

PRELIMINARY MORPHOMETRIC ANALYSIS
OF *STREPTOGNATHODUS* (CONODONT)
FROM THE UPPER PENNSYLVANIAN
AND LOWER PERMIAN OF
SOUTHERN KANSAS

By

TIMOTHY ROBERT WALSH

Bachelor of Science

Phillips University

Enid, Oklahoma

1978


Submitted to the Faculty of the
Graduate College of the
Oklahoma State University
in partial fulfillment of
the requirements for
the Degree of
MASTER OF SCIENCE
May, 1998

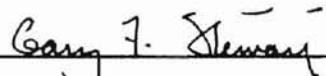
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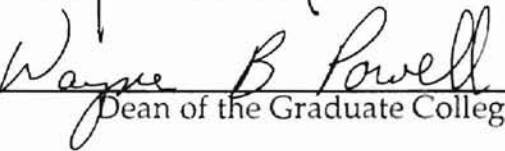
Thesis Approved:



Thesis Advisor







Dean of the Graduate College

ACKNOWLEDGEMENTS

I wish to express my sincere appreciation to my thesis advisor Dr. Darwin Boardman for his guidance, inspiration, patience and friendship. My appreciation extends to my other committee members, Dr. Gary Stewart and Dr. Zuhair Al-Shaieb, whose assistance was also most welcome.

I would also like to thank my friends, especially Mark Bryan, for all their support throughout this process. Their suggestions, encouragement and friendship were invaluable to me.

I should also express my gratitude for the use of computer facilities and office space at Henry H. Gungoll Operating, Inc. of Enid, Oklahoma. This project would not have been possible to complete without their resources.

Finally, and most importantly, I would like to thank my parents and family for their continued support.

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INTRODUCTION

Conodont remains are extremely common fossils. With an evolutionary history dating from the Late Cambrian through Triassic these unique animals ranged in the seas throughout most of the world, leaving an extremely valuable record for paleontologists. Important primarily as temperature indicators in the past, they have realized increasing prominence in biostratigraphic studies and now are regarded as potentially some of the earliest chordates.

Conodonts originally were thought to be a new group of extremely small extinct vertebrate fish (Pander, 1856), based on the few hard parts, or elements, normally recovered. These parts, which are commonly called conodonts themselves, resembled the teeth and jaws of fishes, and some terminology from this early conception remains in use today. For well over one hundred years this fish-related taxonomy was the predominantly held view, although numerous other theories such as annelid-worm jaws, radular teeth of mollusks, and even the remains of plants were put forward. Although great strides in understanding these creatures have been made in recent years a great many questions remain for the conodont researcher, especially in regard to taxonomic classification and true affinities.

This paper deals with certain taxonomic problems through quantitative morphometric analysis of some species of the Pennsylvanian and Lower Permian genus *Streptognathodus*. This is an especially vexing problem with regard to the increasing reliance on conodonts in biostratigraphic studies.

BIOLOGY

Soft Body Anatomy

The first "complete" specimen, that is, a specimen indicating soft body form and structures, was discovered in 1982 (Briggs *et al.* 1983) in the Carboniferous Granton Shrimp Bed of Scotland (Figure 1). The wormlike body was very elongate (approx. 40 mm by 1.8 mm), flattened and possibly segmented, and contained limited internal structures (lines). These lines were interpreted as traces of a nerve chord, a digestive tract, a major blood vessel, etc. (Aldridge *et al.* 1986), with Sweet (1988) giving more credence to a gut, but with some reservations. V-shapes along the trunk may have indicated musculature, but again Sweet reminded us that this interpretation was equivocal when other structures, such as gut diverticula, might yield similarly shaped impressions. Traces of what may be a posterior ray-supported fin are evident, along with an enlarged end with flat disks interpreted as eyes. This 'cephalic' area is where the element groupings, or assemblages, were recovered.

Currently only 12 specimens are known to exhibit soft body anatomy; most are from the same area in Scotland (Aldridge *et al.* 1986) but one poorly preserved specimen is from the Silurian Brandon Bridge Dolomite of Wisconsin U.S.A. (Smith *et al.* 1987) and a few large individuals, one with excellent preservation, from the Ordovician Soom Shale of South Africa (Gabbot *et al.* 1995). The new specimens, along with further study of the first discovered, indicate that the original interpretation of the paired axial lines as

notochords is most likely true (Briggs and Kear, 1994 and Aldridge and Purnell, 1996). The fine preservation of the anterior of a giant Soom Shale individual exhibits extrinsic eye musculature, although the eye is much smaller proportionally than in the Scottish specimens (Purnell 1995a). Also the V-shapes, or chevrons, preserved along the body represent muscle blocks. Scanning electron micrographs of the tissue from the Soom Shale specimen reveal individual muscle fibers that have been preserved as well. Figure 2 illustrates a current reconstruction of the conodont animal.

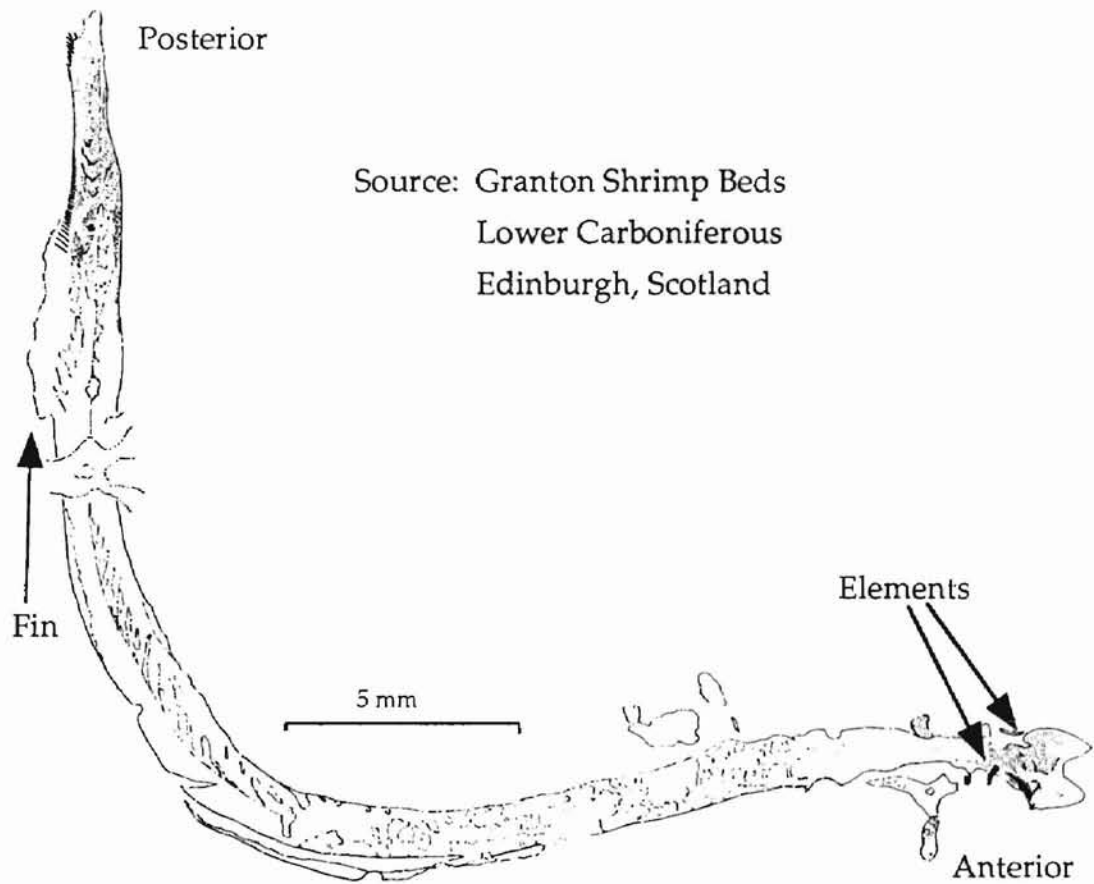


Figure 1

Original soft body 'Scottish' specimen.
From Briggs *et al.* 1983.



Figure 2

Reconstruction of Carboniferous conodont. From Purnell, 1995.

Skeletal Anatomy

While the recent discoveries of soft-body conodont remains have been ground-breaking, the vast majority of conodont workers deal with the hard parts, or skeletal elements of the animal. The elements' composition has lent themselves to ready extraction from surrounding carbonate/shale matrices by dilute acids, resulting in large numbers of dissociated elements being available for study. Individual elements recovered normally range in length from .02 mm to 3 mm.

As first described by Pander in 1856, these microscopic fossils resembled the teeth and jaws of fish. Pander and others asserted that individual conodont animals formed hard parts that were all of the same shape. In the 1930's several workers, Scott (1934) among them, reported of clusters of morphologically different conodont elements on the surfaces of shale slabs. These groupings were regarded as natural assemblages, or the relatively complete element apparatus of individual animals. Although Hinde (1879) was the first to recognize natural assemblages, his findings were disputed at the time, it is now asserted that his clusters were in fact from different individuals. Further discoveries of intact natural assemblages indicate that each component in a conodont element grouping has a very specific spatial relationship to other elements. Many of the multi-element assemblages have been now been given various Type classifications, as in the work of Rhodes (1952) and numerous others. Most of these up-to-septimembrate assemblages exhibit some form of bilateral symmetry. Lane (1968) recognized four classes

of element-pair symmetry (and asymmetry).

Individual elements themselves have been categorized by general shape with groupings such as pectiniform, ramiform, etc. with additional subdivisions (Figure 3). The elements have been further labeled with various terms during the long history of conodont research, causing some confusion for researchers, but this nomenclature has become more standardized (Figure 4).

Purnell's recent work (1995b) of the microwear analysis on elements has lent great credence to the concept of element function as actual teeth— even to the point of precise characterization of food-processing purpose: platform elements (P) used for mashing and ramiform (S and M) for grasping and shearing. The spatial configuration of elements has also been further refined (Figure 5). Bilateral occlusion of pairs, as described by Purnell, occurred in Pa elements with the left member fitted behind the right and hinging at a point close to the junction between the platform and the blade, resulting in crushing but not grinding of food.

Conodont elements are composed primarily of calcium phosphate and as such are part of the apatite group. This significance is twofold. First, the skeletal elements are comparatively heavy and are less soluble in dilute acids than their surrounding carbonate matrix, thus they may be separated much easier than many other fossils. Second, carbon inclusions in the apatite render conodont elements susceptible to changes of color through a fixed range of temperatures. A Color Alteration Index was developed (Epstein 1977) and has

been invaluable to the petroleum industry as post-depositional temperature indicator.

Cell imprints on the surfaces of some elements can further indicate growth pattern and function (von Bitter and Norby, 1994). Histological evidence gathered by SEM of thin-sectioned and etched specimens of pre-Carboniferous elements indicate a two-part construction: a crown and a basal body. The basal body is quite variable, whereas the crown is comprised of two tissues. The first, an apatitic lamellar tissue is possibly homologous with tooth enamel and the second, white matter described as potentially cellular bone (Sansom *et al.*, 1992). Some researchers believe these similarities to vertebrate teeth to be superficial. Aldridge *et al.* (1996) refer to recent histochemical studies of these parts of the elements:

“Partially demineralized conodont element surfaces were found to stain with picosirius red, and this was taken to indicate the presence of collagen, a result at odds with the interpretation of this tissue as enamel. Conversely, white matter did not stain, but if this tissue is bone or dentine, collagen should have been present during life .”

These conflicting results may be due to the age of the materials tested and the resultant breakdown of proteins, so the phrase “during life” takes on added importance. Further research and tests obviously are needed in this area.

Zoological Affinities

Pander's original interpretation of conodonts as fish (and thus the name *Conodontan*), and other affinities, such as the remains of annelids first described by Owen in 1860 and expounded on by many others have for the most part been refuted. One of the major problems in relating these animals to several other phyla is the primary chemical constituent of conodont elements. That is, as Rhodes (1952) and others later pointed out, annelids and mollusks are unable to secrete calcium phosphate. However, even as late as 1986 Tillier and Cuif reported that some aplousophoran teeth and mandibles include calcium phosphate and have body structure similar to the Scottish specimens in their efforts to suggest possible relationships.

The soft-body discoveries of the last 15 years perhaps have done more to portray the true taxonomic relationship of conodonts than any other research. For years many workers in this field, from Clark *et al.* (1981) to Briggs *et al.* (1983) to Sweet (1988), espoused a separate phylum for conodonts.

“Until more specimens with preserved soft-parts are discovered we prefer to assign the conodont animal to a separate phylum Conodonta.” (Briggs, 1983)

This separate phyla concept was convincingly challenged first by Aldridge (1986) in his further descriptions of the new Scottish specimens, which, of course, exhibited preserved soft-body parts. The prevalent theory of conodont as chordate and not separate phyla is bolstered by several lines of reasoning:

1. Element morphology: This is a poor indicator as evinced by the variety of other possible affinities raised historically.

2. Element composition: A more important indicator but far from conclusive, of itself.
3. Presence of possible notochord: A vital point but only indirect evidence is available.
4. Caudal fins.
5. Large eyes with extrinsic musculature.
6. Muscles: Well developed musculature with indications of motile capacity.
7. Recognition of elements as true oral-feeding apparatus with microwear indicating a macrophagous nature. The surface area of proposed filtering arrays (or the lophophore-like structure of Lindström, 1974) over S and M elements as related to estimated metabolic rates is insufficient for microphagous or suspension feeding (Purnell 1993, 1994).

The last three factors strongly indicate a predatory nature of conodonts and may represent a possible shift of the early vertebrates from suspension feeding to predation.

Although the taxonomic relationship of conodonts to other phyla may still be in question, the majority of workers place them with chordates. Even long-time opponents to chordate affinity such as Phillip Janvier believe current evidence of chordate relationships to be too strong to realistically refute, although several major questions remain, such as lack of preserved gill structures (Janvier, 1995). Numerous interpretations of the above data are used to attribute the conodonts to various locations within the chordate clad. Exactly where to position the animals in this lineage remains in flux and is likely to remain the subject of debate for quite some time.

Paleoecology

With such limited (though rapidly increasing) information available on the true nature of conodonts it is not surprising that major debate and controversy exist concerning mode of life and habitat of these creatures. However, some reliable concepts may be squeezed out of our finite resources.

Conodonts undoubtedly were primarily marine organisms, as evidenced by the rocks they are normally recovered from and animal remains found with them. The animal possibly was pelagic, and if so, was most likely nectonic rather than planktonic, vis-à-vis the fin, body musculature and other factors, but even this may not necessarily be true for all forms and is still in debate. Nor may we ascertain exactly how adept or mobile they may have been, although studies of muscle fibers of the Soom Shale specimen indicate an "efficient cruiser incapable of great bursts of speed." (Gabbot 1985). Current studies of the feeding apparatus as described above indicate a predatory nature of some genera. They were also apparently prolific organisms and often cosmopolitan in nature, inhabiting wide areas.

Several paleoecologic models have been developed to account for the distribution of living conodonts. Barnes and Fåhraeus (1975) described a possible nectobenthic mode to account for discontinuities in lateral distribution of conodont remains. Lane (1964) developed a salinity gradient based on correlation between a variety of marine organisms, including a limited number of conodonts.

A more popular concept of a pelagic organism, which was based on

water depth to account for patterns of distribution of Missourian conodonts in Kansas, was that originally posed by Seddon and Sweet (1971). Their model described possible depth zonations for a variety of species, as derived from correlation with the inferred environment of deposition of the rocks the fossils were obtained from. Of course this correlation became more difficult to interpret as water depth increased and as the number of potential depth zones increased proportionately, resulting in mixing of fauna through settling to the point of deposition (sea floor). A further reference to this problem is described as the:

“...potential ambiguity in the term *shallow water deposit*. A shallow-water *deposit* would be understood by most geologists to refer to sediments laid down in water no more than about 200 m deep and probably a good deal less.... a shallow water *fauna*, restricted to the upper photic zone, might be found in the middle of an ocean basin where the actual water depth might be well over 1,000 m.” (Seddon and Sweet, 1971).

Fortunately these problems were overcome and they were able to develop a depth zonation chart comparing species vs. depth during life. Seddon and Sweet strangely cautioned against the use of other marine invertebrates associated with conodonts at other localities for the formulation of ecologic models, calling this practice “unwise” even though a limited number of such comparisons were made in their own work. While their study primarily focused on depth and O₂ levels, during comparisons of conodonts to Chaetognaths and modern planktonic organisms the statement was made that vertical stratification (depth):

“...may be correlated with temperature, light intensity,

nutrient supply and similar factors."

but no attempt to do so was made.

Heckel and Baeseman (1975) provided greater refinement to this depth-zonation model in regards to Pennsylvanian megacyclothems, especially in relation to anoxic bottom conditions in part caused by postulated thermoclines, but made only passing mention of other factors such as density of living organisms and salinity. Klapper and Barrick (1978), in reviewing the various ecologic models at that time, concluded that it was not possible to ascribe a strictly pelagic or benthic mode purely on the basis of conodont distribution patterns. They did however concur with numerous others that conodonts recovered from the black shales interpreted as anoxic bottom environments must be pelagic in nature. The depth-zonation model was revisited and further updated by Boardman and Nestel (1993) to consist of five distinct conodont biofacies along with several other fossil groupings (Figure 7).

It should be noted that a recent work questions the assumed absolute faunal nature of oxygen-deficient zones, i.e., a decrease in oxygen level equates to general decrease in faunal abundance and diversity. Etter (1995) found an increase in diversity in oxygen-deprived bottom layers over that of the region above with higher oxygen levels. The exact nature of the faunal relationship to oxygen gradient for some extinct organisms may require further study and refinement.

Most modern (living) ecologic models rely on a great variety of factors.

Although the models postulated for conodonts may be extremely useful, great care should be taken before fully embracing one particular concept. As

Merrill and Martin (1976) wryly observed,

“ We especially caution against the ready adoption of simplistic models that rely upon single environmental factors. They become extremely precarious....”

Merrill and von Bitter (1984) later attempted to correlate three factors, salinity, ‘energy’ and pH to conodont biofacies groups. Again in 1989 Merrill compared ecological *setting* to ecological *factors* as he championed water chemistry, particularly salinity, as a primary factor controlling conodont distribution, but gave no general template for this concept at that time. The work of Driese *et al.* (1984) in this area concluded in part that conodont distribution was controlled more by temperature and salinity changes and that certain species separated by depth zonations of other workers were actually from the same depth.

An interesting slight variation then on this topic is that of Swade's (1985) interpretation of Heckel and Baeseman's earlier model. His paleoecological model (Figure 6) of the Desmoinesian midcontinent sea at first appears to be another type of purely depth-zonation division. It is in reality dependent on the temperature and oxygen concentration levels of varying water masses, based on revision of the possible circulation patterns and resultant thermoclines as originally addressed by Heckel in 1977.

A number of other methods have been used to help determine the paleoecology of these animals. Wardlaw and Collinson (1984) used

relationships with deposition of phosphate in onshore and offshore facies and correlation with brachiopods. Geochemical analysis of oxygen isotope levels in the apatite of conodont elements has been used as an indicator of water paleotemperatures, with the corollary of determining conodont distribution as to 'exact' temperature controls (Geitgey and Carr, 1987). A correlation this data to depth zonations would be invaluable.

In the end it is very likely, as Sweet (1988) states,

“Although depth itself may not have exerted a primary influence on conodont distribution, factors such as temperature, light penetration, light intensity, turbidity, energy, salinity, and water density fluctuate directly or inversely with depth, and one or a combination of these may have exerted the direct control on distribution.”

