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## **CORRELATION IN THE CAMBRIAN: PUZZLING FACTS OR WRONG CONCEPTS?**

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### **WHY IS BIOSTRATIGRAPHIC CORRELATION IN THE CAMBRIAN SO DIFFICULT?**

The Cambrian System is currently the only Phanerozoic system without any formally agreed international stages. This partly reflects the scarcity of suitable biostratigraphic markers for intercontinental correlation at the stage level and a pronounced faunal provincialism. However, it does not completely explain why the correlation in the Cambrian is so difficult.

When A. R. Palmer raised a similar question some three years ago, he was able to summarize the purely scientific problems for the Early/Lower Cambrian. Faunas from the Lower Cambrian, and particularly trilobites as the major sources for biostratigraphic information, are difficult to utilize for a precise correlation. This is a consequence of three factors: Lower Cambrian faunas have a high endemism caused on one hand by a strong control of both macrofacies (the position on the shelf) and microfacies of the deposits. However, this endemism also existed in reality so that a biogeographic differentiation was developed. Furthermore, considerable stratigraphic intervals of the Lower Cambrian in various regions are devoid of biostratigraphically useful faunas, or substantial hiatuses obscure the four-dimensional pattern to form a pointillistic picture. Finally, inconsistencies of the nomenclature inhibit possible correlation or prompt incorrect comparisons. Palmer (1998) summarized that the Lower Cambrian organisms are generally not widespread and not evolving rapidly enough to permit a precise correlation and to establish a consistent intercontinental biochronology.

The reasons described by Palmer (1998) are sensible and realistic, and the consequence is that there is presently no basis to introduce Lower Cambrian stages. This view is generally agreed among Cambrian stratigraphers as indicated by a ballot of the Voting Members of the International Subcommittee on Cambrian Stratigraphy in January 2001.

The problem of interregional correlation should be less severe for the Middle and the Upper Cambrian because agnostoids, some polymeroid trilobites and conodonts provide more widespread species that at least temporarily assist in a relatively precise age assignment. Nevertheless,

some problems described for the Lower Cambrian can be transferred to the Middle and Upper Cambrian. In addition to the natural limitations and inconsistencies, there exist a number of artificial difficulties and obstacles that equally contribute to the problems of Cambrian interregional correlation, which I will review herein.

A particular taxon may be known under different names in different areas or at different times depending either on insufficient knowledge of the faunas, on nationalistic concepts, or on erroneous assumptions of morphologic characters due to imperfect preservation of the organisms. In other words, there exist "taxonomic barriers" between basins, continents and eras (Koch, 1998). All of these objective mistakes can be avoided by cautionary scientific procedures so that the analytical results would be much more meaningful. However, a preliminary step in the analysis of Cambrian (and not only Cambrian) biotas is to identify distortions in the fossil record. A much more troublesome second step would be to handle them in a proper way and at least to ameliorate the effects.

## **TRUE STRATIGRAPHIC RANGES**

The fossil record is known to be incomplete. This includes an incompleteness of the species that can be found as fossils but also in their stratigraphic ranges. The stratigraphic range is determined by a taxon's exact moment of origin and its point in time of extinction. Both parameters define its longevity, which is crucial for the quality of a taxon as an index fossil.

It is a truism that a stratigraphic range of a taxon is only virtually true if the fossil specimens occur in higher frequency and in monofacial rock successions. These conditions are rarely developed. In practice, observed occurrences are interpreted as approximately true stratigraphic ranges even if they are to some degree controlled by facies changes. Whether the inherent error of this procedure is neglectable or whether the underestimation of the true ranges is significant is usually not debated in detail although a number of scientists were concerned with quantitative methods to estimate the error. However, constructing fossil recovery potential as a function of the stratigraphic position (e.g., relative to fluctuating facies conditions) is extremely laborious. The price to be paid for those statistical methods is usually too high for ordinary index fossils because they should be distributed with enough frequency so that the amount of inaccuracy can be neglected for the stratigraphic resolution at least in the Lower and Middle Cambrian. Statistical methods are also limited in their potential to answer the question of accuracy. Statistical methods are concerned with the problem of precision, and raw data must be examined prior to statistical analysis.

