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Naming the World: Is There Anything Left of Linnaeus?

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Linnean Taxonomy has been ripped from its philosophical foundations, plastered with additional conventions and moulded to serve a variety of functions. Little remains of its original formulation and even that which does has been criticized for being unsuitable for classifying an evolving biota. The chief target for attack is the Linnean rank (Genus, Family, Order etc.). Here, I argue that, while most ranks cannot be defended, the genus and species should be retained as the binomial. This is for practical reasons. Genera are recognized by discrete characters whereas species rarely are. Different workers have very different ideas of species, both theoretically and in recognition criteria. In naming the world our efforts will be more fully rewarded if we concentrate on compiling lists of genera as a proxy for biodiversity estimates.

Carl Linnaeus (1707–1778) laid the foundations of our current systems of taxonomy which are now administered through the various international codes of nomenclature. Nowadays, we accept that it is a system much modified from that which he set up, and some (de Queiroz 1992; Ereshevsky 2001) would say it has outlived its usefulness and deserves to be replaced. So, in answering this question posed by the above title most people would probably agree that the only thing left of Linnaeus is his skeleton, lying beneath an inscribed slab in Uppsala Cathedral.

We no longer share Linnaeus' belief that all of biodiversity was specially created on an island called Paradise, located somewhere in the Indian Ocean. We no longer believe that there is a fixed number of animals and plants. We no longer believe that order in the natural world can be reflected using essentialism and the principles of logical subdivision, and we question many of Linnaeus' practical methods for classifying life, especially the use of ranks (Class, Order, Family, etc.) and the monothetic recognition of groups (groups recognized on the variation of a single feature). Yet, I suggest that there are some elements of the system of taxonomy and nomenclature started by Linnaeus (here called Linnean Taxonomy) that we need to maintain in order to provide effective communication about relationships between organisms, to meaningfully discuss patterns of biodiversity, and in order to be effective in bringing our taxonomic conclusions to as wide an audience as possible. I use the phrase Linnean Taxonomy, rather than refer directly to Linnaeus because many aspects of Linnean Taxonomy are modifications of those proposed by Linnaeus himself.

Linnaeus' Achievements

In our modern world, imbued with very different belief values from those of Linnaeus' day, it is all too easy to lose sight of his achievements and the progress he made relative to what had gone on before him. It may be instructive to review briefly what Linnaeus set up for us in the first place and why. Prior to Linnaeus' work in the 18th century, the names of animals and plants were not fixed. Often the actual name applied was effectively a short description, encapsulating the observable features of the organism. For example, a species of bindweed, *Convolvulus*, was named *Convolvulus folio Althae* by Clusius in 1576. In 1623, Bauhin named it *Convolvulus argenteus Althae folio*. And Linnaeus named it *Convolvulus foliis ovatis divisis basi truncatus: laciniis intermedius duplo longiorubus* in 1738 (Stearn 1971:247).

Linnaeus recognized the potential confusion that could arise by giving different descriptions to the same kind of organism, and he gave us guidance in three main areas:

(1) He provided some rules for sorting organisms into taxa.
(2) He established some rules for naming those taxa.
(3) He provided us with a hierarchy of ranks, or categories by which taxa could be grouped into increasingly more inclusive sets: Variety, Species, Genus, Order and Class (we use many more ranks today).

His rules for sorting taxa were those of Aristotelian logic of subdivision that employs the concept of *genus* and *species*. The *genus* has a recognizable essence: that is, a property or properties "that makes it the type of entity that it is" (Ereshevsky 2001:17). As a subdivision of the *genus* there are the *species* variations on the essence of the *genus* recognized by differentiae. The word genus here is used in a philosophical sense but Linnaeus co-opted it for use as one of the many ranks in the Linnean system.

Linnaeus recognized that the essence of a plant allows the plant to breed true. For Linnaeus, the genus was the crucial entity. He believed that the essence of the genus lay in the fructification (the flowers and fruits). It was the variation in the parts of the flower and fruit that allowed us to discover the essence. Figure 1 shows his descriptions of the essences of two genera of Rannunculacae (buttercups and their allies), where it can be seen that these are combinations of features of the calyx, corolla, stamens, pistil, perianth and the seed. The descriptions of the essences are equivalent to one another; that is, there are descriptions of the same six parts of the fructification. There was for Linnaeus the notion that one genus of plants was equivalent to another.

