Evolution of oral apparatuses in the conodont chordates

JERZY DZIK

Dzik, J. 1991. Evolution of oral apparatuses in the conodont chordates. *Acta Palaeontologica Polonica* **36**, 3, 265-323.

The oldest well known conodonts had seven pairs of their phosphatic denticles arranged into a grasping apparatus closely resembling that of the Chaetognatha. During the Early Ordovician apparatuses with three morphologic groups of elements developed, and a single unpaired element that splits the apparatus into two parts, the posterior one being presumably enclosed into the throat. Subsequent evolution resulted in the development of an incisor-like morphology of the anteriormost pair of elements, a filtratory basket in the remaining exposed part of the apparatus, and a heavily molarized, hidden platform complex. Further development resulted in great diversity of forms of the apparatuses, from secondarily simplified, through robust (of the *Myxine* type), to highly sophisticated apparatuses with all the element pairs being morphologically distinctive. The unusual, ventral location of molarized surfaces in some advanced conodonts suggests some change in muscular armament of the throat. Conodonts reached their greatest diversity in the Middle Ordovician. Co-occurrence of many morphologically similar sympatric species is typical for the Late Paleozoic. A modified classification of the conodonts is proposed.

Key words: conodonts, apparatuses, evolution, Cambrian to Triassic.

Jerzy Dzik, Instytut Paleobiologii PAN, Aleja Żwirki i Wigury 93, 02-089 Warszawa, Poland.

Introduction

Conodonts are known to occur from the Middle Cambrian (or even from the earliest Cambrian if *Fomitchella* belongs here) until the latest Triassic. The most distinctive feature of these animals is the bilaterally symmetrical oral grasping apparatus, analogous to that of the Chaetognatha but composed of phosphatic elements secreted under an epithelial cover in a way similar to the dermal denticles of the vertebrates. As in the chordates, particular elements of the conodont apparatus are composed of two kinds of tissue. The crown was secreted centrifugally from outside, therefore resembling the enamel of the chordates. The conical basal cavity of the crown may be filled with a tissue, which in primitive conodonts is penetrated by channels and minute tubuli (Dzik 1986; Andres 1988), thus somewhat resembling the mesodermally secreted dentine of early vertebrates. Unlike vertebrates, the crown (enamel) formed the main part of the conodont elements and grew steadily, probably without any interruption by piercing. Since the time of discovery of the complete fossil conodont animal in the Carboniferous (Briggs *et al.* 1983, Aldridge *et al.* 1986), it is known that the body was naked, of lamprey shape, with V-shaped myomeres and an asymmetrical caudal fin.

The only other group of fossil organisms that had a similar mode of secretion of a phosphatic skeleton and that preceded the conodonts stratigraphically is represented in the Cambrian and Ordovician by problematic sclerites of *Hadimopanella*, *Utahphospha*, and *Milaculum* (Dzik 1986). It is possible that these belonged to the priapulid-like Palaeoscolecida (van den Boogard 1989; see Kraft & Mergl 1989, Hinz *et al.* 1990). This may mean that the chordates inherited the mode of secretion of their phosphatic dermal scales from worm-like ancestors. In such a case the origin of the conodonts from hypothetical earliest chordates, which had their bodies covered with minute conical phosphatic denticles secreted in epithelial pockets, was connected with transition to a fully pelagic mode of life and loss of the dermal armor. The denticles became restricted to the oral area where they helped in catching prey. The only anatomically known possible westergaardodinid conodont ('paraconodont') *Odontogriphus* from the Middle Cambrian, with its annulated body and an oral apparatus of coniform sclerites, seems to fit this interpretation.

Virtually all we can say about the conodonts is a result of studies of their apparatuses. The apparatuses were composed of several pairs of phosphatic denticles, which were the parts of the conodont body most resistant to decay. Embedded separately in the soft tissue of the head, they occur frequently in fossil sediment as well-preserved, but almost always disarticulated elements. The disparity in chemical composition between the apatite elements and a rock matrix enables their easy extraction. Owing to mass occurrence in marine rocks of Late Cambrian to Late Triassic ages, evolutionary studies of conodont apparatuses is a routine method of time correlation in geology. The present precision and reliability in conodont-based correlation of Ordovician and Silurian rocks could hardly have be reached if apparatus reconstructions were not used. One may expect that further research on the evolution of apparatuses of the Late Paleozoic conodonts will result in a comparable precision in correlation.

The conodont apparatuses are also of great, although still not adequately recognized and appreciated, biological importance. The morphology of an apparatus contains much information, perhaps even more than can be inferred from morphologies of mammalian jaws; conodont apparatuses are comparable in this respect with vertebrate skulls or echinoderm thecae. Unlike these latter fossils, widely used in evolutionary studies, easily identifiable conodont elements occur in great numbers in rock sections covering large amounts of geological time, being also not so sensitive to rock facies changes. This makes them an almost ideal object of studies on evolution.

The present review will start with a presentation of basic arguments, derived from infrequent finds of articulated elements, which indicate that they were always originally assembled into apparatuses. Standard methods enabling reconstruction of the original apparatus composition from isolated elements will be briefly presented subsequently. The inferred three-dimesional organization of the apparatuses in major groups of conodonts and terminology of isolated elements and apparatuses will then be discussed. Later on, a review of apparatus diversity within particular families and patterns of evolutionary transformations will follow. Somewhat speculative interpretations of the functional meaning of particular evolutionary modifications and their implications regarding taxonomy of the conodonts will close the paper.

Natural assemblages and clusters *vs.* the fish-teeth paradigm

Christian H. Pander (1856) believed that the conodont elements discovered by him represented teeth of an unknown group of fish. Conical shapes dominating among elements occurring in the Ordovician 'Glaukonitsand', as well as their coloration and transparency, really very similar to fish teeth, substantiated this view. Although there have been later claims that histologically conodont elements are unlike teeth (Rohon & Zittel 1886; Gross 1954), at least some authors supported homology between the crown tissue of conodonts and the enamel of vertebrates and, consequently, the basal filling tissue and the dentine (Schmidt & Müller 1964; Dzik 1986). The tooth function of the conodont elements has found support also in functional analyses (Jeppson 1979; Nicoll 1985) although the way in which they acted, being covered with an epithelial tissue, remains a mystery (but see Bengtson 1976 and Carls 1977). Anyway, if one, like Pander, accepts the fish-tooth analogy (and/or homology) for the conodont elements, it is reasonable to expect that the diversity of elements within the same conodont animal was similar to the diversity of teeth in fish jaws, that is rather low and with continuous morphologic gradations in series. This is why Pander and his followers considered every discrete type of conodont element as representing a separate species.

G.J. Hinde (1879) was the first paleontologist to differ with the foregoing reasoning. He found inspiration in aggregates of conodont elements occurring on the bedding surfaces of the Late Devonian Genesee Shale. All the diverse elements of the same aggregate were interpreted by him as representing the same species. His reconstruction of the composition of the assemblage of elements belonging to the conodont animal has appeared later to be quite close to the real apparatus but it also has become obvious that these aggregates of elements represent coprolites or food balls of animals eating conodonts (Huddle 1972). This has made subsequent conodont workers extremely cautious in interpreting any assemblage of conodont elements. The first findings of true conodont apparatuses preserved on the bedding surface of the rock (Schmidt 1934; Scott 1935) met therefore much scepticism. It was not until the monographic treatment of natural assemblages of elements by Rhodes (1952, 1954) that most conodont investigators accepted a direct correspondence between the assemblages and conodont apparatuses.

The term 'natural assemblage' is generally applied to an aggregate of elements on the rock bedding surface assumed to represent an articulated conodont apparatus (Fig. 1, 3A). Aggregates of elements that remain connected even after treatment of the rock with acid (owing to an insoluble mineral or organic substances keeping particular elements together) are called 'clusters'. Usually natural assemblages represent complete apparatuses while clusters are their fragments.