Another problem is that incomplete preservation modifies the apparent frequency of occurrence of taxa. Signor and Lipps (1982) studied this phenomenon and recognized that sudden disappearances of taxa may be identified in the fossil record as a pattern reminiscent of a smeared-

out drop. This Signor-Lipps effect (Raup, 1986) is also possible with a sudden appearance of a set of taxa and can provide the incorrect impression of sequential appearances.

## GENUS, SUBGENUS, SPECIES GROUP OR SPECIES?

A fundamental problem of biostratigraphy is what hierarchic level can be utilized for correlation. This of course strongly depends on the temporal distributions of species, subgenera or genera as the essential components of biostratigraphic determinations. A general assumption of early Paleozoic biostratigraphy was that species of a genus have roughly identical stratigraphic ranges. For the purpose of 19<sup>th</sup> century stratigraphy this supposition was commonly acceptable. Exceptions of this conjecture were used to define stages or series as in the case of *Paradoxides* in its traditional concept, which serves to define the Middle Cambrian.

The enormous differences in the application of taxa representing different hierarchic levels are evident. The non-compatibility, however, is not only demonstrated purely by the objecting different stratigraphic ranges. Inherent is also a difference that is inherited by their history of discovery. Concepts of taxa to some degree depend on the history of paleontologic science. This can be illustrated by the accumulation of different species, subgenera, genera etc. within a higher taxon. Graphic plots of the discoveries of new families, genera and species among the Ptychopariida (with the year of discovery plotted against the number of taxa) show that the curves increase in steepness from the family to the species level. This is due to two facts: First, and naturally, early discoveries of species had a high probability to represent also new families which were relatively easy to discover. Second, the number of new genera was raised not only by new discoveries but also by splitting of existing genera. A similar picture was displayed for cystoids (Paul, 1998, fig. 1.4).

Morphologically diverse genera were split over decades of advanced knowledge on Cambrian biotas so that the concept of genera changed considerably from the mid 19<sup>th</sup> century as the starting position of Cambrian paleontology to the 1970s or 1980s. What was held for a genus at the beginning of the century finally matches a subfamily or even a family nowadays. This development parallels the growing number of animal species known from the Cambrian. However, the average number of species in a trilobite genus decreased during the last fifty years.

Species themselves are generally based on more and more delicate characters. This brought up advantages for correlation. Unequivocal identification of a species in different regions allowed the assumption that the strata are more-or-less coeval if the stratigraphic range is proved to be short. On the other hand, the occurrence of the same species in different regions became less frequent due to the more rigid taxonomic concept. Consequently, interregional correlation turned out to be more-and-more difficult.

The exit of this dilemma was tacitly walked by many stratigraphers when not a species but

a genus served as the basic unit for correlation. Regrettably, there was rarely any scrutiny applied to the question whether the species united under such a genus had ranges that allowed the appliance of those genera as stratigraphic markers. Small genera should usually work well as biochronologic markers except they are based on insufficient stratigraphic data or on a wrong stratigraphic concept. As one understands systematics and taxonomy latest since Willi Hennig's approach (Hennig, 1950), the natural system should reflect natural relationships of organisms, i. e. it should portray a genealogical ancestry and descendance. Hence, gaps between the assumed times of existence of organisms can only be interpreted as lacking knowledge on additional species, or the identified species belong indeed to different taxa, or the interpretation of their stratigraphic position is wrong. Genera consisting of many species, by contrast, usually do not have a sufficiently restricted stratigraphic range to be of much help in large-scale correlation.

