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 paraplycheletic 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.