii* and *Osteichthyes* form together the taxon *Teleostomi* Owen 1866 excluding *Chondrichthyes*. The interrelationships within basal *Actinopterygii* and within basal *Sarcopterygii* are unresolved, whereas the clades of the advanced members in each group can be defined.

The name *Actinopterygii* was coined by Cope (1887) to include the *living* ray-finned fishes, the chondrosteans, holosteans and teleosteans sensu Müller (1844). The monophyly of *Actinopterygii*—including both fossil and extant forms—is robustly supported by numerous characters (Schultze & Cumbaa 2001). Most of these analyses are strongly biased by the inclusion of more Paleozoic actinopterygians in contrast to few younger members.

Sarcopterygii represents a monophylum (Zhu & Schultze 2001). Within sarcopterygians, it is now agreed that *Rhizodontida* Andrews & Westoll 1970, "*Osteolepidida*" Boulenger 1901 and *Elpistostegalia* Camp & Allison 1961 are the closest relatives of the *Stegocephali*. All together form the clade *Choanata* Säve-Söderbergh 1934 (= *Tetrapodomorpha* Ahlberg 1991) that excludes *Porolepiformes* Jarvik 1942, *Dipnoi* Müller 1844 and *Actinistia* Cope 1872. The interrelationship of the latter three taxa is currently debated. *Porolepiformes* and *Dipnoi* are considered to represent the clade *Dipnomorpha* when dipnoan features are interpreted in the porolepiform fashion. However, recoding of few characters places the *Porolepiformes* as sister taxon of *Choanata*, and the *Dipnoi* as sister taxon of *Actinistia* or near the base of the *Sarcopterygii*.

DEFINED NAMES:

Teleostomi (*Perca fluviatilis*, *Homo sapiens* and †*Acanthodes bronni* not *Squalus acanthias*)

Osteichthyes (*Perca fluviatilis* and *Homo sapiens*)

Actinopterygii (*Perca fluviatilis* not *Homo sapiens*)

Sarcopterygii (*Homo sapiens* not *Perca fluviatilis*)

Choanata (*Homo sapiens* not †*Porolepis brevis*, *Neoceratodus fortseri* and *Latimeria chalumnae*)

A phylogenetic nomenclature of advanced ray-finned fishes (Actinopterygii)

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During the last 30 years, the monophyly of higher taxa of the ray-finned fishes or *Actinopterygii*, the *Halecomorphi*, and the *Teleostei*, has been established. Thus, the status of the interrelationships of advanced ray-finned fishes (*Actinopterygii*) has reached a certain level of agreement, and the regions of disagreement can be defined. For instance, the unnatural taxon *Holostei* prevailing during most of the 20th century, has been replaced by monophyletic groups. New names have been proposed to clarify the status of older names. This is followed here.

The crown clade *Teleocephala* (created by Pinna 1996) includes all extant teleosts. This clade is supported by about 10 synapomorphies. Among teleocephalans, it is unclear whether the elopomorphs or the osteoglossomorphs are the most primitive group. The phylogenetic position of one or the other is strongly biased by the composition of the ingroup. *Elopomorpha* stand at the base when fossil and recent teleosts are included in the phylogenetic analysis; *Osteoglossomorpha* take the basal position when only recent teleosts are included.

Teleostei Müller 1844 is a taxon based on 15 synapomorphies. This major clade represents all extant and fossil members with cycloid scales (the "true" teleosts) and †*Pholidophorus bechei*. Among advanced actinopterygians, the strongest supported node, with 27 synapomorphies, corresponds to that of "true" teleosts: [*Leptolepis coryphaenoides* + more advanced teleosts]. Different sister taxa of *Teleostei* have been suggested above the branching point of *Halecomorphi*. The clade above the branching point of the *Halecomorphi* has been named *Teleosteomorpha* (erected by Arratia 2001).

The *Halecomorphi* Cope 1872 include *Amia calva* and all its closest relatives, but not *Teleosteomorpha*. *Teleosteomorpha* and *Halecomorphi* together form the clade *Halecostomi* Regan 1923. The *Neopterygii* Regan 1923 include *Halecostomi*, *Ginglymodi* and †*Acentrophorus varians*. However, most Triassic neopterygians are poorly known. A phylogenetic analysis including many fossil and living neopterygians has never been published due to incomplete information of most fossil members of the clade.

DEFINED NAMES:

Teleocephala: Clade (*Perca fluviatilis*, *Osteoglossum bicirrhosum* and *Elops saurus*)

Teleostei: Clade (*Perca fluviatilis* and †*Pholidophorus bechei* not †*Aspidorhynchus acutirostris*, †*Gyrodus hexagonus*, †*Dapedium pholidotum*, †*Pachycormus curtus*)

Teleosteomorpha: Clade (*Perca fluviatilis* not *Amia calva*)

Halecostomi: Clade (*Amia calva* and *Perca fluviatilis*)

Halecomorphi: Clade (*Amia calva* not *Perca fluviatilis*)

Neopterygii: Clade (*Perca fluviatilis*, *Amia calva*, *Lepisosteus osseus* and †*Acentrophorus varians*)

A phylogenetic nomenclature of early limbed vertebrates

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The phylogeny of limbed vertebrates is in a state of flux. Most authors agree that *Panderichthys* and *Elpistostege* are our closest known relatives whose paired appendages are known to have been fins, but this hypothesis has been accepted for only about a decade. Thus, I propose to define the name *Stegocephali* Cope 1868 (converted name) for the most inclusive clade containing *Eryops megacephalus* but not *Panderichthys rhombolepis*, *Elpistostege watsoni*, *Eusthenopteron foordi*, *Osteolepis panderi* and *Strepsodus sauroides*. The name *Stegocephali* formerly included all the earliest limbed vertebrates, but was paraphyletic before it was given a phylogenetic definition in the late 1990s. The name *Anthracosauria* has always included embolomeres; it has sometimes included seymouriamorphs, and much more rarely, amniotes. I propose to define *Anthracosauria* Säve-Söderbergh 1934 (converted clade name) as the largest clade that includes *Anthracosaurus russelli* but neither *Homo sapiens* nor *Ascaphus truei*. Thus defined, the contents of *Anthracosauria* can expand to include seymouriamorphs if they form a clade with embolomeres that excludes lissamphibians and amniotes. The name *Seymouriamorpha* Watson 1917 (converted clade name) is here defined as the largest clade that includes *Seymouria baylorensis* but not *Homo sapiens*, *Anthracosaurus russelli*, and *Diadectes sideropelicus*. *Tetrapoda* has referred to limbed vertebrates in paleontological studies and this is also the intended meaning in many neontological studies. However, most statements concerning tetrapods in the neontological literature describe the crown-group. Thus, the name *Tetrapoda* Goodrich 1930 (converted clade name) is defined as the smallest clade that includes *Ascaphus truei* and *Homo sapiens*. Tetrapods have often been divided into two main groups, one that includes lissamphibians and their extinct relatives, and another that includes amniotes and their extinct relatives. This nomenclature is adopted here by defining the name *Amphibia* Linnaeus 1758 (converted clade name) as the largest clade that includes *Ascaphus truei* but not *Homo sapiens*, and by defining the name *Reptiliomorpha* Säve-Söderbergh 1934 (converted clade name) as the largest clade that includes *Homo sapiens* but not *Ascaphus truei*. Diadectomorphs are generally considered to be closely related to amniotes, but some authors have suggested that they are basal synapsids. Earlier studies also suggested affinities with parareptiles. To ensure that the composition of this taxon will always reflect established usage, the name *Diadectomorpha* Watson 1917 is defined as the most inclusive clade that includes *Diadectes sideropelicus* but not *Solenodonsaurus janenschii*, *Seymouria baylorensis*, *Homo sapiens*, *Eothyris parkeyi*, and *Procolophon trigoniceps*.