Whether a genus includes a large number of species is a matter of convention as is the subdivision of a genus. Different approaches to this problem exist for different stratigraphic intervals of the earth history. Trilobitologists working in the Devonian established an often sophisticated system with genera being divided into numerous subgenera, whereas subgenera are rarely applied in Cambrian trilobite genera. Notable disparities exist even between different Cambrian intervals. Lower Cambrian trilobite genera are usually narrower defined and thus have fewer species (frequently only one or two). Upper Cambrian trilobite genera have broader concepts, and some have numerous species which are often subdivided into subspecies. This discrepancy is partly a result of authentic differences, which, however, are often created by facies controlled occurrence of the individuals. More often, the differences document different approaches to nomenclature. In Middle Cambrian genera the number of species correlates largely with the number of revisions in that particular group and with the amount of easily recognizable characters. The philosophy behind the concept does not alter the stratigraphic value. However, one should be aware that taxa from different times can not be used in a similar manner and are particularly not able to be used similarly in a computer-based analysis without a priori scrutiny.

As already discussed for the stratigraphic ranges of taxa, it is a truism that biostratigraphic correlation is only accurate if it is based on the occurrence of the same species in the different areas, and on virtually true ranges of this species in monofacial rock successions. As these conditions are rarely developed, one is inclined to match occurrences of the same species although their stratigraphic ranges are obviously truncated to some degree controlled by facies changes. In the scope of the biochronologic resolution this approach is acceptable.

However, the story is more difficult if there is no species in common between different areas. Is it then appropriate to use genera for correlation? This is one of the problems that is poorly investigated for Cambrian faunas. Recent investigations for genera of the Lower-Middle Cambrian boundary interval (*Kingaspis*, *Kingaspidoides*, *Serrodiscus* and *Hebediscus*; Geyer, unpubl.) clearly indicate that species from multispecific genera usually bear a stratigraphic dis-



parity that is too large to permit a sufficiently precise correlation. However, such genera may be used for correlation if they can be identified to represent species groups, or "morphotypes", that form a closely related clade. As an example, *Serrodiscus* has a rather long range that stretches throughout the upper part of the Lower Cambrian and occurs in different Cambrian continents such as Avalonia, Gondwana, and Siberia. Useful for correlation, however, is only the *Serrodiscus bellimarginatus* group, and their stratigraphic position should not be confused with those of other species of *Serrodiscus*.

Other trilobites with fairly widespread occurrences are of little value because of totally different problems. *Calodiscus* is a genus also known from the upper Lower Cambrian of a number of Cambrian continents. The most frequent species identified is termed *Calodiscus lobatus* (Hall). However, due to neotenic development, this "species" expresses an immature morphology rather than representing a true species that is readily identifiable. As a consequence, "*C. lobatus*" is dispersed over an unusually long stratigraphic range although the occurrences in particular areas may be relatively sharp within the sections.

## SPLITTERS AND LUMPERS

Over the last two decades there was a movement that separated systematic paleontologists into "splitters" and "lumpers". The assignment to the splitters group identified scientists as dividing taxa into the smallest possible fractions, to hash genera often into monospecific taxa, and to base species and subspecies on small, or smallest, differences. Lumpers, on the other hand, amalgamate taxonomic material to large units, create genera with a broad-based taxonomic concept and to unite species that apparently were based on material with insufficiently studied intraspecific variability.

The existence of lumpers among the scientific community requires the earlier existence of taxonomists that tend to oversplit existing taxa. Obviously, lumpers turn profit from the grace of the later generation. Their criticism is commonly well based and usually founded on, or at least sustained by, biometric studies. Careful examination of poorly, and superficially, described material is important and contributes to a better knowledge on the diversity. Such studies are prerequisite if Cambrian biota are examined paleoecologically.

However, it should be brought to consciousness that subsequent taxonomic amalgamation needs to be based on well preserved and therefore unequivocally determinable material. This, however, is often not the case. Species based on distorted or incompletely preserved specimens are usually undeterminable. Biometric studies are able to show that such specimens fall within the range of what can be regarded as intraspecific variation. Nevertheless, diagrams are no evidence that those specimens represent indeed the same species even if they were collected at the same locality. It is an ill-defined action to unite under one species deformed material on which