The species of genera are recognized by the differentia — variations on the generic essence. He used features of the leaves, stems, roots, etc., as descriptors of such variation. For instance, when diagnosing two species of plantain (genus *Plantago*) he named one "*plantain with pubescent ovate-lanceolate leaves, a cylindric spike and a terete scape*" and distinguished from *"plantain*

Thalictrum

CALYX: nullus
COROLLA: petala quator, subrotunda, obtisa, concava, caduca
STAMENS: *Filamenta* plurima, superne latiora, compressa, corolla longiora, *antherae* oblongae, didymae.
PISTIL: *Styli* plurima, brevissima. *Germina* singulis stylis solitaria, subrotunda. Stigmata crassiscula
PERIANTH: *Cortex* sulcatus, carinatus, unilocularis, non discedens
SEED: solitaris, sublonga

Trollius

CALYX: nullus
COROLLA: petala quatuordecim circiter, subovata, coniventia, decidua; in seriebus exterioribus tribus terna; in intima feriequina
STAMENS: *Filamenta* numerosa, setacea,corolla breviora, *antherae* erectae.
PISTIL: *Germina* numerosa, sessilia, columnaria. *Styli* nulli. Stigmata mucronata, staminbus breviora
PERIANTH: *Capsule* numerosa, in capitum collectae, ovate, acumine recurvo
SEED: solitaria

FIGURE 1. Generic essences for two genera of Rannunculacae as spelled out by Linnaeus. Note there are descriptions of the same parts of the fructification in both.

with lanceolate leaves, an almost ovate naked spike and angled scape" (I have taken this example from that given by Stearn 1971). These were the distinguishing features of the species within the genus *Plantago* that had already been recognized and described by its essence. But a species could not stand by itself. You could not call something "lanceolate leaves, an almost ovate naked spike and angled scape." The diagnostic attributes had to be linked with a genus name. Therefore, there were always two parts to a biological species name — the genus, with its essence, and the species, with its differentia. Like the genus, Linnaeus regarded one species as equivalent to another.

Quite a lot has been written (see Härlin and Sundberg 1998 for discussion) about how a name that we give to something is quite separate from the description of that entity — or how we recognize it. This was not so for Linnaeus and, in practical terms, this does not seem to be the case in day-to-day taxonomic practice. When, we speak of *Rannuculus repens* or *Clupea harengus* we imply certain morphological attributes: characters that we have learned and identify with the name. Modern formal nomenclature still retains this association between the name and characters in two ways. First, the nomenclatural codes insist that there is a description with a name of a species. If not, the name is a *nomen nudum* — a name without a description — and is invalid. Additionally, if the description is ambiguous or too general to be of any diagnostic use it is a *nomen dubium* and similarly is invalid. Secondly, we insist on an actual specimen — a type specimen which must be there to be consulted at any time to check to see what the original author was describing. The insistence of the type specimen was not Linnaeus' idea. That came much later (Strickland et al. 1843 for zoology and Arthur et al. 1904 for botany). Despite being bolted on to Linnaeus' original method, it is this link between a name and characters through the intermediary of the type specimen that remains of Linnean Taxonomy.

There are other reasons why maintenance of the binomial may be advantageous. Linnaeus was a very practical person who realized that it would be impossible for people to remember all the long descriptions of genera and species, so he shortened them to two — the binomial — which, by convention is italicised to distinguish it from all other Linnean ranks. But in shortening the name he did not expect the descriptions to be dropped. He also realized that it would be impossible for anyone to remember all the species names (for example, about 8000 species of plants were known to Linnaeus), but he considered that it was well within capabilities to remember 300 generic names. Furthermore, current generic diagnoses — while they are based on a completely different theoretical footing than those of Linnaeus — tend to be relatively clear cut with presence/absence features most often used. This contrasts with the species diagnoses which are, more usually than not, combinations of morphometric variables (length/breadth, patterns of color, counts of parts). These are far more difficult to commit to memory, as well as being susceptible to the sample available at hand when the species is named. Combining the generic and species names allows a much more complete, manageable and accurate description to be implied by the name. Even today, it is perfectly possible to remember generic names and their meaning, although such practice is limited to much smaller taxonomic groups than "plants" or "animals".

Another reason for maintaining the binomial is that it does give us some indication of the relationships of that species. This is because a Linnean binomial, such as *Clupea harengus*, tells you something about relationships. In other words, it implies a taxonomic address. It tells you that species *harengus* (Atlantic herring) is in the genus *Clupea* and therefore is probably more closely related to the species *pallasi* (Pacific herring) — which is also in the genus *Clupea*, than it is to species in the genus *Salmo*. There is a downside to this. If our ideas of relationships change, then so must the name. And an investigator may be forced to place it in a genus even if the relationships are uncertain, or create a new genus, only because of the demands of the Linnean system (Cantino et al. 1999).

A final reason why the maintenance of the binomial is advantageous is that species names, used by themselves as uninomials, might lead to confusion. Many species epithets are the same, even though they are used for very different animals and plants. For instance, if we just used a specific epithet to refer to a species, such as *vulgaris* (meaning common), or *sylvaticus* (meaning inhabitant of woodlands) or *borealis* (inhabitant of the Boreal Region), we would have to employ some other convention, such as the attachment of a number (e.g., *vulgaris*623) to be clear to which species the name referred. Such has been suggested by those who would like to move towards uninomial names for species (Cantino et al. 1999).

