Neognathodus and the species concept in conodont paleontology

Glen K. Merrill
Department of Natural Sciences,
University of Houston - Downtown

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ABSTRACT – Evolution has two products: speciation and phylemorphismy. True biologic species are genetically defined whereas morphotypes are produced by phylemorphicgenetic change and have the primary utility in biostratigraphy. Confusion between morphotypes and species is commonplace, does nothing to enhance biostratigraphy, indeed may impede it, at the same time confusing the taxonomy and impairing an underserved taxonomic legitimacy to the morphotypes. Resolution of the paleontologic problem of recognizing species when only morphotypes are available is difficult, but can be more closely approximated than is common practice.

Neognathodus, with its rapidly evolving rate of morphotypes is an ideal taxon to which to apply this concept for revised speciation based upon distributions of morphotypes. Although increased number enhance statistical probabilities, redefining species in this manner based on large collections permit reasonably confident identifications of species and determinations of geologic age in small to very small collections.

INTRODUCTION

"I must conclude, therefore, that the most important rule of paleontologic nomenclature is not the law of priority, as is so often stated, but the Red Queen's Rule that: 'When I use a word, it means exactly what I intend it to mean – no more and no less!'" (Shaw, 1969, p. 1094).

These words were uttered as part of Alan B. Shaw's Presidential Address to the Paleontological Society: Adam and Eve, Paleontology, and the non-objective arts. One can safely assume that much of what he had to say his audience really did not want to hear for he outlined how species concepts, however well and honestly proposed, have a serious failing in their ability to actually transmit the useful information they are intended to convey. Shaw further posited that a more useful procedure would involve some numerical or other encoding system to transmit information about morphologic changes through time produced by evolution. He ended his address with the stirring rallying cry, “Help stamp out species!” (p. 1098). Most of all, this certainly was not the message an audience of systematic paleontologists wanted to hear, despite the fact that Homo sapiens has been most effective at doing just that, especially this century.

Shaw's principle message and his main points contain much truth: species concepts frequently do not convey the useful information we wish them to. This problem is aggravated by our desire, worthwhile and indeed noble, to use organic evolution as a measuring stick against which to calibrate Earth History. Such calibration, biostratigraphy, the effort to use fossils to establish temporal relationships within and between rocks, is an important task for science. Far too often, this laudable goal has been allowed to be the driving force behind our systematics; an effort to find differences attributable to the passage of time has forced taxonomic entities upon us that are really divorced from biologic meaning. We have all been guilty of this to some degree and this so-called "nuts and bolts" approach to paleobiology has usually failed for the biostratigraphy it was intended to serve while simultaneously being devoid of biologic reality. It is an approach, to quote another line from Shaw, albeit on another topic, "so widely condemned and so faithfully practiced." (Shaw, 1964, p. 51).

THE NATURE OF SPECIES

In spite of Shaw's very severe reservations, species exist - they are the fundamental operational units in biology as well as taxonomy and their genetic definition has remained fixed, stable, and generally accepted since
the work of Ernst Mayr (1942). That a species is a potentially interbreeding population of organisms capable of producing fertile offspring is well accepted. Phrased in more modern jargon it might be stated that speciation in eukaryotic organisms reflects sufficient separation of their DNA in two populations that their members cannot transmit their combined DNA through a succession of generations. Those definitions fit with modern eukaryotes and have probably been true since eukaryotes first appeared. The reality that species exist and have existed cannot be avoided simply because of convenience in applying the concepts of paleontologists. Perhaps someone will devise a method to convey morphologic information much in the manner that Shaw envisioned, but that has not happened and quantified or unquantified morphology must be used instead - both for systematics and biostratigraphy. As far as Mayr's definition is concerned, the genetic testing by interbreeding of the vast majority of Earth's several million extant eukaryotic species has never been attempted in spite of their being recognized as "species," and extinct species are totally untestable (barring the unlikely circumstance that fossils of extinct species will yield sufficient DNA to reconstruct their entire genomes). Thus neontologic species are primarily probabilistic constructs and paleontologic ones are entirely so. The best we can ever hope to achieve is the establishment of what was probably an extinct interbreeding population. How well or how poorly we do that is based on many factors, but clearly individual taxonomic philosophies pay a key role.

