## MATTERS OF THE RECORD

## Saving the stem group—a contradiction in terms?

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### Introduction

The classification of fossils has long been controversial. Should traditional taxonomic concepts be expanded to encompass plesiomorphic extinct relatives that exhibit subsets of essential defining characters in so many shades of gray? Should rank taxa, established on extant taxa alone, and in a pre-Darwinian, pre-Hennigian framework, remain restricted to their living constituents and integral extinct relatives? Or should these taxonomic concepts be restricted to a membership exhibiting a defining suite of essential characters, regardless of whether they are extant or extinct?

Hennig (1981) argued that rank taxa should be defined on the basis of extant organisms because the latter are often better known than fossil taxa. However, he further argued that traditional taxonomic concepts should be expanded to include all extinct taxa more closely related to the living members than to any other extant clade. The extant clade he denoted the *group, later renamed the crown group (Jefferies 1979), and its paraphyletic complement of extinct taxa, the stem group; Jefferies (1979) later coined the term ''total group'' to describe the monophyletic sum of the stem and crown group, equivalent to Hennig's (1981) more inclusive version of the rank taxon (see Fig. 1 for a diagrammatic representation of these concepts).

There are, however, inherent problems associated with the implementation of the stem group. This is because fossil organisms may fail to exhibit the full inventory of characters deemed diagnostic of a crown group, not because of genuine plesiomorphy but because of incomplete anatomical preservation. Although this holding position was considered ''unsatisfactory'' even in its original formulation, Hennig (1981) argued that prolonged study of fossils would reveal the structure of stem groups and that, ultimately, this could be reflected in the hierarchy of classification.

Hennig's vision of reconstructed stem groups has begun to be realized, demonstrating that the long inventories of characters that diagnose crown groups were acquired incrementally over a protracted period of time, rather than concurrently during periods of rapid evolutionary change. Thus, the terms stem-, crown- and total group, once considered esoteric (e.g., Jefferies et al. 1987), are now finally achieving common currency (e.g., Fig. 2). However, the reason for this is only partly concerned with maintaining stability in taxonomic concepts and owes more to a timely coincidence with attempts by molecular biologists to unravel the origin of key innovations in terms of changes to the genetic and epigenetic control of development. Although their main modus operandi is to compare patterns of development between extant representatives, the implications of this comparison, in terms of modeling developmental evolution, can only be determined with accuracy in reference to the sequence of intermediate anatomical steps. This requires consideration not just of extant phylogenetic intermediates, but of the stem as well (e.g., Coates and Cohn 1998; Prum and Brush 2002; Donoghue and Purnell 2005). Indeed, it could be argued that an understanding of character evolution in the stem is of greatest significance as it is among the extinct members of these lineages that diagnostic characters of extant taxa were acquired.
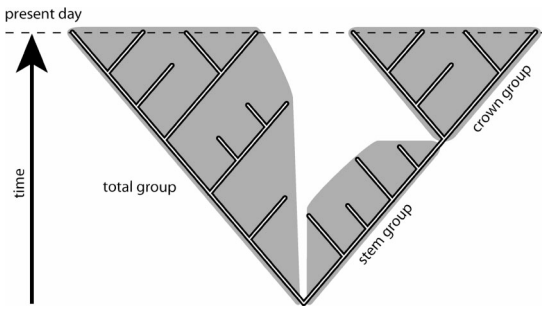
FIGURE 1. The relationship between total-, stem-, and crown-group concepts.



FIGURE 2. Histogram showing the year-by-year appearance of the terms ''stem group'' (gray) and ''crown group'' (white) (using the search string ''stem AND group OR crown AND group'' and filtered for relevance) in titles and/or abstracts of papers included in the Science Citation Index. These counts do not include ''stem'' in the sense of stem-based definitions and do not, therefore, reflect the rise of phylogenetic nomenclature sensu de Queiroz and Gauthier (1990).

The stem-group concept has, thus, become a Rosetta Stone for interpreting evolution from both pattern and process perspectives. However, with the increased currency of these concepts has come confusion and abuse in their use that, unless checked, will inevitably lead to their redundancy.

## Total- versus Crown-group Concepts of Taxa

Despite the widespread adoption of Hennig's stem group and its allied suite of terms, his recommendations on how taxonomic concepts should be adapted to account for total- versus crown-group perspectives have not been widely followed. This occurs mainly because of its potential to disrupt and confuse the entire biological community when the issue is one of fossil classification (Doyle and Donoghue 1993; de Queiroz and Gauthier 1992).