Linnaeus made a logical break between the genus and more inclusive categories (see below). For Linnaeus, the species was nothing special — it was just a variation on the genus essence. Today, species are regarded as the engine of evolution, and if we make a break at all (and not everyone does) it is at the species level. Readers should be aware that there is split in the taxonomic community between those who consider that the species is just like any other rank and should, therefore, be considered and named in the same way (for discussion, see Mishler 1999) and those who consider that the historical connectedness between members of species (individuals) is different from that "connecting" species in genera (Rieppel 1988).

Although Linnaeus was certain that his ranks of Genus and Species were natural (in his terms), he was less certain about the naturalness of the ranks above the level of genus. He used two other ranks, Classes and Orders, which we still use today. However, he claimed that his system of recognizing Orders and Classes was artificial because he differentiated his Orders from one another and Classes from one another on single — not on the combinations of — characters that he had used for his genera and species. That is, his Classes and Orders were monothetic divisions (i.e., based on variations in a single character). For instance, his Classes were distinguished from one another on the numbers and positions of the stamens. As long as the stamens were there the number and position seemed of no biological or vital importance for the maintenance of the genera and species (that is, they were not *essential*). He recognized that such variation, expressed through his recognition of Classes, may be useful to segregate plants into groups as an *aide memoire* even though there was no implied naturalness.

It is also worth emphasising that Linnaeus thought that he had all of the biological universe before him. There were no undiscovered species (although he did acknowledge limited speciation through hybridization), and we had all we need to know in front of us. It was just a case of subdividing that which was on the table — and that was it. Nowadays, of course, we recognize that we do not have the universe; neither, the total number of species nor total knowledge of the variation of those species which we have recognized. This is why our classifications must change, to incorporate new knowledge. So the credo that classifications need to be stable either in content or naming seems an unreasonable expectation. The trick, of course, is to devise systems of classification and naming that will be least perturbed by newly discovered taxa or relationships. Unfortunately, Linnaeus' system, which we have inherited and modified, is particularly bad at this. And this is because of his insistence on rank.

Any newly discovered taxon or newly investigated character complex (for instance molecules) can change our ideas of relationships among taxa. As a paleontologist I am particularly affected by this. Fossils tend to come with particularly unexpected combinations of characters that, more often than not, tend to place them as plesiomorphic taxa to extant sister groups. If we wish to indicate the relationships among the taxa in a written classification, some accommodation is necessary. This is best illustrated by example which I take from Forey et al. (2004). Consider the phylogeny of a group of Recent teleost fishes (Fig. 2A) with a standard ranked classification immediately to the right of it (3C). We may wish to introduce two fossil taxa and write the classification to indicate