Evolution has two products that are commonly confused as if they were one (Turner, 1986, p. 203). Evolution produces species, which simply involves genetic isolation. This can follow a variety of patterns; bifurcation, cladogenesis, anagenesis (phyletic evolution), etc. (Wagner & Erwin, 1995). It also produces phylomorphic genetic change through time. Phylomorphogeny can be defined as the inherited change in form through time within a genetically related lineage. These changes may closely reflect the genetic change or not and assumption that they are parallel is not justified in some cases (Stern, 1949). Although both genetic and morphological changes are products of evolution it is only the second that we can directly observe and a very large part of the uncertainty in taxonomic reconstructions stems from the uncertain correlation between the two. Indeed the best that we can hope to do is to predict that when sufficient morphologic change has taken place that speciation probably will have occurred as well. We must nevertheless keep in mind that these two products of evolution occurred at different rates in most cases. There have been times in Earth History when phylomorphic genetic change seems to have occurred especially slowly and one of these was the Pennsylvanian where, for whatever reason(s), many invertebrate organisms show little or no morphologic change essentially throughout the period. For example, Sturgeon & Hoare (1968) illustrate ranges of seven brachiopod "species" such as Composita subtilissima whose ranges can reasonably be interpreted as from 22 to 35 million years in the Pennsylvanian of Ohio and some are interpreted with still longer ranges elsewhere. Ranges of several other Pennsylvanian brachiopods are nearly as long and other groups of invertebrates record similarly long ranges. These "observations" are at odds with a series of estimates of the life spans of species summarized by Valentine (1970) as from roughly five to ten million years. These estimates are always open to question and may, in fact, be too high, but it emphasizes that we should not expect individual species to range throughout a period. We should expect that speciation really was a continuing process, at least sympatrically, but that there was little or no perceptible morphologic change. Lineages that show rapid evolutionary changes that are easily recognized, probably underwent both speciation and phylomorphic genetic changes through allopatry. Lineages exhibiting little change in morphology could still have had speciation events involving isolate gene pools, but ones retaining generalized and successful morphologies. Long-term genetic shift to satisfy the definition of speciation within sympatric populations remains a possibility, of course, because no gene pool will remain constant through time. Nevertheless, it seems likely that a fair proportion of the debate about punctuated equilibria versus gradualism is really a matter of differing emphasis upon speciation and morphologic change through time (Turner, 1986). Thus speciation may well be allopatric and the resulting speciation punctuated, but the differing pace of phylomorphogenesis and its rather tenuous link to speciation permits it to appear sympatric and gradual and for practical purposes, it is. Speciation is discrete, usually punctuated, generally allopatric, cryptic, and irreversible (Eldredge & Gould, 1972). Phylomorphogenesis is frequently continuous, generally gradual, may be or appear to be sympatric, obvious, and reversible (Boucot, 1978).

MORPHOLOGY IN TIME AND SPACE

Morphologic variation within lineages stems from a variety of sources. Some certainly represents nothing more than simple genetic variation within a population whether involving mutation or not. Within three-dimensional space we can add possible paleobiogeographic differences (probably varieties in the taxonomic sense) and ecophenotypic variations. Quite obviously, this complexity is compounded by changes in populations through time. Unlike speciation with its discrete units, phylomorphogeny commonly produces a continuous range of variables. Dividing such
A morphologic continuum is commonly an arbitrary practice, especially so as differing parts of the morphology may not be changing in anything like a regular, unidirectional manner. Some aspects of the morphology may show directional change, however, and it is these that offer the prospect of utility in biostratigraphy. At a minimum to be useful, however, some differentiation must be made of parts of the continuum. This frequently is done by designating morphotypes although application of morphotypes is generally an artificial attempt to divide the continuous variables into discrete variables. Such a compromise need not have adverse effects - no more serious than dividing the continuum that is Geologic Time into arbitrary segments that we call eras, periods, and epochs, for example - but only as long as we recognize that this is an approximation of variables that are truly continuous.