While the depth zonation model is commonly used, especially for biostratigraphic purposes, it may not provide sufficient insight into the true ecologic factors controlling conodont distribution and mode of life. Additional research and analysis is called for before a more detailed paleoecological model for conodonts may be presented.

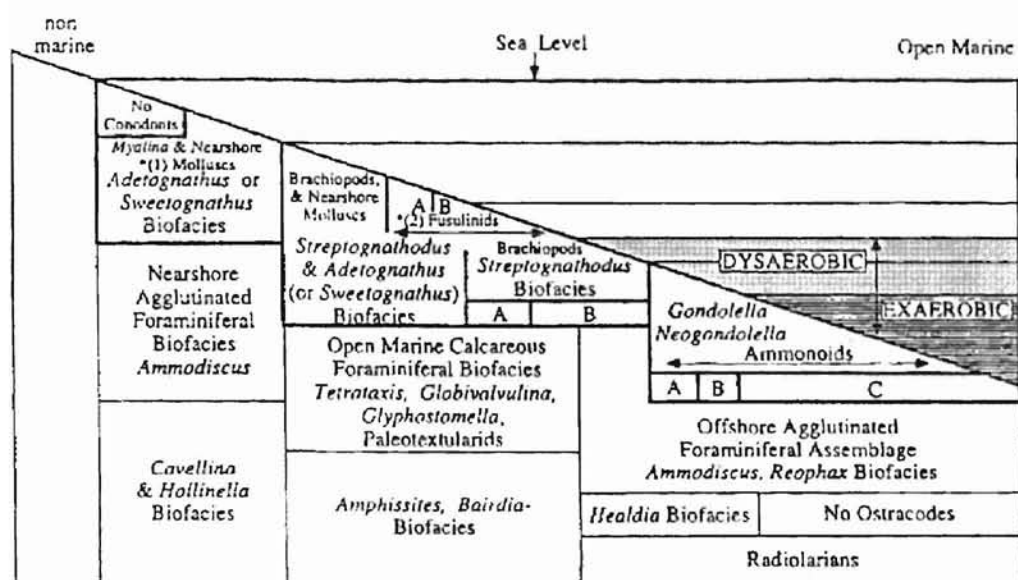


Figure 6
Paleoecologic model.
From Boardman and Nestell, 1993.

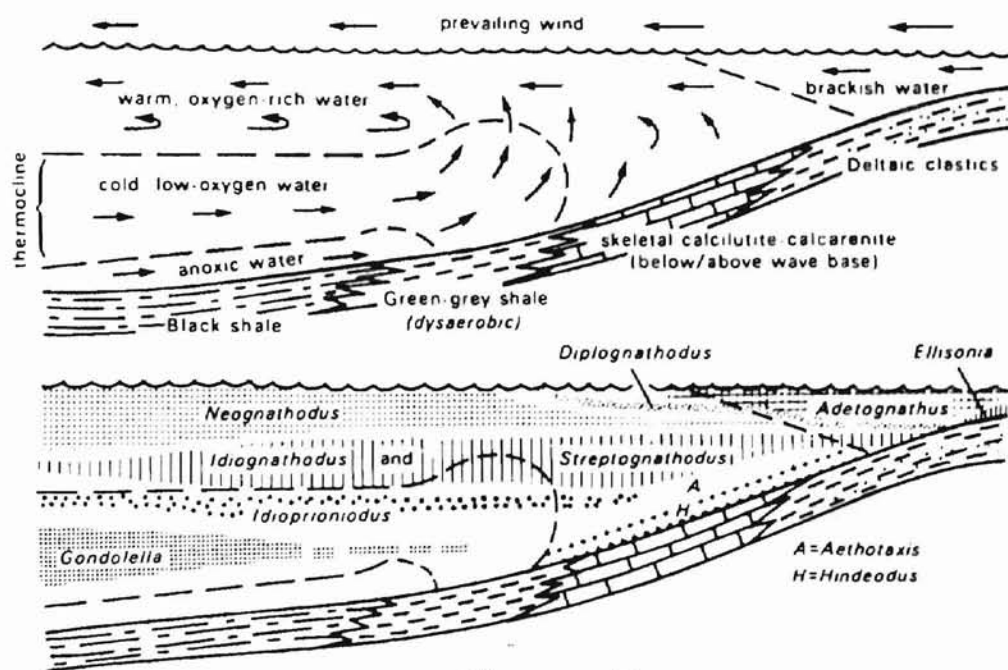


Figure 7
Paleoecologic model.
by Swade, 1985 modified by Sweet, 1988.

IMPORTANCE TO BIOSTRATIGRAPHY

Most studies of Paleozoic and Triassic biostratigraphy now include reference to conodonts. Their long stratigraphic range, along with other factors such as worldwide distribution make them valuable stratigraphic tools. These often ubiquitous fossils have been used by a large number of workers to help delineate strata. Over (1997), in his work on conodont biostratigraphy in western New York State, stated

“The recent use of high resolution conodont stratigraphy and graphical correlation has allowed recognition of global event horizons...”.

One of the more important usage of conodonts was to aid Heckel (1977) in his work on defining the origins of mid-continent Pennsylvanian black shales. The ‘black shale member’ of Heckel and Baeseman(1975) was described to represent deep-water fauna in their paleoecologic model. Although dominated by *Idiognathodus-Streptognathodus*, maximum conodont diversity and abundance occurred:

“...near the lower middle of the limestone formation, specifically in the black shale member and commonly in the adjacent parts of the two limestone members as well.”(Heckel and Baeseman, 1975).

This section was designated as the core of cyclic deposition of specific lithofacies, or cyclothem. The ‘Kansas Cyclothem’ as further refined by Heckel (1983) follows this definite succession.

1. Thick, sandy nearshore to nonmarine *outside* shale.
2. Thin, transgressive *middle* limestone.
3. Thin, offshore *core* shale, commonly black, fissile and

phosphatic.

4. Thicker regressive *upper* limestone.
5. Thick, sandy nearshore to nonmarine *outside* shale.

Conodonts found (or absence thereof) in these sections can be directly correlated to zones of the more recent Boardman and Nestell paleoecologic model. It follows from numerous studies that the *outside* shales, with their low conodont abundance/diversity, represent major sea regression, as opposed to the large abundance/diversity in the maximum flooding zone deposits, or deep water, *core* shale (Figure 8). Other cyclothems have been recognized and described in the mid-continent and elsewhere in the world and may generally follow conodont depth distribution patterns.

Conodonts have then, as a matter of course, played increasingly important roles in sequence stratigraphy. LaMaskin and Elrick (1997) relied solely on conodont zonations for biostratigraphic correlation in their interpretation of sequences recorded in Nevada. Henderson *et al.* (1995), in their work in biostratigraphy and sequence stratigraphy of the Canadian Arctic, made extensive use of conodont and foraminiferan data for correlative purposes. They stated, for example:

“The abundance and diversity of *Streptognathodus* decreases throughout the interval correlated with the Kasimovian and is generally absent in the upper part, where only rare *Adetognathus* specimens are found, confirming the shallow shelf or ramp setting...” (Henderson *et al.* 1995)

(Assuming a depth-zonation model with *Adetognathus* to be a shallow-water inhabitant and *Streptognathodus* to be deeper.)

This common usage does not preclude problems in efforts in conodont biostratigraphy however. There remain a great many areas where conodont successions are not yet well documented. The cosmopolitan distribution of the animal is not fully analyzed, affecting global correlation attempts. Additionally, inconsistent taxonomy for many species further hinders correlative efforts. This last point is especially important with regard to this paper.

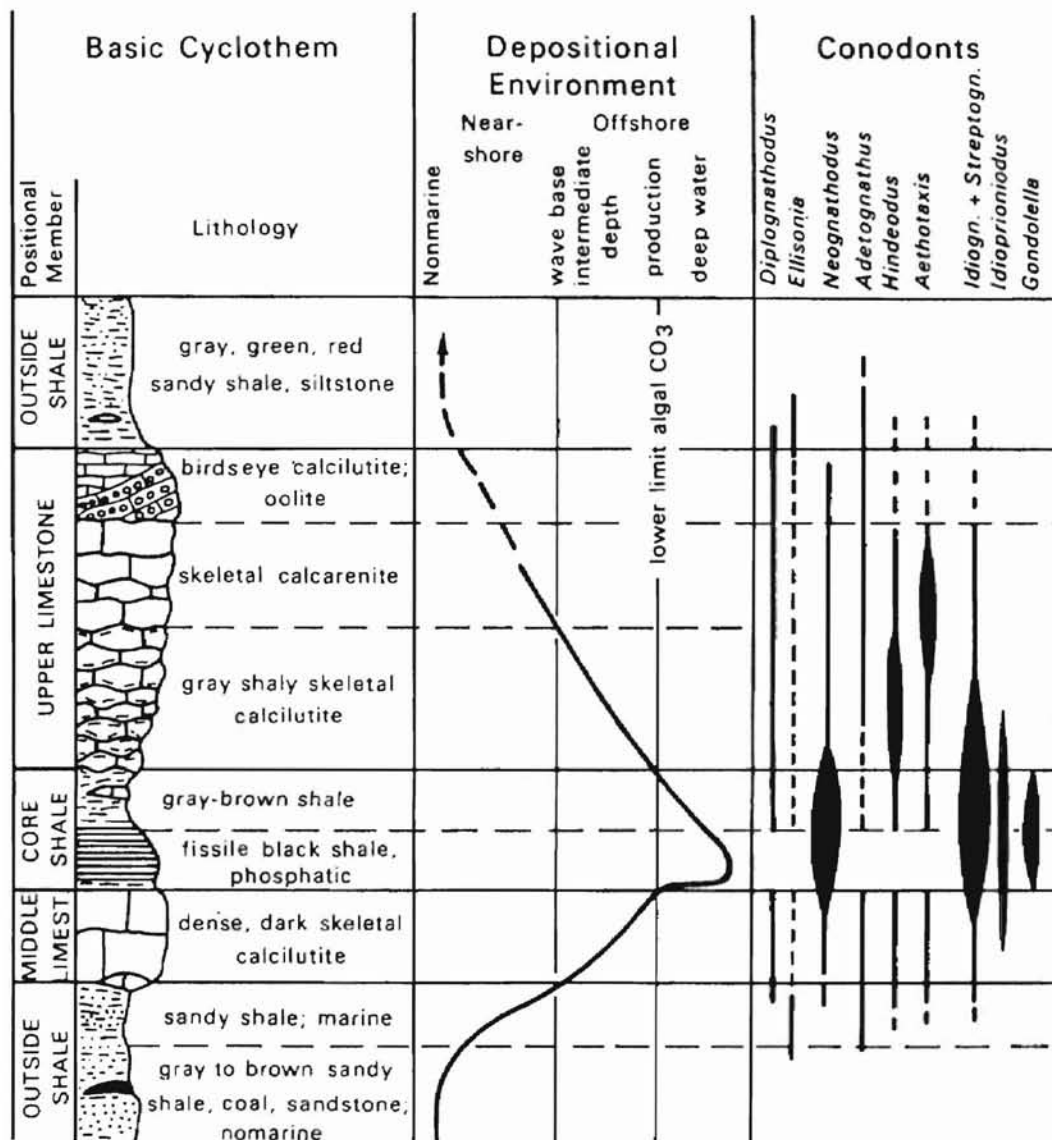


Figure 8

Kansas type cyclothem with inferred environment of deposition and conodont distribution. From Sweet, 1988 as modified and redrawn from Heckell, 1977.

SYSTEMATICS

Current Methodology

Due to the paucity of actual full-bodied specimens, conodont taxonomy has been based entirely on microscopic analysis of skeletal elements. Classification originally was based on the *form* of disassociated elements, which eventually were found to be easily recovered from dilute acid-insoluble residues. In 1934 a new age in conodont taxonomy began with the simultaneous discoveries of Schmidt and Scott of skeletal elements *in situ* on bedding surfaces of Carboniferous black shales. Although this *natural* multi-element type taxonomy was not popular for some time, it is now thought better to indicate a natural biologic classification scheme.

Ideally, complete, intact conodont element apparatus (natural assemblages) or at least 'fused clusters' would be used for all identification. This is seldom possible though, due to the difficulty in recovering these fossil assemblages in such pristine condition(in the early 1990's there were few more than 500 known to exist). Since the mid 1960's the statistical analysis of recurring groupings of discrete elements into 'apparatus types', as equated to natural assemblages, has enjoyed increasing popularity. Horowitz and Rexroad (1981) compared several numerical methods of grouping elements during their analysis while further defining several natural multi-element taxa (as opposed to 'older' form taxa). This type of statistical reconstruction may be based on:

1. Constant numerical ratios of constituent elements in

- collections numbered in hundred thousands.
2. Similarity of stratigraphic ranges of the elements.
 3. Similarity or identity of size, denticulation, character of basal cavity, distribution of white matter, and other morphologic features of the elements.

(Klapper and Philip, 1971)

With little doubt multi-element natural assemblage classification is better zoologically. For many years however, a dual taxonomy, one of form, the other of multi-element relationships in nature, was used for conodonts. This was true for several reasons:

- 1) In many cases, due to the source rock and recovery methods used, statistical multi-element analysis is not possible. Shales in particular may produce large amounts of conodont platform elements as the more delicate shapes may be broken and less abundant (Baeseman, 1973).

2. Formations intrinsically may be excessively dominated by platform elements. In some situations this problem is extremely acute.

“In collection after collection from various levels in the Pennsylvanian and from different places in the world, the platformed Pa elements of *Streptognathodus* dominate the elements that represent other positions in the skeletal apparatus.” (Sweet, 1988).

Sweet speculates that this biased distribution of element types may be due to possible ontogenetic variation. Others believe variation may be caused in some cases by post-mortem sorting (Klapper and Philip, 1971). Current-sorting, breakage, and environmental tolerance may have affected the presence and abundance of conodonts (Horowitz and Rexroad, 1981). McGolf

(1991) analyzed the hydrodynamics of conodont elements, while Broadhead et al. (1990) wrote of the potential distribution-variation resulting during gravitational settling of conodont elements.

3) Perhaps most importantly, is the usefulness of form taxonomy for stratigraphy, which was originally argued by both Rhodes and Müller:

“... that natural species (as represented by conodont assemblages) are represented by a combination of various ‘form species’ which are not duplicated in other natural species. For this reason, and in view of the stratigraphical value of the present {form} classification and the rarity of natural assemblages... ...present system of classification {form} should be retained.” (Rhodes, 1952).

“However, in stratigraphic paleontology the use of a name for the entire assemblage is not practicable with conodonts or other fossils which are isolated parts of skeletons. In biochronology and stratigraphy the description of single elements is unavoidable as only these are available for this type of work. ” (Müller, 1956).

4) Even with current natural multi-element taxonomic studies the correct determination of element components (old form species concept) is vital in determining the associations of apparatus type groupings.

It should be noted that now most form species have been recast as multi-element assemblages. Normally one particular element out of the entire array is used as the primary diagnostic criterion as opposed to the group of elements used in natural species descriptions (for reasons listed above). For many diagnoses the other elements are considered uncommon or too similar to other groups to be used regularly in identification.

New discoveries continue to reduce the need for any type of dual

taxonomy. As more natural assemblages are found or statistically reconstructed paleontologists will gain a better understanding of the taxonomic relationships of these animals. In any case, workers in conodont biostratigraphy still commonly must resort to purely form-diagnosis, especially when the organism's identity is used for correlation and biostratigraphy.

Problem in Systematics (form diagnosis)

Because it is imperative that conodont taxonomy be as accurate as possible, not only as a field of study unto itself but as an important biostratigraphic tool, the correct classification of individuals is vital. Unfortunately problems may arise with many conodont form diagnoses or, specifically, the description of the one part of the beast (commonly the Pa, platform element) normally used for classification and how it is described.

“The study of form may be descriptive merely, or it may become analytical. We begin by describing the shape of an object in the simple words of common speech: we end by defining it in the precise language of mathematics; and the one method tends to follow the other in strict scientific order and historical continuity.” (D’Arcy W. Thompson, 1942)

Unlike many other fossil groups that have followed Thompson’s descriptive to definitive path in classification, conodont form descriptions used for classification generally lag far behind in ‘precision and scientific order’. This is particularly true with the Pennsylvanian and Lower Permian genus *Streptognathodus*...

Streptognathodus isolatus

“Description.— Pa element long to moderately long, widest on anterior part of posterior platform, but nearly as wide [across accessory denticle field near posterior termination of carina in many specimens.]Post carinal platform flat and wedge-shaped with pointed to rounded posterior. ...” (Cherynkh *et al.*, 1997)

In the *S. isolatus* description excerpt above phrases such as ‘long to moderately long’ and ‘pointed to rounded’ are the words of common speech D’Arcy Thompson refers to. With nearly 100 separate species of

Streptognathodus being described in a like manner, from *S. acuminatus* (Gunnel 1933) to *S. zethus* (Chernykh and Reshetkova, 1987) a glaring need for a more precise quantification of conodont *Streptognathodus* descriptions has become all too apparent.

“Study of these forms {*Idiognathodus-Streptognathodus*} has been accompanied by a staggering level of confusion to which we have been as prone as anyone else — meaningful distinctions are genuinely difficult to make... ..problems have prevented the development of a rational biostratigraphy and are now hindering their use in paleoecology as well.” (Merrill and Martin, 1976)

Although a complete quantitative taxonomy based on multielement biometric analysis might be desirable, this may not realistically be possible at this time (or particularly useful for some fields). The vast majority of conodont *Streptognathodus* classification is still normally limited to the platform Pa element form descriptions.

Since these elements are most commonly used for classification, Pa element asymmetry becomes increasingly problematic. Several identified species, especially in older diagnosis, appear to have sinistral and dextral Pa elements that vary in shape and character, that is, exhibit Class III symmetry as described by Lane (1968). Unfortunately they have been classified solely by either the sinistral or dextral description. This problem with element asymmetry for this genus has been previously commented on by various other workers.

Further, problems with the usage of nonstandard terminology to

describe element morphology and the resultant inconsistent selection of homologous reference points and characters for description and comparison have caused even more confusion for *Streptognathodus* identification. For example, some older studies often use element position nomenclature after Jeppsson (1971) and others, which differs from that currently in place (Figure 3). An extensive list of descriptive terminology was listed in the major work of Clark *et al.* (1981) and more current workers have also attempted to alleviate this chaos by publishing additional clarifications. Figure 9, after Boardman *et al.* (1998), is included again here for that purpose.

All these factors help contribute to problems in identification of *Streptognathodus*. Most publications in this field now contain extensive lists of species synonymies. Most of the various authors' interpretations of past speciation and generic status (as defined by others) begin with Gunnell (1931 and 1933) and Stauffer and Plummer (1932), continue with Harris and Hollingsworth (1933), extend through Ellison's revisions (1941), and so on, eventually ending with their own 'corrected' versions, especially in regard to original form vs. natural multielement taxonomies.

For example, Rhodes (1952) defined *Scotella typica* based on a natural assemblage as containing the form genera *Idiognathodus* and *Streptognathodus* (which he combined into one genus). von Bitter (1972) reconstructed assemblages statistically and reinstated *Idiognathodus* and *Streptognathodus* not only as separate genera but as natural multielement assemblages. Baeseman (1973) recombined the two as one multielement

genus. More recently Barrick and Boardman (1992) advocated separating the genera using ontogenetic comparisons, among other factors in their argument. With this type of debate for just generic status, discrimination at the species level of *Streptognathodus* is obviously even more chaotic.

One last point to emphasize is the problem of the variable nature of the platform element itself— perhaps the root cause of most confusion.