earlier discriminated taxa were erected. Specimens that under present-day concepts would be unsuitable for precise determination is undeterminable and cannot be exactly analyzed even if names were based on it previously. Such taxa are simply unrecognizable, and this status cannot be changed further even if this means that apparent valuable information is obscured. *Kunmingaspis stracheyi* (Reed, 1910) has been revised to include six more species and two forms described under open nomenclature (Jell and Hughes, 1997). All were originally introduced by Reed (1910) from the Ladakh-Spiti region. All specimens were considerably deformed. Although it is nearly certain that they all represent the same species, there is no final proof for this assumption. As long as the material comes from a single section, the assumption seems to be reasonably rectified. However, lumping species based on material from different sections, lithofacies, and stratigraphic horizons, lacks a logic base. Computer-based graphic analysis can restore the shape and assess variation in tectonically deformed trilobites and other fossils (Hughes and Jell, 1992), but it cannot restore characters that were lost during deformation.

## RISKS AND DANGERS

It is also a truism that correlation based on the occurrence of organisms strictly depends on the quality of the identification and, thus, the rigid application of a suitable taxonomic concepts. Two problems are connected with these issues.

Firstly, species can only be identified unequivocally if their preservation is "appropriate". "Appropriate" has different aspects in this context. Some groups of animals offer characters that are quite easy to identify, and even slightly distorted specimens can be determined to the species. Other groups rarely show characters that allow an identification below the family when they are found as fossils and therefore would generally have to be treated under open nomenclature.

Trilobites as the major biostratigraphic tools in the Cambrian differ in this aspects from family to family. Ellipsocephaline trilobites, such as the *Kingaspis-Ellipsocephalus* clade, are only identifiable with certainty to the species if the external as well as the internal surface of the cranidium is known (Geyer, 1990). Thus, a number of slightly compressed ellipsocephaline trilobites from western Gondwana show a slightly hypertrophied nomenclature, and meticulous correlations based on such fossils are equally worthless as detailed biostratigraphic concepts. Solenopleurids and redlichiods often bear important characters in the thorax and/or the pygidium, and those characters of usually known only from a low percentage of the formally described species so that different species may be treated under the same species or genus although the additional character may indeed be regarded as autapomorphies for unidentified taxa.

"Lumping" may create a danger for stratigraphic correlation which has two aspects. Synonymization of insufficiently preserved material creates ill-defined taxa they may include species with different stratigraphic ranges. Application of such taxa for correlation will then lead to

wrong results.

A much simpler but equally erroneous method to arrive at incorrect stratigraphic correlations results also from an amalgamation of species or genera. Species or genera that have characters which are at least unusual for their stratigraphic range are mostly regarded as to represent higher taxa. Such taxa, however, are unusual simply because the relevant morphological characters are rarely expressed. The exact systematic relationships for such taxa are often obscure. If their characters are interpreted as apomorphic characters that typify a taxonomically limited unit, the resulting higher taxon ideally consists of one genus with a number of species. Examples for this are known throughout the Cambrian and also from later systems. Known examples include such trilobites as the Bathynotidae, the Emuellidae, or the *Onaraspis* group. Whether the species of such clades are grouped into smaller or larger genera is again a matter of convention. Nevertheless, one should be careful to reiterate from the amalgamation of such straightforwardly recognizable species into larger genera to assume in a circular argument that the resulting species may serve for a precise correlation.

Two examples can be shown. *Onaraspis* is genus introduced with two species (*O. somniura* and *O. adusta*) from the Ordian stage of Australia by Öpik (1968). The cranidium has some allusions to typical species of the Metadoxididae. However, *Onaraspis* has a surprisingly large pygidium and a macropleural segment in the posterior thorax, which clearly differentiates it from those genera and species. A third Australian species was subsequently introduced by Jell (1990) as *Onaraspis rubra*. A similar species was described by Parnes (1971) from the Cambrian of southern Israel under the name *Myopsolenus palmeri*. Öpik (1975) himself founded a new genus on it and named it *Myopsolenites* (which proves that it does not fit into his concept of *Onaraspis*). Another similar species was described from Spain under the name *Perrector? altus* (Liñán and Gozalo, 1986). Gozalo and Liñán (1997) later assigned all five species to the genus *Onaraspis* and argued that they are able to indicate an important level for intercontinental correlation. A species similar to "*Perrector? altus*" was recently discovered in Morocco in the *Cephalopyge* Zone. However, this zone is slightly younger than the upper Bilbilian in which "*Perrector? altus*" occurs in Spain. Even if all species would be assigned to the same genus, this shows that neither the genus nor the species has a stratigraphic range that is exact enough to allow a precise wide-scale correlation.