Morphotypes, produced by random genetic, geographic, ecologic, or phylomorphogenetic changes are not species, but are often confused with them, especially if they are highly idiomorphic and not clearly continuous (Futuyama, 1986).

As is generally recognized, a species may consist of several discrete or continuous, but generally definable and identifiable, morphotypes. What is less commonly recognized is that, because of differing rates of speciation and phylomorphogeny (Schopf et al., 1975), it is extremely likely that indistinguishable morphologies, i.e., morphotypes, may be shared among at least a pair of ancestor-descendant species. Where this is true, one consequence could be that an individual specimen could not be assigned with confidence to a particular species or that a species cannot be positively identified from a single individual specimen. This is in particular contrast with the cherished, but flawed, "index fossil concept" (Shaw, 1964). Consequently, finding of a particular morphotype may be of greater or lesser biostratigraphic utility, but species should be probabilistic reconstructions based upon identifications of populations of fossil organisms, or populations of morphotypes. Additionally, for mobile (pelagic?) organisms with widely distributed gene pools, most species will prove to be chronospecies and, unlike distinct or intergrading morphotypes, more than one is unlikely to occur in a given space at a given time (Ager, 1963, pp. 254-259). Given that we can never genetically test fossil organisms to see if they meet Mayr's criterion of being conspecific, species should be distinguished probabilistically by significant changes in the distribution of morphotypes. Rather than calling morphotypes "species," we should thus use changes in the ranges and abundances of morphotypes in an effort to establish where speciation events are likely to have occurred. Various statistical schemes to measure and quantify the distribution of morphotypes are possible. Some measurements of central tendencies are probably more reliable than others. Because we are dividing a set of continuous variables into classes (forcing them to become discrete variables) this becomes a nominal scale (Sachs, 1984, p.132). With such count data, the mode, especially when modified by secondary mode(s) or next most abundant morphotype(s), is probably a more reliable tool than is the mean and standard deviation (McClave et al., 1998, p.58). Through time these modes should shift from dominance by one morphotype to the next, and the distribution of the other morphotypes should reflect this shift. The product commonly approximates a classic "bell" curve. Ideally, we would like to see such curves that are highly leptokurtic as this should suggest a distribution of morphotypes that is clustered tightly about the dominant one, simplifying the recognition of species, and enhancing the likelihood of precise biostratigraphic correlation. Such increased confidence levels are not always achieved, however, because the transition between species would logically involve more morphotypes and produce curves that are more platykurtic. Biologic populations are usually "noisy," in a statistical sense and this "noise" may also increase platykurtosis. Skewness is helpful in determining from which part of the range of a chronospecies a particular population was derived and thereby reflect sometimes-subtle differences in geologic ages.

For Neognathodus large collections (approximately 11,000 specimens) were used to define "species" (now morphotypes) from rocks of the Appalachians and Illinois Basin spanning approximately 15 million years of geologic time (Merrill & King, 1971; Merrill, 1972, 1975). Several thousand specimens have been added subsequently and used to test the original criteria and as biostratigraphic tools in intra- and inter-basinal correlations. The challenge has been to both recognize species and interpret geologic age from smaller and smaller samples. As will be shown, this can be done with a high probability of success for the former and at least some reasonable level of success for the latter.