Streptognathodus Pa elements exhibit extreme intergradation between forms. Even Rhodes (1952), in first defining his natural genus *Scotella typica* calls the *Idiognathodus-Streptognathodus* component "...most variable element in assemblages ...".

It is in this light then that quantitative morphometric analysis of *Streptognathodus* Pa elements is examined as a possible solution to this taxonomic problem.

Streptognathodus

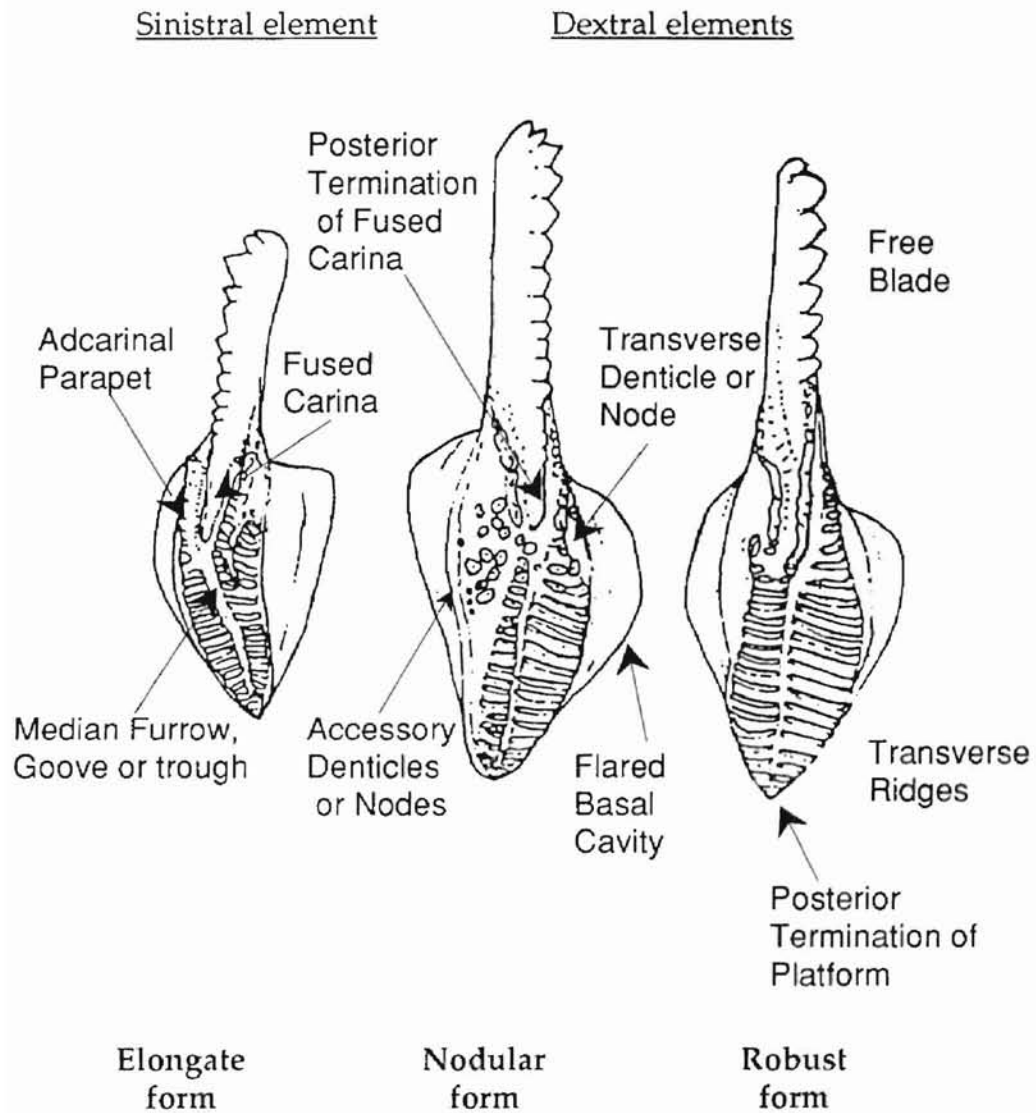


Figure 9

General Pa element morphologic notation.
Proposed cladistic types (Boardman *et al.* 1998) also designated.

MORPHOMETRIC ANALYSIS

General Morphometric Concepts

Several types of character measures may be recorded for use in general quantitative morphometric studies, such as:

1. Binary states, as in presence/absence of some particular attribute of the specimen.
2. Range states, wherein characters measured are noted as being included in some predesignated ranges of variation.
3. Character counts, or actual numbers of a specific feature present in/on the specimen.
4. Distance measures, as in the length, width, etc. of some part of the specimen.
5. Outline, a tracing of the perimeter of part or all of the specimen in question.

This data is then used in a variety of possible numerical procedures loosely called multivariate morphometrics. Most are used and were originally developed for use outside of the field of morphometric analysis. These methods may include principal-component analysis, cluster analysis, linear discriminant analysis, etc. (MacLeod and Carr, 1987).

Traditionally, size and shape analysis of biological specimens commonly employed these various statistical methods on scalar distance measurements such as length, width, and thickness. These distances are measured between landmarks, which are defined as:

“...landmarks are specific locations on specimens that are replicable and identifiable across phylogeny, ontogeny, or pathology.” (Carpenter *et al.*, 1993)

New methods record cartesian coordinates of landmarks rather than interlandmark distances. This allows for the use of 'newer' geometric morphometric analysis techniques (Marcus *et al*, 1993). This type of analysis, such as thin-plate spline and relative warps, attempts to work with the actual 'shape' of the specimen rather than individual components, i.e. length of a blade. Cartesian coordinates may, if needed, easily be converted to interlandmark distances for use in traditional analysis, whereas the converse is not true.

Previous Quantitative Studies

Past research concerning quantitative conodont morphology has been rather limited. Studies of other conodont genera such as *Neogondolella* (Ritter 1989), *Amodrotaxis* and others (Murphy *et al.* 1987, 1989), and *Spathognathodus* (Barnett 1971) have primarily been of a strictly traditional nature using distance measures, various ratios thereof and selected character states. Statistical techniques such as principle components analysis, cluster analysis, etc. were used in efforts to discriminate taxa based on the measured parameters. Klapper (1993) pioneered the use of outline measurements and canonical variate analysis for attempts at discrimination of the genus *Palmatolepis*. Recent quantitative studies of *Idiognathodus* (Braden and Manger, 1995, 1996) have concentrated on the morphology of the aboral surface. All these efforts have met with varying degrees success in delineating the measured groups, with no one particular technique or method of analysis standing out as far superior.

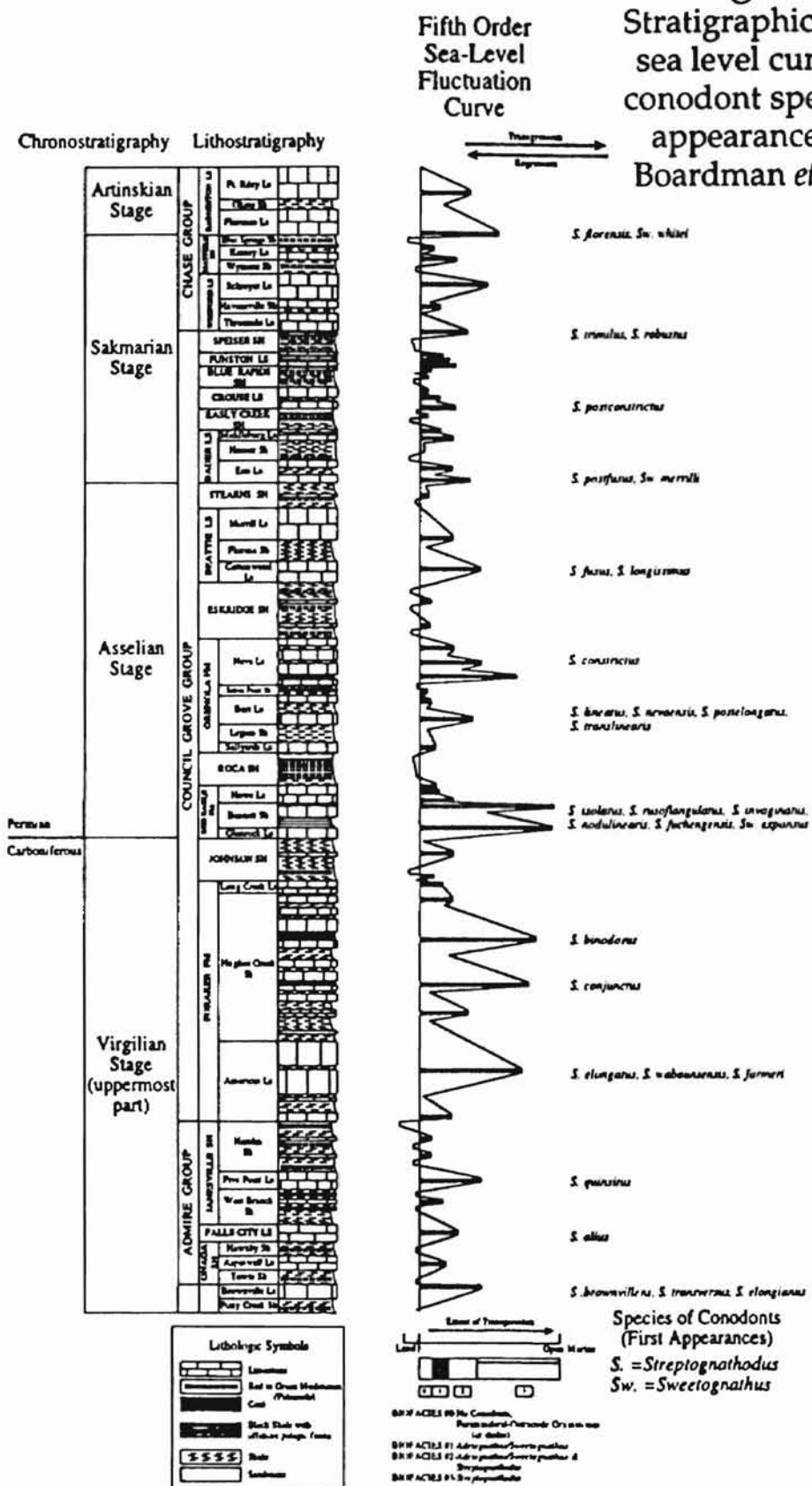
Purpose

The following study is a preliminary effort to solve part of this problem of conodont morphology and provide a means for quantitative classification within the genus *Streptognathodus*. It continues the traditional type of morphometric analysis in an effort to help clarify some of the taxonomic confusion for this group and also lays groundwork for future studies using newer analytic methods.

Materials

Measurements were taken from more than 200 specimens collected from the Upper Pennsylvanian and Lower Permian of central Kansas. Recovery was from formations ranging from the Brownsville Limestone of the Wabaunsee Group to the Fort Riley Limestone of the Chase Group (Figure 10). Complete traditional species descriptions, exact collection localities and detailed biostratigraphic discussion of all specimens used in this study may be found in Boardman *et al.* (1998). In that work individuals were identified to species level using regular diagnoses and were also placed into separate lineages, or clades as follows: Elongate, Robust, and Nodular, along with several shared 'ancestors' classed here simply as Old. (See Boardman *et al.* 1998 for discussion on cladistic delineations.) For each specimen the species determination, possible lineage, formation recovered from and age were entered into the morphometric database for use while seeking possible correlations (Tables 1-4).

Figure 10
Stratigraphic column,
sea level curves and
conodont species first
appearance. From
Boardman *et al.* 1998.



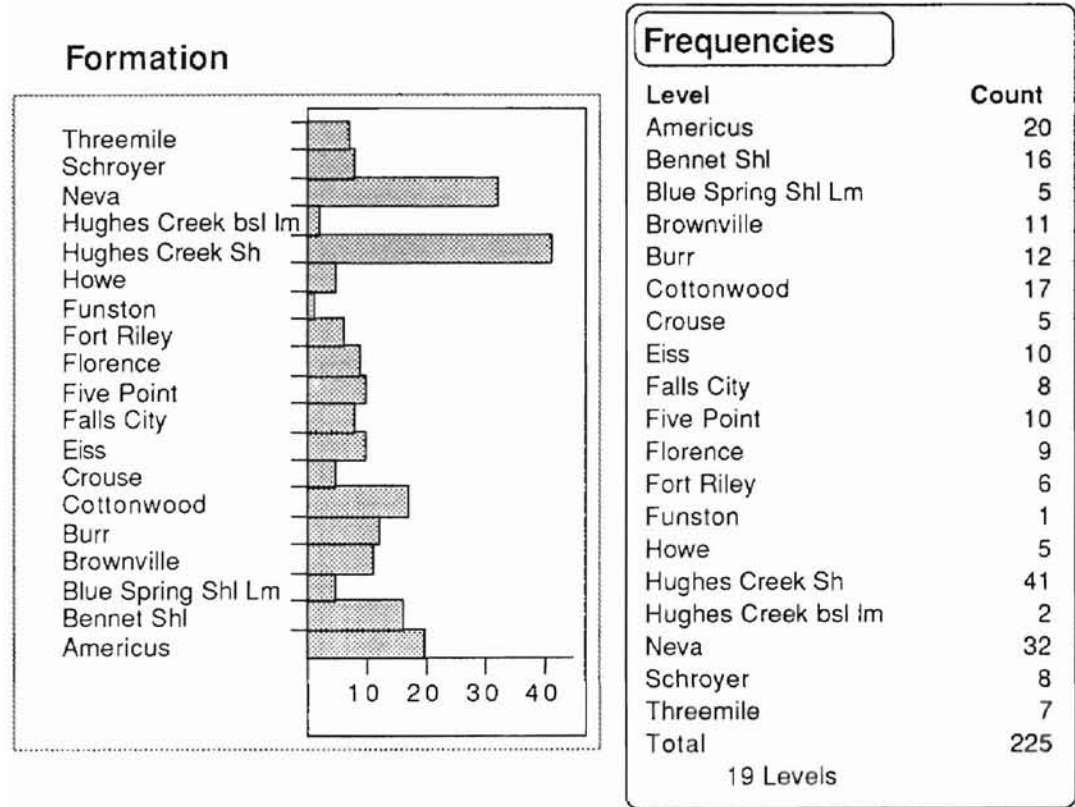


Table 1
 Formation count of individuals
 used in this study.

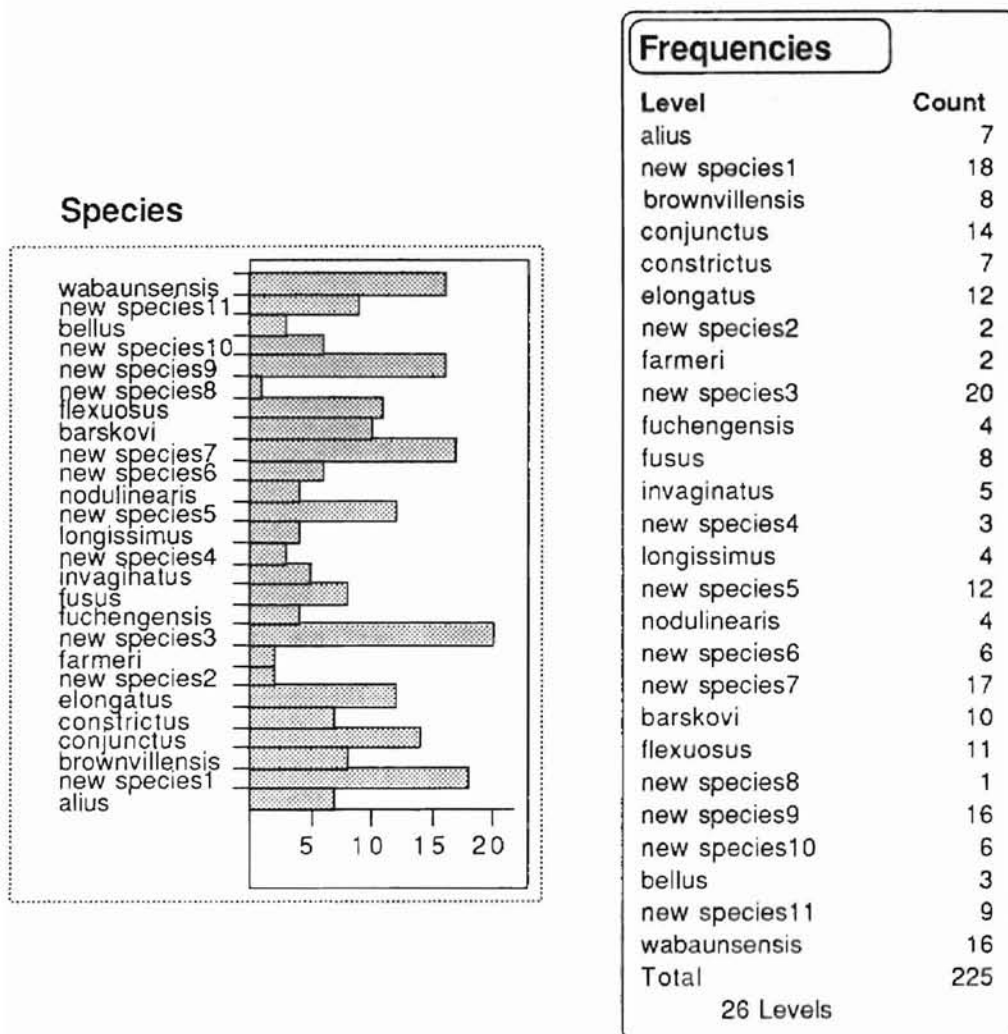
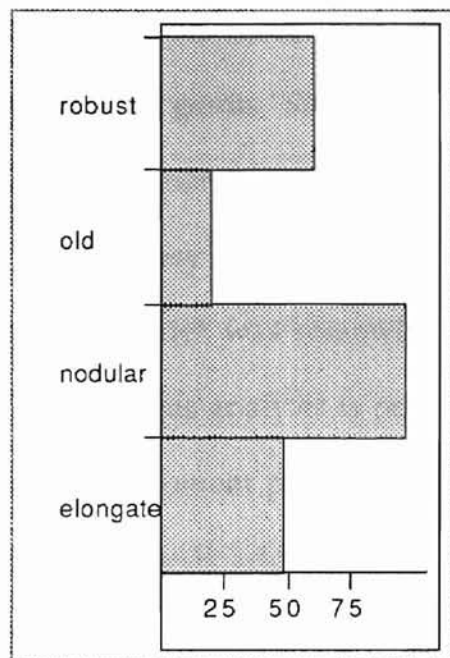


Table 2
Species count of individuals
used in this study.

lineage



Frequencies

Level	Count
elongate	49
nodular	96
old	20
robust	60
Total	225
4 Levels	

Table 3

Cladistic count of individuals
used in this study.

	Elongate	Robust	Nodular
		new species8	
		barskovi	new species3
new species6—new species4		fusus	new species11
constrictus		new species5	new species10
new species7—longissimus		fuchengensis	nodularis—invaginatus
elongatus		conjunctus	new species1—new species9
		flexuosus	farmeri—wabaunensis
Common Ancestral	bellus—alius—brownsvillensis—new species2		

Table 4

Species by lineage.
From Boardman et al. 1998.

Methods

This study follows those traditional morphometric methods in attempting to analyze genus *Streptognathodus* but also sets the stage for use of 'newer' geometric morphometrics (coordinate shape analysis). Of primary importance was the easy reproducibility of the measurements and analytic methods, a feature which was somewhat lacking in a few of the earlier quantitative efforts. This analysis is primarily restricted to ridge/node counts and generalized Pa element platform 'shape' as measured at selected points or 'landmarks'. Obviously additional characters are necessary for a complete taxonomic classification, especially additional surface ornamentation, but several constraints limited the morphologic characters measured in this study.

