

RESEARCH NOTES

THE LIMITS OF STRATIGRAPHIC EVIDENCE IN ASSESSING PHYLOGENETIC HYPOTHESES OF RECENT ARACHNIDS

In recent reviews of the arachnid fossil record, Selden (1990, 1993) suggests that alternative phylogenetic hypotheses of Recent arachnids be evaluated with stratigraphic evidence. He reasons that "successive dichotomies in clades must occur in ascending chronological order; thus a cladogram reflecting evolutionary events should concur with a complete fossil record in the sequence of events" (Selden 1990). Based on this premise, Selden proposes that the relative accuracy of alternative phylogenetic hypotheses can be evaluated by comparing discrepancies between the hypothesized branching orders of extant lineages and the order in which they first appear in the fossil record. Aspects of this proposal may appeal to common sense (e. g., Coddington & Levi 1991) and have been anticipated in a quantitative method called stratocladistics (Fisher 1988, 1991; Maddison & Maddison 1992). However, I argue here that stratigraphic tests of phylogeny are unworkable, as they rest upon the questionable assumption that the origin of extant lineages and the origin of their diagnostic characters are coupled (Fig. 1). In fact, diagnostic characters (unique autapomorphies) may evolve long after a lineage diverges from its sister, and it is likely that the first recognizable fossil members of an extant lineage would appear in the stratigraphic record well after the lineage had originated. This would be the case even if the stratigraphic record was essentially complete. The purpose of this essay is to develop this line of reasoning and to argue against the use of stratigraphic tests of phylogenetic hypotheses.

Phylogenetic systematics and biostratigraphy attempt to estimate the relative timing of events in evolutionary history, but these events differ in kind. Phylogenetic systematics estimates the order in which genetic lineages diverge from one another, and biostratigraphy is concerned with

the order in which morphologically distinguishable taxa appear in the fossil record. According to this reasoning, stratigraphic tests of phylogeny can be successful only to the extent that phylogenetic divergence is coupled with the evolution of diagnostic characters. But phylogenetic systematics and evolutionary theory require no such coupling. In fact, the earliest members of two sister lineages may be indistinguishable from one another and from their immediate ancestors in morphology, behavior, genetics, etc. This situation presents few problems for systematists working on deep divergences of living taxa, since independent lineages are differentiated by features that may have evolved long after their phylogenetic origin. In contrast, sameness among early members of sister taxa and their ancestors creates problems for constructing accurate stratigraphic ranges for clades, as one or both of two sister lineages may exist for long periods before acquiring the characters that are used to recognize their living members. Because there is no necessary connection between the time a lineage first appears and the time it first acquires a diagnostic character of its living members, the order of stratigraphic occurrence and the order of phylogenetic diversification need not correspond (Fig. 1). Thus the order of stratigraphic occurrence should not be used to evaluate phylogenetic hypotheses of extant taxa.

The assumed coupling of phylogenetic divergence and the origin of modern diagnostic characters has also inspired an expectation that a "true" cladogram should predict the stratigraphic occurrence of fossils that have yet to be discovered, such as Devonian palpigrades, Silurian opilionids and Devonian solifuges (Selden 1990; Shear et al. 1989). For example, Selden (1990) states that the van der Hammen and Shultz cladograms (Fig. 2B, C) predict the existence of

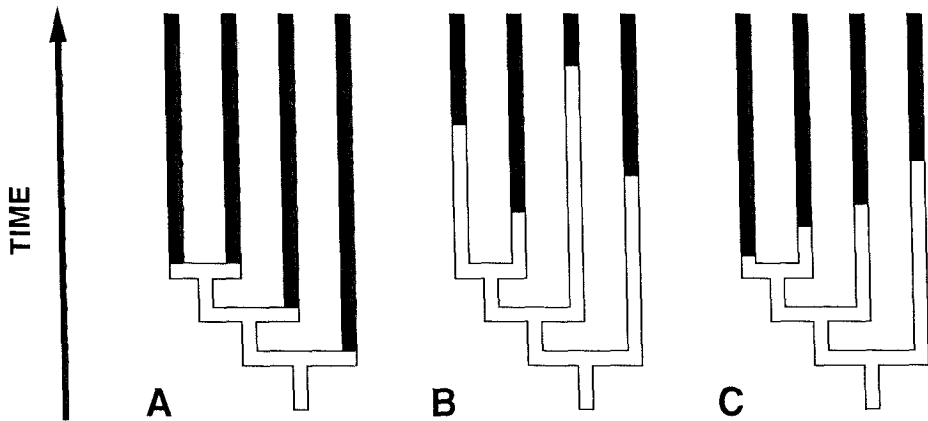


Figure 1.—Trees illustrating the limits of stratigraphic data for evaluating phylogenetic hypotheses of living taxa. Dark regions indicate the occurrence of diagnostic characters (unique autapomorphies) of living taxa within the history of each lineage. Prior to the occurrence of the first modern diagnostic character, members of one lineage are essentially indistinguishable from their immediate ancestors and early members of their sister lineage. Tree A shows coupling between the origin of a lineage and the origin of its modern diagnostic characters, the situation required for stratigraphic assessment of phylogeny. Trees B and C show other possible configurations in which stratigraphic tests would falsify the “true” phylogeny.