DEFINED NAMES:

Stegocephali: Clade (*Eryops megacephalus* not *Panderichthys rhombolepis*, *Elpistostege watsoni*, *Eusthenopteron foordi*, *Osteolepis panderi* and *Strepsodus sauroides*)

Anthracosauria: Clade (*Anthracosaurus russelli* not *Homo sapiens* and *Ascaphus truei*)

Seymouriamorpha: Clade (*Seymouria baylorensis* not *Homo sapiens*, *Anthracosaurus russelli*, and *Diadectes sideropelicus*)

Tetrapoda: Clade (*Ascaphus truei* and *Homo sapiens*)

Amphibia: Clade (*Ascaphus truei* not *Homo sapiens*)

Reptiliomorpha: Clade (*Homo sapiens* not *Ascaphus truei*)

Diadectomorpha: Clade (*Diadectes sideropelicus* not *Solenodonsaurus janenschii*, *Seymouria baylorensis*, *Homo sapiens*, *Eothyris parkeyi*, and *Procolophon trigoniceps*)

Phylogenetic nomenclature of Mesozoic temnospondyls

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The *Temnospondyli* was a diverse and long-lived group of fossil early tetrapods usually considered to contain the ancestors of some or all of the modern lissamphibian groups. *Temnospondyls* diversified in two major radiations, a Carboniferous radiation of primitive temnospondyls, and a Triassic radiation of derived temnospondyls known as the *Stereospondyli*. To date, only two broad-scale studies on the intrarelationships of the *Temnospondyli* have been published, only one of which was based on parsimony analysis of a data matrix. Some of the relationships proposed in those analyses have been challenged by more detailed parsimony analyses of individual clades within the *Temnospondyli*. It has become clear that temnospondyl intrarelationships, particularly amongst the Palaeozoic groups, are far from resolved, and a much more detailed parsimony analysis of the entire *Temnospondyli* is required. Nevertheless, relationships amongst the main groups of Mesozoic temnospondyls have reached a broad level of phylogenetic consensus, and phylogenetic definitions have been provided for a number of clades. Most Mesozoic stereospondyls fall into a large clade composed of the *Mastodonsauria* and the *Trematosauria*. We propose to name this clade *Neorhachitomi* Efremov 1940 (converted clade name), which we define as the smallest clade that includes *Mastodonsaurus giganteus* and *Trematosaurus brauni*. This name was originally applied to an assemblage of Lower Triassic temnospondyls from Russia that included basal members of the *Mastodonsauria* and *Trematosauria*, and therefore captures the historical use of that name. We define the *Mastodonsauria* (new clade name) as the largest clade containing *Mastodonsaurus giganteus* but not *Trematosaurus brauni*. This clade has previously been referred to as the *Capitosauria*, a name which is inappropriate because it is based on the generically indeterminate *Capitosaurus*. Its major subclade, the *Mastodonsauroida* Lydekker 1885 (converted clade name) is redefined as the smallest clade that includes *Mastodonsaurus giganteus* and *Eocyclotosaurus woschmidti*. The *Trematosauria* Yates & Warren 2000 (converted clade name) is redefined as the largest clade containing *Trematosaurus brauni* but not *Mastodonsaurus giganteus*. Its major subclade, the *Trematosauroida* Watson 1919 (converted clade name) is redefined as the smallest clade that includes *Trematosaurus brauni* and *Aphaneramma rostratum*. The *Metoposauridae*, along with some closely related taxa including *Almasaurus*, may be nested within the *Trematosauria* according to some recent analyses, but this hypothesis requires further testing. The phylogenetic position of the other main Mesozoic temnospondyls, the *Brachyopidae*, *Chigutisauridae*, *Plagiosauridae*, *Rhytidosteidae* and *Lydekkerinidae*, is unclear, and some have even been allied with more primitive Palaeozoic temnospondyls. Although some of these groups were defined phylogenetically in a previous study, these definitions will doubtless be challenged by future analyses.

DEFINED NAMES:

Neorhachitomi: Clade (*Mastodonsaurus giganteus* and *Trematosaurus brauni*)

Mastodonsauria: Clade (*Mastodonsaurus giganteus* not *Trematosaurus brauni*)

Mastodonsauroida: Clade (*Mastodonsaurus giganteus* and *Eocyclotosaurus woschmidti*)

Trematosauria: Clade (*Trematosaurus brauni* not *Mastodonsaurus giganteus*)

Trematosauroida: Clade (*Trematosaurus brauni* and *Aphaneramma rostratum*)

Phylogenetic taxonomy of *Lepospondyli*: “top-down” versus “bottom-up” approaches to nomenclature in uncertain topologies.

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Lepospondyli, a diverse assemblage of Paleozoic tetrapods, is becoming central to our understanding of the origins of amniotes and modern amphibians. This important clade and monophyletic constituents (*Aistopoda*, *Adelospondyli*, *Lysorophia*, *Nectridea*, and less inclusive taxa) will be defined to the extent possible given current understanding of their relationships. The paraphyletic “*Microsauria*” will be abandoned, and smaller subclades (e.g. *Recumbirostra*, *Tuditanimorpha*) will be established and defined instead.

Since the late 1990s, lepospondyls have been placed as the most immediate sister group to the amniote stem, and some studies suggest that some, or all, modern amphibians (*Lissamphibia*, assuming monophyly) have their origins within *Lepospondyli*. However, one recent large scale analysis has placed *Lissamphibia* within *Temnospondyli*, consistent with traditional, rank-based classification. This uncertainty creates instability in taxonomy given the definition for *Amphibia* (reproposed in this symposium) that would hold priority were the PhyloCode currently binding. By giving crown taxa primacy in establishing the definition of well-known names, what I call here the “top-down” approach (e.g., *Amphibia* as the largest clade that includes *Ascaphus truei* but not *Homo sapiens*; a stem taxon with extant specifiers), coupled with uncertainty in the position of one of the crown specifiers, two authors can correctly speak of “amphibians” in reference to either temnospondyls or lepospondyls, two morphologically dissimilar taxa, depending on the placement of *Lissamphibia*. The definition of *Amphibia* in this example, while “stable”, leads to instability in taxon composition and discussions of “amphibian” character evolution. Another alternative, which I call “bottom-up”, does not necessarily define well-known stem taxa using crown specifiers of uncertain affinities, but can use fossil taxa historically associated with the name. In the present example, *Lissamphibia* would be a subclade of (stem defined) *Temnospondyli* or *Lepospondyli*, rather than having *Amphibia* shift (and become effectively synonymous with either name) depending on topology. This approach, like “top-down”, uses stable phylogenetic definitions, but additionally it stabilizes taxon content (which is important when converting well-known names), thus stabilizing discussions of character evolution (since the taxa comprising *Amphibia* aren’t changing), and ultimately increases precision in nomenclature. *Amphibia*, in the “bottom-up” scheme proposed here, would be abandoned as a formal taxon, which would permit its continued lay use to refer to the paraphyletic group of non-amniote tetrapods without conflict with new, widely differing phylogenetic meanings. Abandoning *Amphibia*, or not defining it at this time, is consistent with the PhyloCode’s recommendation to avoid establishing definitions when relationships are uncertain.