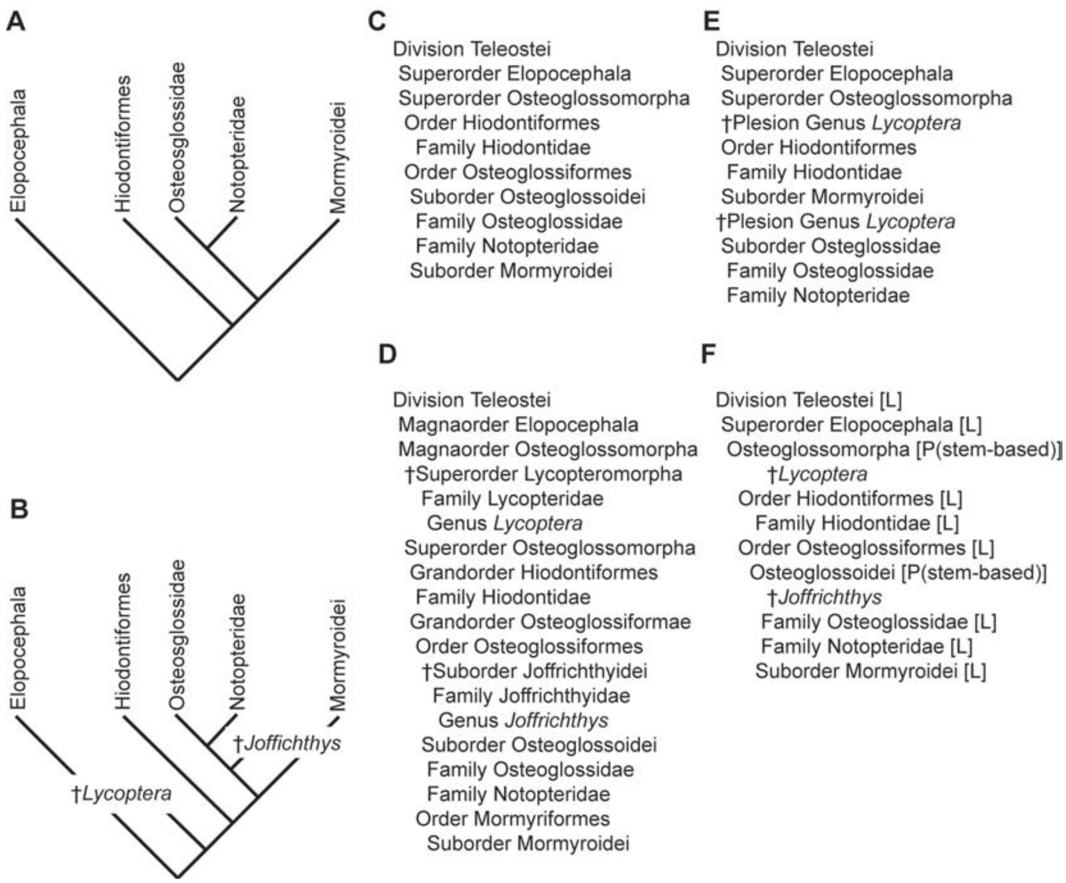


FIGURE 2. Introduction of additional taxa — in this case two fossils — can cause problems for ranked nomenclature. There have been various solutions to this problem, some of which are shown here (see text for discussion).

their relationships. The phylogenetic position of the fossils (†*Lycoptera* and †*Joffrichthys*) are shown in Figure 2B (Note: these could just as easily be Recent taxa but fossils are chosen here to illustrate one of the alternative solutions that caters specifically for fossils). We have a number of alternatives by which we could write a classification to express the phylogeny, only some of which are shown here. We could simply increase the number of ranks as shown in Figure 2D. This has two deleterious effects. It demands that we make new and perhaps unfamiliar intermediate ranks (for example, introducing the ranks Grandorder and Magnaorder, in which I have followed McKenna (1975) who used these in a "real" classification of mammals). It also demands that we change the rank of existing names. For example, the Superorder Elopocephala in the original classification now becomes a Magnaorder Elopocephala. This may also have the unfortunate consequence in demanding a change in the name ending, because the international nomenclatural codes have recommendations for the endings of certain ranks. In addition, different authors may decide to play the rank game in different ways because there are no rules as to what ranks to use beyond the fact that the zoological and botanical Codes demand that species be assigned to ranks up to and including the family.

Other suggestions ignore the rank. There are two shown here. One is called the annotated

Linnean system (Fig. 2E) (Wiley 1979). This uses a sequencing convention in combination with the rankless modifier “plesion.” Here the Recent taxa are listed according to their branching order without indentation. The Recent ranks are retained to provide a link with previous classifications but they have no specific meaning here. The fossils are introduced as a Plesion. Plesion (literally — plesiomorphic sister-taxon) can be associated with any Linnean rank (Order, Family, Genus, Species, etc.) and simply means that it is to be considered as the extinct primitive sister-taxon to the taxon listed below. In other words, the rank of the fossil group Plesion is decoupled from that of the rest of the hierarchy.

A third way (Fig. 2F) is to deliberately abandon Linnean rank and construct names with a specific phylogenetic definition tied to a particular phylogenetic hypothesis. This last is the method suggested by the PhyloCode (Cantino and de Queiroz 2000). Here we have to discriminate between a name to be used in a Linnean sense and that in a PhyloCode sense. That is why, following PhyloCode recommendations, the suffixes [L] and [P] are inserted behind two of the names and the Linnean rank is removed. Furthermore, under PhyloCode we have to stipulate in what sense the particular PhyloCode name has been established. In this case, the stem-based definition of a clade has been chosen, but this is one of many phylogenetic definitions of a name that may be employed.

There are other ways, exemplified by the rank-free classifications of land plants as established by Crane and Kenrick (1997) where there are just names and the indentation on the page of the written classification indicates the shape of the phylogenetic tree. There are also numbering systems where clades are numbered according to an hierarchical fashion (Hennig 1966; Løvtrup 1977) which are perfectly logical but difficult for a biological culture that has grown up with word-based taxonomy to absorb (e.g., Clupeidae may be known as 6.4.5.1.2.3).

Thus, there are many good reasons to agree with the calls to ignore rank. But I say ignore rather than abandon because there are many people who maintain that rank does help them in their everyday work, and I would agree with this latter group up to the genus. As a paleontologist, I cannot ignore the multitudinous graphs and tables showing plots of the diversity of organisms through time. Most of these are compiled from data gathered at the Linnean generic and family levels. But this is a practical necessity of using the genus and maybe the family as a proxy for species durations, rather than a conscious effort to target genera and families.