Silurian opilionids because Silurian scorpions have already been documented. But this is not a precise interpretation. Given the existence of Silurian scorpions, the cladograms predict that a lineage which eventually gave rise to modern opilionids was present during the Silurian, but it does not claim that any diagnostic characters of modern opilionids were present at that time. Opilionid ancestors may have occurred in the Silurian but may be indistinguishable from the common ancestors of Opiliones and their sister group or from early members of the sister group. If arachnologists agreed to include unobserved and unrecognizable opilionid ancestors from the Silurian within Opiliones, then Selden’s statement would be true by definition, but this approach would impose severe problems on the development of any phylogenetic system based on empirical evidence, as some “opilionids” would be indistinguishable from some non-opilionids. Thus, I see no important role for the use of cladograms in forecasting the occurrence of living lineages within particular strata.

The phylogenetic significance of stratigraphic evidence has been questioned repeatedly, primarily from the widely held perspective that the fossil record is incomplete and unreliable. Fisher (1989, 1991; Maddison & Maddison 1992) has countered that if such criticisms are to constitute scientific arguments, they must be accompanied

by evidence or else they are reduced to *ad hoc* assertions. He proposes an optimality criterion termed stratigraphic parsimony which favors cladograms that minimize the number of *ad hoc* hypotheses of unreliable stratigraphic sampling, just as phylogenetic parsimony minimizes *ad hoc* assumptions of homoplasy. In Fisher’s method (stratocladistics) the order in which clades appear in the stratigraphic record is treated as a special kind of ordered multistate character, and the method favors that distribution of stratigraphic appearances that minimizes the number of *ad hoc* assumptions that a clade was present but not preserved in the fossil record. In this way, Fisher claims to give stratigraphic characters empirical equivalence with traditional phylogenetic characters.

Like Selden’s more general approach, stratocladistics is based on the questionable assumption that the origin of clades and the origin of their diagnostic characters are coupled. According to Fisher’s logic, uncertainty as to the first stratigraphic occurrence of a living lineage is derived solely from uncertainty about the completeness of the fossil record; it is assumed that if an organism is preserved and found, its inclusion or exclusion from a clade will be obvious. However, I have argued that stratigraphic tests of phylogenetic hypotheses of living taxa are inappropriate regardless of the quality of the fossil

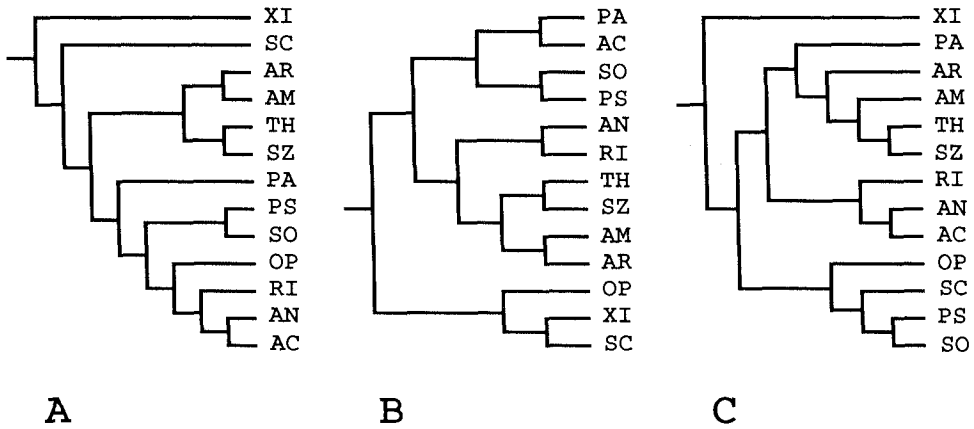


Figure 2.—Phylogenetic hypotheses of Recent Chelicerata. A) Weygoldt & Paulus (1979); B) van der Hammen (1989); C) Shultz (1990). Abbreviations: AC, Acariformes; AM, Amblypygi; AN, Anactinotrichida; AR, Araneae; OP, Opiliones; PA, Palpigradi; PS, Pseudoscorpiones; SC, Scorpiones; SO, Solifugae; SZ, Schizomida; TH, Telyphronida (Uropygi); XI, Xiphosura.

record. The earliest members of an extant lineage would not be recognized as such if none of the diagnostic characters of that lineage had evolved. Early members of a particular clade may be well known as fossils, but their actual phylogenetic affiliation will not be realized because the diagnostic characters are absent. This problem would exist even if early members of a clade were preserved in abundance and in 'perfect' condition. As stratigraphic parsimony fails to accommodate this possibility, stratigraphic 'characters' are inappropriate for evaluating phylogenetic hypotheses of extant lineages.

The most compelling evidence against the use of stratigraphic occurrence in assessing phylogenetic hypotheses has emerged from a recent empirical study. Norell & Novacek (1992) tested for positive correlations between the order of stratigraphic occurrence and the order of phylogenetic divergence in over 20 well-studied vertebrate clades. They found significant positive correlations in only a few examples and many of these showed substantial residual variation. Furthermore, they questioned the reliability of some positive correlations, noting that stratigraphic occurrence may have played a role in the construction of phylogenetic hypotheses; that is, stratigraphic and phylogenetic analyses on which their study was based may not have been independent. Norell & Novacek concluded that stratigraphic occurrence is not a reliable indicator of the order of phylogenetic divergence and that stratigraphic evidence is not appropriate for evaluating the specific predictions of cladograms.

In summary, I have argued that stratigraphic evidence is inappropriate for assessing phylogenetic hypotheses of Recent arachnids or in forecasting the occurrence of clades within particular strata. Stratigraphic methods assume that the order in which diagnostic characters appear in the fossil record reflects the order of phylogenetic divergence. However, this assumption has no logical or empirical justification. Paleontology plays an important role in phylogenetic analysis by discovering and describing new taxa and characters, but fossil evidence has no empirical priority over neontological evidence in reconstructing phylogenetic history.

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