NAMES TO BE DEFINED:

Lepospondyli

Nectridea

Scincosauridae

Diplocaulidae

Urocordylidae

Urocordylinae

Sauropleurinae

Adelospondyli

Lysorophia

Aistopoda

Oestocephalidae

Phlegethontioidea

“*Microsauria*”

Tuditanidae

Recumbirostra

Hapsidopareiontidae

Ostodolepidae

Pantylidae

Gymnarthridae

Urocaecilia

Lissamphibia (assuming it is not defined as a crown clade by others)

A Phylogenetic Nomenclature for the Major Clades of Amniota Haeckel 1866, with Emphasis on Non-Avian Reptilia Laurentus 1768

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We propose phylogenetic definitions for 38 important taxon names associated with the major clades of land-egg laying *Vertebrata*, including the crown clades *Amniota*, *Mammalia*, *Reptilia*, *Testudines*, *Sauria*, *Lepidosauria*, *Archosauria*, *Sphenodon*, *Squamata*, *Crocodylia*, and *Aves*. The importance of these names, particularly for the crowns, is revealed by the frequency with which they are encountered in the scientific literature. A Google search, for example, lists the following approximate citation numbers for each of these names as, respectively: 8,750; 335,000; 142,000; 17,100; 28,400; 4,160; 8,810; 3,840; 44,200; 7,840; 1,190,000. If a scientific publication that inspires 50 citations is “influential,” then these names must be “important.” The challenge for the PhyloCode is that taxonomic names above the “family group” have been unregulated for centuries, so “higher” taxon names were often used for a range of internested clades whose ancestors could be separated by several million years. As a consequence, several semi-synonymous names may be “available” for any given amniote clade, making it difficult to justify choosing one name-clade association over another. We propose to resolve the ambiguity by using nomenclatural conventions that enable taxonomy to be maximally informative about genealogical relationships while minimizing cognitive effort. We propose first to assign the most widely used names to the clades that are of interest to the most biologists, namely, the crown clades. Taxon names in general, and familiar names in particular, should be defined precisely in order to most efficiently connect the scientific community to the data in the printed literature, as well as to a growing digital presence on the internet. We also fix the meaning of additional names for more inclusive clades containing our focal crowns, including node-based “*Archosauriformes*” (203 citations), here tied to one of the two internested clades still being called “*Archosauria*”. And we define some names based on fossils, including “*Diapsida*” (3,550 citations) and “*Rhynchocephalia*” (3,570 citations), with respect to the apomorphies from which their names were originally derived. We propose a single convention for naming the stems of all crowns by adding the prefix *Pan-* to crown names: hence, “*Panreptilia*” for the stem of “*Reptilia*.” That effectively reduces cognitive effort and distinguishes another important class of clades that most biologists, especially paleontologists, want to talk about, namely, the pan-monophylum of each crown. Phylogenetic nomenclature will best serve biology by providing a simple and coherent scheme for converting traditional taxon names while permitting scientists to name all the kinds of clades that they want to talk about.

DEFINED NAMES

Amniota Haeckel 1866 = Crown (*Homo sapiens* + *Chelonia mydas* + *Sphenodon punctatus* + *Draco volans* + *Caiman crocodilus* + *Vultur gryphus*).

Reptilia Laurentus 1768 = Crown (*Chelonia mydas* + *Sphenodon punctatus* + *Draco volans* + *Caiman crocodilus* + *Vultur gryphus*).

Diapsida Osborn 1903 = Apomorphy (1st reptile with *Caiman crocodilus*' two temporal arches/fenestra).

Sauria MacCartney 1802 = Crown (*Sphenodon punctatus* + *Draco volans* + *Caiman crocodilus* + *Vultur gryphus*).

Lepidosauria Haeckel 1866 = Crown (*Sphenodon punctatus* + *Draco volans*).

Rhynchocephalia Guenther 1867 = Apomorphy (1st lepidosaur with *Sphenodon punctatus*' premaxillary chisels).

Sphenodon Gray 1831 = Crown (*Sphenodon punctatus* + *Sphenodon guntheri*).

Squamata Oppel 1811 = Crown (*Draco volans* + *Crotalus horridus*)

Archosauromorpha von Huene 1946 = Node (*Protorosaurus speneri* + *Rhynchosaurus articeps* + *Caiman crocodilus*).

Archosauriformes Gauthier *et al.* 1988 = Node (*Proterosuchus fergusi* + *Caiman crocodilus* + *Vulture gryphus*).

Archosauria Cope 1869 = Crown (*Caiman crocodilus* + *Compsognathus longipes* + *Vultur gryphus*).

Crurrotarsi Sereno and Arcucci 1990 = Apomorphy (1st archosaur with *Caiman crocodilus*' fully rotary, hemicylindrical, fibulocalcaneal crurrotarsal articulation).

Crocodylia Owen 1842 = Crown (*Caiman crocodilus* + *Crocodylus niloticus* + *Gavialis gangeticus*).

Early Amniote Phylogeny and Nomenclature

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Recent work on amniote phylogeny has helped to resolve not only the pattern of relationships within *Amniota*, but also clearly identify the stem amniotes. Most authors agree that *Diadectes*, *Limnoscelis*, and *Tseajaja* are the closest known relatives of animals with an amniotic egg. I therefore define the name *Cotylosauria* Cope 1880 (converted clade name) for the most inclusive clade containing *Diadectes sideropelicus*, *Homo sapiens* and *Iguana iguana*. *Cotylosauria* previously included not only *Diadectomorpha*, but also various other anamniotes and eureptiles, and was paraphyletic before it was given a phylogenetic definition in 1995. *Amniota* has always included all extant tetrapods with an amniotic egg, and as such represents a crown-group. Thus, the name *Amniota* Haeckel 1866 (converted clade name) is here defined as the smallest clade that includes *Homo sapiens* and *Iguana iguana*. Amniotes are into two main groups, one that includes mammals and their extinct relatives, and another that includes reptiles and their extinct relatives. It is this nomenclature that we propose to adopt here by defining *Synapsida* Osborn 1903 (converted clade name) as the largest clade that includes *Homo sapiens* but not *Iguana iguana*, and *Reptilia* Laurenti 1768 (converted clade name) as the largest clade that includes *Iguana iguana*, *Testudo hermani*, *Crocodylus niloticus* but not *Homo sapiens*.

Within synapsids there is strong evidence for a basal division of this group, and I therefore propose to define the names *Caseasauria* Watson 1917 (converted clade name) as the most inclusive clade that includes *Casea broilii* but not *Homo sapiens* and *Eupelycosauria* Kemp 1982 (converted clade name) as the most inclusive clade that includes *Homo sapiens* but not *Casea broilii*. Historically there is a paraphyletic division of non-mammalian synapsids into pelycosaur and therapsids. Although the former can no longer be used within a phylogenetic context, the name *Therapsida* Broom 1905 (converted clade name) is defined here as the most inclusive clade that includes *Homo sapiens* but not *Sphenacodon ferox*.