Supposedly most of such associations of elements originated through fossilization of conodont animal bodies in extremely quiet environments of sedimentation. However, at least some of them represent remnants of conodonts, that passed through digestive tracts of scavengers. In some cases this is clearly evidenced by the preservation of apparatuses of more than one animal together (Lange 1968), an admixture of elements representing another species (von Bitter 1976), or inferred features of displacement of elements in the apparatus (Dzik & Drygant 1986). Natural assemblages could thus represent contents of coprolites even if any obvious evidence of this is lacking. Anyway, whether they passed through a digestive tract or not, assemblages of conodont elements remain a valuable source of data as long as there is independent evidence for their completeness. Such an evidence can be provided by other natural assemblages showing identical composition, as well as by apparatus reconstructions based on other lines of reasoning. The term 'coprolitic association' has to be applied only to associations of elements which are clearly unnatural and are supposed to originate by assembling together remnants of different species of conodonts in a scavenger stomach.

The most important result of early investigations of natural assemblages was the unequivocal conclusion that conodont apparatuses were bilaterally organized, with elements arranged in morphologically distinct pairs. The fish-tooth (as well as fish scale) model was thus finally refuted. The conodont apparatus appeared to be similar rather to that of the eunicid polychaetes (Rhodes 1952) and hagfishes (Huddle 1973; Dzik 1986; Sweet 1988).

Detailed studies on the spatial organization and functional morphology of conodont apparatuses, based on natural assemblages and clusters, had to be preceded by recognition of their exact element composition. The natural assemblages themselves are not convenient objects of morphologic investigation of particular elements because they are almost always crushed (an effect of sediment compaction), incomplete, and obscured by the rock matrix. The three-dimensional morphology of elements can be adequately studied only with elements freed from the rock either by washing of a loose sediment (as Pander did) or by dissolving the limestone matrix with acetic or formic acid, as for the first time was reported by Graves & Ellison (1941). The latter method appeared especially profitable, resulting in extraction of complete elements in their original shape, as when they were enclosed by the sediment (Fig. 2).

Acid in the hand of stratigraphic paleontologists tremendously increased the value of conodonts as age indicators in geology. In fact, hundreds of thousands of specimens have been collected and identified. It was only a matter of time that methods of reconstruction of the original apparatus composition based on these isolated elements were developed.

The symmetry transition series and the platform complex

The first step in the recognition of the original composition of conodont apparatuses on the basis of isolated elements was the observation that at least some element types recurrently occurring in samples can be arranged in morphoclines with stepwisely increasing asymmetry of particular elements (Sweet & Bergström 1962). Such a morphocline was named the 'symmetry transition series' by Lindström (1964). To apply separate Linnean names to each member of a symmetry transition series would be tantamount to a highly unrealistic assumption that there are series of closely morphologically related species, which always occur together in stable numerical proportions. Another interpretation, that the symmetry transition series represents apparatuses or, at least, their parts, was thus reasonable, the more so because such a gradation of element shapes was already recognized in natural assemblages.

Recurrent association and morphologic similarity characterize also another series of elements, usually composed of two types of robust elements, which was named the 'platform complex' by Lindström (1964). Later Sweet & Schönlaub (1975) introduced a term 'pectiniform' for elements of the platform complex, derived from their usual shape in early ozarkodinids, while Nicoll (1985) proposed to name them the 'contundens elements', referring to their proposed grinding function.

The symmetry transition series and platform complex are supplemented in many conodonts by a single element type, which is morphologically quite distinct from the rest of the apparatus, and which was named the 'makelliform element' by Sweet & Schönlaub (1975).

Homologues of particular elements of the platform complex, symmetry transition series, and the makelliform element can be traced even among conodonts having very simple apparatuses, which are not differentiated into discrete series of element types. In several apparatuses the homologue of the makelliform element appears to be the end-member of the symmetry transition series. In some simple apparatuses of coniform elements there is only a single symmetry transition series embracing all element types. There are also rare apparatuses in which quite different, sometimes unique, morphologic series of elements had developed or there is no apparent similarity between particular element types at all.

Inductionist approaches to apparatus reconstruction

While studying numerous samples of isolated conodont elements one can easily notice that some platform complexes, symmetry transition series, and makelliform elements are recurrently associated, while others occur in changing combinations. As all these three groups of discrete element types are known to occur in complete natural assemblages, this is just enough to assemble them together to reconstruct the exact composition of particular apparatus. For the first time this was done by Huckriede (1958) who gave a list of element types proposed to represent apparatuses of two Triassic conodont animals.

If many samples from strata of approximately uniform age are available, the above method of inference appears simple enough to allow apparatus reconstruction by a single inspection of the frequency data matrix. It is tempting to apply then one of several available methods of numerical analysis of data matrices and this was performed by Kohut (1969), von Bitter (1972), and other early students of conodont apparatuses. Most of these studies were based on presence/absence methods and they generally supported reconstructions of apparatuses proposed earlier on the basis of more or less intuitive approaches.

A wider application of inductionist statistical methods to reconstruction of conodont apparatuses is hampered by two features of data sets: nomenclatorial inconsistencies caused by mosaic evolution of elements within the apparatus and unbalancing of samples. The latter factor, resulting in unstable ratios between element types, dependent on the energy of the environment of sedimentation, appeared to be especially destructive in this respect and mostly because of it statistical methods have not helped in apparatus studies as much as was expected. Rather, numerical methods are used to test hypotheses proposed without such sophisticated soft- and hardware.

It is rarely possible to gather extensive collections of conodont elements from a single geological horizon in many localities, like those from the Late Ordovician of the North American Midcontinent, on which the first monographic presentations of reconstructed conodont apparatuses were based

Fig. 1. Natural assemblage of conodont elements of an early species of *Hemilistrona* from the Famennian of Moravský Beroun, Czechoslovakia (photograph courtesy of Dr. Jana Zikmundová, Prague; published also in Habětín, V. & Knobloch, E. 1981. Kapesní atlas zkamenělin. SPN, Praha).

(Bergström & Sweet 1966; Webers 1966). What one usually has are samples covering a significant geological time span. This strengthens the bias introduced by mosaic evolution of conodont apparatuses and complicates handling of data even in the most simple cases. As a result of this particular feature of evolution the same kind of element may occur in several different apparatuses (Klapper & Philip 1971) and practically each element type has its own, different stratigraphic range. To overcome this obstacle one has to base considerations not on particular morphologic types but rather on whole series of homologues of elements (Dzik 1976;

van den Boogard & Kuhry 1979). Thus apparatus reconstruction should be involved in a feedback with phylogenetic studies.

Numerical proportions among particular element types in samples are virtually never consistent with expectations derived from our knowledge of natural assemblages. Usual overrepresentation of the platform complex and underrepresentation of gracile elements of the symmetry transition series suggest that this is a result of selective sorting and preservation of elements (McGoff & Briggs 1988). It has been shown that due to the action of these factors almost all chi-square tests applied to quantitative data on conodont element distribution lead to rejection of apparatus reconstructions (van den Boogard & Kuhry 1979: p. 4).

Hypothetico-deductive methods in the apparatus studies

It can safely be said that it is not so important what was the reason for presentation of particular apparatus reconstruction but, instead, it is of crucial importance how this reconstruction behaves in tests. This Popperian approach to apparatus reconstruction appears to be the most efficient tool in conodont studies.

Because of the biases cited above the applicability of statistical methods to testing apparatus reconstructions is somewhat restricted. Perhaps the most appropriate method of data processing is factor analysis (van den Boogard & Kuhry 1979) although there is a great diversity of useful methods (see e.g. Horowitz & Rexroad 1982; Sweet 1988). One may doubt, however, whether it is possible to reject definitively any hypothesis in this way. At best, they can be graded as less or more probable.

Although it is generally true that the efficiency of testing hypothetical apparatus reconstructions depends on the number of available samples, it is also not without importance what size are particular samples and what is their stratigraphic and geographical provenance. In fact, even a few large samples may allow severe tests of a hypothesis, granting that they are different enough in composition to have their component species in combinations excluding certain associations. Therefore it is helpful to have samples from at least different facies if not biogeographic provinces. They should be close enough to share some species but different enough to ensure that other species are missing in some of them. Then negative arguments can be used for reconstruction of the apparatuses, which otherwise are difficultly separated from their close allies. Some possible combinations of elements in apparatuses can be definitely rejected in this way.

