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Representing supraspecific taxa in higher-level phylogenetic analyses

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REPRESENTING SUPRASPECIFIC TAXA IN HIGHER-LEVEL PHYLOGENETIC
ANALYSES: GUIDELINES FOR PALAEONTOLOGISTS

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Abstract: As phylogenetic analyses become larger, one of the greatest methodological
difficulties is representing speciose supraspecific clades in higher-level analyses (e.g., trilobites
within studies of arthropod phylogeny). Several strategies have been proposed, including using
representative single composite terminals or species-level exemplars, and various methods are
currently used in the palaeontological literature. However, this is problematic, as simulation
studies and empirical arguments in the systematics literature have clearly identified multiple
exemplars as the optimal method. The continuing usage of suboptimal strategies in
palaeontology may lessen the accuracy of phylogenies and hampers comparison between
alternative studies. Here I outline problems with suboptimal strategies, review arguments in
support of multiple exemplars, and provide guidelines for palaeontologists undertaking higher-
level phylogenetic analyses.

Key Words: cladistics, evolution, exemplars, missing data, phylogeny, supraspecific taxa,
Archosauria

RH: BRUSATTE: REPRESENTING SUPRASPECIFIC TAXA IN CLADISTIC ANALYSES

THE goal of assembling a comprehensive "Tree of Life" has promoted extensive phylogenetic research at all levels, and such work has become a primary aim of palaeontological research programs. Palaeontologists often concentrate on broad scale, higher-level cladistic analyses that aim to discover relationships between major clades, which are crucial for macroevolutionary studies. Many of palaeontology's most important contributions to uncovering the tree of life, such as the interrelationships of long extinct taxa and the phylogenetic backdrop to the origin of major body plans, fall into this category. However, conducting large-scale analyses is not always straightforward. How should palaeontologists represent a group such as Trilobita, which contains ~17,000 species, within a higher-level analysis of arthropod phylogeny? Aside from techniques such as supertrees and supermatrices (see Gatesy *et al.* 2002 and Bininda-Emonds 2004), many systematists carry out higher-level analyses in which major supraspecific clades are treated as terminals. For instance, in the above example, Trilobita may be treated as a single unit rather than including all individual species. But this raises another problem: how to best construct such a terminal to represent the group as a whole. This has been the subject of much debate, and unfortunately the palaeontology literature is rife with problematic examples that may produce inaccurate phylogenies. Here I review different strategies, present arguments in favour of an optimal approach, and provide guidelines for palaeontologists undertaking higher-level phylogenetic analyses.

DIFFERENT STRATEGIES AND AN OPTIMAL APPROACH

Accurately and appropriately representing a speciose group such as Trilobita is neither trivial nor straightforward. Different authors have used numerous strategies in situations such as these, and

most of these methods have been utilised in the palaeontological literature. Some studies score a single species or multiple species as exemplars (e.g., Parrish 1993; Clark *et al*. 2002; Ruta *et al*. 2003). These exemplars are intended to be representative of the larger group, but are faithfully scored with the character states of the species, even if these are not uniformly present in all members of the group. Other authors create a composite single terminal, which is scored based on amalgamated data from several species. There are many methods for scoring a composite terminal, and often authors simply present data with little or no explanation for how it was derived. Three of the most widespread explicit methods score the composite terminal based on the most primitive or common states exhibited by the group (e.g., Estes *et al*. 1988; Trueb and Cloutier 1991; Carroll 2007) or with the reconstructed ancestral states of the group, usually with reference to existing ingroup phylogenies (e.g., Langer and Benton 2006; Bloch *et al*. 2007).