There is also a well-supported dichotomy of reptiles into two groups, one that includes forms most often referred to as parareptiles, and another that includes most extant reptiles and their fossil relatives. Although variously employed, the name *Parareptilia* Olson 1947 (converted clade name) is defined here as the most inclusive reptilian clade that includes *Procolophon trigoniceps*, but not *Iguana iguana*, and *Eureptilia* Olson 1947 (converted clade name) is defined here as the most inclusive reptilian clade that includes *Iguana iguana* but not *Procolophon trigoniceps*. The controversy surrounding the position of mesosaurs and turtles does not effect these clades, as both groups are encompassed within the larger clade of *Reptilia*. Studies of early diapsid reptiles have dramatically modified our views on the early history of this important group. *Diapsida* Osborn 1903 (converted clade name) is defined as the most inclusive eureptilian clade that includes *Petrolacosaurus kansensis* and *Iguana iguana*, but not *Paleothyris acadiana* or *Captorhinus aguti*. The latter eureptile taxa are employed because the pattern of relationships between these stem diapsid taxa remains poorly supported, and requires additional work. There is strong evidence for a basal dichotomy of diapsids into two groups, and I propose to define *Araeoscelidia* Williston 1913 (converted clade name) as the most inclusive clade of diapsids that includes *Araeoscelis gracilis* and *Petrolacosaurus kansensis* but not *Iguana iguana*, and *Neodiapsida* (converted clade name) as the most inclusive clade of diapsids that includes *Iguana iguana* but not *Araeoscelis gracilis*.

DEFINED NAMES:

Cotylosauria: Clade (*Diadectes sideropelicus*, *Eothyris parkeyi*, *Homo sapiens*, *Captorhinus aguti*, not *Seymouria baylorensis*, *Ascaphus truei*, *Anthracosaurus russelli*)

Amniota: Clade (*Homo sapiens* and *Iguana iguana*)

Synapsida: Clade (*Homo sapiens* not *Hylonomus*, *Procolophon trigoniceps*, *Petrolacosaurus kansensis*)

Therapsida: Clade (*Biarmosuchus tener*, *Homo sapiens*, not *Sphenacodon ferox*, *Ophiacodon uniformis*, *Varanops brevirostris*)

Reptilia: Clade (*Testudo hermani*, *Crocodylus niloticus*, *Sphenodon punctatus*, *Iguana iguana*)

Parareptilia: Clade (*Procolophon trigoniceps*, *Pareiasaurus serridens*, not *Homo sapiens*, *Iguana iguana*)

Eureptilia: Clade (*Captorhinus aguti*, *Iguana iguana*, not *Procolophon trigoniceps*, *Milleretta rubidgei*)

Diapsida: Clade (*Petrolacosaurus kansensis*, *Iguana iguana*, not *Captorhinus aguti*, *Procolophon trigoniceps*, *Paleothyris acadiana*)

Phylogenetic nomenclature for stem crocodylians and birds, exclusive of Pterosauria

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Crown clade *Archosauria* contains crown clades *Crocodylia* and *Neornithes* and their respective stem clades that arose and went extinct during the Mesozoic. Fundamental advances in phylogeny over the last 20 years include consensus regarding the disbanding of “ancestral” paraphyletic groups, namely Thecodontia, and repositioning of *Aves* and crown group birds (*Neornithes*) within *Dinosauria*.

The following list of shorthand definitions includes these three crown clades (*Archosauria*, *Crocodylia*, *Neornithes*) and a sampling of stem clades outside *Crocodylia* and *Neornithes*, exclusive of Pterosauria. In contrast to the current draft PhyloCode, “crown” clades are employed below as originally conceived and most commonly used (i.e., clades defined by living specifiers with immediate outgroups that are extinct), and nested specifiers are preferred over more basal alternatives that owe their selection to their inclusion in a traditional paraphyletic group (e.g., *Megalosaurus* and *Iguanodon* as specifiers for *Dinosauria*). The definitional shorthand employed below, furthermore, does not always capture important functional components of phylogenetic definitions, such as the polarity of inclusiveness or certain qualifying phrases. A modified shorthand scheme will be compared to that given here.

DEFINED NAMES FOR CROWN CLADES:

Archosauria: Crown Clade (*Crocodylus niloticus* and *Passer domesticus*)

Crocodylia: Crown Clade (*Crocodylus niloticus* not *Passer domesticus*)

Neornithes: Crown Clade (*Passer domesticus* not *Crocodylus niloticus*)

SAMPLE CLADES CLOSER TO CROCODYLIA:

Crocodyliformes: Clade (*Protosuchus richardsoni* and *Crocodylus niloticus*)

Protosuchia: Clade (*Protosuchus richardsoni* not *Crocodylus niloticus*)

Mesoeucrocodylia: Clade (*Crocodylus niloticus* not *Protosuchus richardsoni*)

Metasuchia: Clade (*Notosuchus terrestris* and *Crocodylus niloticus*)

Notosuchia: Clade (*Notosuchus terrestris* not *Crocodylus niloticus*)

Neosuchia: Clade (*Crocodylus niloticus* not *Notosuchus terrestris*)

SAMPLE CLADES CLOSER TO NEORNITHES:

Dinosauria: Clade (*Triceratops horridus* and *Passer domesticus*)

Ornithischia: Clade (*Triceratops horridus* not *Passer domesticus*)

Genasauria: Clade (*Ankylosaurus magniventris* and *Triceratops horridus*)

Thyreophora: Clade (*Ankylosaurus magniventris* not *Triceratops horridus*, *Pachycephalosaurus wyomingensis*,

Parasaurolophus walkeri)

Euryopoda: Clade (*Stegosaurus stenops* and *Ankylosaurus magniventris* not *Pachycephalosaurus wyomingensis*,

Parasaurolophus walkeri)

Stegosauria: Clade (*Stegosaurus stenops* not *Ankylosaurus magniventris*)

Stegosauridae: Clade (*Stegosaurus stenops* not *Huayangosaurus tabaii*)

Stegosaurinae: Clade (*Stegosaurus stenops* not *Dacentrurus armatus*)

Ankylosauria: Clade (*Ankylosaurus magniventris* not *Stegosaurus stenops*, *Pachycephalosaurus wyomingensis*,

Parasaurolophus walkeri)

Ankylosauridae: Clade (*Ankylosaurus magniventris* not *Panoplosaurus mirus*)

Ankylosaurinae: Clade (*Ankylosaurus magniventris* not *Shamosaurus scutatus*, *Minmi paravertebra*, *Gargoylesaurus parkpini*, *Mymoorapelta maysi*)

Nodosauridae: Clade (*Panoplosaurus mirus* not *Ankylosaurus magniventris*)

Nodosaurinae: Clade (*Panoplosaurus mirus* not *Sarcolestes leedsi*, *Hylaeosaurus armatus*, *Polacanthus foxii*)

Neornithischia: Clade (*Triceratops horridus* not *Ankylosaurus magniventris*, *Stegosaurus stenops* and *Parasaurolophus walkeri*)

Ornithopoda: Clade (*Heterodontosaurus tucki* and *Parasaurolophus walkeri*)

Euornithopoda: Clade (*Parasaurolophus walkeri* not *Heterodontosaurus tucki*, *Ankylosaurus magniventris*, *Stegosaurus stenops*, *Triceratops horridus*)

Hypsilophodontidae: Clade (*Hypsilophodon foxii* not *Parasaurolophus walkeri*, *Heterodontosaurus tucki*)