Thus, it is generally more profitable to consider a few large samples than many small ones. The sample size has to be large enough to ensure that the majority of element types are represented in statistically significant numbers. In practice this means that in the case of rather well balanced samples from the Early Paleozoic an optimum number of elements per

Fig. 2. Isolated elements of hibbardellid *Prionidina* sp. (A-H) and palmatolepidid *Mesotaxis* sp. (I-R) from the earliest Frasnian of Wietrznia in the Holy Cross Mountains (sample WTR-11), all × 66.

sample would vary from one to three thousand (depending on diversity of a fossil assemblage), while in the case of unbalanced Devonian ones identification of apparatuses may require even greater numbers of elements.

Three-dimensional organization of the apparatus

In early reconstructions of conodont apparatuses, based on natural assemblages of Carboniferous age (Schmidt 1934; Rhodes 1952, 1954) it was assumed that the most common orientation of elements on the rock surface roughly corresponds to their original life position. Elements were thus reconstructed as arranged parallel to the long axis of the apparatus, attached to a common surface with all the cusps oriented in the same direction (Schmidt 1934; Nicoll 1985), medially (Rhodes 1952, 1954; Collinson *et al.* 1972), or radially (Lindström 1964, 1973, 1974). Most of the Carboniferous natural assemblages are preserved in a way which does not contradict these interpretations. Nevertheless, there are some natural assemblages, the most important being that of Mashkova (1972; here Fig. 3A), and many clusters with an organization totally incompatible with all the above reconstructions. To explain at least some peculiarities of these clusters an idea of 'tetanus' was introduced, according to which a post-mortem muscle contraction resulted in the present opposing position of elements in clusters (Rexroad & Nicoll 1964). It seems more reasonable, however, to interpret these natural assemblages and clusters as resulting from different directions of compression of the original apparatus structure in the process of fossilization. The three-dimensional organization of the apparatus, from which all configurations known among natural assemblages can be easily derived in this way, is that with particular elements arranged almost parallel to each other but transversely to the apparatus long axis and with opposing cusps (Fig. 3B; Dzik 1976, 1986; Aldridge *et al.* 1987; Smith 1990).

An even more precise analysis of the element orientation is enabled with well preserved natural assemblages and clusters. One may note thus that:

(1) Laterally compressed undisturbed natural assemblages have cusps of their elements oriented always toward that end of the apparatus that bears the makelliform element pair (that is, anteriorly).

(2) Elements of the symmetry transition series have their cusps either hidden under processes of these elements which are located in front of them (sinistral series) or lying on the elements located in front of them (dextral series; see Fig. 3A). These two observations indicate that during life the element cusps were inclined somewhat anteriorly. This led Aldridge *et al.* (1987) to propose that the elements of the symmetry transition series had cusps oriented anteriorly. Such a model, however, is a poor fit with natural assemblages arranged in a linear pattern (Aldridge *et al.* 1987: Fig. 4.12) and its weakness is clear even if the parallel or perpendicular

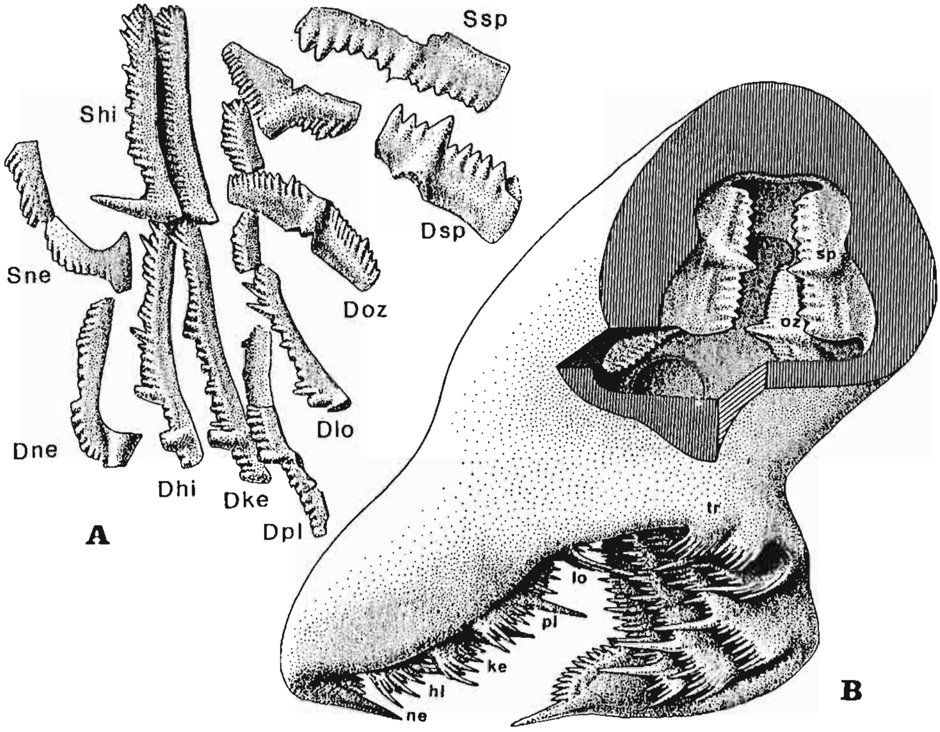

Fig. 3. □A. Identification of elements, following Jeppson's (1979) suggestions, in the assemblage of *Pandorinellina remscheidensis* (Ziegler 1956) from the Gedinnian of Tadjikistan described by Mashkova (1972). □B. Three-dimensional reconstruction of the apparatus of the same species. A postero-ventral view of the head of the conodont animal 'cut out' in a way allowing presentation of the platform complex in the throat (modified after Dzik 1986).

patterns are considered. It seems thus that the left and right series of the symmetry transition series formed rather a V-shaped structure which gaped anteriorly (Fig. 3B).

(3) Elements of the platform complex deviated slightly in the orientation of their processes from the rest of the apparatus and their cusps are distributed randomly in natural assemblages either forward or backward (although always opposed in every pair). In clusters they occur usually in precise occlusion (Pollock 1969; Mietto 1982; Nicoll 1987, and others). This, in turn, indicates that their cusps during life were exactly opposed, unlike the symmetry transition series elements.

(4) In well preserved clusters of ozarkodinid conodonts (Lange 1968; Nicoll 1985, 1987) a bilaterally symmetrical element seems to bind posteriorly the left and right wings of the symmetry transition series. This element has its cusp oriented forward (Fig. 3B). However, in clusters of *Cordylodus* (Andres 1988) and *Besselodus* (Aldridge 1982) all the elements are arranged linearly and there is no evidence for any medial element

disturbing this arrangement (Fig. 4A), although isolated symmetrical elements are known at least in some species (Nicoll 1990).

Accordingly, a provisional reconstruction of the apparatus of the ozarkodinid conodonts shows (Fig. 3B) a basket formed by the two mirror-image parts of the symmetry transition series connected into a single functional unit by the medial symmetrical element. The platform complex, set somewhat apart, has its elements opposing each other in pairs. Descriptive terminology for sides of the whole apparatus and elements will follow in this paper this proposed arrangement instead of the traditional convention based on the fish-tooth model of the conodont elements.