No matter whether a genus or family is used, it is imperative that the status of that group is given by the author. The PhyloCode insists that only monophyletic groups be named. No one would disagree with the desirability of monophyletic groups. However, it is unrealistic to expect the PhyloCode to be capable of naming but a small percentage of life. It is much more practical to include all taxa that you may wish to name, with or without rank, but to identify them as monophyletic, paraphyletic and polyphyletic groups, or even status unknown. It would then be up to the consumer to decide whether certain named groups are going to be useful for his or her purpose. A great deal of the confusion surrounding the calculation of diversity curves is caused by not knowing the phylogenetic status of the taxa listed in the various data bases (see Smith and Patterson 1988 for a good example).

Therefore, I would agree that we have abandoned all of Linnaeus’ theoretical underpinning. Despite this, and despite all the modifications to Linnaeus’ original system of taxonomy and nomenclature, we have retained the binomial and the link with characters through type specimens. I do not find this surprising because the advantage of the Linnean system is that it is basically agnostic to any causal explanation we may invoke to explain diversity.

Future of Taxonomy

So what about the future of taxonomy? I would like to address this in the field I know best — paleontology. For this I would like to draw information from Forey et al. (2004). In this paper we first asked ourselves how good we were, as a paleontological community, at documenting the fossil record.

There are at least two aspects to "how good". How well have we sampled the fossil record and how good are we at documenting it. In terms of sampling paleontologists have done well. Given the constraints of fossilizable parts of animals and plants (probably about 5–10% of all organisms that have ever lived entered the fossil record, Paul 1998). Given the constraints that some paleoenvironments will be preserved (near shore marine environments) and some will not (e.g., high montane regions), and given the constraint that only a fraction of the rock record survives today — it as has been estimated that more than 50% of the species in rocks available at outcrop are now documented. If we add the fossilizable component to that which has been lost due to the attrition of the rock record through erosion, subduction, etc., then probably 1–5% of the biota is preserved as collectable fossils. Low as this may seem, we do seem to be getting better at documenting the record we have. Paul (1998) looked at the proportion of new species in monographs throughout the latter half of the 20th century that represented genuinely new finds, as opposed to reinterpretation of earlier collected material and concluded that only about 40% of the newly erected species were the result of new collections. Sixty percent (60%) were discovered as the result of revision.

How good are we at documenting the fossil record? It turns out again that paleontologists are quite good — at least superficially. This is probably because paleontologists have a long history of documentation as part of their everyday work and the fact that many fossils are used for stratigraphic and commercial purposes encourages this.

Table 1 lists some of the major compendia for fossil groups, and without going into detail most of the fossilizable animal and plant groups are covered. However, a number of comments are in order. Virtually none are web-based and/or updated on a regular basis. If they are updated it is more usual for wholesale revisions to replace earlier attempts than for constant updating. Since most are hard copy or even CD Rom-based, then any information is always immediately out of date. Most often wholesale revisions are done by authors different from the original or preceding author(s). Because of this, there can be very different concepts of species and genera, and especially very different ideas of higher classification leading to very little continuity between revisions.

This last point is best illustrated by example from the field of fossil fishes, although other people can substitute their own case histories. In the history of paleoichthyology there have been only two people who were in a position to fully appreciate the total diversity: Louis Agassiz who wrote *Les Poisson Fossiles* between the years 1833–1844, and Arthur Smith Woodward, who wrote the *Catalogue of Fossil Fishes* between the years 1889–1901. These two people in their own eras saw at first-hand all, or nearly all, the specimens of fossil fishes that were in existence. Agassiz and Woodward saw the same specimens. Woodward, of course, saw many more collected in the heyday of the Victorian accumulation which separated these two works. Therefore, like Linnaeus and his plants, Agassiz and Woodward each had the contemporaneous universe of fossil fishes before them. All they had to do was to divide that universe.

Agassiz divided his fishes into four groups characterized by their scales — placoids, ganoids, cycloids and ctenoids. He recognized a total of 1223 species in 348 genera, an average of 3.5 species per genus, split into the systematic groupings as shown here (Table 2). Woodward recognized 1167 species in 391 genera, an average of three species per genus. The numbers are comparable. If we look at just two of these groups the comparison becomes even closer. Agassiz' cycloids

TABLE 1. This table lists some of the major data-bases, compendia and lists of fossils with some indication of their information content. From Forey, *et al.* (2004) where further annotation of this table is given.