Iguanodontia: Clade (*Parasaurolophus walkeri* not *Hypsilophodon foxii*, *Thescelosaurus neglectus*, *Parksosaurus warreni*, *Orodromeus makelai*, *Othniellia rex*, *Zephyrosaurus schaffi*, *Yandusaurus hongheensis*)

Ankylopollexia: Clade (*Camptosaurus dispar* and *Parasaurolophus walkeri*)

Camptosauridae: Clade (*Camptosaurus dispar* not *Parasaurolophus walkeri*)

Styracosterna: Clade (*Parasaurolophus walkeri* not *Camptosaurus dispar*)

Hadrosauriformes: Clade (*Iguanodon bernissartensis* and *Parasaurolophus walkeri*)

Iguanodontidae: Clade (*Iguanodon bernissartensis* not *Parasaurolophus walkeri*)

Hadrosaurioidea: Clade (*Parasaurolophus walkeri* not *Iguanodon bernissartensis*)

Sauropodomorpha: Clade (*Plateosaurus engelhardti* and *Saltasaurus loricatus*)

Prosauropoda: Clade (*Plateosaurus engelhardti* not *Saltasaurus loricatus*)

Plateosauria: Clade (*Plateosaurus engelhardti* and *Massospondylus carinatus*)

Sauropoda: Clade (*Saltasaurus loricatus* not *Plateosaurus engelhardti*)

Eusauropoda: Clade (*Saltasaurus loricatus* not *Vulcanodon karibaensis*)

Neosauropoda: Clade (*Diplodocus longus* and *Saltasaurus loricatus*)

Theropoda: Clade (*Passer domesticus* not *Saltasaurus loricatus*)

Neotheropoda: Clade (*Coelophysis bauri* and *Passer domesticus*)

Tetanurae: Clade (*Passer domesticus* not *Ceratosaurus nasicornis*)

Aves: Clade (*Archaeopteryx lithographica* and *Passer domesticus*)

The nomenclature of *Pterosauria* (*Reptilia*, *Archosauria*)

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The distinctiveness of pterosaurs has made them a well recognized group for two centuries, ever since Cuvier first realized in 1800 that Collini's original specimen, described in 1784, was of a flying reptile. Cuvier first described the animal in 1809, and coined the term "ptéro-dactyle" or "wing-finger" to describe it. (Actually, the name first appeared as the misprint "péto-dactyle," or "rock-finger.") Cuvier did not provide a formal Latin name; the first to do so was Th. von Soemmerring (1812), who called it *Ornithocephalus antiquus*. Cuvier first used the Latin name *Pterodactylus longirostris* in 1819. History has accorded priority to Cuvier for the genus name *Pterodactylus* and to Soemmerring for the species name *antiquus*; hence the first named pterosaur taxon is known as *Pterodactylus antiquus*. The name *Pterosauria* was coined by Owen (1840).

Until the mid-1800s most pterosaurs found were generally referred to *Pterodactylus*, often with new sub-generic or species names. In 1846 H. von Meyer recognized a completely new kind of pterosaur, with a longer tail, shorter metacarpus, and longer fifth toe than in *Pterodactylus*, which he called *Rhamphorhynchus*. From that point on, as new genera of pterosaurs were discovered, they were usually grouped with either *Rhamphorhynchus* or *Pterodactylus*. In 1901 Plieninger formalized this division of the Order *Pterosauria* into the Suborders *Rhamphorhynchoidea* and *Pterodactyloidea*, and henceforth all pterosaur taxa were assigned to one of those two categories.

Until the 1970s there were few attempts to develop evolutionary trees of pterosaurs, and these were not based on much beyond Plieninger's subordinal division. Family or sub-family names were based at one time or another on nearly every genus name, but in most cases, these were given to emphasize the distinctness of the genus in question from other genera, and less to unite different genera evolutionarily.

In the 1980s and 1990s some limited phylogenetic studies of pterosaurs were published, mainly of pterodactyloids. However these did not largely agree with each other, apart from the conclusion, widely recognized with the advent of cladistics, that *Rhamphorhynchoidea* was a paraphyletic taxon, because some members of that group (including its eponymous genus) were closer to *Pterodactyloidea* than to other rhamphorhynchoids. *Pterodactyloidea* was recognized as a monophyletic group.

In more recent years a few more detailed phylogenies have been published, and phylogenetic nomenclature has been developed for some sub-clades. However, as before, there is substantial disagreement about phylogeny. Unwin (2003) and Kellner (2003) produced sharply differing schemes of non-pterodactyloid ("rhamphorhynchoid") relationships, with very different character polarities. Their schemes of pterodactyloid relationships, along with that of Bennett (1994), agree in some major respects but differ in others, partly because their choices of taxa do not completely overlap, partly because their character choices and analyses differ, and partly because the suprageneric names they use in their analyses are different. Further critical work on the phylogenetics is needed before the relationships of pterosaurs find the consensus necessary to establish a detailed, stable nomenclature in the phylogenetic system.

DEFINED NAMES:

Pterosauruomorpha (*Archosauria* closer to *Pterodactylus antiquus* than to *Vultur gryphus*)

Pterosauria (*Pterosauruomorpha* with fourth metacarpal and digit hypertrophied to support wing membrane synapomorphic with *Pterodactylus antiquus*)

Pterodactyloidea (*Pterosauria* with metacarpus at least 80% as long as humerus synapomorphic with *Pterodactylus antiquus*)

The phylogenetic nomenclature of ornithischian dinosaurs (*Vertebrata: Reptilia*) and a consideration of the difficulties in converting the names of extinct clades

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Ornithischia is one of the most diverse entirely extinct tetrapod clades. There is one published phylogenetic nomenclature for the group, based on a single phylogeny. Use of this scheme with other published phylogenies results in drastic changes to taxon content and diagnosis. A more circumspect approach to conversion is adopted here, one that accounts for topological uncertainty. My goal is to facilitate access to the literature and minimize the need for emendation, except in the case of a major topological revolution, by constructing definitions that conform to widely accepted “taxon concepts.”

I convert the major divisions (Linnean suborders) of *Ornithischia* using mutually exclusive, stem-based definitions. More exclusive, generally dichotomous divisions (subfamilies) are given reciprocally exclusive stem-based definitions, and are united by node-based (family) names. Use of restrictive definitions for these “families” is similar to the crown clade convention; such definitions ensure the association of the name with well-known group members and widely accepted diagnostic characters in the light of major topology shifts. However, they will inevitably exclude some species regarded as the “first” or “most primitive” members, or which exhibit the taxon’s “key apomorphies.”

The choice of names, and of concepts, is necessarily arbitrary. Preference is given to names that have been in constant or consistent use, or that fit well within the overall scheme. The majority of available names are redundant or nearly so, including obligatory family-rank names uniting a set of putatively allied, fragmentary fossils with at most one well-known species, or names recognizing the association of a single outgroup with another named clade. Such names are ignored unless they are widely applied. Few internal names are converted where accepted tree topologies are strongly asymmetrical, poorly supported, or probably based on symplesiomorphy (*e.g.*, within stegosaurs and pachycephalosaurs). Names are carefully defined and sequenced so that better known or more conceptually appropriate names will be retained in synonymy, while conceptually restricted (*e.g.*, *Marginocephalia*) or traditionally paraphyletic (*e.g.*, *Ornithopoda*) names will be lost. Accommodation is made for some previously accepted arrangements that have fallen out of favor, (*e.g.*, pachycephalosaurs in *Ornithopoda*), although others (*e.g.*, ceratopsians in *Thyreophora*) are ignored to preserve current usage.