Any speculation about functions of the conodont apparatus unavoidably leads to the conclusion that the robust elements of the platform complex, supposed to crush food particles, must be located behind the basket of the symmetry transition series, believed to perform filtering or grasping functions (Dzik 1976; Jeppson 1979; Nicoll 1985, 1987b; Aldridge *et al.* 1987). These expectations were confirmed fully by the discovery of a Carboniferous conodont with preserved remnants of soft parts (Briggs *et al.* 1983). Furthermore, the distribution of elements in laterally compressed natural assemblages (see Fig. 1A,B) clearly indicates that in the Ozarkodinida the makelliform element pair was located in front of the rest of the apparatus, being followed by two pairs of 'hindeodella' elements, a pair of 'plectospathodus' elements, a pair of angularly bent elements, and an unpaired medial symmetrical element. The presence of the pair inserted between the 'plectospathodus' and the symmetrical element is evident in *Manticolepis* and *Polygnathus* (Lange 1968), *Gondolella* (von Bitter 1976; Rieber 1980), *Gnathodus* (Lane & Ziegler 1984) and *Ozarkodina* (Nicoll & Rexroad 1987). Its presence seems typical for all conodonts. Two types of 'plectospathodus'-like elements seem to occur in the Late Ordovician ancestor of the *Ozarkodina* lineage (Nowlan *et al.* 1988) and even in the Early Ordovician *Microzarkodina* (Stouge & Bagnoli 1991), the oldest representative of the order. Perhaps numerical domination of the 'tetraprioniodus' element type in samples of the Ordovician Balognathidae is a result of its occurrence in two pairs. No such domination in number of associated elements of the symmetry transition is observed and this is interpreted as the evidence for two separate element types being present in the Prioniodontida in positions homologous to two ozarkodinid 'hindeodellas' (Dzik 1976). In the Gondolellidae there were five, instead of two, pairs of almost identical 'hindeodella' elements (Ramovš 1977, 1978; Rieber 1980).

Elements of the platform complex are rarely found together with the rest of the apparatus in clusters, and in natural assemblages they are somewhat apart. There is a distinct morphologic discontinuity between them and the rest of the apparatus. The most robust pair of the complex is invariably located at the posterior end of the apparatus. Judging from this position of the platform complex and the orientation of its elements it seems that it was hidden inside the body, probably in the throat.

The model of the conodont apparatus with seven pairs of elements with an additional median one allows for potential occurrence of eight element types but the usual number is lower. Virtually all well known natural assemblages of conodont elements are of the Late Paleozoic age and they represent a single branch of the evolutionary tree, the derivatives of the Silurian *Ozarkodina*. Another great branch of the mostly Early Palaeozoic relatives of the Ordovician *Prioniodus* is known exclusively from isolated elements. They show a similar pattern of morphologic variability within the apparatus as the Ozarkodinina. It is possible to trace homology of elements in both these groups back in time to the stage of coniform common ancestors of *Prioniodus* and *Ozarkodina*. *Drepanodus*-like apparatuses composed of robust coniform elements appear to be the most archaic ones that still show the presence of distinct element series supposedly homologous to those in advanced ozarkodinid and prioniodontid apparatuses (Dzik 1990a). The homology can be traced to *Prioniodus* through *Acodus* and to *Ozarkodina* through *Rossodus*, *Oistodus*, and *Microzarkodina* (Dzik 1983). Except that probably in the Prioniodontida instead of two identical element pairs there were two distinct types homologous to 'hindeodella' while their 'tetraprioniodus' elements correspond to two distinct element pairs in the Ozarkodinida, they all are basically similar. An unexpected complication appears when tracing of homologies between elements of the *Drepanodus* and *Panderodus* apparatuses are attempted. Although there seems to be a consensus regarding homology of their main element types (Barrick 1977; Sweet 1979; Dzik & Drygant 1986; Smith *et al.* 1987) the apparatuses seem to show opposite polarities in size gradients of their elements, with the supposed homologues of the platform series being the smallest ones in the apparatus of *Panderodus* (Dzik & Drygant 1986). No discontinuity in distribution of morphologies within the apparatus of *Panderodus* is observed that could be compared with the distinction between the platform complex and the symmetry transition series in the Ozarkodinida and Prioniodontida. All elements of each side of the apparatus in *Besselodus*, *Panderodus*, and *Cordylodus* seem to compose a single symmetry transition series (Andres 1981, 1988; Aldridge 1982; Dzik & Drygant 1986; Smith *et al.* 1987). In several genera belonging to this group (*Dapsilodus*, *Scabbardella*, *Belodina*) symmetrical elements are completely lacking in the apparatus, while in *Panderodus* some species possess them, others do not. Thus, it seems possible that, when symmetrical elements occurred, they were located behind the whole apparatus or, perhaps more likely, were paired (Fig. 4A). Consequently, any homology between the symmetrical elements of *Panderodus* and *Drepanodus* remains problematical.

It may be provisionally concluded that the most primitive conodonts had seven pairs of coniform elements in their apparatuses, while in later conodonts a symmetrical element was inserted between the fourth and fifth pair.

Element notation: location and homology

In early apparatus studies particular element types of the apparatus were labelled with binomens of former single-element species or with such generic names alone. This was rather inconvenient and easily led to confusion with the taxonomic nomenclature of the whole apparatus. Because of this, several special nomenclatorial systems, designed solely for elements within the apparatus, have been proposed.

The idea of element notation was thus derived from, and remains nothing more than a modification of, the earlier monoelemental taxonomy. An element type is a unit that groups corresponding elements from different apparatuses. The correspondence is generally accepted to be of an evolutionary nature, morphologic differences being assumed to be a result of the divergent evolution of the apparatuses. A common ancestry is, in the framework of this concept, the basis for identification of different elements as representing the same type. The ancestry can be identified on the basis of a similarity in morphologic design of elements and/or their position in the apparatuses. Thus, for instance, elements with a long, robust cusp and characteristically bent processes, which occupy the frontal position in the apparatuses of the ozarkodinid conodonts and are derivatives of the common geniculate ancestor, are classified as the makelliform elements. Particular notation symbols are thus implicitly designed to designate homologues, even if one declines to admit this (like Sweet *in* Clark *et al.* 1981: p. W20). In this respect all the different notation schemes are quite uniform, being based on the same philosophy.

Provenances of particular notation symbols are very diverse. The system of Jeppson (1971), which has priority being, among widely used ones, published first, derives its symbols from the first two letters of former generic names of elements that appeared to belong to the apparatus of *Ozarkodina.* This apparatus was thus implicitly indicated as the reference standard for homologization. This remains well within the spirit of biological terminology, where many anatomical terms were derived in a similar way. Other notation systems refer rather to morphologic groups of elements in the apparatus. The most widely used system of this kind is that of Sweet (Sweet & Schönlaub 1975, modified by Sweet *in* Clark *et al.* 1981). The symbols of the element types are composed of a capitalized letter, indicating an assignment to a morphologic series of elements in the apparatus, and a small letter indicating proposed position in the series (Table 1). Although Sweet (*in* Clark *et al.* 1981: p. W18) clearly stated that his system is applicable only to morphologically discrete element types he, in fact, introduced the idea of a location in the apparatus, which does not necessarily need to correspond to any recognizable morphologically (para)taxonomic unit. It is quite common that several locations are occupied by the same element type.

Any notation system may thus serve both for indicating the homology of elements and their position in the apparatus. It is, however, rarely

Table 1
Homology between locations in different element notation systems.

used here	Jeppson (1971)	von Bitter (1976)	Klapper & Philip (1971)	van den Boogard & Kuhry (1979)	Sweet & Schönlaub (1975)	Sweet & Clarke *et al.* (1981)	Sweet & Clarke *et al.* (1981)	Barnes *et al.* (1979)	Sparling (1981)
Ozarkodina	*Ozarkodina*	*Gondolella*	*Manticolepis*	*Manticolepis*	*Oulodus*	*Oulodus*	*Amorphognathus*	*Prioniodus*	*Polygnathus*
ne	ne	Ne	N	N1	M	M	M	e	N
hi	hi	Hi	A1	N2	Sc	Sc	Sc	a	A1
ke	hi	Hi	A1	N2	Sc	Sc	Sb	b	A1
pl	pl	Syn	A2	A1	Sb	Sb	Sd	d	Aa
lo	pl	Lo	A3	A2	Sb	Sb	Sd	d	Ap
tr	tr	Tr	A3	A3	Sa	Sa	Sa	c	A3
oz	oz	Oz	O1	O	Pa	Pb	Pb	f	O1
sp	sp	Sp	P	P	Pb	Pa	Pa	g	P

possible to determine the exact number of elements in the apparatus on the basis of the morphology of isolated elements. Well preserved clusters show that, even if every pair may be somewhat different morphologically, this is frequently expressed only in small differences of the length and curvature of their processes (see Ramovš 1978; Nicoll 1985, 1987). In this sense most, if not all, apparatuses are octomembrate. Nevertheless, such a slight morphologic difference can hardly be discerned in samples of loose fossil elements being completely obscured by ontogenetic and population variability. Moreover, as a result of evolution not only a single element type can diversify into several others but an opposite process, in which two element types can be reduced to a single one, has been documented (Dzik 1976, 1990a). One has then to decide at what stage of such evolutionary convergence there are still two discrete element types and when to start counting them as a single type. The concepts of penta-, sexti-, or septimembrate apparatuses remain only a convention to express a degree of diversification of elements within the apparatus. It definitely depends on the personal preferences of students to exaggerate or rather ignore the differences between element types and, being subjectively biased, cannot be considered as a strict measure in the apparatus taxonomy.