Group	*Most exclusive taxonomic level*	*Diagnosis most exclusive level*	*Species listed*	*Synonymy included*	*Higher classification*	*Stratigraphic resolution*	*Geographic location*	*Hard/CD/Web*	*Updated*	*Reference*
All taxa	Family	n/a	No	No	Yes	Stage	Yes	Hard/Web	No	Benton 1993
Marine animals	Genus	n/a	No	part	part	Stage	No	Hard/CD	?	Sepkoski 2002
Marine animals	Family	n/a	No	No	Yes	Stage	No	Hard	No	Sepkoski 1992
Fungal spores and mycelia	Species	Species	Yes	Yes	No	Stage	No	Hard	No	Kalgutkar and Jansonius 2000
Dinoflagellates	S (var)	n/a	Yes	Yes	No	Variable to Stage	No	Hard	Yes	Wiiliams et al. 1998
Dinoflagellates	Species	Species	Yes	Yes	No	Variable to Stage	Yes	Hard	Yes	Cramer and Díez (1979)
Acritarchs	Species	n/a	Yes	Yes	No	Variable to Stage	No	Hard	No	Fensome et al. 1990
Palynomorphs	Species	Species	Yes			Stage	Yes	Hard	Yes	Jansonius and Hills 1978
Foraminifera	Genus	Genus	Yes	Yes	Yes	Stage	Yes	Hard	No	Loeblich and Tappan 1988
Invertebrates	Species	Genus	Type	Yes	Yes	Stage	Yes	Hard	Yes	Moore 1955
Echinoids	Species	Genus	Yes	Yes	Yes	Stage	Yes	Hard/Web	Yes	*<www.nhm.ac.uk/science/echinoids>*
Echinoids	Species	No	Yes	No	Yes	Stage	Yes	Hard	No	Kier and Lawson 1978
Fishes	Species	Genus	Yes	part	Yes	Stage	Yes	Hard	No	Schultze 1978
'Reptiles'	Species	S	Yes	Yes	Yes	Stage	Yes	Hard	No	Kuhn 1969
Birds	Species	No	Yes	Yes	Yes	Epoch	Yes	Hard	No	Brodkorp 1963–1978
Mammals	Genus	No	No	Yes	Yes	Epoch	Yes	CD	No	McKenna and Bell 1997
Land plants	Species	Species	Yes	Yes	Yes	Variable to Stage	Yes	Hard	No	Boureau 1964–1975
Plants	Species	Species	Yes	No	Yes	Stage	Yes	Web	No	*<http://ibs.uel.ac.uk/ibs>*

and ctenoids make up what we now know as the teleosts — the dominant group of fishes today. Woodward recognized 387 fossil species in 190 genera while Agassiz recognized 342 fossil species in 173 genera. The comparison is remarkable. And if we compare the actual names of the genera we find that out of Woodward's 190 generic names 75, or 40%, are shared with Agassiz names. And some of those that were not shared were only minor changes in name such as Woodward preferring to refer to the fossil form as Eo- or Pro- rather than Agassiz' preference to refer fossil species to Recent genera whenever he thought possible.

TABLE 2. Recognition of genera and species of fossil fishes according to Louis Agassiz and Arthur Smith Woodward. (A) For all fossil fishes. (B) For the teleost fishes. See text for discussion.

A	*Genera*		*Species*		*Species per genus*	
	Agassiz	*Woodward*	*Agassiz*	*Woodward*	*Agassiz*	*Woodward*
placoids	81	97	406	341	5	3.5
ganoids	94	104	475	439	5	4.2
cycloids	86	95	178	218	2.1	2.3
ctenoids	87	95	164	169	1.9	1.8
Totals	348	391	1223	1167	3.5	3

B	*Genera*		*Species*	
	Agassiz	*Woodward*	*Agassiz*	*Woodward*
cycloids	86	95	178	218
ctenoids	87	95	164	169
Totals	173	190	342	387

But the situation is far worse with species. There was, in fact, very little overlap in the species names. Woodward had sunk most of Agassiz' into synonymy and erected many new ones. This may give us a message, at least for paleontology. Species names are far more labile, far more difficult to apply in systematic revisions, and, in effect, far more difficult to document. This is because species boundaries are far more ambiguous than genera, etc.