Discussion of which strategy is best has largely bypassed the palaeontological literature, but was the subject of several contributions in the systematics literature beginning well over a decade ago (e.g., Yeates 1995; Bininda-Emonds *et al*. 1998; Wiens 1998; Prendini 2001). From these and other papers emerged a general consensus that scoring multiple exemplar species is the best approach. The utility of multiple exemplars was well-articulated by Prendini (2001), but these arguments have not yet swayed many in the palaeontological community. A survey of higher-level morphological phylogenetic analyses published from 2003-2007 in both the paleontological and neontological literature is striking: only 38% of paleontological analyses use multiple exemplars, compared to 85% of neontological studies (Table 1). In other words, more than 60% of paleontological studies continue to neglect multiple exemplars in favour of other methods shown to be less accurate and justifiable by Wiens (1998), Prendini (2001), and others. Thus, it is worthwhile to briefly review arguments in favour of multiple exemplars.

ARGUMENTS FOR MULTIPLE EXEMPLARS

In general, multiple exemplar species are thought to produce the most accurate results (Wiens 1998; Salisbury and Kim 2001; Simmons 2001) and are held as the most defensible technique empirically and theoretically (Yeates 1995; Prendini 2001; Prendini *et al*. 2003; Malia *et al*. 2003). Simulation studies indicate that scoring multiple species (i.e., at least two) results in more accurate trees than using a single exemplar or a representative composite terminal based on the most primitive or common states exhibited by the supraspecific group (Wiens 1998). From an empirical perspective, scoring exemplar taxa is generally more transparent than creating composite terminals, which are often constructed based on inexplicit and unstated methods (Yeates 1995; Prendini 2001). Scoring exemplars also more faithfully represents variation within the supraspecific taxon, and allows for the ancestral state of the taxon (which is ultimately what is important to represent in a higher-level analysis) to be inferred simultaneously from the higher-level analysis itself instead of assumed a priori (Yeates 1995; Prendini 2001). Similarly, including many exemplars in a higher-level analysis also serves to test the monophyly of the supraspecific group, which is useful and necessary when monophyly is unknown or poorly-supported (Yeates 1995; Prendini 2001).

Scoring a single composite terminal based on Inferred Ancestral States (IAS: Rice *et al*. 1997) circumvents some empirical and theoretical drawbacks of composite terminals, but is problematic for other reasons. Most troublesome, IAS requires the ingroup phylogeny of the supraspecific group to be known, which is often unrealistic. Additionally, reconstructing the ancestral state relies on reference to an outgroup (Rice *et al*. 1997), the closest of which is often

unknown. Indeed, identifying the closest outgroup (sister taxon) to a supraspecific taxon is often the object of higher-level analysis.

WHY ARE MULTIPLE EXEMPLARS NEGLECTED?

In light of the well-articulated advantages of multiple exemplars, it is alarming that less optimal strategies persist in palaeontological studies. This is likely due to many factors, several of which are practical. First, adding copious exemplars is time consuming and adds considerable worker-hours to a project (the "extra effort" identified by Prendini [2001]). Second, multiple exemplars will often increase computational time and greatly enlarge the number of possible trees, making it more likely that heuristic search options will fail to find the most parsimonious tree(s). Third, a particular problem in many palaeontological analyses is that many species-level exemplars are characterized by an abundance of missing data due to incomplete preservation and deformation. Fourth, adding multiple exemplars often entails adding a multitude of new characters to both support the monophyly of the supraspecific taxon and resolve ingroup relationships, which may increase homoplasy, computational time, and worker-hours.

Each argument has been raised in the literature (e.g., Bloch *et al*. 2007:S51), but is probably less of a problem than is often assumed. First, at the most basic level, it is debatable whether the "extra effort" of scoring multiple exemplars is any more time and labour intensive than the work needed to condense observations from numerous taxa into a representative terminal. For instance, would it not be quicker and easier to simply score several dinosaur exemplars than to review scores from many taxa and reconstruct ancestral states using the lengthy process of Langer and Benton (2006)? From an analytical standpoint, if the addition of

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exemplars and characters increases computational time and the number of possible trees, this can be alleviated with certain computational strategies, such as the parsimony ratchet (Nixon 1999; Quicke *et al*. 2001) and a litany of approaches outlined by Goloboff (1999) and Roshan *et al*. (2004). In fact, such strategies are commonplace in current neontological phylogenetic analyses and are included in phylogenetic software packages such as TNT (Goloboff *et al*. 2003). Although missing data is often a problem, ignoring taxa simply because of missing data is dangerous (Wiens 2003, 2005, 2006) and the use of several exemplars can alleviate missing information in one or two fragmentary exemplars (see below). Finally, although scoring multiple exemplars can be time consuming and sometimes difficult due to funding constraints, the *a priori* decision to abandon the more defensible use of multiple exemplars in favor of the less time-consuming use of suboptimal methods is unwise, and runs counter to the ultimate aim of rigorously and accurately reconstructing phylogenies.