THE BASIS FOR SPECIATION AMONG CONODONTS

In spite of both predictions and fears that multielement reconstructions would drastically revise conodont taxonomy, most workers would probably now agree that the turbulence produced has been less destructive than was feared. Too often reconstruction of the apparatuses is performed as an almost mandatory exercise, followed by assignment of these apparatuses as parts of species, genera, and families originally defined on single-element criteria. This is especially unfortunate at the generic- and familial-levels where much information is contained in parts of the apparatus other than the Pa elements (Merrill, et al., 1990). At the specific level this practice is probably less harmful
because, unlike genera and families, most if not all of the differentiated morphologic characters occur in the Pa elements. Thus, traditional practice of basing taxonomy on the Pa elements is more justifiable at the specific level. Although there seems to be a reluctance to do so, "genera" containing species that have significantly different, phylomorphogenetically stable, distinctive Pb, M, and S elements are ripe candidates for division, into separate genera or subgenera at the very least. That was suggested several years ago as likely outcome given the genetic diversity probably present among elements belonging to *Palmatolepis* (Merrill et al., 1990, p. 399).

ONTGENY AND PHYLOMORPHOGENY OF *NEOGNATHODUS*

In common with the Pa elements of many genera, those of *Neognathodus* show an ontogeny in which the less mature elements are generally simplified versions of the more mature elements. Element size does seem to be a good predictor of the maturity of the animals that bore them, however, and terms such as "juvenile" and "mature" seem to be justified (Merrill & Powell, 1980). Just how simplified the juvenile Pa elements of *Neognathodus* are in comparison with the adults is not uniform. Although many are more simplified others are essentially miniatures of the adults and in general they are reasonably good predictors of how the final morphology will appear. How much imprecision a large number of juveniles will introduce into morphotype analysis remains uncertain, but it is clear that an analysis performed solely on "adult" specimens should be more reliable. This question is somewhat addressed later in this paper under Morphotypes, Species, and Biostratigraphy of *Neognathodus*. Nevertheless, in any phylogeny that features morphologic simplification through time, juveniles will bear a strong resemblance to their descendants. This situation in *Neognathodus* exactly parallels the one encountered by Carruthers (1910), summarized by Moore et al. (1952) dealing with Lower Carboniferous zaphrentid corals from Britain. Carruthers found adult corals of ever-increasing morphologic simplicity through succeeding stratigraphic levels. At any given level he found a distribution of several different morphotypes that he referred to as individual species. Moreover, at each stratigraphic level Carruthers found ontogenetic successions featuring increasing morphologic complexity during growth, a predictable enough situation. Not so predictable, however, was the realization that, phylogenetically, there was simplification in the morphology of the adults so that descendant adults resemble the juveniles of their ancestors (paedomorphosis). The situation in *Neognathodus* is exactly parallel. Ontogenetically, some simplification in morphology occurred so that juveniles are less reliable for placement into morphotypes and species or for use in biostratigraphy than are the adults. Through time the morphology of the adults simplified in a highly predictable manner being reminiscent of the juveniles among their ancestors. The earliest known species of *Neognathodus* in the Morrowan (*N. basleri*) has wide platforms with widely flaring parapets.

Text-figure 1 - (all figures X55)