Specifiers are carefully chosen to ward against phylogenetic uncertainty, and to ensure the association of eponymous taxa with the clades named for them. Long term use in the Linnean system seems to divorce taxon names from eponymous apomorphies; I use apomorphy-based definitions only for relatively new or rarely used names, and in other cases I use node-based definitions specified by species possessing the eponymous apomorphy. Poorly known, inadequately described, or topologically labile taxa are avoided as specifiers, except in the case of eponymy. Where type material of an eponymous taxon (*e.g.*, *Ceratops*) is considered nondiagnostic at lower levels, definitions are supplemented with additional specifiers at those levels.

DEFINED NAMES (Abridged):

Ornithischia: Clade (*Iguanodon bernissartensis* not *Megalosaurus bucklandii* or *Cetiosaurus medius*)

Genasauria: Clade (*Ankylosaurus magniventris*, *Pachycephalosaurius wyomingensis*, *Stegosaurus armatus*, *Hypsilophodon foxii*, *Heterodontosaurus tucki*, *I. bernissartensis*, and *Ceratops montanus*)

Ankylosauria: Clade (*A. magniventris* not *H. foxii*, *P. wyomingensis*, *S. armatus*, *I. bernissartensis*, or *C. montanus*)

Ceratopsia: Clade (*C. montanus* not *H. foxii*, *P. wyomingensis*, *A. magniventris*, *I. bernissartensis*, or *S. armatus*)

Stegosauria: Clade (*S. armatus* not *H. foxii*, *P. wyomingensis*, *A. magniventris*, *I. bernissartensis*, or *C. montanus*)

Pachycephalosauria: Clade (*P. wyomingensis* not *H. foxii*, *A. magniventris*, *S. armatus*, *I. bernissartensis*, or *C. montanus*)

Ornithopoda: Clade (*I. bernissartensis* not *A. magniventris*, *S. armatus*, or *C. montanus*)

Thyreophora: Clade (*A. magniventris* not *I. bernissartensis*, *P. wyomingensis*, or *C. montanus*)

Ceratopoda: Clade (*C. montanus* and *I. bernissartensis*)

Marginocephalia: Clade (*C. montanus* and *P. wyomingensis*)

Phylogenetic Nomenclature for *Crocodylia*: a success story in the face of phylogenetic uncertainty

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Phylogenetic definitions for clades within *Crocodylia* have been refined ever since the group was first phylogenetically defined in 1988. These have achieved broad acceptance among crocodyliform systematists, and they dramatically demonstrate one of the greatest strengths of phylogenetic nomenclature - a stable framework around which newly-discovered fossils can be added. They also illustrate the challenges posed by competing phylogenetic hypotheses.

This contribution formalizes the definitions currently in use.

Crocodylia is the last common ancestor (LCA) of *Gavialis gangeticus*, *Alligator mississippiensis*, and *Crocodylus niloticus*, and all of its descendents. First-order stem-based group names are made in reference to these three species:

Gavialoidea : *Gavialis gangeticus* and all crocodylians more closely related to it than to *C. niloticus* or *A. mississippiensis*.

Alligatoidea : *Alligator mississippiensis* and all crocodylians more closely related to it than to *C. niloticus* or *G. gangeticus*.

Crocodyloidea : *Crocodylus niloticus* and all crocodylians more closely related to it than to *A. mississippiensis* or *G. gangeticus*.

Each of these groups can include a crown clade based on living members. These crown clades can, themselves, be subdivided. However, because of controversy surrounding the relationships of the living gharials (*Gavialis gangeticus* and *Tomistoma schlegelii*), these are dependent on phylogenetic context. Based on the tree preferred by morphological analyses (in which *G. gangeticus* is basal to all other living crocodylians), these are as follows :

Alligatoridae : LCA of *Alligator mississippiensis*, *A. sinensis*, *Caiman crocodilus*, *C. yacare*, *C. latirostris*, *Melanosuchus niger*, *Paleosuchus palpebrosus*, and *P. trigonatus* and all of its descendents.

Alligatorinae : *Alligator mississippiensis* and all crocodylians more closely related to it than to *Caiman crocodilus*.

Caimaninae : *Caiman crocodilus* and all crocodylians more closely related to it than to *Alligator mississippiensis*.

Crocodylidae : LCA of *Crocodylus niloticus*, *Crocodylus cataphractus*, *C. siamensis*, *C. palustris*, *C. porosus*, *C. johnstoni*, *C. novaeguineae*, *C. mindorensis*, *C. acutus*, *C. rhombifer*, *C. moreletii*, *C. intermedius*, *Osteolaemus tetraspis*, and *Tomistoma schlegelii* and all of its descendents.

Crocodylinae : *Crocodylus niloticus* and all crocodylians more closely related to it than to *Tomistoma schlegelii*.

Osteolaeminae : *Osteolaemus tetraspis* and all crocodylians more closely related to it than to *Crocodylus niloticus*. (In the morphological context, this is nested within *Crocodylinae*).

Tomistominae : *Tomistoma schlegelii* and all crocodylians more closely related to it than to *Crocodylus niloticus*.

As there is only one living gavialoid in this phylogenetic context, *Gavialidae* would be redundant with *Gavialis gangeticus* and would not be used.

If *Gavialis* and *Tomistoma* are sister taxa, as supported by molecular data, *Crocodylidae* is reduced to the LCA of *Crocodylus spp.* and *Osteolaemus tetraspis* and all of its descendents, and *Gavialidae* is the LCA of *Gavialis gangeticus* and *Tomistoma schlegelii* and all of its descendents. *Tomistominae* is *Tomistoma schlegelii* and all crocodylians more closely related to it than to *Gavialis gangeticus*. Definitions of *Crocodylinae*, *Osteolaeminae*, and *Tomistominae* remain unchanged.

Crown clade definitions specifying *living* or *extant* species (rather than specifying the species themselves) resemble apomorphy-based definitions, but they rely on a plesiomorphic state («extant») rather than the apomorphic condition («extinct»). Moreover, multiple crocodylians became extinct during the Holocene, including gharials from the Solomon Islands and crocodyloids from Australasia, but at dates with associated uncertainty. This renders such definitions ambiguous, as we cannot say the derived state was attained before historical times, and the hypothesis that members of these groups might be found alive remains unfalsified. Their inclusion would support very different group memberships under the competing phylogenetic contexts. The context must always be specified when context-dependent definitions are based on species rather than vital status, but such definitions are less ambiguous and provide greater stability of group meaning.

A Phylogenetic Nomenclature for the Major Clades of Amniota Haeckel 1866, with Emphasis on Aves Linnaeus 1758

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As explained by Gauthier et al. (this volume), we propose application of a single convention for naming the stems of all crowns by adding the prefix *Pan-* to any crown name: hence, “*Panaves*” for the stem of “*Aves*.” That effectively reduces cognitive effort while distinguishing another important class of clades that most biologists, particularly paleontologists, want to talk about, namely, the pan-monophylum of each crown. We also fix the meaning of additional names for more inclusive amniote clades containing our focal crown *Aves*. Among the most important of these names, “*Dinosauria*” (1,893 citations), “*Saurischia*” (1,374) and “*Theropoda*” (870), were first proposed for fossils, and did not include *Aves*, though the latter clade is now widely regarded to be part of all three taxa. Two additional names, both apomorphy based, are proposed for clades that are currently associated with the name “*Aves*”. Phylogenetic nomenclature will best serve biology by providing a simple and coherent scheme for converting traditional taxon names while permitting scientists to name all the kinds of clades that they want to talk about.