ONE EXAMPLE OF THE PROBLEM

The use of composite terminals in the palaeontology literature is problematic for two reasons. First, as reviewed above, multiple exemplars are simply a *better* approach: they are more accurate in simulation studies and are more defensible empirically. Second, the use of different methods hampers comparison between competing phylogenetic analyses, something that is becoming increasingly necessary as the number and size of datasets increase (e.g., Harris *et al*. 2007; Brusatte and Sereno 2008). This is well illustrated by one recent example.

One of palaeontology's most notable contributions to evolutionary biology is the phylogenetic context to the origin of land-living vertebrates, the tetrapods. Two of the most

comprehensive phylogenetic analyses of early tetrapods are the recent studies of Ruta *et al*. (2003), which was updated by Ruta and Coates (2007), and Carroll (2007). These analyses use vastly different representation strategies for supraspecific clades: Ruta *et al*. (2003) utilise multiple species-level exemplars for higher-level clades such as Amniota and various lepospondyl subgroups (e.g., Nectridea, Microsauria, Aïstopoda), whereas Carroll (2007) employs a single terminal for these clades, which is scored on a complex strategy that takes two pages to explain. With these differences, it is not surprising that the analyses generate remarkably different topologies. For example, Ruta *et al*. (2003) place extant lissamphibians within the speciose temnospondyl group, whereas Carroll (2007) finds lissamphibians more closely related to lepospondyls and amniotes (thus rendering the entire temnospondyl radiation outside of the tetrapod crown group as defined by living taxa). Additionally, groups such as Anthracosauria, Microsauria, and Nectridea, which are assumed to be monophyletic by Carroll (2007), are recovered as paraphyletic grades by Ruta *et al*. (2003).

Which of these two topologies is more credible? As an evolutionary biologist interested in the radiation of major groups, but not an expert in the minutiae of early tetrapod anatomy, which analysis should one favour? These are not trivial questions, since the conflicting topologies have very different implications for the evolution of certain character complexes (Ruta and Coates 2007), divergence times for living lissamphibian clades (Anderson *et al*. 2008), and the development of metamorphosis and other ontogenetic changes in living groups (Schoch 2009). For example, a temnospondyl origin suggests that lissamphibians evolved from small ancestors that fed on land and underwent remarkable ontogenetic changes in a short period of time, whereas a lepospondyl origin implies that the ancestral lissamphibian may have been aquatic and that "metamorphosis" identified in temnospondyls was a convergent acquisition

(Schoch 2009). The practical consequence of different supraspecific taxon representation strategies is that it is extremely difficult to compare studies such as these. This only obfuscates resolution of important phylogenetic debates and obstructs the use of these phylogenies in macroevolutionary studies.

STRATEGIES FOR SELECTING EXEMPLARS

There is little justifiable reason for palaeontologists to use any representation method other than multiple exemplars. However, which species should be targeted as exemplars? Previous authors (e.g., Yeates 1995; Prendini 2001) have listed several qualities important in an exemplar, and here I review ideal qualities demanded of exemplars in most common palaeontological analyses. Thus, the focus here is on exemplars representing supraspecific clades which are most likely monophyletic, but whose monophyly and higher-level relationships to other taxa (including other supraspecific clades) are the subject of study. This discussion also applies to selection of exemplars more generally, and more detailed explanation is provided by Yeates (1995) and Prendini (2001).