A method using computer image analysis software was used to obtain consistent specimen orientation of SEM images and for obtaining the measurements (both landmark and character) of specimens. Consistent specimen orientation is vital for accurate reproducible measurements and for future morphometric analysis of the data. Unfortunately this was not an automated process and was the most time-consuming portion of the research.

SEM images were recorded in Kodak PhotoCD format for ease of storage and for transfer to image analysis computer programs. NIH Image version 1.6 from the National Institute of Health was the primary program used for image analysis in this study. During the original SEM process specimens were oriented essentially with the platform surfaces normal to

direction of viewing. However many of the specimens did not have the same vertical orientation. That is, the platforms (and blades) were slightly rotated clockwise or counterclockwise about their center. Using NIH Image the angle between the blade axis and true vertical was determined for each specimen. They were then rotated that amount (on screen) so that the blade axis was in 'true' vertical orientation. Coordinates of landmarks were then collected while in this standardized position. At this time ridge/node counts were also taken.

The number of individual transverse ridges on the platform were recorded for both left and right sides of each specimen. A total ridge count and a count from just posterior tip of platform to a point even horizontally with posterior end of carina were made. On some specimens ridges on the anterior end of the platform degraded into single or binodal form. These nodes were included in the ridge count when they followed a regular spacing as found in the true ridges. The number of nodes in the central trough or groove posterior to the carina end was also noted.

Record was made of the coordinates of landmark positions (Figure 11) rather than the interlandmark distances, which was common practice in previous studies. This method allows for calculation of distances between any landmark pair, calculation of various angles between landmarks, and future use in geometric morphometric analysis. The landmark positions are described as:

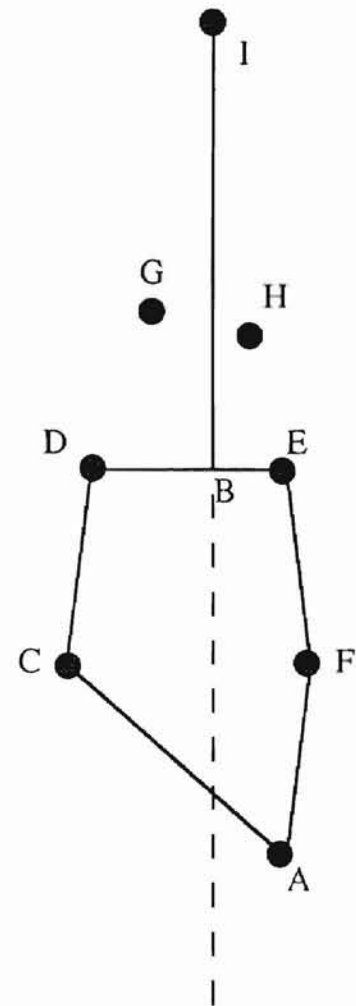
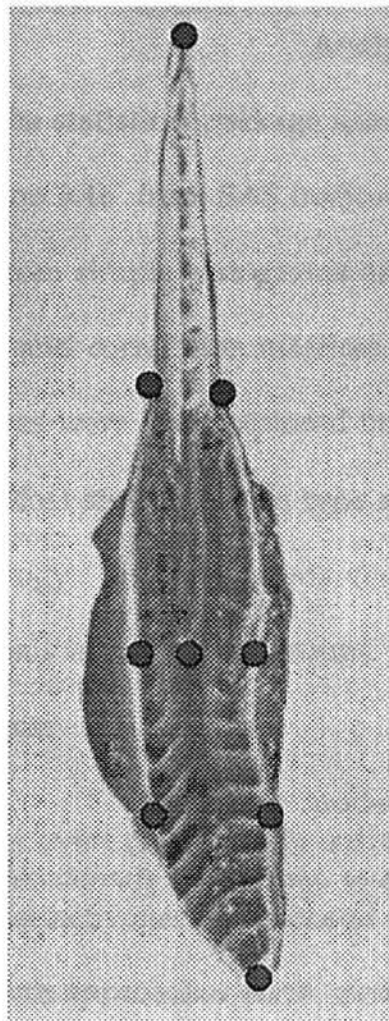
A. Posterior tip of platform.

- B. Posterior tip of carina.
- C. Left platform edge equidistant vertically between A and B.
- D. Left platform edge horizontal to B.
- E. Right platform edge horizontal to B.
- F. Right platform edge equidistant vertically between A and B.
- G. Left side of blade where completely free of platform or ramp.
- H Right side of blade where completely free of platform or ramp.
- I. Anterior tip of blade.

**Platform*, as used throughout, includes node fields.

These points are referred to throughout the remainder of this paper. Points A through F were selected not only because they indicate the general platform shape but especially for reproducibility. Points C and F, horizontally equal and equidistant between specific vertical landmarks, were selected as an indicator of width rather than the 'widest' measure which is sometimes very difficult to determine. Correct specimen orientation is vital for collection of these landmarks (see also points D and E). Coordinate data was stored and later converted to a number of interlandmark distances and various angular measures. Collected and converted data was then available for use in statistical and morphometric analysis programs.

To gather the complete set of measurements for every specimen was impossible due to the poor condition of some individuals, i.e., broken blades, residue on the sample, etc. As Rhodes *et al.* (1973) noted in their quantitative morphometric studies, "...even broken individuals can provide meaningful data..." and may indicate a specific group more prone to damage than others.



Landmark locations:

- A Posterior tip of platform
- B Posterior tip of carina
- C Left platform edge equidistant vertically between A & B
- D Left platform edge horizontal to B
- E Right platform edge horizontal to B
- F Right platform edge equidistant vertically between A & B
- G Left side of blade when completely free of platform or ramp
- H Right side of blade when completely free of platform or ramp
- I Anterior tip of blade

Specimen oriented:

1. Platform surface level
2. Blade vertical with page

Figure 11
Landmark positions used in this study.

Analysis and Interpretations

The statistical package used for the majority of examination was JMP IN version 3.16 from SAS Institute, Inc. A variety of analyses was used in this study, from simple histograms and bivariate scatters to principle component analysis and correlation matrices. Additionally several geometric analysis techniques were also explored but are not included in this report.

Most studies of this type are examinations of patterns of variation in morphology. In other words, they are the comparison of form between individuals in pairs or in groups. There are two basic approaches to this type of analysis:

“...*exploratory* mode (e.g. examinations of single sample for overt clustering of individual morphotypes ...) ... or *discriminate* mode (e.g. examination of hypothesis of group distinctiveness). (MacLeod and Carr, 1987)

Both approaches were used at various stages of this research. Current analysis and interpretations of this data has been divided into the major categories listed below. The interpretation and discussion of this analysis follows.

1. Element Asymmetry - dextral and sinistral variation
2. Shape vs. Size Variation - factors of growth or shape
3. Lineage Discrimination - cladistic separation
4. Variation through Time - evolutionary trends

Element Asymmetry

One of the first shape observations is the simple variation between sinistral and dextral elements. Although Rhodes (1952), in commenting on 'left and right forms' states that "No specimen studied has revealed any significant difference between two such components...", others have noted this variation to be more pronounced, especially in Permian individuals. In fact, more recent diagnoses of new species usually include descriptions or comparison of both sinistral and dextral forms often with reference to the symmetry types of Lane(1968).

This issue is one that could be easily addressed through quantitative measure. The means of various measured and derived data were calculated and are provided in Table 4, with several major points summarized as follows.

There was little variation between between sinistral and dextral elements in length, either total (A-I vertical component) or platform length (A-B vertical component) only. The same is true for blade 'width', whereas the difference in platform width at carina (D-E) was relatively minor, with sinistral forms 90.7 % of dextral width. Platform width at the middle of the platform (C-F) was 84.3% of dextral in sinistral elements. The primary variation appears to be not in the actual dimensions but in their placements within the element.

Dextral elements are relatively symmetric about their own vertical axes except for slight horizontal displacement of the posterior platform tip from

the vertical axis. Sinistral elements exhibit a shift in the platform width and positioning. This occurs slightly at the carina and is very pronounced at the midpoint, with the mean of the width of the outer portion of the platform (from central vertical axis to platform edge) less than 50% that of dextral elements. The sinistral platforms then may be described as slightly thinner and having a midsection shifted to the right.

Along with the variation of middle platform shift, the displacement of posterior platform tip is notable. Although the total range of displacement is similar in both groups the sinistrals are offset relative to the dextrals. For dextral elements the mean displacement is slightly to the left of the vertical axis as normally viewed, with some dextral specimens exhibiting displacement to the right (again, general symmetry about vertical axis). No sinistral elements have any such 'reverse' shift. That is, all sinistral elements have platform posterior tip displacement to only the right side of the vertical axis. This variation is also observable in the mean of the angle between vertical axis and line from carina posterior tip to platform posterior tip (14.1° sinistral, 4.5° dextral). A reconstruction based on means of both sinistral and dextral elements is provided in Figure 12.

It becomes apparent then that complete diagnosis and analysis must include descriptive and quantitative detail of both elements. These symmetry variations can affect other morphometric analysis, so in most cases further analysis was performed on the separate sinistral and dextral groupings. Of the 225 specimens in this study, 115 were dextral and 110 were sinistral.

Element		Character	
Sinistral	Dextral	Landmarks	Description
30.0	31.0	G-H	Blade width(horizontal component of G-H)
398.0	397.0	A-I	Total Length (vertical component of A-I)
142.0	148.0	A-B	Platform length (vertical component of A-B)
37.0	11.5	Vert. axis to A	Horizontal displacement posterior platform tip
14.2°	4.5°	Vert. axis -B-C	Angle vertical axis to posterior platform tip
59.4	70.5	C-F	Width of platform at middle
54.4	60.0	D-E	Width of platform at carina
16.2	35.8	C-Vert. axis	Width of left side platform at middle
43.2	35.0	Vert. axis-E	Width of right side platform at middle
23.8	31.8	D-Vert. axis	Width of left side platform at carina
30.6	30.2	Vert. axis-F	Width of right side platform at carina

Table 5
Mean values of selected measures.

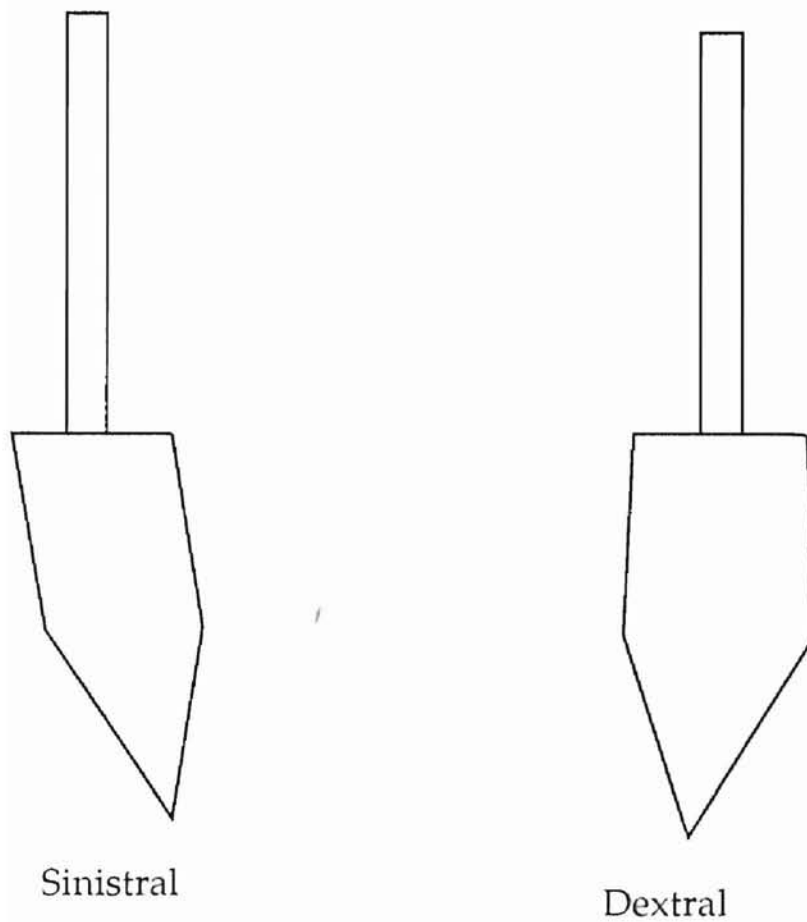


Figure 12
Sinistral and dextral elements
as reconstructed from mean values.

Shape vs. Size Variation

While conducting morphometric analysis it is sometimes necessary to determine whether shape parameters are invariant to change of scale (size). In other words, is the measured variation due to ontogenetic change or phylogenetic change (assuming measured size variation is due to growth)? Allometric analysis was performed on a few selected groups even though most of the specimens were considered adults in this study, due to their overall size .

Allometry is the study of size and its consequences (Gould, 1966), particularly for this study, consequences in relation to shape. The concept of allometry was first fully quantified by Huxley (1924) in the allometric growth equation, $y = bx^a$, where y = variable whose increase is considered relative to that of another variable (size of individual organ or 'part'), b constant scale factor for size, x total 'body' size (usually a mean of several/all measures) and constant a the percentage rate of growth. Its log transformation, $\log y = a \log x + \log b$ as described by Huxley (1932) is in the familiar $y = ax + b$ notation where slope a and intercept b may be easily determined. Additional justifications of using log transforms in some morphometric analysis techniques were expounded on by Bookstein *et al.* (1985).

Isometry is the case of growth without change in shape and results in growth factor(a above) of 1 (if compared values are both linear measure). This value varies then for isometric growth with the type of comparisons

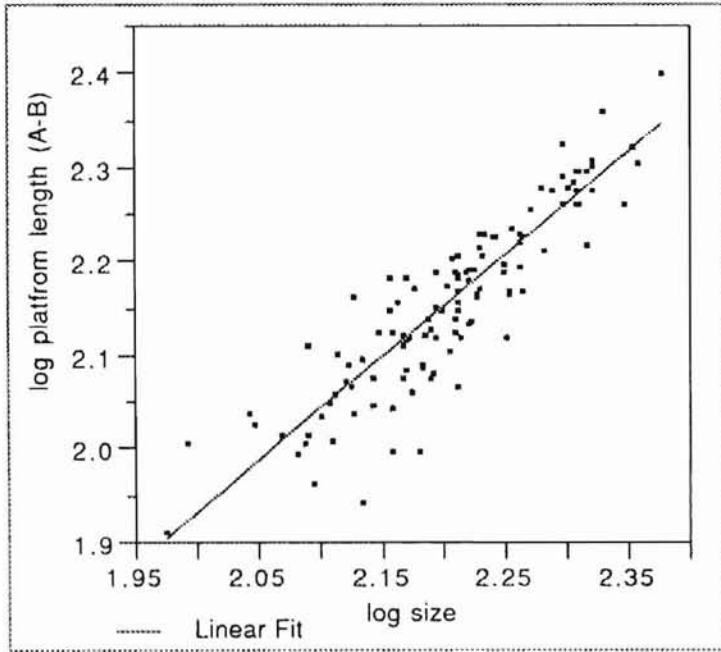
made, i.e., a factor of 2 for linear to area or factor of 3 for linear to volumetric measures. For allometric growth (non-isometric), relative-size increase occurs at a rate above or below that of isometric growth (Purnell, 1994).

Several parameters assumed to be size-related were tested for isometry. One member each of the three clades previously described along with total sinistral and dextral groupings (for control) were examined. In general, for characters with true isometric growth, species groups should have index closer to 1 (for linear measures) than the entire genus. This was often the case, but the character of width at middle (C-F), which was assumed to be growth related, consistently had values that did not concur (Chart 4, B for example). Sample scatterplots with regression data are provided in Charts 1, 2, 3 and 4. Slightly positive allometric growth is indicated for most of the tested parameters, but the values are well within the range expected, except as noted above.

Ridge counts were compared to length as a possible indicators of growth. Common sense might presuppose that the longer the individual, the more ridges, but as is apparent from the correlation matrices in charts 5 and 6 this is not the case. Ridge counts were not correlatable in this study.

It is usually important to distinguish between growth-dependent characters vs. size-independent morphologic attributes. Much of this analysis followed expected patterns, but a few tests returned inconsistent values. A much larger sample size is probably needed before more conclusive interpretations in this area can be formulated.