In practice, it makes little difference whether long-established taxonomic concepts are adapted to total- or crown-based phylogenetic definitions, so long as there is consistency. For example, tetrapod (e.g., Laurin *in* Laurin and Anderson 2004) and angiosperm (e.g., Doyle and Donoghue 1993) systematists have adopted crown-group concepts of established taxa whereas specialists in almost all other areas have adopted a total-group perspective (e.g., Runnegar 1991; Budd 1993; Donoghue et al. 2000; Wills and Fortey 2000; Collins and Valentine 2001). Unfortunately, this difference in approach has led to considerable confusion over the time of divergence of modern mammal orders. Molecular biologists and paleontologists have unwittingly attempted to date
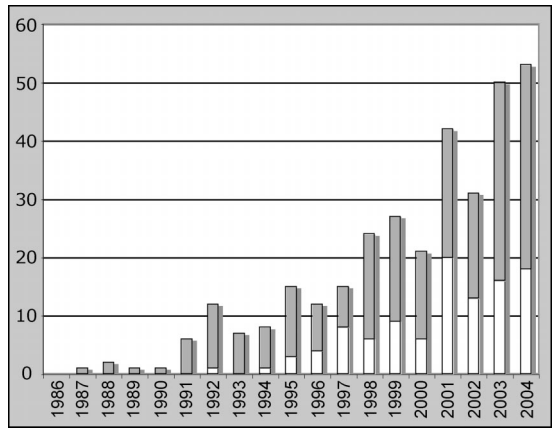
total versus crown group concepts of the same taxa (see, e.g., Bromham et al. 1999; Archibald 1999). This is not a problem peculiar to mammals (Brochu et al. 2004), nor to debate on the timing of evolutionary events, but it impacts upon any research based on taxonomy.

The need for consistency is clear, and the choice of total- or crown-group definition for long-established extant taxa may be little more than arbitrary, particularly given the hierarchical relationship between the two concepts. Total-group definitions passively facilitate the classification of extinct organisms amongst their extant relatives, obviating the need to formally erect new suites of taxa (Hennig 1981) and force biologists to confront the deep history of the lineage leading to the crown (Patterson 1993). However, these benefits are outweighed by the problem of total-group diagnoses that are entirely reliant upon basal members of the stem, those taxa that, by definition, share fewest synapomorphies with the crown. To make matters worse, these organisms are often the least well preserved. Thus, it can be difficult to reconcile among basal membership of the stem of one total group, terminal membership of the stem of the next more inclusive total group, and basal membership of the stem of the sister total

group. Meanwhile, the systematic disparity of a crown group is fully encompassed by its extant members and so, together with data from extinct members, we may have greater confidence in membership, the inferred nature of their last common ancestor, and, ultimately, the diagnostic characters of the clade.

Thus, for practical reasons, crown-group rather than total-group definitions are preferred for long-established extant taxa. However, it does not necessarily follow that new names need to be coined for their total-group counterparts (Rowe 1988; de Queiroz and Gauthier 1990, 1992; Bryant 1996). As Doyle and Donoghue (1993) have argued, the terms ''stem'' and ''total group'' may still be used as modifiers with reference to revised crown-based definitions. Thus, for example, stem-mammals are non-Mammalia (crown group) Synapsida (total group). Given that this is the way in which advocates of total-group definitions utilize these concepts (e.g., Donoghue et al. 2000; Ruta et al. 2003) such a proposal should lead to minimal disruption in working practice.

## Abolish the Stem Group?

Perhaps the greatest source of dissatisfaction with the stem group suite of concepts has been the paraphyletic nature of the stem group itself, which contravenes the Hennigian principle of formally recognizing only clades. A variety of remedies have been suggested.

Patterson and Rosen (1977) and Wiley (1979) argue that extinct taxa are better accommodated in existing classifications using Nelson's sequencing convention for successive sister taxa to the extant crown group, which indicates extinct status by using a dagger epithet (Nelson 1972). However, this does not provide a means of discussing the relationships of stem taxa to the crown group, which is the main utility of the stem group concept.

Ax (1984, 1985, 1987) proposed the elimination of the stem-group concept and its replacement with the ''stem lineage,'' restricted in its constitution to members of the direct lineage leading from the earliest member of the total group to the earliest member of the crown group. However, this concept is even more paraphyletic than the stem group in that it excludes not only the crown group but also all the side branches of the stem group, which he referred to as ''stem representatives'' (Jefferies 1985, 1986). Clearly, Ax's stem lineage, despite its distinct and precise definition, is a stem group in all but name.