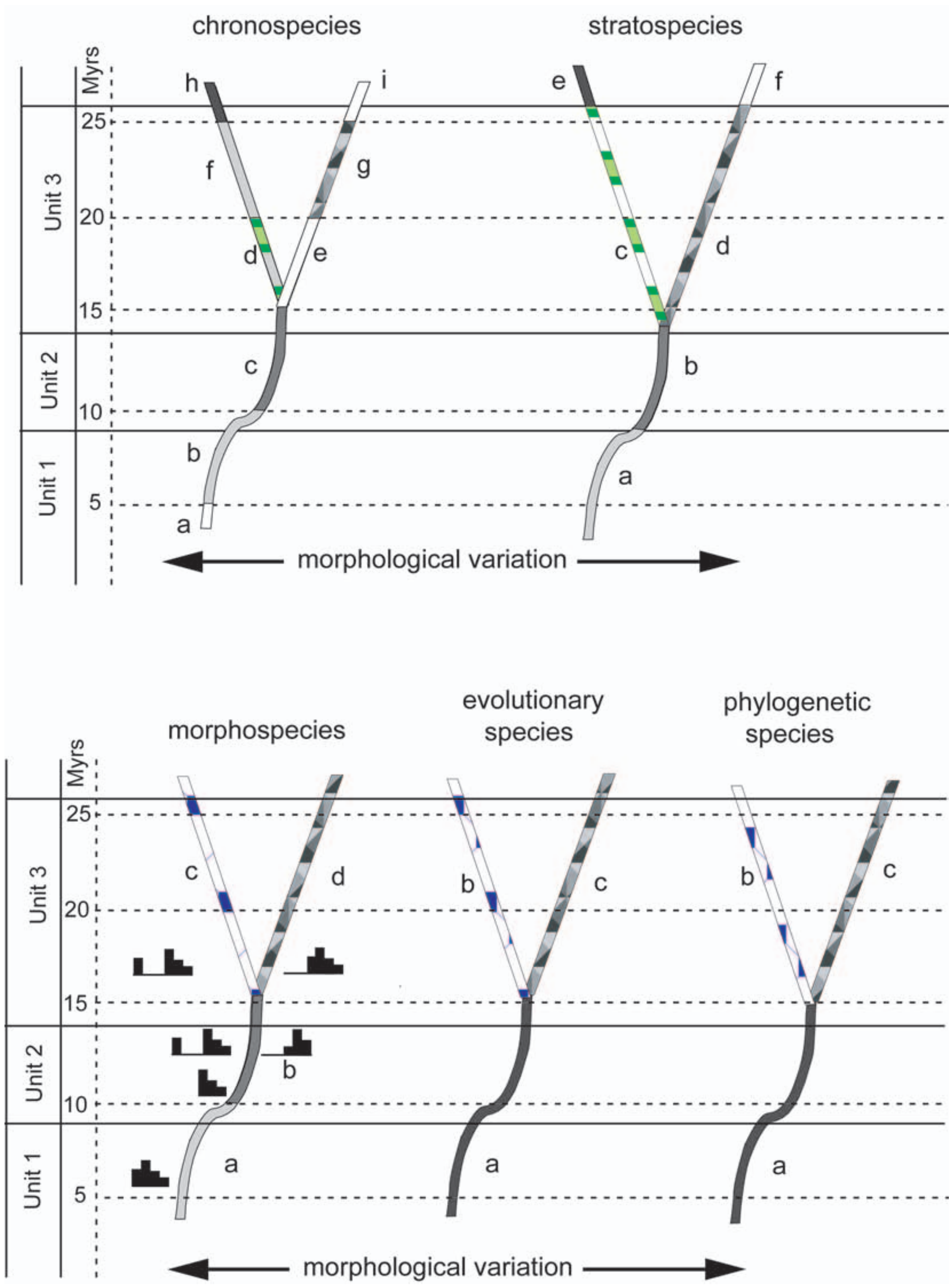
Paleontological species come in many guises, mostly due to the fragmentary nature of fossils, which are always incomplete in some way or other. Even if they are complete we generally do not have the geographic sampling or ontogenetic continuity to truly say whether we have one or more species. There are, of course, echoes of this in the Recent world but the resonance is far greater in paleontology.

Different species names have often been given to different parts of animals found isolated. For plants this is particularly true where the fructifications, stems, roots, leaves and spores are each given separate names as form taxa.

For paleontologists there is an additional dimension when we consider the time aspect of fossils. The problem of recognizing species is exacerbated because there are different ways to divide a stratigraphic continuum, based on different concepts of species and leading to different species recognition and the names applied (see Forey, *et al.* 2004). Sometimes this is done by simply dividing the continuum in segments of equal time — the chronospecies. Others give different species names where the continuum intersects with a stratigraphic boundary or sometimes with a break in the succession — the stratigraphic species. Others divide the continuum into segments according to the degree of variation seen in the modern representatives, should there be any. Yet others divide the continuum according to deviations in morphological trends — the evolutionary species concept of George Gaylord Simpson, while others will give new species names only at inferred cladogenetic events — the phylogenetic species concept.

Clearly, with such a multitudinous variety of species concepts and recognition criteria, the units to which we give species names have to be regarded with suspicion and the calculations of species duration through time must also be regarded with great care. Many of these problems, such as form taxa, with different species representing parts of the same organism or stages of life histories will be difficult to overcome. Their solution depends upon fortuitous finds of fossils. However, it is reasonable to suggest that the concepts of chronospecies, stratigraphic species, evolutionary species, and phylogenetic species be discouraged, and that species be established and named on unique combinations of characters as advocated by Wheeler and Platnick (2000). This will allow closer comparison with Recent species that, despite the domination of the biological species concept, are most often recognized on combinations of morphological characters. By doing so, esti-