First, it is roundly agreed that selected exemplars must be able to accurately represent the basal condition of a supraspecific taxon, as this condition includes "all the apomorphies necessary to correctly infer the position of the group it represents, but lacks those that have subsequently evolved among only some of its descendants and are either uninformative at the higher level (autapomorphies) or suggest an erroneous placement for the group when taken to be representative of it (homoplasies)" (Bininda-Emonds *et al*. 1998:104). This raises a critical question: how should researchers select taxa that are most likely to possess the "basal

condition"? This is straightforward if there is prior information on character polarity, since in these cases individual taxa can be assessed and those with the greatest amount of plesiomorphic states (and the least amount of autapomorphies or homoplasies) can be targeted. In the absence of this information, species that occupy a basal position within the supraspecific clade may be selected as a proxy for the "basal condition." "Basal position" is a relative concept: taxa are more or less basal relative to a certain node (in this case, the ancestral node of the supraspecific group) depending on how many internodes are between the taxa and the node in question (Jenner 2006).

However, these approaches may be problematic for two reasons. First, both require some knowledge of the ingroup phylogeny of the supraspecific group, which itself is difficult to determine without reference to an ougroup. In many higher-level analyses the main objective is to recover the relative relationships of the supraspecific taxa, and thus finding the closest outgroup to a particular taxon is a goal of the study itself. In these cases, outgroups cannot be assumed a priori, and therefore the primitive and derived character states within the supraspecific taxon can only be determined after the analysis. A similar problem is that, for some groups, ingroup phylogenies are available, but are rooted based on questionable techniques such as all zero outgroups, composite outgroups, or hypothetical ancestral outgroups (e.g., basal gnathostomes: Sansom 2008). Thus, researchers must carefully consider the intrinsic merits of ingroup phylogenies, including underlying assumptions and methodological protocols, before using them to help select exemplars. Second, using a basal taxon as a proxy for the "basal condition" is only justifiable if phylogenetic position corresponds to degree of character change (in other words, if more basal taxa are more plesiomorphic and closer to the ancestral condition). This is a common assumption, but Jenner (2006:392) argues that it is based on "no convincing theoretical or empirical justification." Jenner (2006) recommends that testing this assumption is

paramount, and until such research is carried out, I assume here that basal position is a reasonably proxy for the "basal condition" in the morphological datasets that are common to palaeontological analyses. For instance, I assume that *Archaeopteryx* is a better representation of the primitive avian condition than a penguin or a hummingbird.

Several additional qualities are desired in exemplar species. When multiple exemplars are used these should be selected from each branch that arises from the basal node of the supraspecific group, if this information is known (Prendini 2001). Preferably, each should be a basal taxon within its respective clade. If a more conservative approach is sought, multiple exemplars may also be selected so as to represent maximum character diversity within the clade, which potentially provides a more stringent test of ingroup monophyly and ancestral character states (Prendini 2001). Furthermore, from a practical perspective the selected exemplars should be known from a reasonable number of specimens, be characterized by minimal missing data, and should be well-described in the literature, which facilitates transparency in scoring decisions and further testing by alternative researchers.

Number of Exemplars

In addition to these guidelines, the number of exemplars to use is also an important consideration. Previous literature has argued for a "more is better approach" (Wiens 1998; Salisbury and Kim 2001), which means that in practice systematists must choose a number that is a tradeoff between phylogenetic accuracy on one hand and computational time and worker-hours on the other. Previous authors have frequently used two exemplars to represent a supraspecific taxon, as this is the *minimum* number to test ingroup monophyly and distinguish ingroup

synapomorphy from homoplasy. Selecting a minimum of two exemplars was explicitly

recommended by Prendini (2001), but such usage was unfortunately not modeled by Wiens

(1998). However, although two exemplars is an absolute minimum, three exemplars is a more

secure baseline.

Support for the preferred use of three exemplars comes from theoretical consideration

of polymorphism (variation) and empirical examples. First, utilizing at least three exemplars is

critical when there is ingroup polymorphism, which is almost always the case in practice.