The simplest solution of the problem is to accept the idea that the element notation refers strictly to locations in the apparatus, whether respective elements are distinct morphologically or not. This enables application of the same system to both natural assemblages and isolated elements. In the latter case it is possible only to indicate all locations in the apparatus that are expected to be occupied by an element type (Dzik & Drygant 1986). Thus, for instance in the *Baltoniodus variabilis* apparatus where the elements occupying locations **ke** and **hi** are hard to recognize, it seems reasonable to label all of them **ke**-**hi**.

A lack of a clearly indicated reference standard for a notation system is always a potential source of misunderstanding. I thus firmly support the original indication of *Ozarkodina* as the reference standard for homologization (Jeppson 1971). At the present stage of knowledge of the conodont apparatuses it seems necessary to have also some other, provisional standards, more or rather less precisely homologized with the *Ozarkodina* apparatus. Well suited for such a purpose are among the prioniodontids *Amorphognathus*, the palmatolepidids *Manticolepis*, and among the simple-cone apparatuses *Drepanodus* (Dzik 1990a).

Taxonomy and nomenclature of apparatuses

When early reconstructions of the conodont apparatuses based on isolated elements were proposed by Walliser (1964), he labelled each apparatus with letter symbols followed by a list of binomens that can be used for the element types included in the reconstruction. However, according to the nomenclatorial law of priority, only a single one of these binomens may be the valid name for the species. This rule was applied to natural assemblages already by Schmidt (1934) and to reconstructed apparatuses, in a sense, by Huckriede (1958). It has been fully executed for the conodont apparatuses for the first time by Bergström & Sweet (1966) and Webers (1966).

It is quite clear that virtually every conodont element type has its own stratigraphic range different from ranges of other element types in the apparatus. A range of an apparatus chronospecies is therefore usually defined as tantamount to the range of the element type which shows the highest rate of evolution. When ranges of different element types only partially overlap, the range of the apparatus chronospecies may be defined as being shorter than any particular element type. This, however, does not

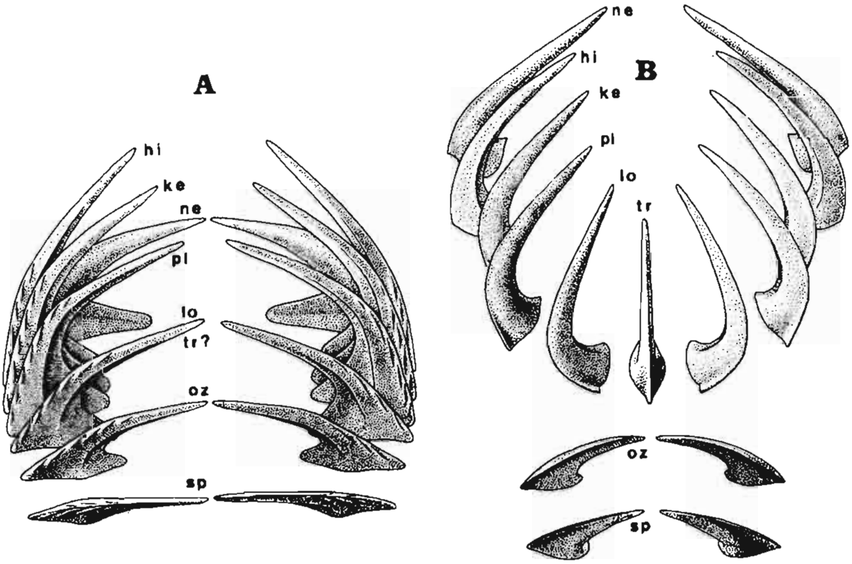

Fig. 4. Proposed arrangement of elements in panderodontid and distacodontid conodont apparatuses. ❑A. Apparatus of *Besselodus arcticus* Aldridge 1982; a reconstruction based on the cluster of Aldridge (1982). Note that in the possibly related *Dapsilodus* (Fig. 5C) all elements are also asymmetrical. ❑B. Apparatus of *Drepanodus robustus* Hadding 1913 *sensu* Lindström 1971; a reconstruction based on isolated elements tentatively homologized with the elements in the apparatus of *Ozarkodina* by Dzik (1990a).

mean that the morphologically diagnostic element type must necessarily give its name to the apparatus. Often the law of priority does not permit it.

To be efficient in conodont apparatus studies it seems better to forget at the beginning about the isolated element taxonomy. Any nomenclatorial search for the proper name of a biological (chrono)species has little to do with the morphological typology of its disarticulated elements. It has to be preceded by a standard taxonomic procedure, with recognition of paleophena, populations, biospecies, and definition of chronospecies (Dzik 1990b). A recognition of populations belonging to the species is thus crucial in any taxonomic study and this must precede any nomenclatorial decision. All the type specimens of every named species that are included into the range of the apparatus chronospecies are candidates for being its holotype. The first proposed type is the bearer of the valid name, regardless of whether it represents a long or short ranging element type, diagnostic or not (Klapper & Philip 1971). It is enough to have reasonable suspicion that this holotype was a part of the body of a member of a population belonging to the chronospecies. In some cases it is possible to reach a high level of certainty in this respect (for instance, when only a single conodont species occurs in the type locality), even if the holotype specimen otherwise is an unidentifiable fragment. Its original diagnosis is not binding at all.

According to the same methodology the proper generic name of the apparatus is the oldest one proposed for any genus, as long as the type species of that generic name is a component of an apparatus species included in the apparatus genus. The originally designated type species of the genus may appear to be a junior synonym of one of its proper apparatus species names.

An application of the above rules is rather simple in practice and if still so much confusion arises, this is mostly because of difficulties in the identification of exactly to which populations the holotypes belong. Sometimes in the topotype bed many species occur that have in their apparatuses elements identical with that to which the name is attached (this is the case with the type species of the Devonian *Palmatodella*; van den Boogard & Kuhry 1979). Sometimes it is no longer possible to make additional sampling in the type locality to identify the apparatus species occurring there (this is the case with the type species of the Ordovician *Cyrtoniodus* and the family Cyrtoniodontidae; Sweet *in* Ziegler 1981).

It has to be stressed that the recently accepted procedures of apparatus taxonomy require consistent application of the horizontal concept of chronospecies (see Dzik 1990b). Whenever the vertical concept, inherited from element taxonomy, is applied confusion is almost unavoidable.

Ancestral conodonts

It is still a matter of dispute when the first conodont appeared. The earliest Cambrian conical fossil *Fomitchella* shows the same mode of formation of the crown tissue (Bengtson 1983) as the conodonts. It shares it, however also with another group of fossils, represented by Cambrian to Ordovician possible palaeoscolecid worms *Hadimopanella* and *Milaculum*, with more widely conical crowns and a well mineralized tissue filling the basal cavity (Dzik 1986; van den Boogard 1989). Similarly to *Fomitchella* they had randomly distributed small crystallites in the crown tissue, which makes them similar also to the oldest agnathans. Like agnathans their sclerites covered a dermal skeleton. It remains unclear whether *Fomitchella* had sclerites restricted to the oral apparatus, being thus a conodont, or, as in the agnathans, they covered its whole body.