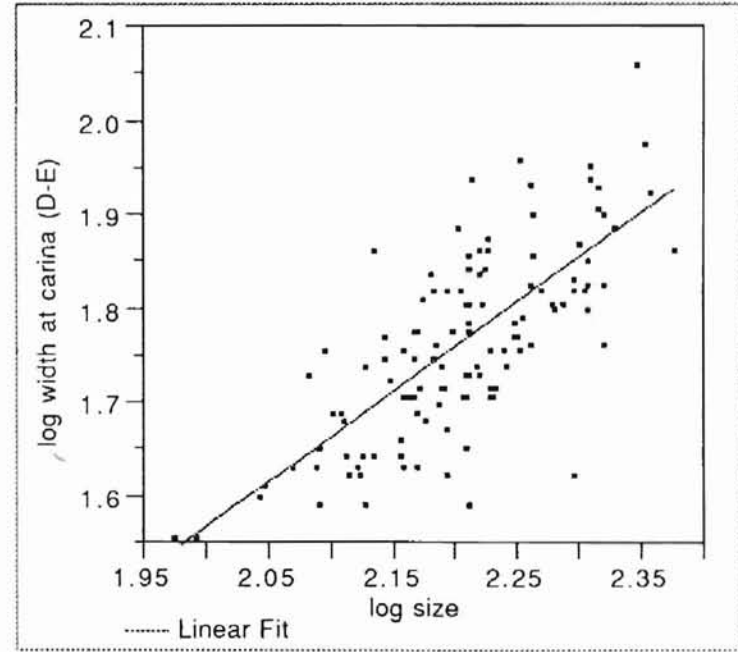
A



$$\text{log platform length} = -0.2729 + 1.10234 \text{ log size}$$

$$a = 1.10$$
$$\text{isometry} = 1.00$$

B

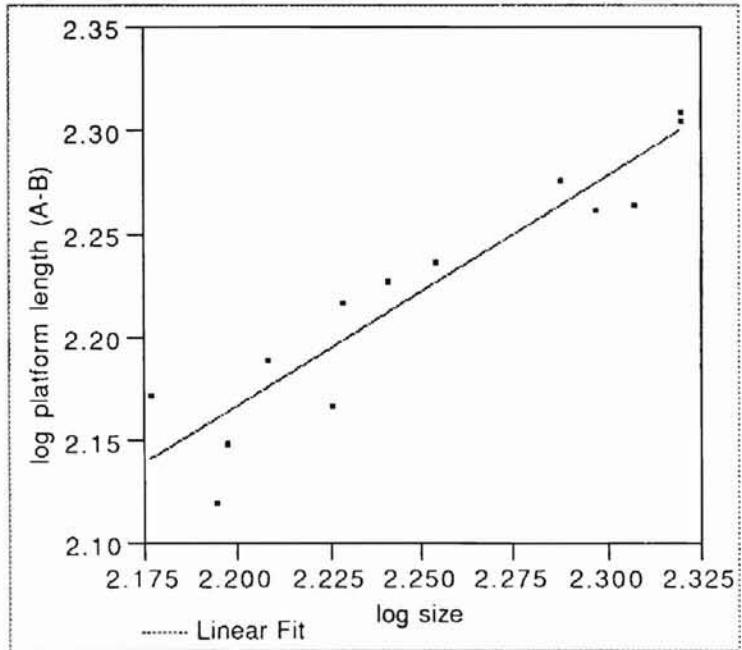


$$\text{log width at carina} = -0.341 + 0.95389 \text{ log size}$$

$$a = .95$$
$$\text{isometry} = 1.00$$

Chart 1

Samples of allometric analysis
for all dextral elements

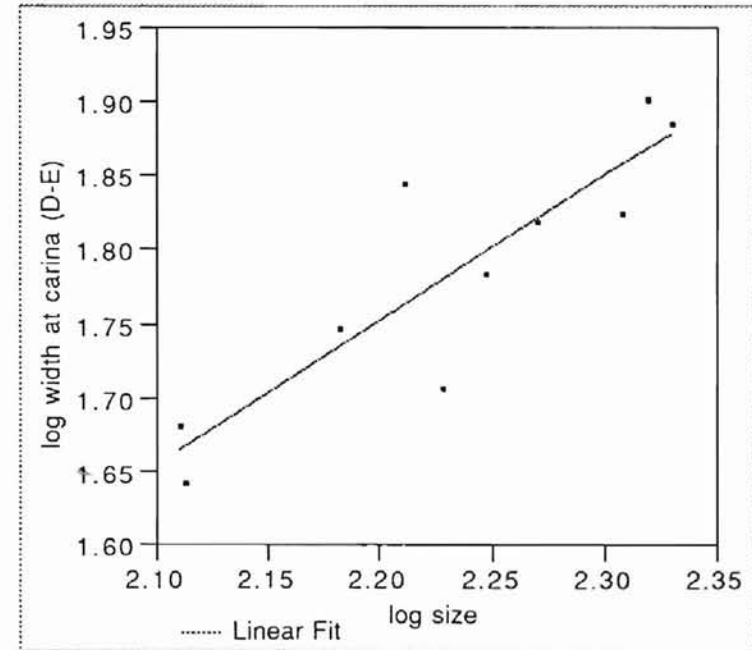
A

$$\text{log platform length} = -0.2802 + 1.1124 \text{ logsize}$$

new species 1

$$a = 1.12$$

$$\text{isometry} = 1.00$$

B

$$\text{log width at carina} = -0.3814 + 0.97043 \text{ log size}$$

new species 3

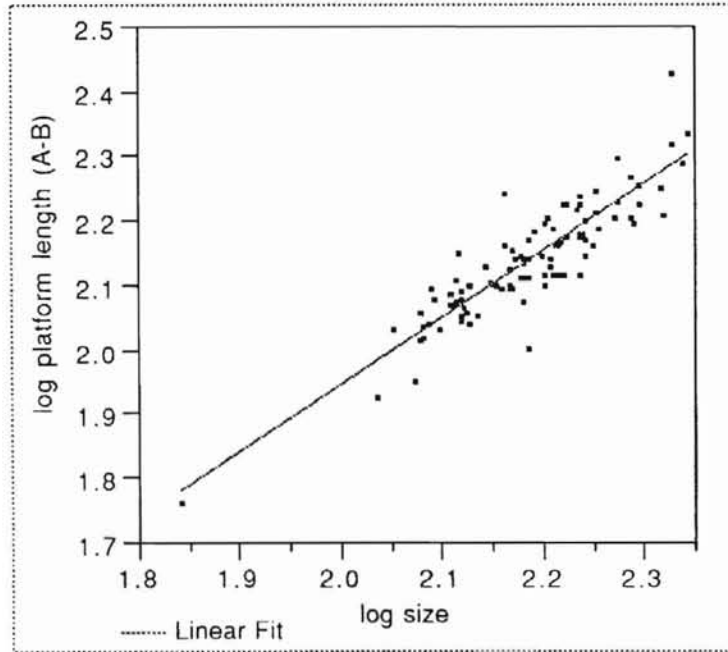
$$a = .97$$

$$\text{isometry} = 1.00$$

Chart 2

Samples of allometric analysis
of dextral elements selected by species.

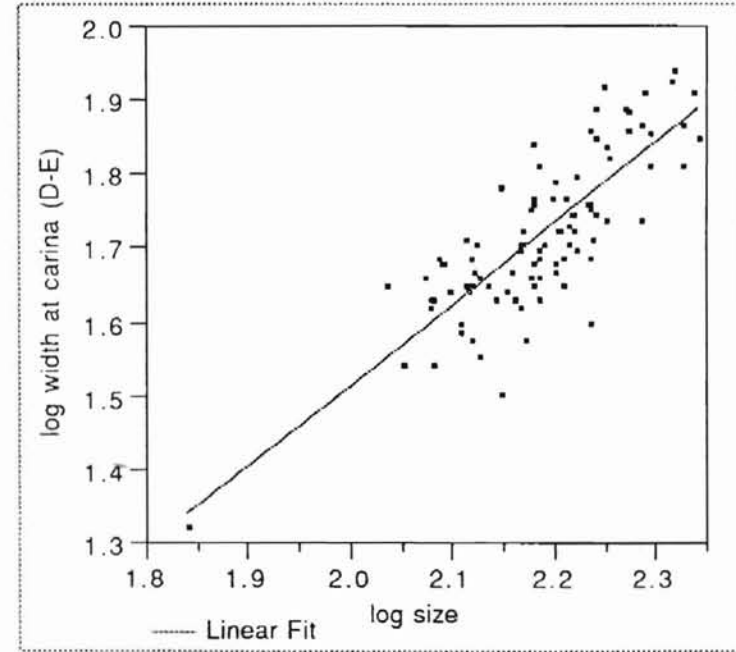
A



$$\text{log platform length} = -0.1394 + 1.0431 \text{ log size}$$

$$a = 1.04$$
$$\text{isometry} = 1.00$$

B

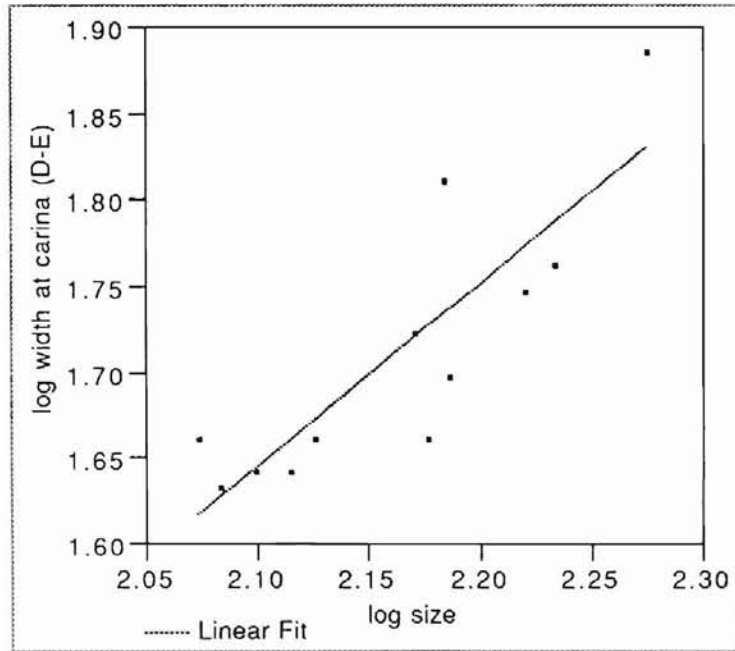


$$\text{log width at carina} = -0.6756 + 1.09519 \text{ log size}$$

$$a = 1.10$$
$$\text{isometry} = 1.00$$

Chart 3

Samples of allometric analysis
for all sinistral elements

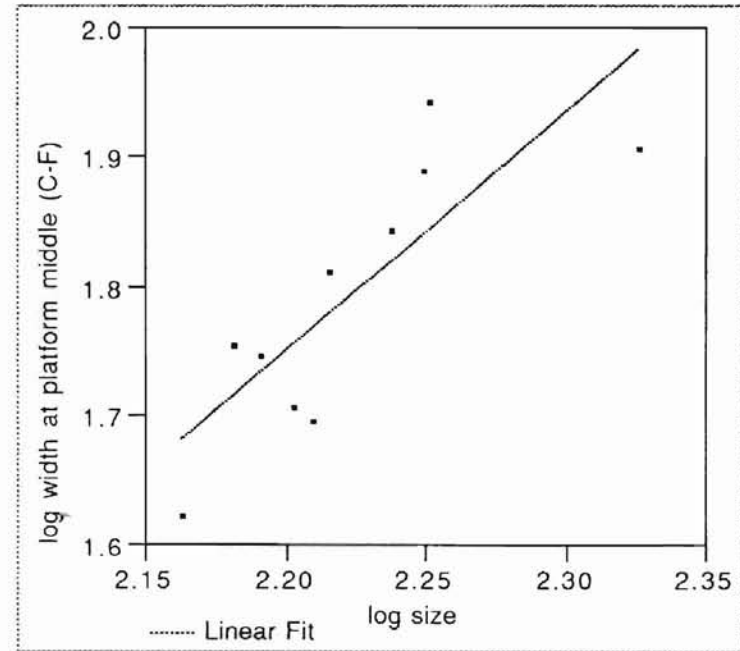
A

$$\text{log width at carina} = -0.5723 + 1.05642 \text{ log size}$$

new species 7

$$a = 1.06$$

$$\text{isometry} = 1.00$$

B

$$\text{log width at platform middle} = -2.3045 + 1.84348 \text{ log size}$$

S. wabaunsensis

$$a = 1.8$$

$$\text{isometry} = 1.00$$

Chart 4

Samples of allometric analysis
of sinistral elements selected by species.

Correlations

Variable	tot len	ridgL2car	ridgR2car	ridgLtot	ridgRtot
tot len	1.0000	0.4636	0.5472	0.2405	0.4283
ridgL2car	0.4636	1.0000	0.8923	0.6423	0.6626
ridgR2car	0.5472	0.8923	1.0000	0.5387	0.6954
ridgLtot	0.2405	0.6423	0.5387	1.0000	0.6838
ridgRtot	0.4283	0.6626	0.6954	0.6838	1.0000

Scatterplot Matrix

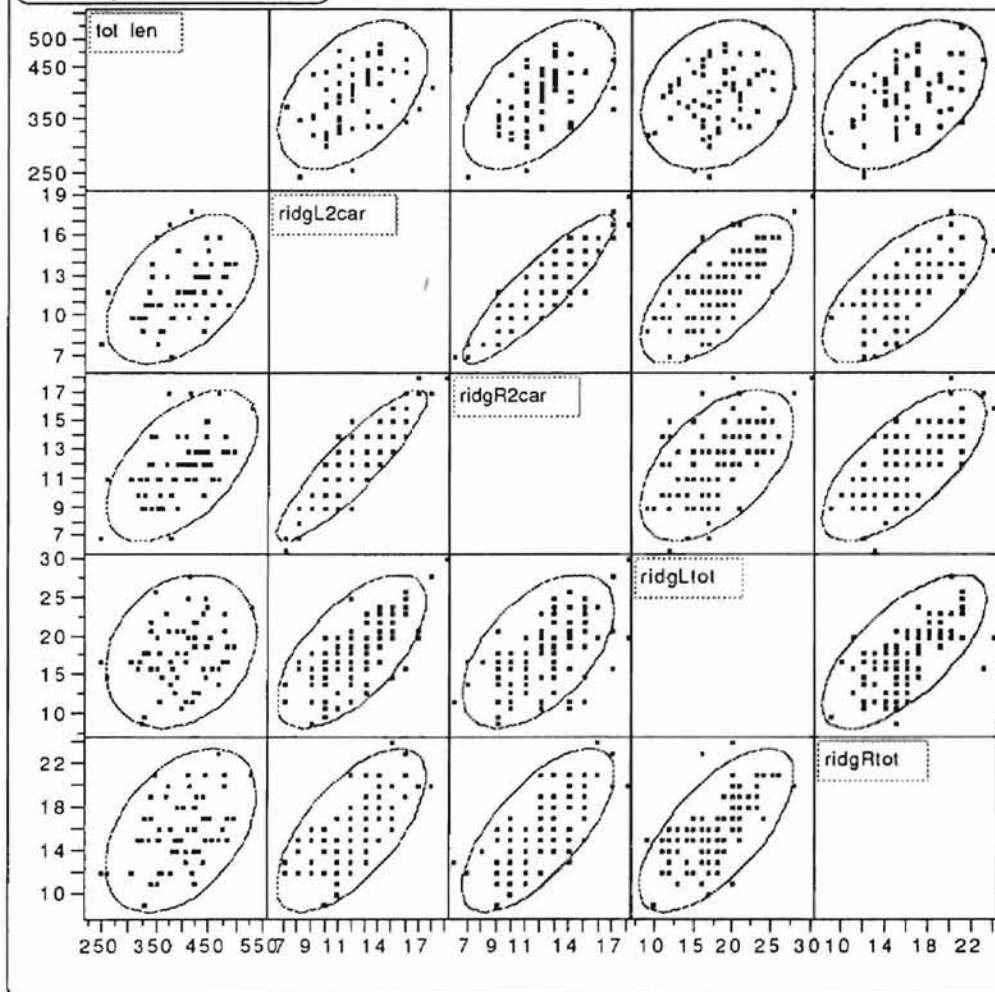


Chart 5

Correlation of ridge counts to total length for dextral elements.

Correlations

Variable	tot len	ridgL2car	ridgR2car	ridgLtot	ridgRtot
tot len	1.0000	0.3335	0.2330	0.2524	0.0136
ridgL2car	0.3335	1.0000	0.8555	0.7636	0.5414
ridgR2car	0.2330	0.8555	1.0000	0.5902	0.5528
ridgLtot	0.2524	0.7636	0.5902	1.0000	0.6651
ridgRtot	0.0136	0.5414	0.5528	0.6651	1.0000

Scatterplot Matrix

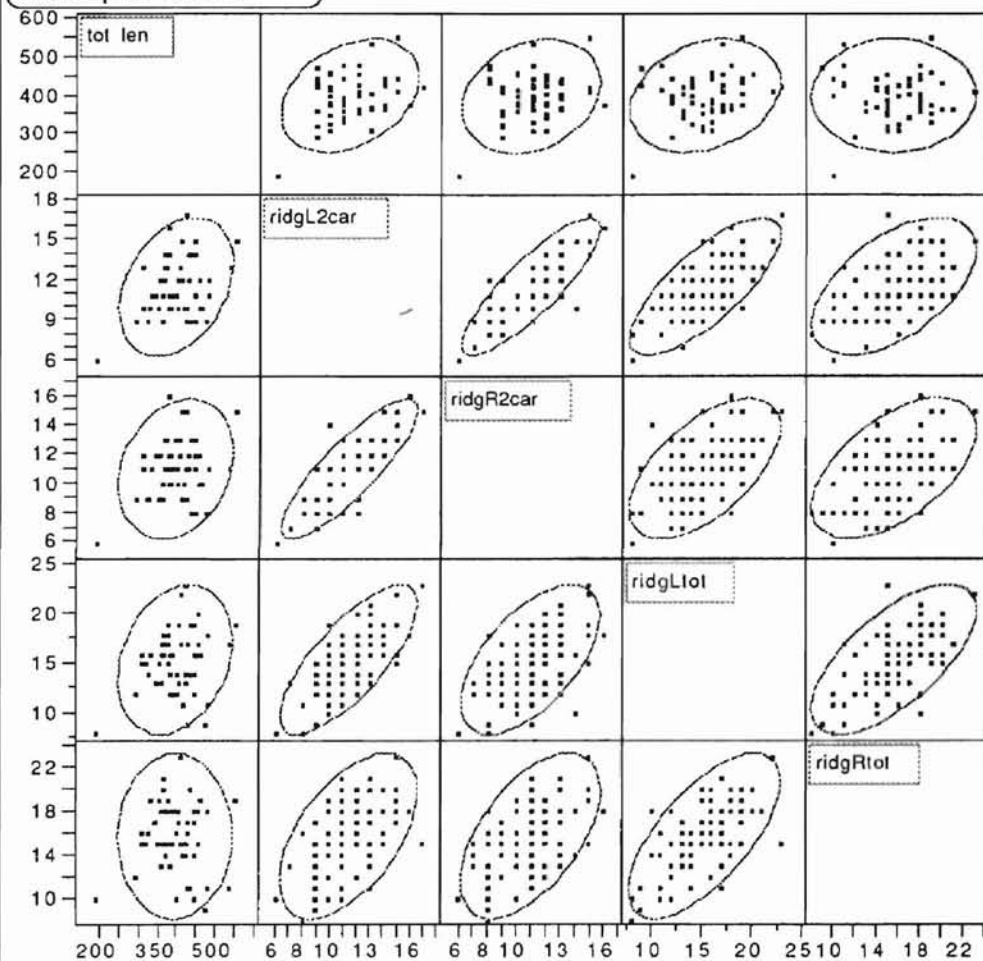


Chart 6

Correlation of ridge counts to total length for sinistral elements.

Discrimination among Lineages

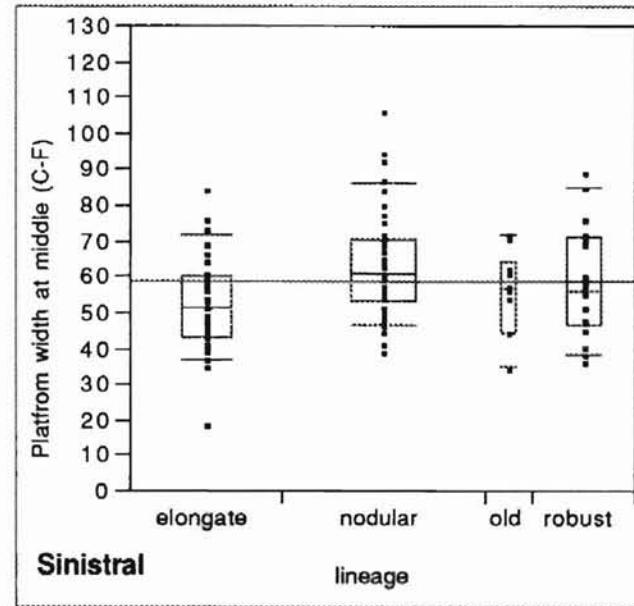
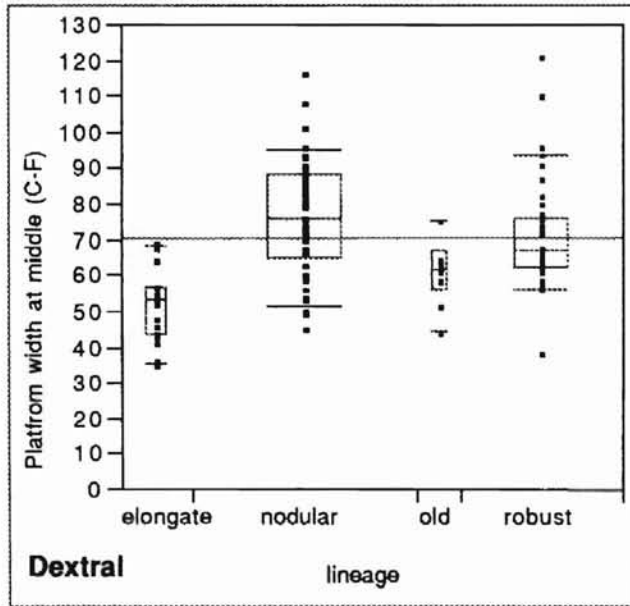
As described above the specimens were divided into three lineages with a common ancestral group. For most of the morphometric characters analyzed, variation was insufficient to discern groups. Among the numerous characters tested the single character of platform width at middle (C-F) provided by far the most cladistic separation (Chart 7), although there was still significant overlap of values. However, when combined in a ratio with length a very clear discrimination occurs in dextral elements. The {total length}/{width at midpoint} ratio (A-I-/C-F) clearly divides elongate specimens from all others with two exceptions (Chart 8, section A). After re-examination, the first outlier, in the nodular clade, may simply have been misidentified. However, the second, classified as *new species 2*, is more interesting. Its placement in the common ancestral grouping and identification appears to be correct. The question then arises: Is this an ancestor of only the elongate lineage, with the three groups having split earlier than previously postulated and not sharing the other ancestral members? Further research with more individuals and of earlier specimens is required to address this issue properly .