Assuming that taxa with no missing data are selected, three ingroup taxa is the minimum number

needed for ingroup relationships to bear on the ancestral state when there is ingroup

polymorphism and the outgroup is unknown. For example, consider two exemplars that exhibit

the states 0 and 1 for a binary character in which the primitive and derived states are unknown,

as is often the case in higher-level analysis when character polarity at the base of an ingroup is

not known *a priori*. A global parsimony analysis attempting to find the sister taxon to the

supraspecific taxon could place the latter anywhere on the tree based on this character, a problem

that is exacerbated when numerous characters exhibit interspecific polymorphism within a group.

However, selecting three or more exemplars allows for ingroup topology to influence

optimization of the ancestral state, which is essential when discovering the closest outgroup is an

object of the higher-level analysis.

Second, empirical studies (e.g., Donoghue and Smith 2001) have shown that using

three or more exemplars is imperative for testing the monophyly of clades lacking unambiguous

synapomorphies and instead united by homoplasy (reversals). This is an important point to

consider for higher-level analyses examining the relationships of numerous supraspecific taxa.

Authors of these analyses may often want to exclude synapomorphies of supraspecific taxa in

order to save both computational time and worker hours, as well as the introduction of additional homoplasy into the dataset. Three exemplars is the minimal number that will allow a researcher to test the monophyly of supraspecific taxa without including additional character data superfluous to the higher-level relationships that are often the main goal of study.

The use of additional exemplars depends intimately on many factors, including ingroup polymorphism and morphological variability. Taxa that exhibit little ingroup polymorphism and morphological variability and are known from many well-studied species may be well represented by two or three exemplars only, while those characterized by more extensive polymorphism and variability may require additional exemplars in order to more confidently reconstruct the ancestral state. The exact choice depends on the reality of the group being studied. For instance, a group with several morphologically-distinctive subclades may warrant one or more exemplars from each subclade, while a group with rampant polymorphism should be represented by a healthy sampling of basal species.

An especially important consideration for choosing exemplars is missing data. As argued above, the ability of three exemplars to resolve ingroup polymorphism depends on the use of three complete taxa. Thus, a group in which many basal species or other exemplars are fragmentary, as is often the case with fossil data, may necessitate a greater number of exemplars to compensate for the uncertainty of missing data. Perhaps more critically, however, highly incomplete taxa near the base of a clade may preserve crucial phylogenetic information. Although highly incomplete taxa are often implicitly assumed to worsen accuracy and resolution, their inclusion may increase the accuracy of an analysis by breaking up long branches and preserving unique combinations of characters (e.g., Wiens 2003, 2005, 2006). Many clades may include highly incomplete basal members that may serve these functions, but otherwise would

make poor exemplars because their shear amount of missing data would have little bearing on reconstructing the ancestral state or testing the monophyly of the clade. In these cases, including such fragmentary taxa with at least three more complete exemplars is recommended.

Finally, exemplar choice also depends on the scope of the analysis. If testing monophyly of the supraspecific groups is a primary objective then numerous exemplars representing all potential major subclades and morphological variants (e.g., body plans) should be selected (Prendini 2001). If monophyly is well-corroborated and the main objective is to reconstruct relationships between supraspecific taxa, then exemplars should be chosen to represent major basal subclades, and enough exemplars should be selected to represent and resolve polymorphism at the base of the taxon, if this information is known. Finally, if monophyly of ingroup clades is uncontested, ingroup exemplars could be constrained as monophyletic in the global analysis. This approach should only be used cautiously, however, as testing clade monophyly is one of the primary goals of most global analyses.

As is clear, the appropriate number of exemplars to use is dependent on the analysis at hand: both the taxa being studied and the scope of the analysis. However, three recommendations are paramount: 1) the use of at least two exemplars in all cases, in order to test monophyly and distinguish synapomorphy from homoplasy; 2) the use of at least three exemplars if there is any ingroup polymorphism or missing data, as is most often the case in palaeontological analyses, to better reconstruct ancestral states; 3) careful consideration of polymorphism, morphological variability, missing data, and the goals of the analysis, which will allow the researcher to determine the need for and prudent choice of additional exemplars.

