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Matters of the Record

The stability of species in taxonomy

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Many questions of evolutionary pattern and mechanism must be addressed at the species level, because species are a fundamental unit of biology. Even studies which examine patterns of morphologic (as opposed to taxic) diversity rely on species as a basic unit of analysis. Species also provide the backbone for both biostratigraphy and biogeography. Consequently, the definion of individual species is an important and influential aspect of paleontology. Most fossil species have been erected using brief descriptions of small numbers of specimens. The vast majority of these species, even those that characterize biostratigraphic units, are poorly known. Recovery of new material often necessitates re-evaluation of species definitions as specimen numbers rise and variations among specimens are assessed more rigorously. How stable are species definitions in the light of increasing knowledge?

Answering this question will allow us to estimate confidence limits on geological or paleobiological interpretations which utilize fossil species. To address this issue we need well-known species that have been subject to intensive and sustained research effort. At present the numbers of fossil taxa that have been subject to such detailed analysis is minimal. However, recent morphometric studies of ammonites (Hohenegger and Tatzreiter 1992) and foraminifera (Tabachnick and Bookstein 1990) have shown that in both these cases characters once thought to define biostratigraphically significant taxa failed closer scrutiny. Trilobites are commonly used as index fossils, and here we explore the history of a striking example of the instability of species definitions within the Trilobita. In each of these three cases it has been concluded that the species-level taxonomy was previously substantially over split, and the implications of these observations are potentially far-reaching. By detailing the history of a well documented example below we aim to draw attention to the problem, and to suggest possible solutions.

The Late Cambrian asaphide trilobite *Dikelocephalus* occurs in large numbers in the St. Lawrence Formation of Wisconsin, Minnesota, and Iowa. Since its first description in 1852 the systematics has received substantive revision approximately once every 30 years (fig. 1). Over the same time period there has been an exponential increase in the numbers of specimens reposited in museums (fig. 1). The result of this prolonged series of studies is that *Dikelocephalus* is one of the best-documented trilobite taxa. The most recent revision (Hughes 1994), based on analysis of patterns of variation within and among collections from single bedding planes, has resulted in synonymizing all St. Lawrence Formation specimens into a single species, *Dikelocephalus minnesotensis.* While there are considerable morphological differences among the 2750 specimens analyzed, these variations are concentrated within collections made from single beds, and are best interpreted as intraspecific variations. This revision forms a basis from which we review the taxonomic history of the taxon.

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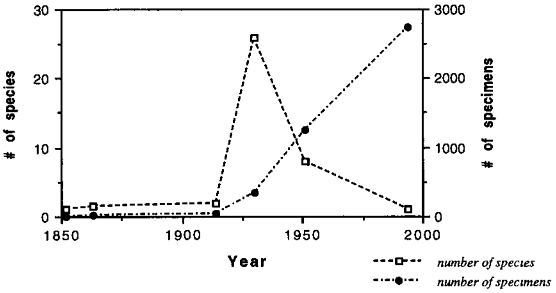

FIGURE 1. Numbers of species (left y axis) and numbers of specimens (right y axis) of trilobites now assigned to *Dikelocephalus minnesotensis*, since its first description in 1852. Only those papers in which new taxa were erected or synonymized are shown, and include Owen (1852), Hall (1863), Walcott (1914), Ulrich and Resser (1930), Raasch (1951) and Hughes (1994). Estimates of numbers of specimens available were made either from statements in publications or accession data from U.S. museums.

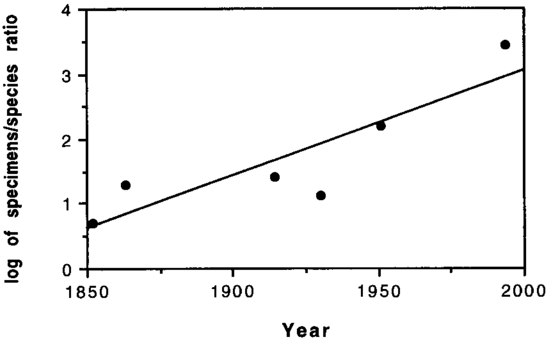

FIGURE 2. Log of ratio of average number of specimens per species now assigned to *D. minnesotensis*, since its first description in 1852. Least squares regression line shows the general increase in the ratio through time.