*Neognathodus* sp. cf. *symmetricus* (Lane) - Maggiefl Member, Brethitt Formation, (sample from D. Chesnut, his locality 1422), N. side of Daniel Boone Parkway, KY. 23°1'73 235°05'150°50'17°9" N 83°27'19" W Leslie Co., KY. *Neognathodus* "preatokaensis" - Stoney Fork Member, Brethitt Formation, type section, strip mine W. of KY Rte. 1201, KY Coordinates South 211°250N 2.640,550E., 36°34'49" N 83°33'24" W Bell Co., KY. *Neognathodus* arkoahesis Grayson - "Boggs" Member, Pottsville Formation, near OH Rte. 93, N. of Mt. Pleasant, 17SLP74806268 39°23'53" N 82°24'24" W Hocking Co., OH. *Neognathodus* sp. cf. *columbiensis* (Stibane) - Lower Mercer Member, Pottsville Formation, bed of Blunt Run, 40°1'12" N 81°57'46" W Muskingum Co., OH. *Neognathodus* biolfo Merrill - Upper Mercer Member, Pottsville Formation, bed of Little Beaver Creek, 40°41'38" N 80°31'54" W Columbiana Co., OH. *Neognathodus* medarditius Merrill - Putnam Hill Member, Allegheny Formation, type section, Putnam Hill in Zanesville, 39°56'15" N 82°00'52" W Muskingum Co., OH. *Neognathodus* medarditius Merrill - Obryan Member, Allegheny Formation, strip mine S. of U.S. Rte. 50 E. of McArthur, 17SLP73614444 39°14'32" N 82°27'54" W Vinton Co., OH. *Neognathodus* roundyi (Gunnell) - St. David Member, Carbondale Formation, Jubilee College (Merrill, 1979, Stop 1), 16TBA509402221 40°49'12" N 89°46'52" W Peoria Co., IL. *Neognathodus* dilatus (Stauffer and Plummer) - Sparland Member, Carbondale Formation, along creek W. of Smithville, 16TBA61670443 40°38'54" N 89°56'48" W Peoria Co., IL. *Neognathodus* oligenus Merrill - Lonsdale Member, Modesto Formation, waterfall locality (Merrill, 1979, Stop 7), 16TBA50940360 40°38'54" N 89°56'48" W Peoria Co., IL. Oak Grove Grouping - Oak Grove Member, Carbondale Formation, Wolf Bridge (Merrill, 1979, Stop 3), 15TYR45592665 40°51'23" N 90°06'36" W Knox Co., IL. Obryan Grouping - Obryan Member, Allegheny Formation, along U.S. Rte. 52, 17SLN55836429 38°31'08" N 82°49'16" W Lawrence Co., OH.
generally higher than the carina (Lane, 1967). The carina usually does not extend to the posterior junction of the parapets. Later forms are narrower, more symmetrical, but still retained high and somewhat flaring parapets Neognathodus sp. cf. *symmetricus* on text-fig. 1 (Lane, 1967; Grayson, 1984). This part of the phylogeny is least well known, at least to me. The Atokan forms continue the wide flare of the parapets with some reduction in their length (compare with the form referred to informally as *Neognathodus "preatokaensis"* on text-fig. 1). It was followed by forms considered transitional to the younger Atokan forms that showed reduced flare and lowering of the outer parapet, maintaining an inner parapet much like their ancestors *N. atokaensis* (Grayson, 1984). The younger Atokan phylogeny features parapets reduced in lateral flare and more consistently, reduced in height to, or even below, the height of the carina. Additionally, the carina was shortened (or the parapets were extended!) so that the carina does not extend to the posterior junction of the parapets. This form is somewhat homeomorphic with *N. basteri* and I erroneously used that name in earlier works. It appears to be what Sibane (1967) called "*Streptognathodus colombiensis*" and is presently assigned there provisionally. Later in the Atokan the parapets fused with the carina posteriorly (*N. botrops*). It was followed later, mostly in Desmoinesian time, by shortening of the outer parapet by progressively more anterior fusion with the carina (*N. medadulitimus* and *N. medexultimus*). This shortening continued until the outer parapet was reduced to a few nodes, commonly a single node (*N. roundyi*) and was finally eliminated altogether in *N. dilatus* (Merrill, 1972). Following the loss of the outer parapet, the inner one began to disappear in an almost identical progressive fashion, first by fusing farther and farther anteriorly (*N. metadulitimus* and *N. polyadulitimus*) until it was reduced to a few nodes (*N. oligonadulitimus*) to a final few specimens encountered that had lost all vestiges of either parapet (*N. anadulitimus*) virtually at the end of Desmoinesian time (Merrill, 1975). These are the last neognathodontids known and the extinction of the genus should be a leading candidate for the paleontologic placement of the Desmoinesian-Missourian boundary. The phylomorphogenetic progression from approximately the middle of the Atokan to essentially the end of the Desmoinesian is quite clear: it was one of continuous morphologic simplification. The rate and the constancy of rate of this simplification is hard to determine, but there does seem to be an acceleration in the simplification in the later part of the range of the genus, although this may in part be an artifact of the paucity of marine units representing the necessary times to show the final simplification in as much detail as the part preceding it.