AN EXAMPLE OF EXEMPLAR CHOICE

In practice, the choice of exemplars will depend on the scope of the analysis and the availability of data, and it would be foolish to suggest a universal method. However, here I present one example of how to use the above guidelines to choose exemplars for one type of cladistic analysis common to palaeontological research: a higher-level analysis focusing on the relationships between supraspecific groups.

Archosauria is a diverse and long-lived clade that includes extant birds and crocodilians, as well as numerous extinct groups such as dinosaurs, phytosaurs, and aetosaurs. The monophyly of most of these lower-level supraspecific clades is accepted, as they are characterized by a highly unique body plan and copious synapomorphies. Additionally, decades of lower-level phylogenetic study have outlined the basic ingroup relationships of these clades. However, despite this lower-level resolution the higher-level phylogeny of Archosauria remains contentious in spite of considerable study. Essentially, researchers agree that many discrete monophyletic clades of archosaurs exist but are unsure of the relationships between these clades.

Current systematic consensus recognizes six major speciose supraspecific taxa within Archosauria: Aetosauria (Stagonolepididae), Crocodylomorpha, Ornithischia, Phytosauria (Parasuchia), Pterosauria, and Saurischia. Each taxon is known from numerous species, and including even a reasonable sample of all species is impractical, at least for initial cladistic analyses. This is especially true for Saurischia, which includes not only hundreds of species of non-avian dinosaurs but also ~10,000 species of living birds. Such difficulty has likely led previous authors to use suboptimal representation strategies. Most previous studies scored a single composite terminal with assumed ancestral states, which are not reconstructed based on a quantitative optimization but rather on an "intuitive" (sensu Yeates 1995) approach (e.g., Sereno

and Arcucci 1990; Sereno 1991; Juul 1994; Bennett 1996; Novas 1996; Benton 1999; Benton 2004; Nesbitt 2007). Other studies score a single exemplar species for supraspecific taxa (e.g., Parrish 1993; Benton and Walker 2002). It is likely that these problematic and inconsistent strategies have, at least in part, contributed to the lack of consensus among published studies.

Each of the six major supraspecific archosaur subclades should be represented by multiple species-level exemplars. Since the six subclades are likely monophyletic and their basic internal relationships are well-corroborated, but missing data and ingroup polymorphism do exist, three exemplars should suffice for each. Table 2 outlines possible three exemplar sets for each supraspecific archosaur taxon, chosen because they best fulfill the requirements outlined above (see Text-fig. 1). Namely, for each subclade I aimed to select the basal-most taxon for which sufficient data is known, as well as basal taxa from divergent branches one or two steps above the basal node of the clade, based on a careful review of numerous published ingroup phylogenies. Additionally, I targeted taxa with divergent morphologies (which provide a more stringent test of clade monophyly and ancestral character states) and minimal missing data. Of course, several possible three exemplar sets exist for each taxon, and the choice of exemplars can be modified with discoveries of new taxa or altered consensus on internal phylogenetic relationships of the supraspecific taxon.

Caveats. The above strategy for archosaurs is only one possible method, which is well-suited to the practical realities of the question at hand. Using three exemplars for each supraspecific clade may suffice for Archosauria, but may be inadequate in other instances. For example, if the monophyly of the subclades was disputed or internal relationships were poorly known, then it would have been beneficial to select at least three morphologically divergent exemplars for each subclade, as outlined by Prendini (2001). As divergence cannot be assessed with reference to an

ingroup phylogeny in these situations, gross morphological difference or geographical

disjunction are reasonable proxies (Prendini 2001). It is also easy to imagine numerous other

scenarios that would necessitate slightly modified exemplar strategies. In some cases a basal

taxon may sit at the end of a long branch, and is thus poorly suited for inferring the

plesiomorphic condition of its larger taxon. In other cases a subgroup may be demonstrably

monophyletic, but is so morphologically variable (or characterized by variable rates of evolution)

that additional exemplars are needed. The same holds true for missing data, as reviewed above:

often the most basal and/or plesiomorphic taxa are woefully incomplete, requiring additional

exemplars to compensate for rampant missing data. The single most important point, however, is

that at least two, and more ideally three, species-level exemplars should be used, and these

should carefully be selected based on the reality of the analysis.