DEFINED NAMES

Dinosauria Owen 1841 = Node (*Megalosaurus bucklandii* + *Iguanodon bernissartensis*).

Saurischia Seeley 1887 = Branch (*Megalosaurus bucklandii* + *Plateosaurus engelhardti*, not *Iguanodon bernissartensis*).

Theropoda Marsh 1881 = Branch (*Allosaurus fragilis*, not *Plateosaurus engelhardti*).

Avipluma New = Apomorphy (1st theropod with *Vultur gryphus*' hollow-based, branched, filamentous epidermal appendages [= feathers]).

Avialae Gauthier 1986 = Apomorphy (1st theropod with *Vultur gryphus*' powered flight supported by feathered wings).

Aves Linnaeus 1758 = Crown (*Struthio camelus* + *Tinamus major* + *Vultur gryphus*).

A Phylogenetic Nomenclature for the Major Clades of Amniota Haeckel 1866, with Emphasis on Mammalia Linnaeus 1758

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We propose phylogenetic definitions for 38 important taxon names long associated with the major clades of land-egg laying *Vertebrata*, including the crown clades *Amniota*, *Mammalia*, *Reptilia*, *Testudines*, *Sauria*, *Lepidosauria*, *Archosauria*, *Sphenodon*, *Squamata*, *Crocodylia* and *Aves*. The importance of these names, particularly for the crowns, is revealed by the frequency with which they are encountered in the scientific literature. In the past 25 years alone, for example, the Zoological Record lists the following citation numbers for each of these names as, respectively: 101; 223,196; 72,770; 15,060; 21,962; 40,159; 5,679; 210; 40,044; 3,462; 251,491. If a scientific publication that inspires more than 50 citations can be said to be influential, then all of these names must be “important” to science. It makes sense to define well-known names precisely so that they can be the most efficient passwords connecting us to the vast trove of information already stored in, and retrievable from, the scientific literature, as well as a growing presence on the internet. Of course, crown clades are not the only clades of scientific interest. So we take this opportunity to fix the meaning of additional names for some more inclusive amniote clades containing our focal crown: “*Mammalia*”. These include some much less well known node-based names (e.g., “*Mammaliaformes*” with only 7 citations), here tied formally to one among the set of interested clades commonly called “*Mammalia*”. We also define some names based on fossils, including “*Synapsida*” (558 citations), “*Therapsida*” (446 citations), and “*Cynodontia*” (61 citations), with respect to the synapomorphies from which they were originally derived. These have the added virtue of being consistent with current ideas about taxonomic composition, even if they do not actually specify the same ancestors. We also propose application of a single convention for naming the stems of all crowns by adding the prefix *Pan-* to any crown name: hence, “*Panmammalia*” for the stem of “*Mammalia*.”

DEFINED NAMES

Synapsida Osborn 1903 = Apomorphy (1st panmammal with *Homo sapiens*'s lower temporal arch/fenestra).

Therapsida Broom 1905 = Apomorphy (1st panmammal with *Homo sapiens*' enlarged, dorsally-oriented, lower temporal fenestra and ventrally emarginate lower temporal arch).

Cynodontia Owen 1861 = Apomorphy (1st panmammal with *Homo sapiens*' differentiated jaw dentition including spatulate incisors, large canines, and 3-cusped cheek teeth with cingulum on inner face of upper postcanines).

Mammaliaomorpha Rowe 1988 = Node (*Tritylodon longaevus* + *Homo sapiens*).

Mammaliaformes Rowe 1988 = Node (*Morganucodon oehleri* + *Homo sapiens*).

Mammalia Linnaeus 1758 = Crown (*Homo sapiens* + *Didelphis marsupialis* + *Ornithorhynchus anatinus* + *Tachyglossus aculeatus*).

Phylogenetic nomenclature of carnivoran mammals

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Although the modification of the upper fourth premolar (P4) and lower first molar (m1) as carnassial teeth has been considered a synapomorphy for carnivorans, here we follow a recent convention employing the name *Carnivoramorpha* for that clade and restricting the meaning of the widely known name *Carnivora* to the smaller crown clade delimited by the extant species regarded as carnivorans. Accordingly, *Carnivoramorpha* Wyss and Flynn 1993 (converted name) is here defined as the smallest clade containing the earliest organism to have the P4/m1 carnassial shear synapomorphic with that in *Felis catus*. Morphological and molecular evidence indicates that the carnivoran aeluroid, cynoid and arctoid clades share an exclusive common ancestry. Species representing these three major carnivoran clades are used as specifiers in the definition of *Carnivora* Bowdich 1821 (converted name), which is here defined as the smallest clade containing *Felis catus*, *Canis familiaris* and *Mustela erminea*. Within *Carnivora* there exists a well-supported dichotomy between catlike (*Feliformia*) and doglike (*Caniformia*) carnivorans. Given this evidence and following recent usage of these names, we define *Feliformia* Kretzoi 1945 (converted name) as the largest clade containing *Felis catus* but not *Canis familiaris*. *Caniformia* Kretzoi 1943 (converted name) is defined as the largest clade containing *Canis familiaris* but not *Felis catus*. The widely known name *Pinnipedia* has traditionally referred to a taxon containing sea lions (*Otariidae*), the walrus (*Odobenidae*) and seals (*Phocidae*), but none of the terrestrial carnivoran taxa. However, some phylogenetic hypotheses have suggested that sea lions are most closely related to bears (*Ursidae*), whereas seals are most closely related to weasel-like carnivorans (*Musteloidea*). To ensure that *Pinnipedia* Illiger 1811 (converted name) will only be applicable to phylogenetic contexts that are consistent with its widely recognized historical meaning, we propose to define this name as the smallest clade containing *Otaria byronia*, *Odobenus rosmarus* and *Phoca vitulina*, but not *Ursus arctos* or *Mustela erminea*. In addition to these five definitions, node- and stem-based definitions for some other carnivoran clades are proposed.

DEFINED NAMES:

Carnivoramorpha: Clade (P4/m1 carnassial shear in *Felis catus*)

Carnivora: Clade (*Felis catus*, *Canis familiaris* and *Mustela erminea*)

Feliformia: Clade (*Felis catus* not *Canis familiaris*)

Caniformia: Clade (*Canis familiaris* not *Felis catus*)

Pinnipedia: Clade (*Otaria byronia*, *Odobenus rosmarus* and *Phoca vitulina* not *Ursus arctos* or *Mustela erminea*)