FIGURE 3 (right). Species problems in paleontology. There have been various ways in which lineages of fossils traced through the rocks have been partitioned into species. Both the different implied theoretical concepts and the different practical ways in which this is done lead to very different concepts of species. In this diagram five concepts are shown against a common background showing a lineage of fossils collected from successively earlier strata in which the morphology (horizontal axis) changes and at one point diverges into two distinctive morphotypes. Thick continuous lines are stratigraphic boundaries; dotted lines are subdivision into equal time bands. Top diagram: two concepts which depend exclusively on the time aspect. The chronospecies is recognized as units delimited by arbitrary units of time (in this case every five million years). The stratospecies is delimited at stratigraphic boundaries. Lower diagram: three concepts centered on the intrinsic morphological variation. The morphospecies is recognized when overall morphology or some morphological variable has changed through time sufficiently to consider a new species (the histograms represent some measure of variation of populations). The evolutionary species recognizes species boundaries where some evolutionary trend changes beyond that expected from stochastic variation. The phylogenetic species is recognized only when a cladogenetic event takes place.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morphological variation

mates of species longevity can be comparted in a more realistic way with likely fates of modern species.

At the end of the day disagreements over recognizing species, at least in the fossil record, may be counterproductive to effective production of taxonomic information, web-based or otherwise. Full species listings for many groups are just not feasible propositions. Listings at the generic level are possible and achievable. On the whole, genera are recognized on clear-cut characters such as presence/absence characters that can be evaluated more easily than those used at the species level — which are often proportions and counts of parts, patterns of ornament, colour patterns etc. And for this reason alone I would advocate maintenance of the Linnean binomial. Descriptions at the generic level would be given, still tied to the type species and the type specimen — both of which I recommend we keep.

When my colleagues and I sat down to discuss web-based taxonomy (Forey et al. 2004) we all agreed that paleontology would benefit for exactly the same reasons that are cited by neontological taxonomists, namely:

1. Web-based taxonomic databases can significantly reduce the time lag between the acquisition and dissemination of knowledge.
2. The ability to constantly update taxonomic data is an obvious advantage of the web.
3. Pertinent primary literature for fossil genera and species is scattered through a huge number of books and journals, many of them restricted to specialist libraries. If basic taxonomic informa tion can be placed on the web, it will help standardise the use of names by allowing easier access to critical data by a larger number of people. Technically, it would be possible to include tracts of text and illustrations from the relevant original literature, but this demands cognisance of copyright laws.
4. Web-based lists make it potentially easier to collate information (i.e., numbers of genera/species from named horizons etc) with the possibility of calculating rates of origination and extinctions (e.g., this is now possible with the web-based Fossil Record II, Benton 1993).
5. The description of fossil taxa can often involve reference to many different partial specimens in order to capture the complete morphology. The unlimited space for illustration on the www is clearly an advantage. However, there remains no substitute for examining actual specimens.

There are some potential disadvantages of a web-based taxonomy, but none are unique to paleontology. The main problem to be solved is how web-based taxonomy is to gain validation. Taxonomic data can be posted on the www without passing through any review process and thereby run the risk of erecting poorly diagnosed taxa. It might be necessary to establish accredited host sites and/or panels of experts who could ensure quality control, however authoritarian this may seem. No such system currently exists and the erection of such panels would not be an easy exercise in a science where individuals have had free reign. Perhaps, like journals, the respect for some web sites may become self-regulating. The best taxonomy has always come from individuals with the experience and breadth of knowledge to provide an authoritative overview — Agassiz and Woodward once again. It is probable that data-rich and scientifically useful sites will soon become self-evident to the wider community.

An important consideration of www-based reference taxonomy is the feasibility of its goals. Many web sites have started, only to fizzle out. For the www to be any advantage over our current vehicles for disseminating taxonomic information it must capitalize on its strengths, accessibility and instantaneousness.

I have pointed out above that taxonomic problems associated with defining species are far more complex than those associated with genera and monophyletic clades. Species-level taxonomy usually requires data on large numbers of individuals and is often based on very subtle character assessments. Consequently, species boundaries are rarely unambiguous and obvious. By contrast, generic and higher taxonomic levels are usually established on the basis of more major character traits that are easier to define and illustrate. Whereas a web-based taxonomy at genus level and above may be relatively easily achieved, the goal of placing all species on the web seems over-ambitious given present resources devoted to taxonomy.

Summary

I would maintain that despite shedding the theoretical basis of Linnaeus we have and indeed need to retain the binomial, type species and type specimen. I would advocate recognition of species based on unique combinations of characters and reject the chronospecies, stratospecies, evolutionary species (of Simpson) and phylogenetic species as useful entities by which to name the world. I would further recommend that it be mandatory for an author to designate the phylogenetic status of genera and more inclusive taxa, irrespective of whether rank is applied or not.

With respect to any future taxonomic compilations that may be put on the Web (www), we should concentrate our efforts on revision and documentation on genera, rather than species.

The biggest challenge over the next few years will be to devise methods for validating web-based taxonomy. Certainly the international codes of nomenclature will have to change to give guidance on naming genera and species on the Web. There needs to be a clear distinction between authoritarianism, which will simply fragment our science of taxonomy, and authoritiveness which will secure its future.

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