Additional Examples. Several published phylogenetic analyses include well thought out, detailed

explanations for exemplar choice. Useful case studies to consider include Prendini (2000, 2003),

whereas Prendini and Wheeler (2005) provide a stirring critique of a problematic study using

composite terminals. Additionally, Scott (2005) discusses exemplar choice in the context of

combined morphological and molecular studies, which are becoming an integral component of

paleontological research programs (e.g., O'Leary 1999).

DISCUSSION AND CONCLUSIONS

One of the most arbitrary, variable, and problematic practices in higher-level phylogenetic

studies is parsing the often abundant and limitless observations of species and individuals into a

more manageable format representative of their supraspecific group as a whole. Accurate and

empirically-defensible representation strategies are essential for higher-level analyses that attempt to find relationships between major clades. As these analyses are often used as the framework for large-scale evolutionary studies, systematists should be especially careful in their choice of representation method. A rich literature of simulation studies and empirical arguments supports multiple species-level exemplars as the best strategy, but several less optimum methods continue to enjoy widespread usage among palaeontologists. The above discussion and recommendations are intended as a guide for palaeontologists actively conducting systematic research but less familiar with the systematics literature. Much of the above is a review, and the most important cited papers (Yeates 1995; Bininda-Emonds *et al*. 1998; Wiens 1998; Prendini 2001) should be consulted. At a very minimum, palaeontologists should embrace the use of multiple exemplars. If palaeontologists are committed to accuracy then suboptimal techniques cannot stand.

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FIGURE CAPTION

TEXT-FIG. 1. An example of judicious selection of three species-level exemplars to represent a supraspecific clade when previous hypotheses of ingroup phylogeny exist. The example given involves Saurischia, a speciose clade that includes sauropodomorph dinosaurs, theropod dinosaurs, and birds. The phylogeny is a consensus tree taken from many sources, which mostly agree on these relationships. Triangles represent speciose subgroups. Birds are members of Tetanurae.

TABLE 1. Literature Review of Exemplar Strategies[1]

Journal	Analyses	Multiple Exemplars	Percentage
Journal of Paleontology	3	1	33%
Journal of Systematic Palaeontology	7	4	57%
Journal of Vertebrate Paleontology	22	7	32%
Palaeontology	16	5	31%
Zoological Journal of the Linnean Society[2]	12	6	50%
Palaeontological Literature Pooled	**60**	**23**	**38%**
Biological Journal of the Linnean Society	7	7	100%
Cladistics	31	26	84%
Organisms, Diversity and Evolution	5	3	60%
Systematic Biology	9	8	89%
Zoological Journal of the Linnean Society[3]	27	23	85%
Neontological Literature Pooled	**79**	**67**	**85%**

1: Morphological phylogenetic analyses focusing on the higher-level relationships between supraspecific clades (usually subfamily or higher levels). Combined morphological and molecular studies are included, but not studies that are solely molecular. Five well-known and high impact journals have been surveyed for each field.
2: Palaeontological analyses only
3: Neontological analyses only

TABLE 2. Three Exemplar Sets for Archosauria

Taxon	Number of Ingroup Species[1]	Three-exemplar Sets[2]
Aetosauria	~20	*Aetosaurus, Desmatosuchus, Stagonolepis*
Crocodylomorpha	~300	*Protosuchus, Sphenosuchus, Terrestrisuchus*
Ornithischia	~150	*Heterodontosaurus, Lesothosaurus, Psittacosaurus*
Phytosauria	~20	*Mystriosuchus, Paleorhinus, Rutiodon*
Pterosauria	~100	*Dimorphodon, Eudimorphodon, Pteranodon*
Saurischia	10,000+	*Coelophysis, Herrerasaurus, Plateosaurus*

1: Number of accepted species varies by author, and the given figures are intended to be a general estimate. As most of these taxa are completely extinct, these are minimum estimates for species diversity.

2: These genera are mostly monospecific, as is often the case with fossil reptiles.