**MORPHOTYPES, SPECIES, AND BIOSTRATIGRAPHY OF *NEOGNATHODUS***

The various points of biologic theory and reality that are discussed above were generally well known to me when I studied *Neognathodus* in 1972 and 1975. To reiterate, these were:
1. Congeneric species are unlikely to co-occur;
2. Species frequently consist of populations composed of several morphotypes;
3. Morphotypes are not equivalent to species and a single morphotype may be shared among several related species;
4. Morphotypes can be used in an attempt to recognize species, but because of 3., an individual specimen may not unequivocally identify a species.

It is this last point that caused me to depart from what I considered sound biologic practice and to give Linnaean binomen to morphotypes. This was done in the belief that it was preferable to have a workable abstraction with biologic flaws than it was to erect sound biologic categories that departed dramatically from common paleontologic practice. I have had a quarter of a century to regret having made that choice.

*Neognathodus* illustrates a long geologic range with a huge amount of phylogenetic change. Therefore it is not reasonable to yield to the idea that only a single, highly variable species was involved. Rather it is a question of trying to select places that are likely points where genetic separation was sufficient that parts of the morphologic continuum should be recognized as distinct species. The number of species involved that can be redefined on the basis of the distribution of their morphotypes should not exceed the number of morphotypes and may be fewer. Thus one might redefine *Neognathodus medadulitimus* as a population whose most common morphotype (mode) agrees closely with the description of it as a species by Merrill (1972, pp. 824-825) and that also contains lesser numbers of morphotypes with such names such as *botrops* and *medexultimus*, *columbien sis* and *roundyi*, etc. Other species would be redefined in a similar fashion. Redefining species based upon central tendencies of their morphologic ranges rather than single, fixed, morphologies is not entirely a new concept (Wagner & Erwin, 1995) and has little negative impact other than to make a few specific assignments uncertain. Some units have yielded so few specimens belonging to the genus that specific determination must remain questionable. This is especially true near the termination of the range of the genus. However, this may not preclude making a reasonable biostratigraphic interpretation from such faunas. Such redefinition of species should lead to no reduction in the biostratigraphic utility of *Neognathodus*. The distributions of
morphotypes have been, and will continue to be, the criteria used for age determination. The precision possible by this method is extremely high. Brown et al., (1998) in their analysis of some Desmoinesian marine units used a numeric analysis of the means of morphotype distribution to demonstrate differences in age among units previously considered coeval. Rexroad et al. (1998) made use of these ratios in correlation and more recently did a numerical analysis in the same manner as Brown et al. (1998). Application of modes seems a more robust procedure, but we are still attempting to determine the best way to apply these chronologically very sensitive tools.