The taxonomic history of specimens now assigned to *D. minnesotensis* shows marked instability, with a peak of 26 species erected in 1930 (fig. 1). Initial slow growth in the numbers of collected specimens of *D. minnesotensis* was succeeded by rapid growth after 1914 (fig. 1). This initial period is also characterized by slow growth in the numbers of species, with one "variety" described by Hall in 1863, and another species added by Walcott in 1914. The stability in species numbers during this early phase may have been due in part to the small but relatively constant specimen numbers, because proliferation of species in Ulrich and Resser's 1930 monograph was coincident with a sharp, seven-fold rise in specimen numbers (fig. 1). This dramatic rise in species descriptions was attributable to: (1) an expanded sample that presented a significantly greater variety of morphologies than had been available previously, and (2) the authors' zest for defining new species that reflected an explicit commitment to provide tools for high resolution biostratigraphy. Their taxonomy was also influenced by the fact that the sample they examined, despite containing 350 specimens, was too small to demonstrate the continuity of variation evident among larger numbers of specimens. By 1951 the numbers had risen sharply to about 1250 specimens, and it proved impossible to apply the species definitions proposed in 1930 to the new material. With this specimen base Raasch (1951) was able to note that variation within *Dikelocephalus* is continuous, and consequently he reduced the species diversity drastically. The eight species he recognized were defined using stratigraphic criteria to draw arbitrary boundaries within ranges of continuous variation. Once again, the desire to define zonal taxa generated a taxonomic scheme that was based on perceived stratigraphic utility rather than intrinsic patterns of biology.

The discussion above explains the taxonomic history of *Dikelocephalus* in terms of two factors: (1) patterns of morphologic variation evident at particular sample sizes, and (2) the historical agendas of particular scientists. What was the relative contribution of these factors? We have approached this question by assessing how far particular works deviate from a general trend in the taxonomic history of *Dikelocephalus.* We calculated the ratio of specimens available to species described for each major revision, took the log of this ratio because of the exponential growth of specimen numbers, and plotted it against time (fig. 2). The steady increase in the ratio of specimens to species is summarized by a regression line. Ulrich and Resser's 1930 monograph forms a clear outlier to this general trend. The average ratio of specimens per species was 14:1 in that work, whereas Walcott in 1914 had a ratio of about 25:1, and Raasch in 1951 about 160:1. Hence the specimen support for each of Ulrich and Resser's species was, on average, anomalously low, and the deviation of their study from the regression line may approximate their particular predilection for defining new species. However, while Ulrich and Resser were notorious taxonomic splitters the regression suggests that other contemporary workers might have recognized an inflated number of species given the same sample (the regression predicts four or five species among 350 specimens). This result compliments the contention that insufficient sampling may give rise to the appearance of discrete morphologic character states, which can be misinterpreted to have taxonomic significance (Labandeira and Hughes 1994). This pitfall is likely most dangerous in cases where finding discontinuous variation is a primary object of the analysis.

The wide disparity in numbers of *Dikelocephalus* species has implications for estimates of diversity within the dikelocephalid clade and for regional biostratigraphic schemes. A larger question is the extent to which the taxonomic history of this species has relevance for understanding other taxa. The issue is important because our knowledge of the vast majority of fossil species is comparable to the knowledge of *D. minnesotensis* during the period from 1914 to 1930. The answer depends on the extent to which the patterns seen in *D. minnesotensis* can be generalized to other organisms. As mentioned above, there are noteworthy parallels in ammonites and foraminifera, two groups widely used in biostratigraphy. Therefore, we should be aware that taxonomies proposed primarily to serve biostratigraphy may, in some cases, have resulted in inflated estimates of species abundance. Moreover, as taxa of higher rank have sometimes been defined on the basis of numbers of constituent lower taxa rather than specified quanta of morphologic variation, the diversity of superspecific taxa may also be inflated in some cases. In addition to the importance of inflated estimates of taxic diversity for biostratigraphy, there are implications for evolutionary models which use taxa as a primary database, and for assessments of biogeography and faunal provinciality.

Two approaches may allow us to better understand the significance of this potential bias. The first is to increase the number of studies of variation at low taxonomic levels, and document the effect of these studies on previous taxonomic schemes. The second is to explore whether particular workers had characteristic "taxonomic signatures." If, for example, a constant specimen/species ratio is characteristic throughout Ulrich and Resser's work, and if this is significantly different from that of other workers, it may be possible to compute error estimates that can be applied to their work when using their data in comprehensive analyses of taxic diversity. While particular personalities and philosophies have had marked effects on taxonomic interpretations of the fossil record, analysis of the historical consistency of these effects may allow us correct for these anomalies in our understanding of species-level diversity in the fossil record.

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