Quite inconsistent stratigraphic ranges of regionally dispersed species of a genus are particularly notorious for groups of organisms which are comparatively rare, relatively poorly known, and fairly inadequately understood. Bradoriids are known from various Cambrian continents, and the stratigraphic ranges of the genera differ widely which is partly an effect of the insufficient state of knowledge. Genera such as *Hipponicharion* are identified from middle to late Early Cambrian deposits, but at least one species is known from the basal Middle Cambrian of Morocco so that a possible stratigraphic correlation based on the genus is undermined.



## COMPUTER ARTISTRY

Reconstructing phylogeny has been among the fundamental interests of paleontologists. Early attempts to unravel the pathways of organic life relied to a large degree on stratigraphic data when estimating phylogenetic developments. Recent workers, particularly those from the cladistic school, considered stratigraphic information as either useless or of minor impact for assessing phylogeny. Although most paleontologists with stratigraphic interests clearly rely on stratigraphic information, systematic studies, and cladograms as the icon of modern systematics, are almost exclusively generated by means of computers and without stratigraphic data.

Computers revolutionized human life in general and science in particular. This text is written on a personal computer, and it would have required a pile of paper, scissors and lot of glue to bring the bits of text into this order without a word processing program. However, the basic application of a computer was to calculate, and in this respect the computer is a miraculous tool. Programs exist to bring into a precise order entities of life. One can code genera or species of animals and let the computer set up a tree that may reflect the pathways of evolution.

Most of us know that we should be careful with our believe in such trees. Everybody who has worked with such programs (may it be PAUP, MacClade, etc.) is aware that the results directly depend on (i) the amount of input of data and (ii) the weighting of characters. Usually, the program produces a number of trees that are of equal significance. The brain of the user selects and thus sets preferences which the program never intended. Insofar, the user is an additional modul of the program that performs a last filtering of the output.

Of course, the entire process of computing trees can be done without electronic devices and just on paper with result of equal quality. The process would be far more time consuming but not more incorrect. A human processing of trees would probably start the same way as the computer. One would have to select those *two* taxa that according to best knowledge are closest relatives. To avoid mistakes, one would have to control oneself asking whether the facts that make the two taxa the apparently closest relatives are objective (i.e., no convergence). This would be more reliable than any program is in the moment because coding characters creates a character set that may or may not include convergence.

Computer-based cladistic analyses based on broad data sets in greater part turn out to conflict with well-established character evidence. Cladistic analyses should therefore avoid computerization by such programs and only operate with clearly recognized primary and subsequent evolutionary novelties, or apomorphic characters. This theoretically saves our scientific paradigm. However, the key issue is to recognize apomorphies.

## HOW DO I RECOGNIZE AN APOMORPHIC CHARACTER?

Apomorphic characters are evolutionary novelties which first of all characterize a pair of species with closest genealogic relationship. In general, they are regarded as an objective way to identify such genealogic relationships.

However, two complementary ways exist to achieve an understanding of the relationships of organisms (and taxa). One is to reconstruct the basic pattern, or ground plan, of the groups, the other to analyze excellently preserved fossils. The Cambrian has turned out during the last decade to be among the time intervals which delivered the most proliferous and best preserved fossils during earth history. Burgess Shale, Chengjiang, Orsten, Sirius Passet, and others became icons of the so-called "fossil lagerstätten". The fossil remains unearthed from such sites deliver the most comprehensive characters to unravel the body plans of early bilaterian animals. Whenever one should be able to identify characters that can be called "apomorphic" with some certainty the carriers of such characters would probably come from those natural archives of fine details.