Magallón and Sanderson (2001) proposed that the problem be remedied by redefining the stem group such that it is monophyletic, encompassing also the crown group to make it synonymous with the total group, which they deem redundant. Members of the stem group that are not also members of the crown group are referred to as ''stem-lineage representatives,'' compatible with the use of this phrase by Ax (1984, 1985, 1987), though incompatible with his stem-lineage concept.

None of these solutions are entirely satisfactory. The problem with the paraphyletic nature of the stem group seems to be based entirely on theoretical objections to the formal taxonomic recognition of paraphyletic groups. However, discussion of a paraphyletic assemblage is not formal taxonomic recognition, and the need to refer to such groups is evident from the various attempts to replace or redefine the stem-group concept.

In essence, the problem lies with status of ''group,'' and this is very clear from the many ways in which Ax (1984, 1985, 1987) uses his stem-lineage concept. However, the stem lineage and stem group are not interchangeable concepts, as their distinct definitions indicate. In referring to the direct lineage of common ancestors intermediate to the base of the stem and the base of the crown, the stem lineage remains a useful concept because it is the nature of its component nodes, rather than the plesia they subtend, that reveals the steps through which anatomy evolved intermediate to the base of the stem and crown. Thus, it would be preferable to find an alternative term that would convey the meaning of a stem group, but without the implication of a taxonomic group.

The simplest of all solutions to theoretical objections to the stem group would be to drop ''group'' from the name of the concept, and refer instead to the ''stem,'' or to ''stem-[crown taxon name].'' Indeed, the simplicity of this solution is evident from the fact that it has

emerged as common parlance in the recent relevant systematic literature.

## Extant Stem Groups and Extinct Crown Groups

Although all stem taxa are, by definition, extinct (Hennig 1981; Ax 1987), extant taxa have begun to be described as members of stem groups. For instance, tunicates have been recognized as stem-chordates (Bassham et al. 1999), and many exclude extant protists from ''crown-eukaryotes'' if they fall outside the clade encompassing Plantae, Fungi, and Animalia (e.g., Best et al. 2004). At the same time, a wide variety of entirely extinct clades, from trilobites to sauropterygians, have been partitioned into stems and crowns (e.g., Ax 1985, 1987; Janvier 1996; Lenz and Melchin 1996; Rieppel 1998; Monks 2002).

The fashion of subdividing extinct clades into stems and crown groups was first advocated by Ax (1987) on two premises: (1) the need to subdivide taxa in scientific communication and (2) the view that taxa are both diagnosed and defined on the basis of an essential suite of characters, or ''ground plan.'' From this perspective, there is no logical impediment to the extension of the stem-group suite of concepts to extinct clades. However, this logical inequality of this perspective is that taxa should be defined on the basis of characters—precisely the driver that led Hennig (1981) to erect the stem group and its associated suite of concepts. Taxa defined on the basis of characters give rise to as many competing taxonomic definitions as there are characters or opinions to be held (e.g., Rowe 1988; Rowe and Gauthier 1992; Gauthier and de Queiroz 2001). This extremely liberal (and ironic) interpretation is eroding the value in the intended purpose for which stem- and crown-group concepts were devised.

Nevertheless, the prevalence with which this kind of abuse of Hennig's concepts occurs indicates that there is a need for a suite of terms articulating the relationship between components of an extinct clade in a manner that it is analogous to stems and crowns and even total groups in the true sense. Ideally, such a suite of concepts could be applied within a frame of reference that is objectively de-finable, as are the stem-, crown-, and total-group concepts.

Craske and Jefferies (1989) devised just such a suite of concepts but their scheme is overly complex and the objectivity of definition fails in clades that are perfectly balanced, or even clades in which the most distal branches exhibit perfect balance.

Monks (2002) instead recognized extinct stems and crowns with respect to a geological time horizon, but the analogy clearly distinguished through use of a dagger epithet. However, although a clear definition of a †crown group is provided, none is provided for the †stem group and this creates difficulty in applying these terms hierarchically. Thus, their utility within cladistic frameworks is very limited. Furthermore, the choice of time horizon against which †stems and †crowns are identified is far from objective, and is hostage to the incompleteness of the fossil record. Finally, the use of a dagger epithet hardly aids communication.