If platform length instead of total length is used in the ratio the lineage separation is not so clearly distinct (Chart 8, B). However well over 75% of individuals are still discriminated by this ratio (see Chart 8 quantiles). Chart 9 displays the means of the ratio used above (platform length to width at middle) for all species. A line is drawn at value 2.5, which separates all but

two members of the elongate clade from others. The two species that are not split, *new species 4* and *S. longissimus*, have a wider platform middle in general and interestingly, are shown as 'dead end' branches in this group (Table 4).

Unfortunately, the use of a ratio to clearly separate members of the elongate lineage from others applies only to dextral elements. The comparable sinistral analysis, as shown in Charts 10 and 11, does not strictly divide the clades and no other statistical method attempted to date has done so.

The only other clade with apparent statistical separation is the old, Virgilian 'ancestral' group. They may be distinguished in dextral elements by comparing the platform width at carina (D-E) and the platform length (A-B). This clearly is visible in Charts 12 and 13 where strong correlations exist between these two characters, except in three 'old' species. Again, *new species 2* stands out from the others in this ancestral grouping, bolstering the earlier argument for its separation from this group. Correlation matrices of these factors for each lineage are shown in Table 6 and display a relatively low value for these factors in the ancestral group. Unfortunately, this variation is readily apparent only in the dextral members, not the sinistral (Chart 14 and Table 7).



Dextral

Level	minimum	10.0%	25.0%	median	75.0%	90.0%	maximum
elongate	36	36.8	44.5	54	58	69.2	70
nodular	46	52.5	66.25	77	89.25	96	117
old	45	45.7	57.25	62.5	67.75	76	76
robust	39	57	63	68	77	95	122

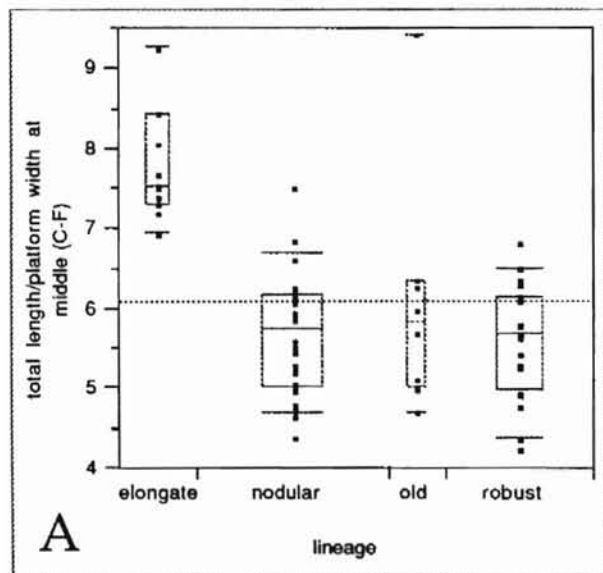
Quantiles

Sinistral

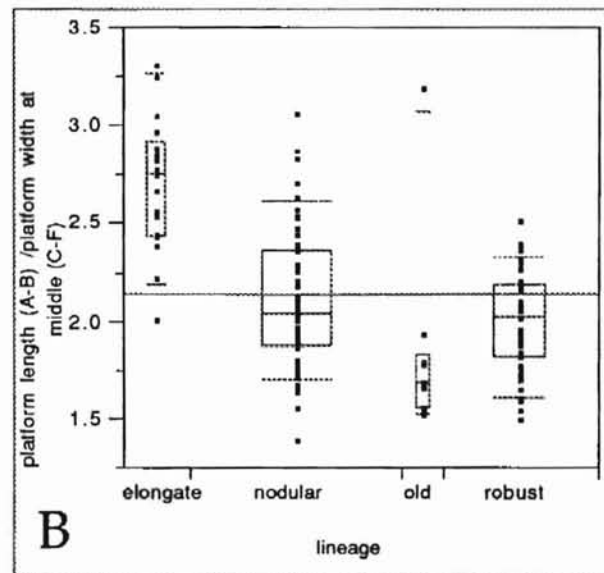
Level	minimum	10.0%	25.0%	median	75.0%	90.0%	maximum
elongate	19	38	44.25	52	60.75	72.8	85
nodular	40	47.6	54.25	61.5	71.5	87.1	107
old	35	36	45	57.5	65	72.8	73
robust	37	39.4	47	57	72	86	90

Chart 7

Platform width at middle (C-F)



Dextral



A
Quantiles

Level	minimum	10.0%	25.0%	median	75.0%	90.0%	maximum
elongate	6.927273	6.978855	7.327586	7.553191	8.45283	9.285012	9.295455
nodular	4.40367	4.709387	5.042614	5.743284	6.190141	6.697826	7.529412
old	4.723684	4.723684	5.01905	5.838441	6.34874	9.422222	9.422222
robust	4.23913	4.391577	5.009841	5.695472	6.157617	6.493792	6.833333

B

Level	minimum	10.0%	25.0%	median	75.0%	90.0%	maximum
elongate	2.018182	2.189144	2.445437	2.757143	2.930931	3.272867	3.318182
nodular	1.404255	1.703587	1.88666	2.045381	2.36964	2.61443	3.0625
old	1.526316	1.528372	1.563642	1.693611	1.841681	3.074737	3.2
robust	1.5	1.614035	1.828829	2.030769	2.189655	2.337349	2.525424

Chart 8
Dextral length/width ratio comparisons by lineage

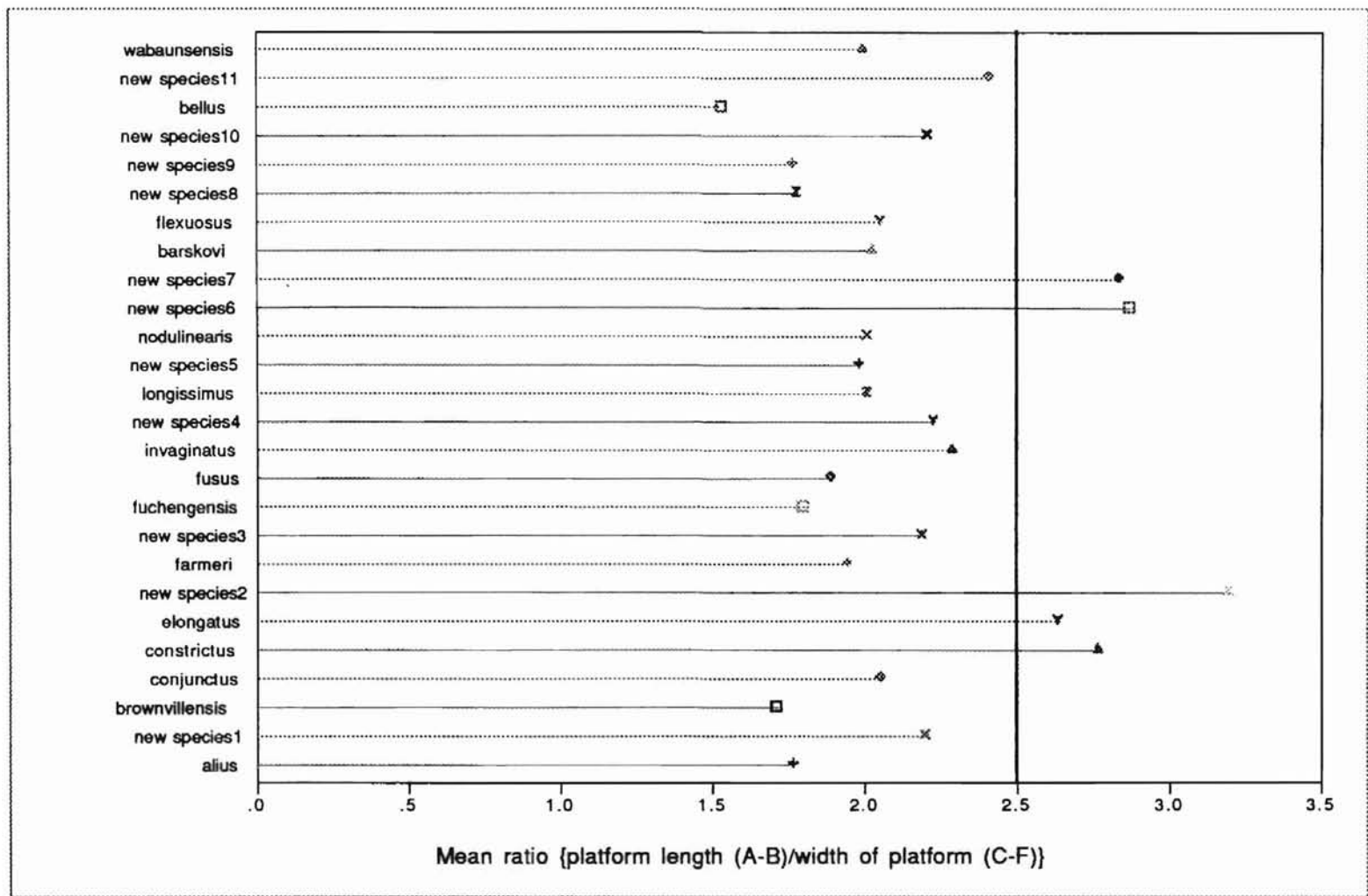
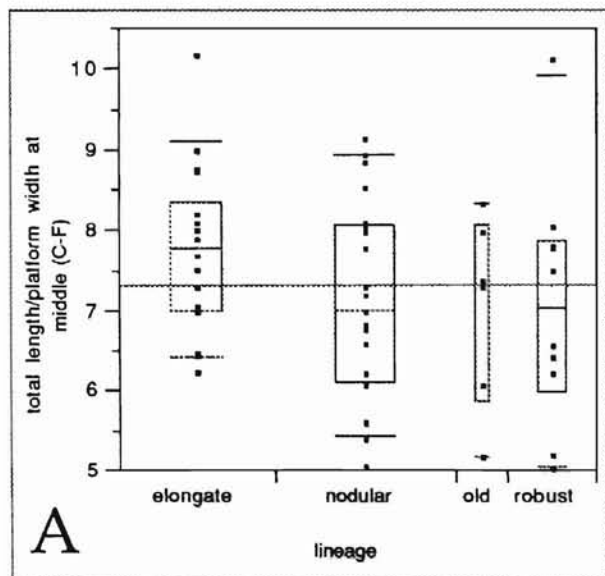
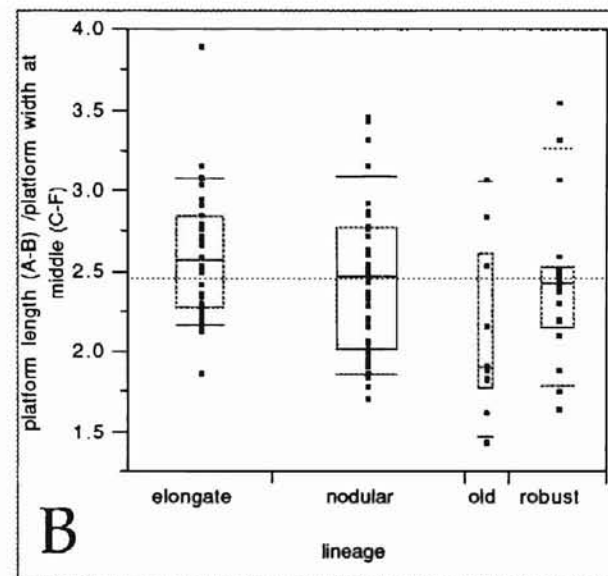


Chart 9
 Dextral mean length/width ratio comparisons by species.



Sinistral



A

Quantiles

Level	minimum	10.0%	25.0%	median	75.0%	90.0%	maximum
elongate	6.258065	6.438306	7.026316	7.803686	8.363558	9.121053	10.21053
nodular	5.068182	5.450558	6.128571	7.018182	8.083824	8.937415	9.16
old	5.197183	5.197183	5.870724	7.335354	8.085714	8.342857	8.342857
robust	5.055556	5.07093	5.985465	7.038001	7.880435	9.925969	10.13514

B

Level	minimum	10.0%	25.0%	median	75.0%	90.0%	maximum
elongate	1.882353	2.167692	2.279014	2.577594	2.846552	3.085789	3.911111
nodular	1.715789	1.860267	2.027284	2.470098	2.777679	3.096639	3.47619
old	1.452055	1.469753	1.780498	1.909357	2.624904	3.061587	3.085714
robust	1.642857	1.793953	2.15478	2.423077	2.530154	3.274844	3.560976

Chart 10

Sinistral length/width ratio comparisons by lineage

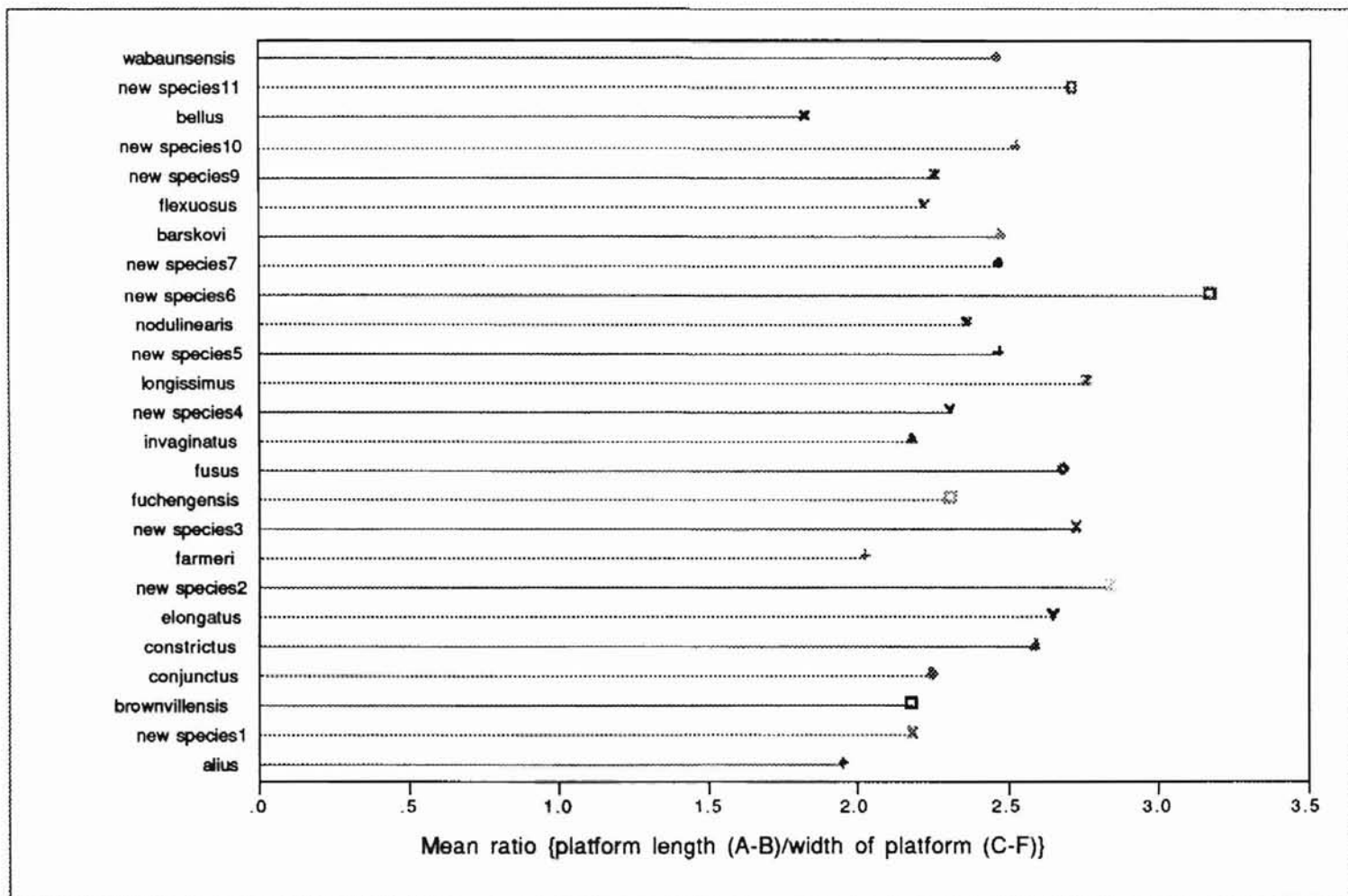


Chart 11
Sinistral mean length/width ratio comparisons by species.

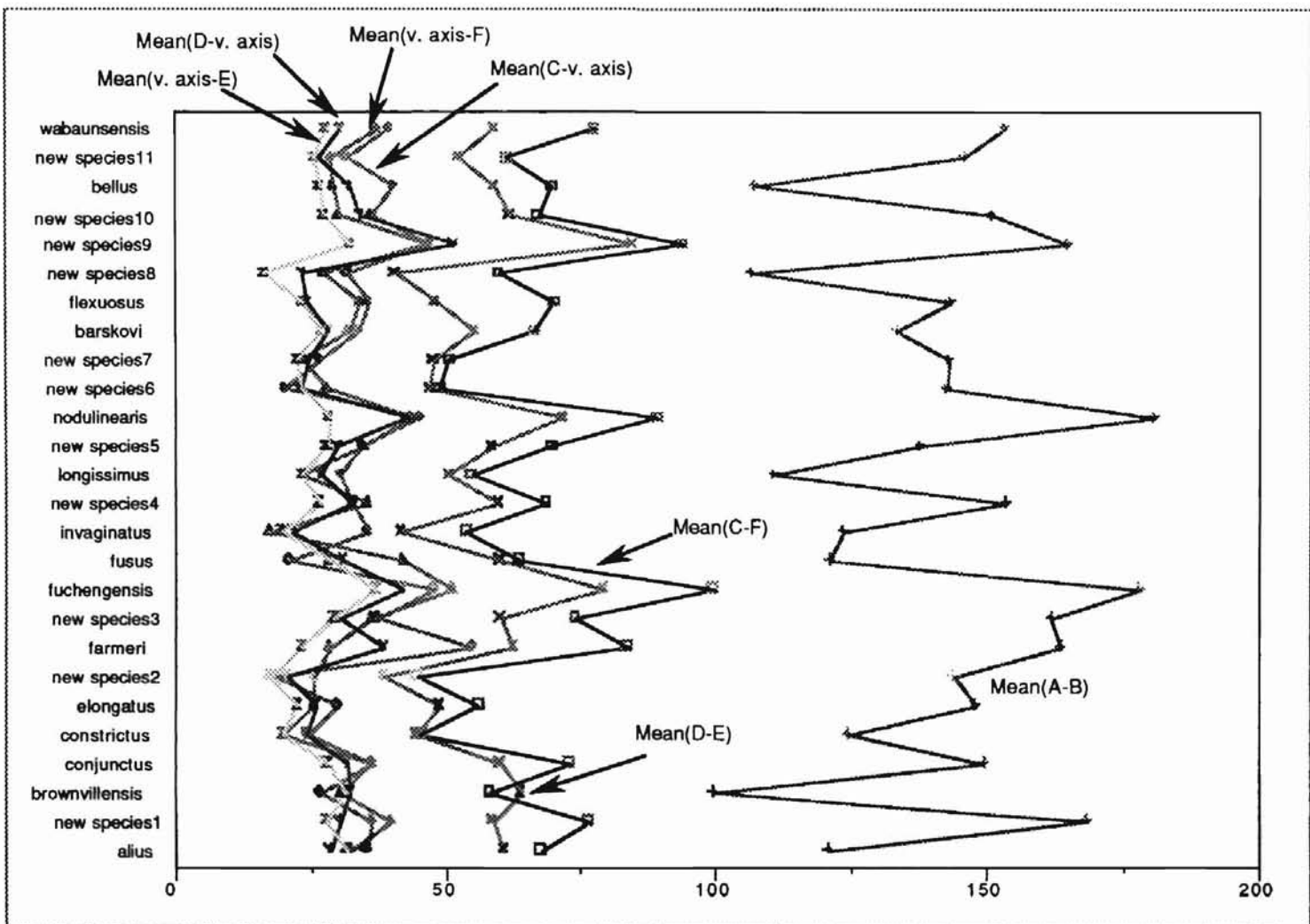


Chart 12
Dextral mean comparisons by species.