The undoubtedly Cambrian conodonts represent three types of internal element structure. The most unusual mode of the early development of sclerites characterizes the Furnishinidae ('paraconodonts'). Their elements initiated as minute rods surrounded by the epithelium, lacking any basal cavity (Müller & Nogami 1971; Szaniawski 1971). Only with subsequent growth the element became more conical as an effect of decreasing activity of the secretory tissue at the center of its base. A layer of weakly mineralized basal filling tissue sometimes covers the interior of the basal cavity in larger elements (Andres 1988). The secretory activity of the epithelium

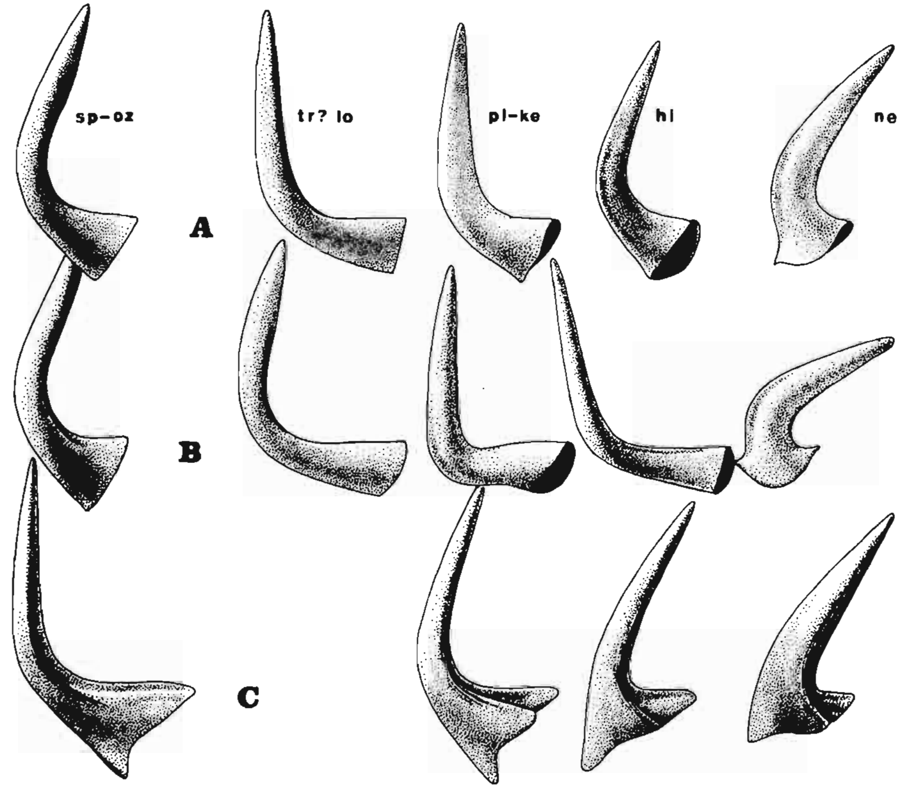

Fig. 5. Discrete element types in apparatuses of the Strachanognathidae (after Dzik 1990a). □A. *Cornuodus longibasis* (Lindström 1955), Arenig (Kundan) of the Holy Cross Mts, Poland. □B. *C. bergstroemi* Serpagli 1967, Llanvirn of the Holy Cross Mts. □C. *Dapsilodus viruensis* (Fåhræus 1966), same strata. Note: In this and following figures the elements that are suggested to be homologous to each other are arranged in vertical rows. Their homology is indicated with Jeppson's (1971) modified notation and in some well established cases also Sweet's (1981) notation symbols are added. Reconstructions of particular elements are based on camera lucida drawings and/or photographs with their sizes roughly accomodated according to estimated means in the sample, magnification is thus approximately × 30.

seems also to have been very weak or completely stopped at the element tips, perhaps an effect of its periodic penetration (Bengtson 1976).

The remaining conodonts had conical elements from the beginning of their secretion. In the Fryxellodontidae, Proconodontidae, and Cordylodontidae the crystallites of the crown tissue were arranged radially, perpendicularly to the cusp surface (Miller 1980; Landing *et al.* 1980; Andres 1988; Nicoll & Shergold 1991), while in typical conodonts the crystallites are oriented along the axis of the cusp (Barnes *et al.* 1973; Lindström & Ziegler 1973). The longitudinal orientation of the apatite fibres is most visible in cusps of the Middle Ordovician 'Neurodontiformes' (Lindström & Ziegler *in* Clark *et al.* 1981). The basal filling tissue in early conodonts may be penetrated with tubuli (Klapper & Bergström 1984) showing some similarity to mesodermal tissues in vertebrate dermal sclerites (Dzik 1986).

Apart from fragmentary associations of a couple of elements of *Furnishina* (Andres 1988) and the somewhat problematic specimen of *Odontogriphus* (Conway Morris 1976) the only evidence on the organization of apparatuses in the earliest conodonts provides a cluster of elements that represents probably a complete one half of the apparatus of an early species of *Cordylodus* (Andres 1988). The cluster is composed of seven elements having cusps oriented approximately parallel to each other. All elements are similar in size and shape, the largest one being located in the center of the series. In the apparatus of *Cordylodus* alreadty wo discrete element types can be distinguished. One of them is similar to the 'cyrtoniodus' **ne** element of some later conodonts and, being most probably its homologue, occupies the anteriormost location in the apparatus. The second type dominates numerically in samples and seems to correspond to all the remaining locations, showing some morphological diversification (Nicoll 1990).

According to Andres (1988) the denticulation of the inner processes developed gradually during ontogeny in *Cordylodus*. The genus derived from earlier conodonts with elements of a widely conical shape (from *Proconodontus*, with *Eoconodontus* and *Cambrooistodus* as transitional forms; Miller 1989; Andres 1988). It seems reasonable to conclude that, except for the element denticulation, the apparatus of *Cordylodus* represents the most archaic stage in the evolution of the typical conodont ('euconodont') apparatuses. Judging from the available data the ancestral conodont apparatus was thus composed of seven pairs of rather widely conical elements of similar shape and size (Andres 1988).

Grasping apparatuses of the chaetognath type

Little is known about the three-dimensional apparatus organization of coniform-element conodonts. It seems that they shared their pattern of element arrangement with Late Ordovician *Besselodus*, known from a seven-element, probably half-apparatus cluster (Aldridge 1982). This assumption finds support in a close similarity of the *Besselodus* apparatus to that of *Cordylodus*. In both cases only two types of elements were developed, one represented by six pairs and another by a single one, all elements being of similar size. The single pair element type, characterized by a more inclined cusp as in *Cordylodus* occupies the marginal position in the apparatus. In the *Besselodus* apparatus a slight size gradient can be detected, with the smallest element pair located posteriorly. It remains to be determined whether the genus is related to Early Ordovician *Paltodus* or rather to *Dapsilodus*, both having somewhat more diversified apparatuses, as indicated by morphologic distribution in samples of discrete elements (Cooper 1976; Dzik 1990a), with up to four element types (Fig.