Phylogenetic nomenclature of living and fossil catarrhines

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Anthropologists and primatologists have been among the last researchers to adopt phylogenetic methodology and taxonomy. As such, a number of important primate clade names remain paraphyletic. The name *Catarrhini* É. Geoffroy Saint-Hilaire 1812 (converted clade name) is here defined as the most inclusive clade containing *Aegyptopithecus zeuxis*, *Pliopithecus antiquus*, *Macaca fuscata* and *Homo sapiens*, but not *Cebus capucinus*. There is substantial debate about the nature of the “Propliopithecoidea” and the “Pliopithecoidea”- they have alternately been described as basal hominoids, basal cercopithecoidea, basal catarrhines and sister taxa to the Catarrhini (Ross et al., 1998; Begun, 2002; Rasmussen, 2002). Either or both groups may be paraphyletic. We include these fossil taxa within the Catarrhini here, but more phylogenetic work needs to be done to determine their position within the group. If *Catopithecus browni* and *Aegyptopithecus zeuxis* form a monophyletic group that excludes *Dionysopithecus shuangouensis* and *Plesioliopithecus lockeri*, the clade name Propliopithecoidea will be available. If *Dionysopithecus shuangouensis* and *Plesioliopithecus lockeri* form a monophyletic group that excludes *Catopithecus browni* and *Aegyptopithecus zeuxis*, the name Pliopithecoidea will be available. *Victoriapithecus* and *Prohylobates* are African early to middle Miocene monkeys, generally agreed to be basal to the extant Old World monkeys (Benefit and McCrossin, 2002). We define the name *Cercopithecoidea* Gray 1921 (converted clade name) as the largest clade containing *Victoriapithecus macinnesi* and *Papio hamadryas*. If *Victoriapithecus macinnesi* and *Prohylobates tandy* are found to form a monophyletic group that excludes *Presbytis melalophos*, the name Victoriapithecidae will be available. The clade *Colobinae* Jerdon 1867 (converted clade name) is here defined as the largest clade containing *Presbytis melalophos* but not *Macaca silenus*. The *Cercopithecinae* Gray 1821 (converted clade name) is the clade stemming from the most recent common ancestor of *Cercopithecus diana* and *Papio hamadryas*. Recent analyses of newly discovered fossil hominoid taxa have resulted in conflicting hypotheses of relationships. The *Hominoidea* Gray 1821 (converted clade name) is defined as the largest clade containing *Proconsul heseloni* and *Homo sapiens*. There are a number of unplaced taxa, including *Rangwapithecus gordonii* and *Dendropithecus macinnesi*, but there is no consensus on the position of these and many other non-*Proconsul* taxa (Harrison, 2002; Begun, 2001). If future analysis determines that they fall within the Hominoidea, the contents of the taxon may expand. We propose to redefine *Hominidae* Gray 1821 (converted clade name) as the most inclusive clade containing *Homo sapiens* and *Pongo pygmaeus*. We redefine *Homininae* Gray 1825 (converted clade name) as the most inclusive clade containing *Homo sapiens* and *Gorilla gorilla* not *Pongo pygmaeus*. *Hominini* Gray 1825 (converted clade name) includes *Homo sapiens* but not *Pan troglodytes*. The Ponginae has traditionally been paraphyletic, separating *Pongo pygmaeus*, *Gorilla gorilla* and *Pan troglodytes* to the exclusion of *Homo sapiens*. *Ponginae* Elliot 1913 (converted clade name) is defined as *Pongo pygmaeus* but not *Homo sapiens*. These converted clade names preserve the established endings of the older system in order of most to least inclusive. Reevaluation continues within fossil taxa, therefore the majority of these defined names are based on living taxa whose relationships are well known and largely uncontroversial.

DEFINED NAMES:

Catarrhini (É. Geoffroy Saint-Hilaire 1812): Clade (*Aegyptopithecus zeuxis*, *Pliopithecus antiquus*, *Macaca fuscata* and *Homo sapiens*, not *Cebus capucinus*)

Cercopithecoidea (Gray, 1821): Clade (*Victoriapithecus macinnesi* and *Papio hamadryas*)

Colobinae (Jerdon, 1867): Clade (*Presbytis melalophos* not *Macaca silenus*)

Cercopithecinae (Gray, 1821): Clade (*Papio hamadryas* and *Cercopithecus diana*)

Hominoidea (Gray, 1825): Clade (*Proconsul heseloni* and *Homo sapiens*)

Hominidae (Gray, 1825): Clade (*Homo sapiens* and *Pongo pygmaeus*)

Homininae (Gray, 1825): Clade (*Homo sapiens* not *Pongo pygmaeus*)

Hominini (Gray 1825): Clade (*Homo sapiens* not *Pan troglodytes*)

Ponginae (Elliot 1913): Clade (*Pongo pygmaeus* not *Homo sapiens*)

New non-Linnaean, neo-cladistic nomenclature and classification conventions exemplified by recent and fossil hominids

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A phylogenetic classification is developed to satisfy the needs of biology, palaeontology and a precise general reference system, which should be able to indicate exactly the present state of our knowledge as well as what we do not know or are uncertain about.

To this end in evolutionary biology a (neo-)cladistic classification has to be based on not only a cladogram, but rather on a phylogenetic tree (a model) where all its complications should be mirrored as precisely as possible in the system to produce a one to one (isomorphic) correspondance. The consequent nomenclature has to deal with names (taxonomy) of terminal taxa, be they 'species' or not, monophyletic, metaphyletic, paraphyletic, fossil and ancestral (and hybrid) taxa, and with sistergroup relations, relative rank, ages, origins, extinctions and ancestry, and should in a meaningful way indicate diversity. All should be expressed in a simple list of names with prefixes and suffixes and age, which is conform with the best model of the stem-tree.

Conventions are suggested to do the job, such as traditional subordination of clades, sequencing for (some) fossil taxa (as 'plesions') to reduce the need of relative ranking between the extant taxa (and 'important' fossil taxa), making it possible to remove all fossils from the classification without changing that of the recent ones. Rather traditional conventions for subordination, uncertainty and mutability of taxa, less traditional ones for paraphyletic (including ancestral), metaphyletic and extinct taxa, which are specially marked. We provide non-traditional, non-Linnaean conventions for naming terminal and other unit taxa, which should be LITU-s (Least Inclusive Taxonomic Units. LITUs are smallest diagnosable groups by which the phylogenetic history can be mapped in a hierarchy. Some LITUs, including some extant ones, may be paraphyletic. Others may correspond to the 'chrono[-sub-]species' of palaeontologists and be 'ancestors'); they are given a single name in lower case letters. Clades are given single names (Capitalized), and so are other groups, be they 'stemgroups', paraphyletic or metaphyletic ones, some of which are only preliminary or 'left over' groups and marked as such, to signal that they are not necessarily 'natural groups', but remain problematic because of the lack of precise knowledge. Ways of converting the traditional Linnaean names are suggested to create continuity ('stability').

Classification of recent and fossil hominids (including some apes) will be used to exemplify these principles and conventions on a detailed phylogenetic tree (model), which has about 35-40 LITUs on our branch since it separated from the chimps about 7 million years ago. Age will be used as a measure for 'rank' if one wishes to compare taxa on a rational and evolutionary relevant basis. Several 'famous ancestors' are synonymized in a 'controversial' way and new LITUs are named.

Modern biological systematics, like all sciences, should be logically consequent, tentative and open to critical discussion, rather than being bound to traditions, authoritative and 'stable', but also inconsequent. It should mirror our knowledge of well tested phylogenetic relationships as precisely and simply as possible, and provide information about the limits of that knowledge. The often highly prized 'stability' of the general klassifikation is illusory, and is perhaps the last remnant of the belief in a 'harmonic, divinely created' world of the 18th century.

Bonde, N. & Westergaard, B. 2004 Progress in hominid classification: cladistic approaches. *In* E. Baquedano (ed.): Homenaje Emiliano Aguirre, p. 2-23 (Museo Arqueologico Regional, Madrid).

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