The following examples may help to illustrate both concepts of speciation based upon the distribution of morphotypes and the biostratigraphic application of those morphotypes. To do this, two samples were chosen not quite at random. The first is from the Obryan, formerly “southern” Vanport Limestone (Allegheny Formation) in southern Ohio at a well-known locality (Ferm et al., 1971; Rice et al., 1992). The second is the transitional shale at the top of the black shale at Wolf Bridge, Oak Grove Beds (Carbondale Formation), northwestern Illinois. This is also a well-known conodont locality (Merrill & King, 1971; Merrill, 1975, 1979; von Bitter & Merrill, 1998). Each was chosen not only because they are well-known, but also because each sample yielded a convenient number of neognathodontid Pa elements (coincidentally 13 in each case), permitting a small, but relevant number of specimens to be analyzed. Thus these entire populations could be fit on a single figure (Text-fig. 1). The units chosen were not entirely arbitrary either, because through a tortured chain of reasoning, they are supposed to be “correlatives” (Moore et al., 1944; Rice, et al., 1994). Even a cursory glance at the two groups of illustrations on Text-fig. 1 indicates that they are drawn from different populations. The Obryan population contains more juveniles and a wider range in morphologic variation, likely resulting in large part from that juvenility. The Oak Grove population has fewer juveniles and that may be largely responsible for a curve that is extremely leptokurtic; seven specimens would be assigned to roundyi and six to medexultimus. Indeed, such a distribution, although excellent for biostratigraphic determinations, makes specific assignment somewhat uncertain. A larger population is necessary to determine the dominant morphotype (Merrill, 1972, et seq.) and these larger populations show that the dominance makes a specific assignment to N. roundyi the correct one. For the Obryan sample the curve is far more platykurtic and exhibits an apparent skewness that is an artifact of its juvenility. Thus a calculation based on the pure form of morphotypes would show three specimens that would be assigned to medadulitimus, three specimens that would be assigned to medexultimus, two specimens that would be assigned to roundyi, and five specimens that would be assigned to dilatus. This is the apparent skewness toward the younger end of the phylogeny. That this is an artifact is borne out by the fact that it is the five smallest specimens that have the dilatus morphology, one of these having a platform that is well under 0.1 mm in length. In a similar context the next two smallest specimens from this sample are the ones with the roundyi morphology and the largest half dozen exhibit medadulitimus and medexultimus morphologies. Indeed, if the six largest specimens are arrayed from largest to smallest they would correspond to these morphotypes: medexultimus - medadulitimus - medadulitimus - medadulitimus - medadulitimus - medadulitimus. Analysis of many more specimens from many more samples and localities in the Obryan shows that the single most common morphotype (mode) for these samples is in fact the medadulitimus one with a strong secondary mode of the medadulitimus morphotype (Merrill, 1972). Thus a specific assignment of all of these forms to the species Neognathodus medexultimus is justified.

Applying a similar analysis to the Oak Grove specimens shows that the half dozen largest specimens from largest downward in size belong to the roundyi - roundyi - medexultimus - medexultimus - roundyi - medexultimus morphotypes. As stated above, this sample has lower juvenility than the one from the Obryan and continuing with successively smaller specimens would have no effect on the basic distribution pattern begun with the six largest specimens. This once again emphasizes that arraying the morphotypes so that more mature specimens are emphasized is an effective way to analyze phylo-morphogenetic development and genuine distribution of morphotypes. By diminishing or eliminating the apparent “younging” effect that juvenility would force upon the population, such analysis emphasizes both the importance of adults in the analysis and the importance of central tendency statistics based upon the mode(s).

Clearly, removal of the “younging” effect of juvenility in the Obryan population shows that the phylomorphogenetic development of the Obryan neognathodontids is more primitive and the Obryan is distinctly older in both a phylogenetic and a chronological sense than the Oak Grove population.

CONCLUSIONS

Neognathodus remains the preeminent conodont, possibly the preeminent fossil, for biostratigraphy in Lower - Middle Pennsylvanian rocks. Analysis of the distribution of morphotypes can lead to very precise age determinations. It is also the distribution of these morphotypes, rather than the single morphotypes
themselves, that should be used in the identification and redefinition of species. Such redefinition will not adversely effect the genus for biostratigraphy, but will more closely conform to biologic reality. 

The situation in Neognathodus where species consist of several morphotypes and individual morphotypes are shared by more than one species is unlikely to be unique. Indeed, this is probably the norm with most populations of fossil organisms. It certainly should impact those interpretations where a large number of congeneric species are presently recognized within single samples.

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Glen K. MERRILL
Department of Natural Sciences,
University of Houston - Downtown
1 Main Street, Houston, TX 77002 USA
e-mail: merrillg@zeus.dt.uh.edu