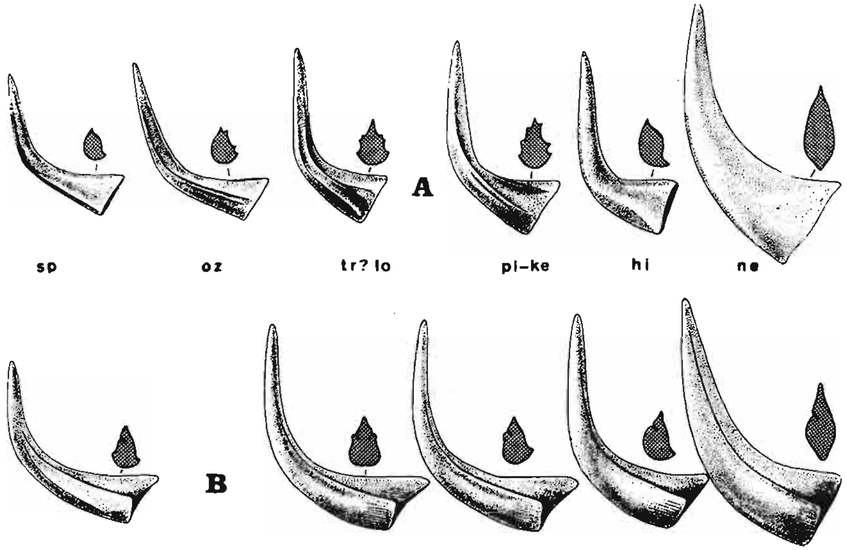

Fig. 6. Discrete element types in apparatuses of the Belodellidae and Panderodontidae (after Dzik 1990a). □A. *Walliserodus costatus* Dzik 1976, Arenig (Kundan) of the Holy Cross Mts, Poland; costate elements, being very variable may actually not form any discrete morphologic classes. □B. *Panderodus sulcatus* (Fåhræus 1966), Llanvirn of the Holy Cross Mts.

4A). All elements of *Dapsilodus* are asymmetrical, which seems consistent with the interpretation of the apparatus of *Besselodus* as having also all elements paired (Fig. 4A).

The ancestry of *Dapsilodus* remains unknown, but the morphology of its oldest known Late Arenig species suggests one of the most generalized simple-cone conodonts, *Cornuodus*, as a possible ancestor. Despite superficial simplicity the apparatus of *Cornuodus* is quite diversified (Fig. 5A, B) and gives an opportunity to homologize through it the element types with more advanced Ordovician conodonts. *Cornuodus*, if it really belongs with *Besselodus* and *Dapsilodus* to the same group, is its earliest representative. A large stratigraphic gap separates it from the similarly organized early cordylodontid *Eoconodontus* that could potentially be its ancestor. It remains to be proven that the seven-pair apparatus is inherited by both the cordylodontids and *Besselodus* from a common ancestor.

Even more enigmatic is the ancestry of another group of simple-cone conodonts, the Panderodontidae, with apparatuses known from clusters (Dzik & Drygant 1986) and even a soft-body impression (Smith *et al.* 1987). The panderodontids are different from all the remaining conodonts in having opposite polarity in element size distribution. The largest element pair is located anteriorly (Dzik & Drygant 1986). This pattern has been documented by clusters also in Late Ordovician *Belodina* (Nowlan 1979) and Devonian *Belodella* (Lange 1968). Although elements of *Belodella* are serrate it is otherwise closely similar to *Walliserodus* (Fig. 6A; see Cooper

1975). *Walliserodus* shares its ancestry in *Scalpellodus* with *Panderodus* (Dzik 1990a), thus it seems reasonable to conclude that the peculiar size gradient of the elements in the apparatus developed close to the base of the whole clade. It is suggestive of a grasping function and morphologically the apparatus of *Panderodus* is almost identical with that of the Chaetognatha despite a different mode of formation of the elements (Dzik & Drygant 1986b).

Some species of *Panderodus*, *Walliserodus*, and *Belodella* posess a bilaterally symmetrical element type in their apparatuses. It occurs in samples with frequencies that rather suggest paired occurrence in the apparatus. Nevertheless, in other species of the same genera, as well as in several other genera related to *Belodina* (Sweet 1979), no symmetrical element is present (Klapper & Barrick 1983). A plausible interpretation is thus that a pair of symmetrical elements occurred in some apparatuses that was homologous to a pair of asymmetrical elements in other apparatuses (Dzik & Drygant 1986).

All these most primitive conodonts thus had a grasping apparatuses with seven pairs of elements probably arming a fissure-like mouth and all being located outside the throat, as is required by the proposed grasping function. This seems to provide evidence of a significant difference in anatomical organization from the remaining conodonts, which have their apparatuses subdivided into morphologic (and thus obviously functional) groups of elements. Despite a functional similarity between the panderodontid conodonts and the chaetognaths, the differences in structure and mode of secretion of elements exclude their closer relationship (but see Bengtson 1976 and Szaniawski 1982).

Differentiation of element series

Homology of elements can be traced from the best known Late Paleozoic conodonts as far back in time as their Early Ordovician distant relatives with coniform elements, to *Protoprioniodus* and *Acodus* (Dzik 1983). The apparatuses of these conodonts are not unlike those of such early distacodontids as *Paltodus* and *Drepanoistodus* (Fig. 7C; van Wamel 1974). The most primitive conodont still having distinguishable element series in the apparatus that can be identified with those in the advanced conodonts is the Early Ordovician *Drepanodus* (Fig. 7B; Dzik 1990a).

Isolated elements of *Drepanodus* form two morphoclines of discrete types. One of them is bracketed by a homologue of the **ne** element and a symmetrical proposed homologue of the **tr** element at its ends. All elements of this series have long cusps and can be arranged according to a stepwise-changing curvature and degree of asymmetry (Fåhræus & Hunter 1986). A distinct morphologic gap separates another two kinds of elements that have rather short cusps and a wide base (Fig. 7B). Perhaps these are homologues of the platform complex of later conodonts. The fragmentary

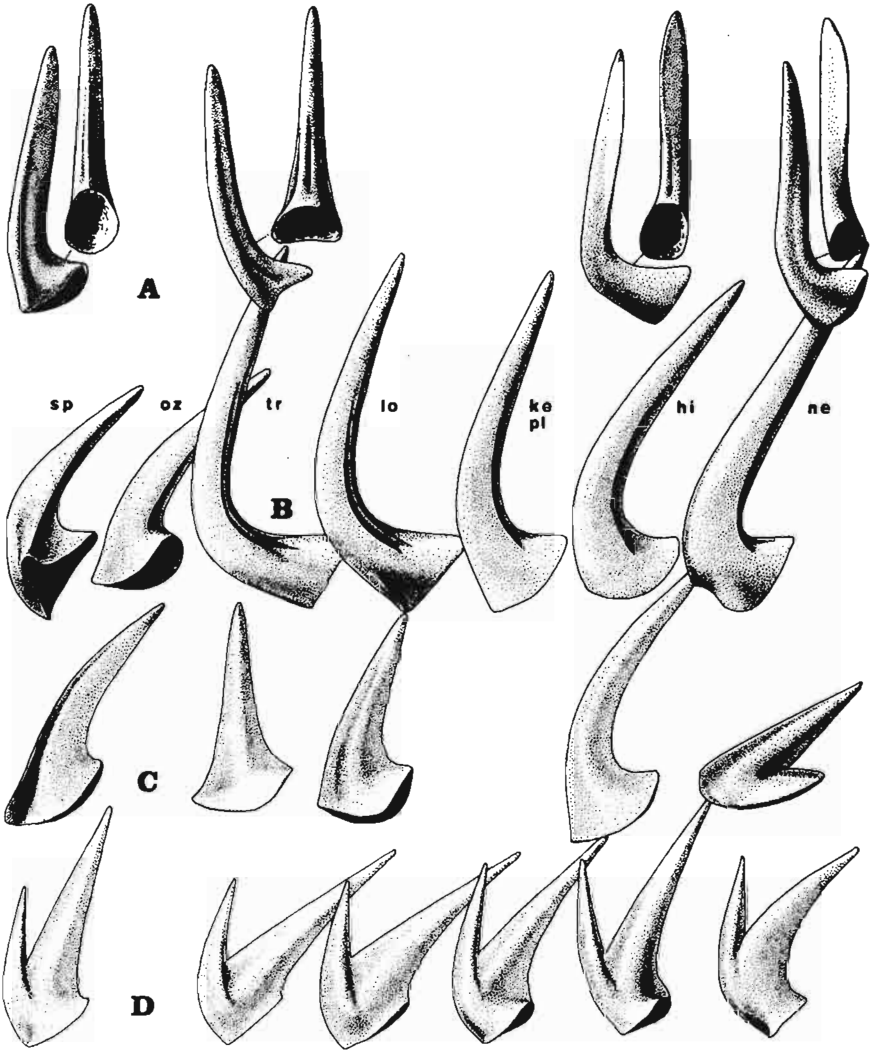

Fig. 7. Discrete element types in apparatuses of the Protopanderodontidae and the Distacodontidae (after Dzik 1990a). ❑A. *Semiacontiodus cornuformis* (Sergeeva 1963), Arenig (Kundan) of the Holy Cross Mts, Poland. ❑B. *Drepanodus robustus* Hadding 1913, Llanvirn of the Holy Cross Mts (see also Fig. 4B). ❑C. *Drepanoistodus basiovalis* (Sergeeva 1963), Arenig (Kundan) of the Holy Cross Mts. ❑D. *Strachanognathus parvus* Rhodes 1955, Llandeilo of the Holy Cross Mts.

cluster of *Drepanodus* described by McCracken (1989; classified by him as *Protopanderodus* n. sp. A) confirms this interpretation showing that the two element pairs interpreted as the platform complex really occupied the marginal position and that the homologue of the **ne** element was at the opposite end of the apparatus.