Particularly meticulous analyses was performed to reconstruct the origin of the Crustacea. The main source of information were the secondarily phosphatized arthropod remains from the Orsten-type assemblages of Sweden. Numerous publications on these Upper Cambrian arthropods (e.g., Müller and Walossek, 1985, 1986, 1988, 1998; Walossek and Müller, 1990, 1992; Walossek, 1993) show an extremely large array of details, which allow, combined with data from other Cambrian *lagerstätten*, to reconstruct developmental changes of the appendages of the crustaceans and thus the evolution of the crustacean types of limbs (Walossek, 1995; Walossek and Müller, 1998). The investigations proved that the innovations of the Crustacea s.l. were the development of a mobile enditic process at the basipod. This "proximal endite" (Walossek, 1993; Walossek and Müller, 1998) is in strong sense the autapomorphy of the Pan-Crustacea.

Almost certainly this character would have remained unidentified without the wealth of almost perfectly preserved fossil material. Moreover, it would have been highly unlikely that this type of apomorphy ever could have been identified in ordinary fossil material. Nevertheless, other apomorphies for the different crustacean groups are equally difficult to identify, and none of the eye catching features seen in the carapace plays a major role in the development. We may thus assume that this is the rule for most of the invertebrate fossil groups. The dorsal carapace of trilobites in this respect usually may not bear any characters that are true apomorphies. As a consequence, apomorphies recognized, announce and applied in cladistic analyses of trilobites or other frequent groups in all probability have little in common with authentic apomorphic characters.

## HOW CAN WE IMPROVE CORRELATION WITHIN THE CAMBRIAN?

The comments and remarks presented above are unsophisticated and known by virtually every Cambrian worker. However, daily life often obscures clear assessment so that I used to opportunity to bring the facts into mind again. Biostratigraphic correlation in the Cambrian does not generally differ from correlation in other stratigraphic intervals. Careful application of nomenclature and taxonomy avoids unnecessary distortions of the fossil record and prepares the platform on which correlation takes place. Nonetheless, this is not always a simple task. Some fossil groups are in strong need of alternative taxonomic concepts. As an example, ptychopariacean trilobites as one of the decisive groups of Middle Cambrian index fossils are in urgently await a comprehensive revision. Such a monographic treatment, however, appears to be beyond the capacity of a single scientist.

Active improvement of the correlatability commences with an enhancement of the fossil record. Trilobites as the primary source of stratigraphic information in the major part of the Cambrian need to be examined as thorough as possible. More trilobite species have to be recovered from the section to support assumed correlations which are based on the occurrences of a single taxon. In addition to trilobites, more stratigraphic information on other fossil groups needs to be collected to establish additional, not to say auxiliary biostratigraphic schemes. This is particularly important for the acritarchs, which have proved to be of enormous biostratigraphic significance (Palacios and Moczydlowska, 1998; Moczydlowska, 1998), and for the sub-trilobitic portion of the Cambrian.

The increase of the number of species, or genera, of fossils grows with additional collections in a logarithmic scale. Consequently, it appears to be more rewarding to examine sections, which were not studied yet in detail, instead of reworking well-known sections, or to look at new sections which are recognized to have some potential for important biostratigraphic information. Well-known sections, however, should be examined in terms of non-conventional methods to calibrate biostratigraphic data with isotope curves, magnetostratigraphy, etc.

Significant differences also exist in the intensity of the studies. Due to historical reasons, sections in Europe, the United States and also in parts of Siberia were more intensely explored than others. In addition, different stratigraphic intervals are studied in the same areas to very different degrees. As a consequence, new and important additional stratigraphic information is to be expected from fairly neglected areas and stratigraphic intervals.

Paleontologists traditionally play a key role in the *International Subcommission on Cambrian Stratigraphy*, and the overwhelming majority of stratigraphic information for the Cambrian is coming from biostratigraphy. Biostratigraphic information will certainly remain the primary tool for international correlation. However, non-conventional methods are required to permit a fine

calibration of biostratigraphic data and to build a global framework. A sufficiently reliable portrait of Cambrian times can only be achieved if techniques such as isotope profiles (based on carbon, oxygen, strontium, sulfur, and other elements), magnetostratigraphy, and radiometric dates as well as the examination of depositional environments and the analysis of eustatic sea-level changes are employed for correlation.

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