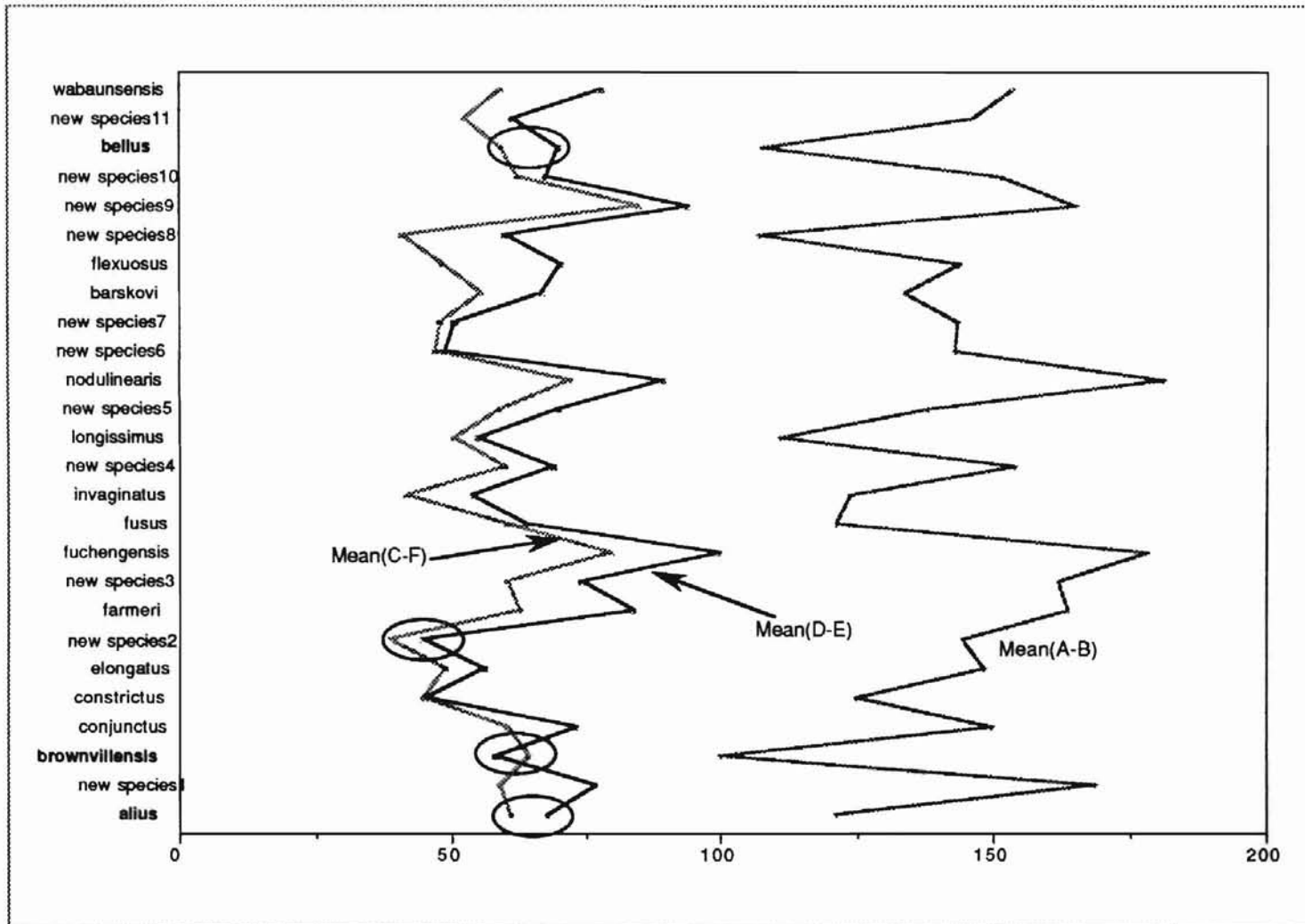


Chart 13
 Enhancement of three mean-value comparisons by species.

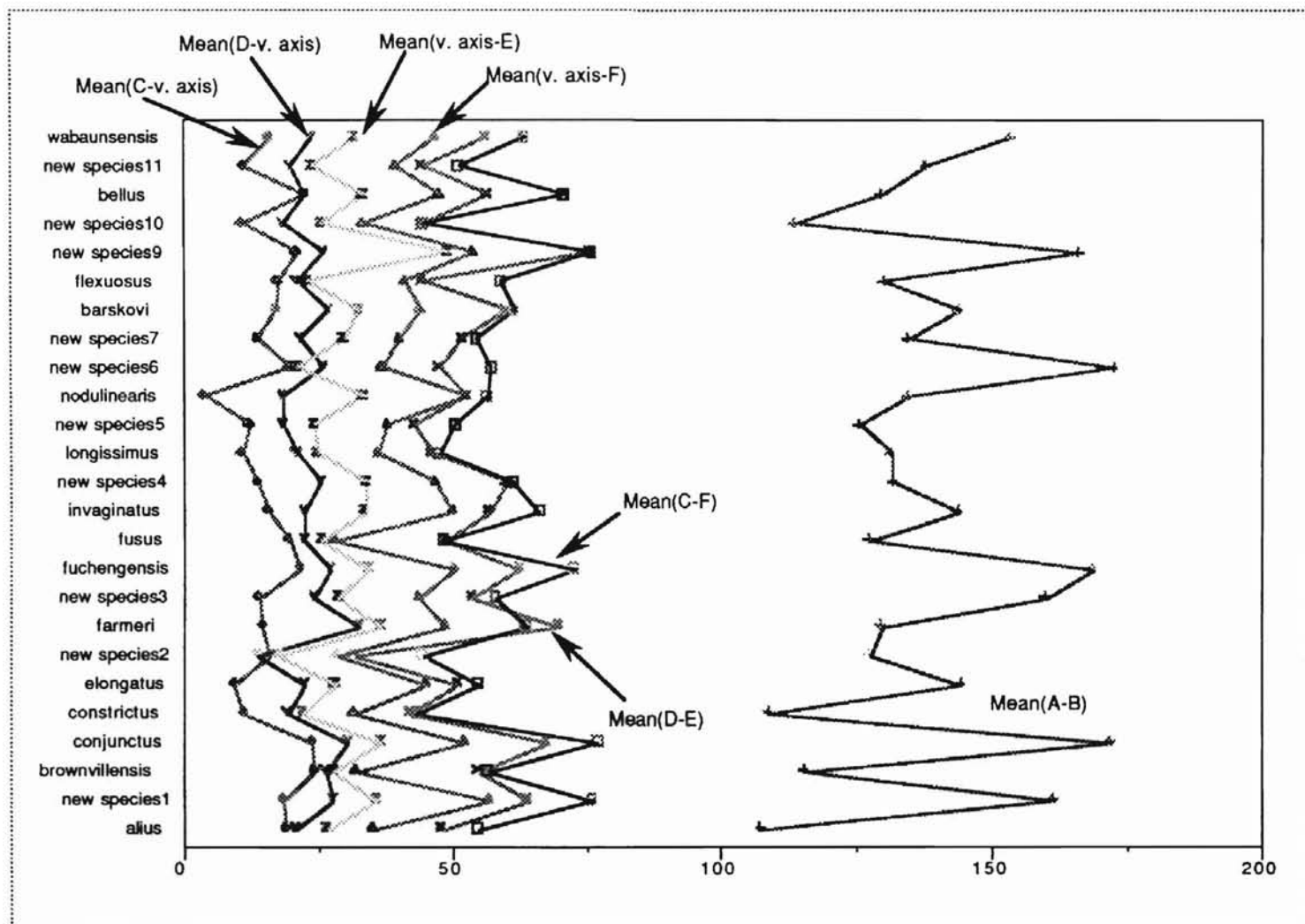


Chart 14
 Sinistral mean comparisons by species.

Old

Correlations

Variable	pltfm	end/...	wid/mid	wid/car
pltfm end/...		1.0000	0.1557	0.1166
wid/mid		0.1557	1.0000	0.4939
wid/car		0.1166	0.4939	1.0000

Robust

Correlations

Variable	pltfm	end/...	wid/mid	wid/car
pltfm end/...		1.0000	0.7898	0.6277
wid/mid		0.7898	1.0000	0.8089
wid/car		0.6277	0.8089	1.0000

Nodular

Correlations

Variable	pltfm	end/...	wid/mid	wid/car
pltfm end/...		1.0000	0.6821	0.4666
wid/mid		0.6821	1.0000	0.8324
wid/car		0.4666	0.8324	1.0000

Elongate

Correlations

Variable	pltfm	end/...	wid/mid	wid/car
pltfm end/...		1.0000	0.7612	0.7863
wid/mid		0.7612	1.0000	0.9027
wid/car		0.7863	0.9027	1.0000

Table 6
Dextral correlation matrices by lineage.

Old

Correlations				
Variable	pltfrm	end/...	wid/mid	wid/car
pltfrm	end/...	1.0000	0.2084	0.0282
wid/mid		0.2084	1.0000	0.8477
wid/car		0.0282	0.8477	1.0000

Robust

Correlations				
Variable	pltfrm	end/...	wid/mid	wid/car
pltfrm	end/...	1.0000	0.7421	0.6347
wid/mid		0.7421	1.0000	0.7946
wid/car		0.6347	0.7946	1.0000

Nodular

Correlations				
Variable	pltfrm	end/...	wid/mid	wid/car
pltfrm	end/...	1.0000	0.5413	0.5284
wid/mid		0.5413	1.0000	0.7579
wid/car		0.5284	0.7579	1.0000

Elongate

Correlations				
Variable	pltfrm	end/...	wid/mid	wid/car
pltfrm	end/...	1.0000	0.7974	0.7419
wid/mid		0.7974	1.0000	0.8969
wid/car		0.7419	0.8969	1.0000

Table 7
Sinistral correlation matrices by lineage.

Variation through Time

In an effort to unravel the evolutionary history and due to their importance to biostratigraphy, to understand the morphologic variation of *Streptognathodus* Pa elements through time is paramount. To this end several examinations of the data using time (stratigraphic) reference points were performed. Again, separation into dextral and sinistral groups was used during this analysis.

No strict 'time-based' pattern was presently discernible from the data for an entire left/right group. Mean values of a variety of parameters were traced through 'time' (stratigraphically) (Charts 15 and 16). Plots for total ridge counts of the left and right groupings are also provided in Chart 17, A and B.

Further analysis of separate clades yielded minor, but notable variation. For example, elements from the sinistral elongate lineage have a very high correlation between horizontal displacement of posterior platform tip and platform length (A-B). In general this correlation was higher for all sinistral members, but this was not true of dextral members (Charts 18 and 19).

Discrimination among Lineages

As described above the specimens were divided into three lineages with a common ancestral group. For most of the morphometric characters analyzed, variation was insufficient to discern groups. Among the numerous characters tested the single character of platform width at middle (C-F) provided by far the most cladistic separation (Chart 7), although there was still significant overlap of values. However, when combined in a ratio with length a very clear discrimination occurs in dextral elements. The {total length}/{width at midpoint} ratio (A-I-/C-F) clearly divides elongate specimens from all others with two exceptions (Chart 8, section A). After re-examination, the first outlier, in the nodular clade, may simply have been misidentified. However, the second, classified as *S. elongianus*, is more interesting. Its placement in the common ancestral grouping and identification appears to be correct. The question then arises: Is this an ancestor of only the elongate lineage, with the three groups having split earlier than previously postulated and not sharing the other ancestral members? Further research with more individuals and of earlier specimens is required to address this issue properly .

If platform length instead of total length is used in the ratio the lineage separation is not so clearly distinct (Chart 8, B). However well over 75% of individuals are still discriminated by this ratio (see Chart 8 quantiles). Chart 9 displays the means of the ratio used above (platform length to width at middle) for all species. A line is drawn at value 2.5, which separates all but

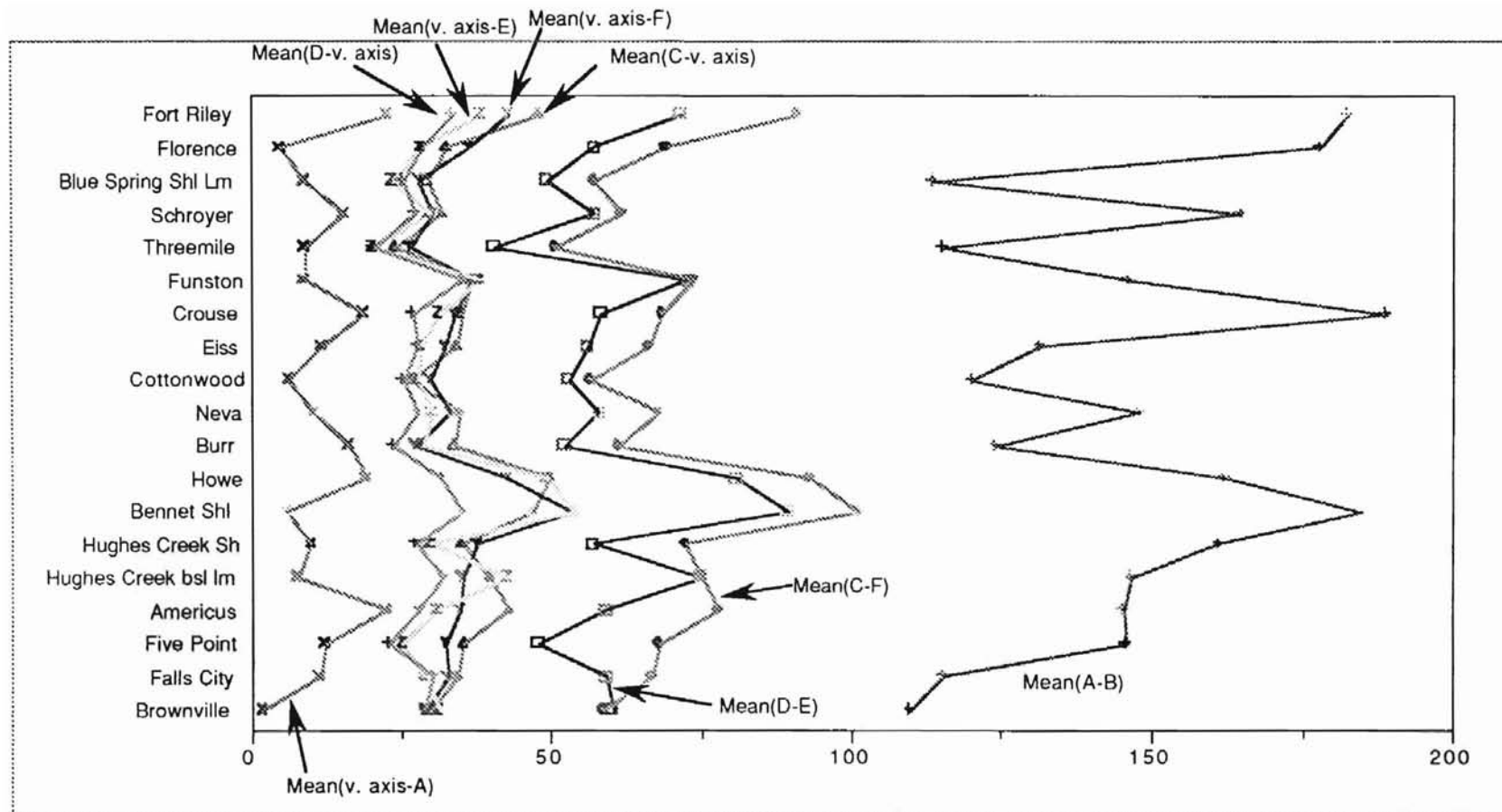


Chart 15
 Mean values of
 dextral elements
 by formations through 'time'

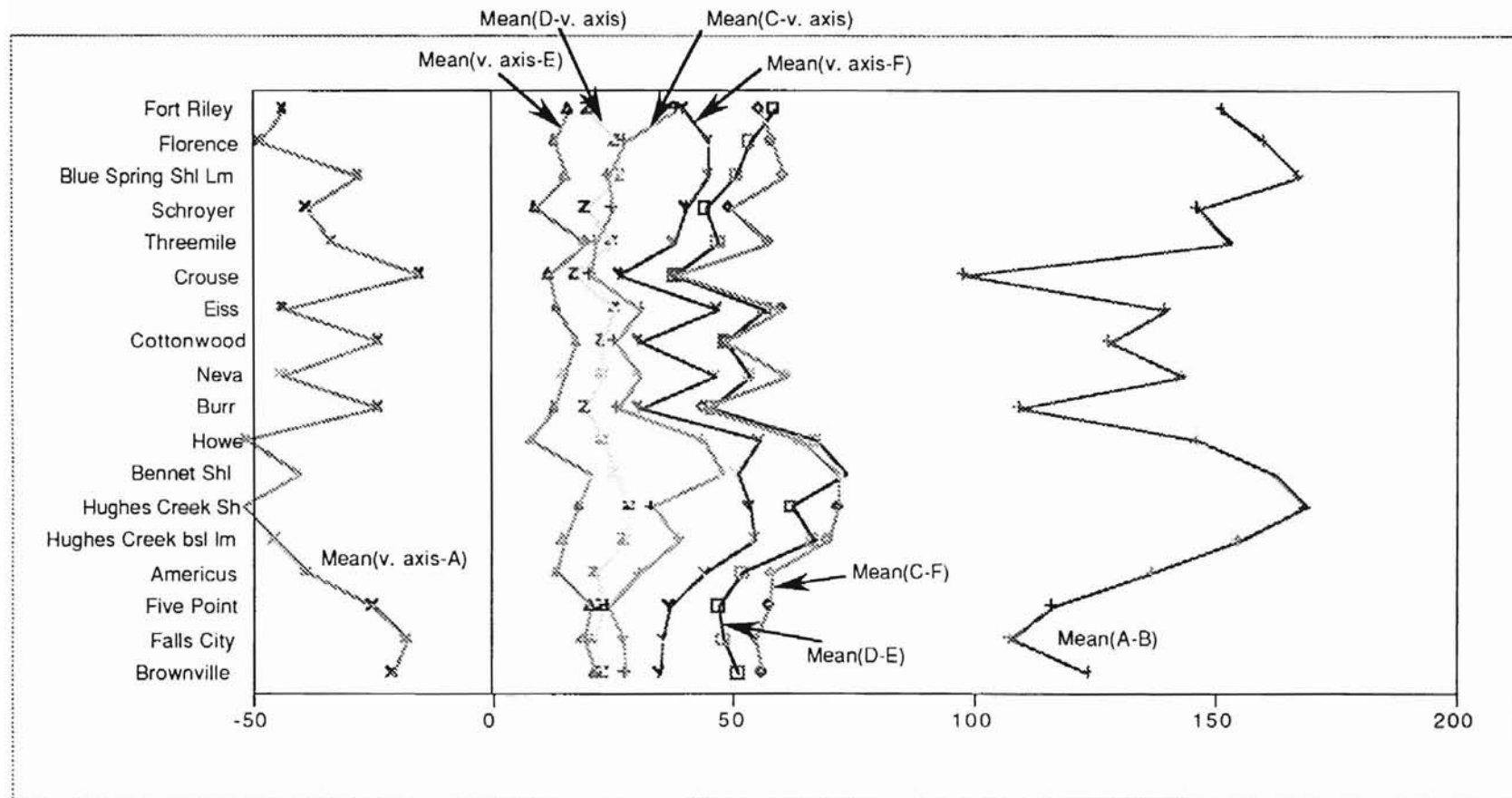


Chart 16
 Mean values of
 sinistral elements
 by formations through 'time'