The solution is to accept the fact that in defining new clades there is no objective criterion on which plesia may be subdivided, but also that objectivity is not a necessary criterion so long as the frames of reference with which plesia are subdivided are clear. Following the principles of phylogenetic nomenclature, taxonomic concepts defined on the basis of genealogy and diagnosed on the basis of characters can be used to subdivide plesia into component clades, and they are also the appropriate frame of reference from which to discuss polarity. Whether those clades are identified because they coincide with changes in diagnostic characters that are deemed important is not significant; taxonomic concepts are, and always have been, defined so that their membership may be discussed. The key distinction from character-based clade definitions is that such taxa cannot be redefined if the diagnostic suite of characters is diluted or otherwise changes, as might be expected to occur with the discovery of new taxa and/or with a modified phylogenetic hypothesis. Nevertheless, Bryant (1996) has proposed various means of devising phylogenetic definitions such that they may be falsified if mem-

bership changes radically with systematic revision.

*Phylogenetic Nomenclature.*—A special class of further confusion is emerging from the development of phylogenetic nomenclature. This has the laudable aim of defining taxa on the basis of evolutionary relationships in the face of differing interpretations of the ''essential'' qualities of a taxon and the discovery of stem taxa. Phylogenetic nomenclature recognizes three classes of phylogenetic definition: (1) a node-based definition circumscribes the clade derived from the most recent common ancestor; (2) a stem-based definition relies instead upon sister-group relations, and a clade so defined encompasses all more closely related to one specified taxon than to another; and (3) an apomorphy-based definition circumscribes a clade as the descendants of the first ancestor to possess a particular synapomorphy. These relate to the three criteria that Hennig (1981) entertained for the classification of fossil taxa among their extant relatives. Indeed, de Queiroz and Gauthier (1990) recognize the crown-group, total-group, and structural-type definitions of Hennig (1981) as special cases of their node-, stem-, and apomorphy-based phylogenetic definitions. The key distinction hinges on the fact that phylogenetic definitions are not restricted to the classification of extinct organisms about their extant relatives and can be extended to the subdivision of entirely extinct clades. Thus, node-, stem-, and apomorphy-based phylogenetic definitions refer to the architecture of a cladogram and, though the stem-, crown-, and total-group concepts of taxa are also phylogenetic in their definition, they are also formulated with reference to which members are extant and which are extinct, making best use of variability in data quality.

Problems emerge, however, from the dual meaning of the term ''stem'' and from the fact that the cause célèbre of phylogenetic nomenclature has been the redefinition of traditional Linnean taxonomic concepts (Rowe 1988; Gauthier and de Queiroz 2001). In such instances phylogenetic nomenclature has been used in a manner equivalent to the total- and crown-group concepts and it is only in the subdivision of extinct clades that the distinc-

tion has emerged most obviously, with the erection of a whole new class of ''stem'' taxa that lack complementary crowns (e.g., many contributions in Weishampel et al. 2004). Further diminishing the distinction between stem-based taxa, stems, and total groups, Joyce et al. (2004) have coined a new term, the ''panstem,'' which is identical in meaning to the total-group concept. The need for a new term is justified on the basis that the term ''total group'' implies that other clades are somehow incomplete (Gauthier and de Queiroz 2001), but these authors miss the point that the total group is defined with reference to the crown group and its closest sister-crown. Thus, it is the most complete of all possible component clades. How duality in the use of the term ''stem'' may be resolved is far from clear as both are now heavily entrenched within the literature.

Although most authors have found it possible to juggle ''stem groups,'' stem groups, panstems, and stem-based definitions in the same text without losing clarity, it is perhaps not surprising that others have confused the concepts and begun to identify the ''stem'' portions of stem-based taxa as ''stem lineages'' (e.g., Weishampel et al. 2004). Indeed, this novel use of the term ''stem'' is hardly compatible with the stated aim of phylogenetic nomenclature (de Queiroz and Gauthier 1990). Obtaining stability in the meaning of taxonomic concepts would be better served by providing an alterative name for the ''stem-based definition'' such as ''sister-taxon-based definition.''

## Conclusions

Stem-, crown- and total-group concepts provide a framework within which extinct organisms may be classified alongside their living relatives, leading to a holistic nonpartisan perspective on organismal diversity and evolutionary history in the Tree of Life. Paleontological data organized in this way provide a more complete understanding of the pattern of anatomical evolution that process-based hypotheses seek to explain. This is arguably the greatest value of the paleontological record (Patterson 1981). Given the importance of stem-, crown-, and total-group concepts in fa-

cilitating interpretation of the fossil record, we should avoid ambiguity in the way in which they are interpreted and applied, recognize semantic criticisms for what they are, and adopt new concepts rather than adapting existing ones and thus diminishing their utility.

## Acknowledgments

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