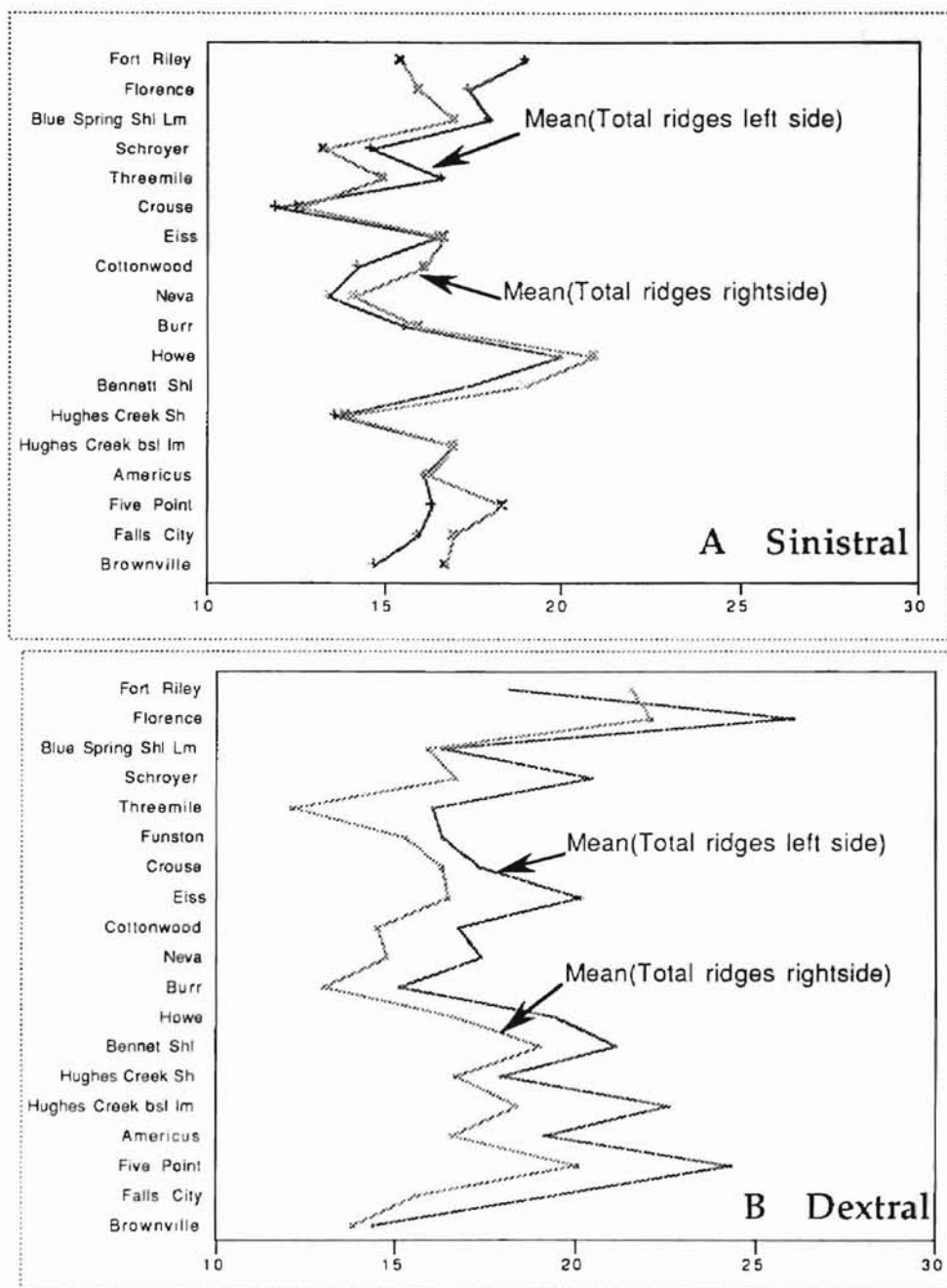
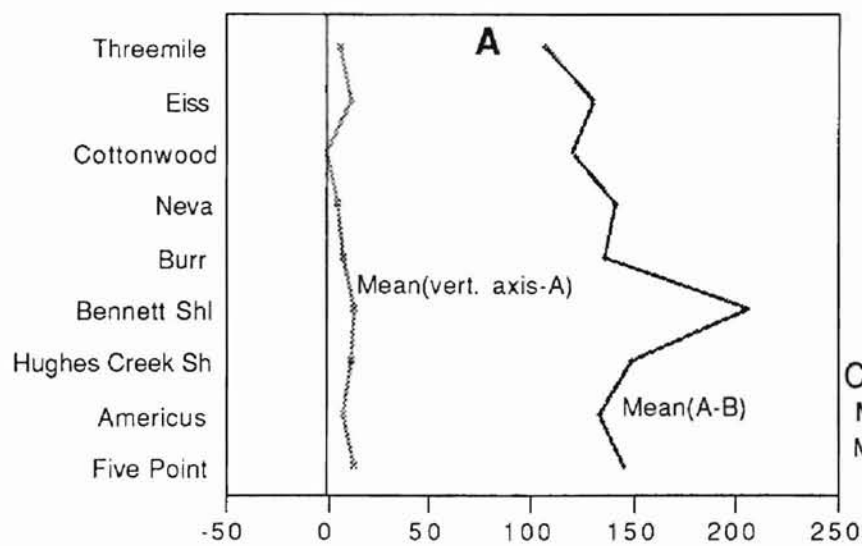


Chart 17

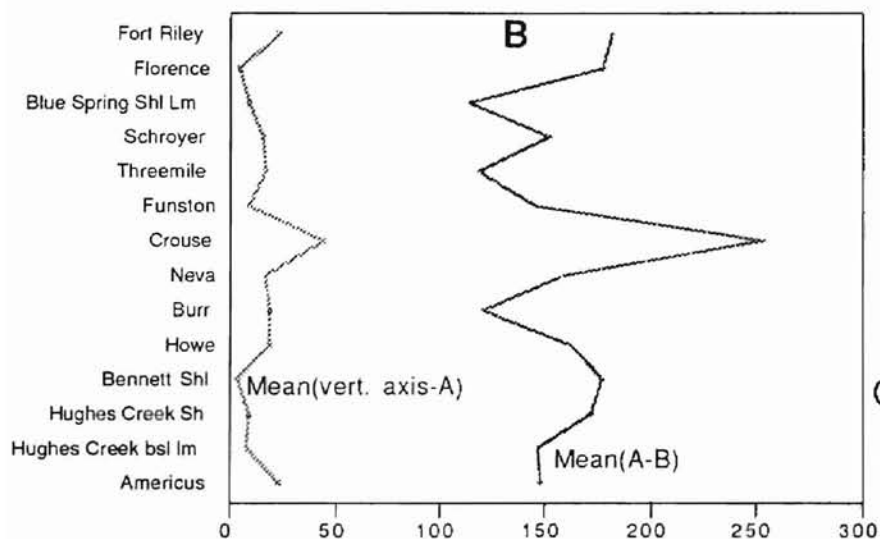
Mean values of
dextral and sinistral element
transverse ridge counts through 'time'.

Chart 18

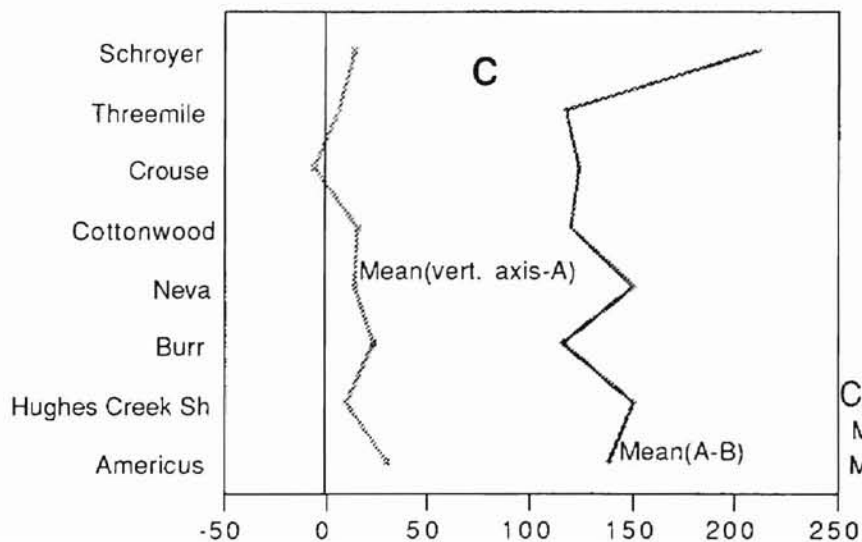
Dextral
mean
comparisons
through
time.



Robust
Correlation
Mean(A-B)
Mean(vert. axis-A)
0.5914



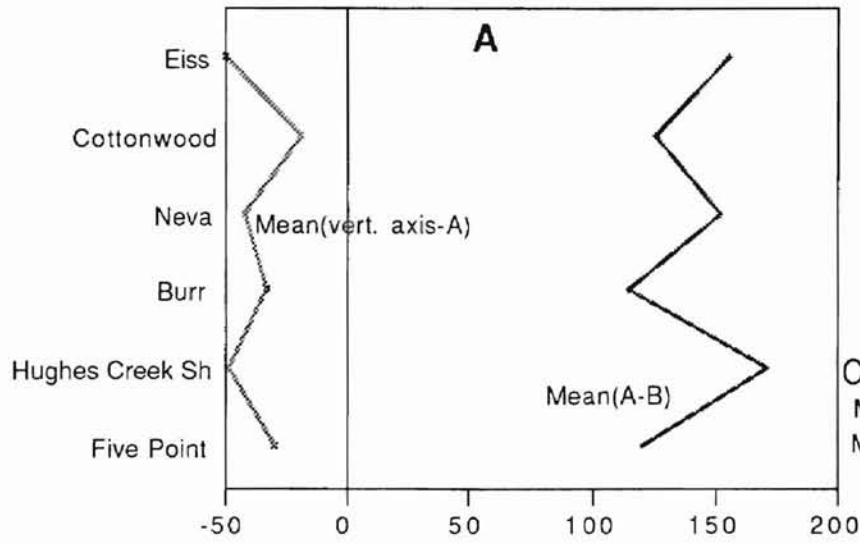
Nodular
Correlation
Mean(A-B)
Mean(vert. axis-A)
0.5387



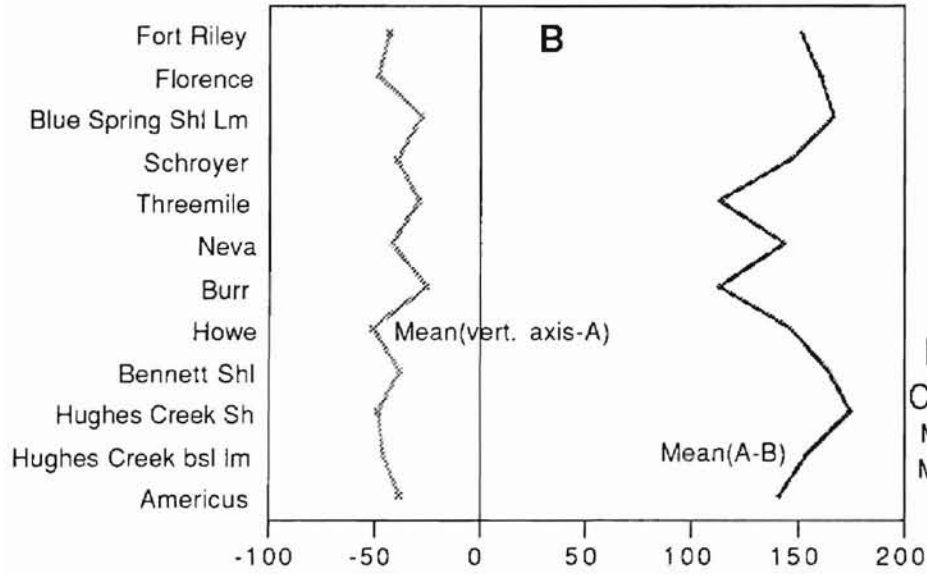
Elongate
Correlation
Mean(A-B)
Mean(vert. axis-A)
0.0710

Chart 19

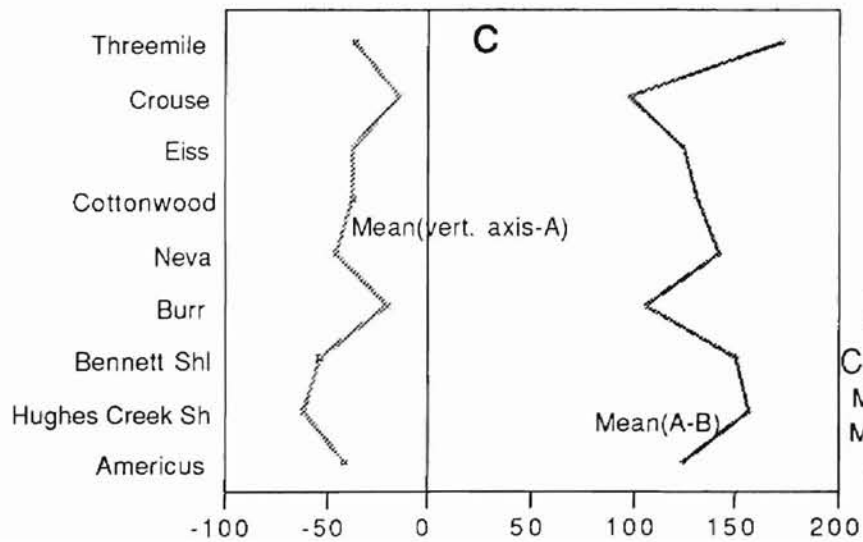
Sinistral mean comparisons through time.



Robust
Correlation
Mean(A-B)
Mean(vert. axis-A)
-0.7986



Nodular
Correlation
Mean(A-B)
Mean(vert. axis-A)
-0.5457



Elongate
Correlation
Mean(A-B)
Mean(vert. axis-A)
-0.7400

CONCLUSIONS

"In comparison with the complex discrimination of shape achieved by the human visual systems and its subsequent analysis by the trained observer, the parameters commonly used to quantify shape seem crude indeed." Todd, 1980

Although the above statement is true, the need for quantitative morphometric analysis is more vital than ever. Even simple statistical analysis can verify or disprove assumptions and empirical observations. In this vein it should be noted that preconceptions may be damaging to even this type of numeric effort and can blind a researcher to certain character relationships or methods of analysis.

This paper attempted to provide uncomplicated means for consistent orientation and measurement of a variety of morphological characters of *Streptognathodus* Pa elements. These efforts were limited to *Streptognathodus*, although these concepts may be applicable to other genera, particularly *Idiognathodus*. Statistical analysis used here reveals that variation within the specimens studied is sufficient to form several conclusions.

However, in many respects there was no appreciable variation in characters measured. Test after test proved inconclusive in efforts to separate the individuals into coherent and distinct groups, either cladistic or by species. In some ways these results are disappointing, in revealing a small amount of variation, but they are still significant. Sometimes it is as important to disprove as much as prove. In all, several groupings with

distinct morphometric variation were found.

This study verified previous observations of asymmetry between left and right Pa elements. This point actually may strengthen the argument of element function as tooth. If, as Purnell strongly advocates, the platforms were used for crushing, it is necessary that the elements be asymmetric. The platforms of truly symmetric element pairs matched at equal positions would not meet, as the height of blade and denticles would effectively prevent motion and surface contact. With truly symmetric elements and a positioning of the left blade behind the right (see Figure 5) to allow for motion, the resulting 'H' position would decrease surface area for crushing. For maximal surface contact area it is thus imperative that at least one platform be more curved than the other. This is the case for sinistral elements, especially for more recent individuals. In fact, when mean reconstructions of sinistral and dextral pairs are aligned (with the blade of the left individual behind the right blade), platform tips nearly match. This is due to the variation in the sinistral elements –i.e.– greater horizontal displacement of posterior platform tip. Speculation such as this can raise more questions than it answers, but is fodder for research and analysis.

Cladistic separation was also accomplished, albeit to a limited extent. The use of simple ratios to separate lineages was demonstrated, along with refinement of previously conceived concepts, as in the possibility of redefining the Elongate group ancestor. Additionally, this type of analysis can be a valuable tool in establishing evolutionary morphologic trends.

For research of this type to succeed the obvious need to quantify additional characters, especially patterns of surface ornamentation (i.e. node fields), would be a primary concern. Quantification of surface ornamentation can be difficult, as noted by Ritter(1989) and it presents special problems in regard to reproducibility. Other morphologic features, such as outlines of platforms, groove depths, etc. also should be examined in detail.

Because coordinate pairs of landmarks were collected rather than inter-landmark distances, use geometric morphometric techniques on this data is possible. These methods may reveal other relationships while using the 'true' shape characteristics of elements as an integral whole. However, these procedures normally cannot include characters such as surface ornamentation, but many traditional statistical approaches can. Further, different methods of traditional statistical analysis of previously derived characters may also be performed.

Subsequent efforts to verify and/or discover distinct groupings within *Streptognathodus* through quantitative morphometric analysis will rely on many of the above concepts. This type study is essential in efforts to resolve various questions of conodont taxonomy, particularly with regard to genus *Streptognathodus*.

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VITA

Timothy Robert Walsh

Candidate for the Degree of

Master of Science

Thesis: PRELIMINARY MORPHOMETRIC ANALYSIS OF
STREPTOGNATHODUS (CONODONT) FROM THE UPPER
PENNSYLVANIAN AND LOWER PERMIAN OF SOUTHERN
KANSAS

Major Field: Geology

Biographical:

Personal Data: Born in Enid, Oklahoma, On January 9, 1957, the son of
Robert and Mary Lou Walsh

Education: Graduated from Chisholm High School, Enid, Oklahoma in
May 1975; received Bachelor of Science degree in Geology from
Phillips University, Enid Oklahoma in May 1978. Completed the
requirements for the Master of Science degree with a major in
Geology at Oklahoma State University in May, 1998.

Experience: Employed as field geologist for private petroleum geology
consulting firm. Formed partnership, Geo-Logic Consultants, with
former employer and acted as general manager and lead geologist
from 1979 to 1984 . Employed as geology and computer science
teacher in Waukomis Public School, Waukomis, Oklahoma 1984 to
present.