The apparatus of *Drepanodus*, being the most diversified among all conodonts with coniform elements, is thus a suitable auxillary reference standard enabling homologization of elements of the Protopanderodontidae and related groups. The earliest member of the family having a morphologically distinct symmetrical element in the apparatus was probably *Semiacontiodus* (Miller 1980; Ji & Barnes 1990). This element type (Fig. 7A) occurs in samples with too high frequency to represent only a single medial location. Its homology to the symmetrical elements occurring in the apparatus of *Panderodus* remains unclear and, unless a well preserved cluster is found, detailed evolutionary studies are required to solve this question. One may speculate that the medial element developed at the junction of the V-shaped exposed part of the apparatus when the elements of the platform series migrated inside the oral cavity.

Origin of the filtratory basket

The morphology of the symmetry transition series elements in the apparatus of *Drepanodus* strongly suggests their grasping function, similar to that of the whole apparatus of *Panderodus*. The development of prominent, flat and high ridges (here termed 'cristae') along the cusp and with a tendency to be prolonged basally into processes seems to mark development of a new function of the elements. Cristate elements occurred among primitive members of several lineages of the conodonts and usually their appearance was soon followed by transformation into finely denticulated processes (see Dzik 1983). Obviously a presence or absence of denticulation in these lineages is of little diagnostic value and cannot be used to define high-rank taxonomic units. Such a widespread convergent development of ramiform elements suggests that the function, to which they served, had developed already earlier.

The cristae originated in early conodonts usually along the inner and outer (following the physiologic orientation; see Fig. 3B) margins of their elements. Sometimes an additional medial (anterior) crista developed in the **tr** element and four cristae were present in the **pl** element. This pattern has been preserved in denticulate elements. Quite an elaborate arrangement of additional secondary processes may be found among more advanced forms, especially in platform elements. Still, only two basic plans of the element ramification can be traced along the evolution back to the coniform stage. The simpler one is well exemplified by *Histiodella*, *Protoprioniodus*, and *Rossodus* (Fig. 10). In their apparatuses the elements of the platform series are biramous while the **tr**, **lo**, and **pl** elements bear three cristae or processes. Another pattern is represented by *Acodus* and its relatives, with originally triramous elements of the platform complex (as well as in the **tr** and **ke** locations) and the tetraramous **lo** and **pl** elements.

Both these basic branches of the ramiform conodonts can be rooted in coniform ancestors. The lineage of *Protoprioniodus*, probably ancestral for the order Ozarkodinida seems to be related to *Histiodella*, which was traced back to the earliest Ordovician *Utahconus* by Repetski & Ethington (1983). The lineage of *Acodus*, ancestral to the order Prioniodontida, derived perhaps from *Paltodus*, a form transitional to the distacodontids.

Relationships of another early conodont with well denticulated elements, *Paracordylodus*, remain unclear. A cluster found by Stouge & Bagnoli (1988) in the early Arenig of Newfoundland is composed of a geniculate **ne** element, located marginally, and five morphologically identical denticulated elements. The apparatus embraces also a more robust element type, presumably occupying the location opposite to the **ne** one, thus being homologous to elements of the platform series. No triramous symmetrical element seems to be present in the apparatus. Either one of the identical elements in the cluster is the homologue of the **tr** element or the symmetry transition series in *Paracordylodus* had one more pair of elements than other ramiform conodont apparatuses.

The prioniodontid apparatus

Cold and deep-water conodont faunas of the late Early and Middle Ordovician were dominated by conodonts that developed from *Acodus* by means of transforming cristae into finely denticulated processes. Although the composition and evolution of their apparatuses is relatively well known (Bergström 1971, 1983; Dzik 1976, 1983, 1990a) in only a few cases the development of denticulation was traced (McTavish 1973; van Wamel 1974; Stouge & Bagnoli 1988). In several lineages at least the **sp** elements were subsequently molarized by thickening of the element crown just basally of the denticle row (the 'platform')(e.g. see Löfgren 1990). Among the most advanced stellate platform elements the left and right counterparts frequently do not form a mirror-image pair (Bergström 1971, 1983), which was probably an adaptation to a grinding function. The **ke** elements initially had a long denticulated anterior process, being thus unlike the **hi** elements, but in the course of evolution the morphologic discontinuity between these element types gradually disappeared (Dzik 1976, 1990a). Percent contribution of **hi**-type elements in later *Baltoniodus* in well balanced samples (those not showing strong overdominance of platform elements) is twice that of the contribution of **sp**, **oz**, or **ne** elements. That is, it is equal to the contribution of **ke** and **hi** elements together in older species and to that of the 'tetraprioniodus' elements. The latter indicates that also locations **pl** and **lo** were occupied by morphologically indistinguishable elements. Although such elements do not occur in the Ozarkodinina they can be step-by-step homologized with *Microzarkodina*, which may serve as an intermediate link. Symmetrical elements are four times less common in *Baltoniodus* samples than the tetraramous **pl**-**lo** or biramous **ke**-**hi**, which testifies to their being unpaired.

The only Ordovician natural assemblage of conodont elements, *Promissum* from the Ashgill of South Africa (Theron *et al.* 1990), contains tetraramous **lo** and **pl** elements which, being confined to the prioniodontids, indicate taxonomic position of the fossil. Most interestingly the platform series of *Promisssum* seems to be composed of three pairs of elements, two of them being probably identical morphologically. Usual domination of **oz** elements in samples of older prioniodontids may thus find explanation in their possible repetition in the apparatus.

In the Middle Ordovician some prioniodontid and balognathid lineages invaded equatorial seas and underwent a profound morphologic diversification that obscured the real basic plans of their apparatuses and hampered tracing their origins. The most important branch of this kind is represented by *Phragmodus*, which was derived from the balognathids in the Late Arenig (Watson 1988; Dzik 1990a). As a result of evolution all but the inner processes in **tr**, **pl**, and **ke** elements in its apparatus were reduced (Fig. 8B) and subsequently denticulation of the inner processes of the **tr** and **pl** elements became undulated (Fig. 8C). Possibly *Paraprioniodus* is an early sister lineage of *Phragmodus* confined to equatorial regions (Dzik 1983). During the Llandeilo and Caradoc a few other warm-water lineages developed within the *Phragmodus* branch (Sweet *in* Ziegler 1981). An exclusively Siberian branch of *Acanthocordylodus* (Fig. 8D) developed a peculiar serration of elements that initially appeared only in the **ne** elements and later expanded to other ramiform elements of the apparatus, which simultaneously underwent some morphologic simplification (Moskalenko 1972).

An odd tendency is shown by the apparatus morphology of *Complexodus* (Fig. 9A; Dzik 1990a) a typically South Chinese form. While in other supposedly related prioniodontids an introduction of secondary processes in **sp** elements was preceded by a development of the platform, in the *Complexodus* lineage during the late Llanvirn two anterior processes originated without building any platform. Somewhat later the element was molarized by a widening of the denticle tips, forming what I here propose to name 'icrions'. Rather unusual is also the evolution of its symmetry transition series. The elements **tr** and **pl** at the beginning had typical features of the balognathids (which make their identification in samples dominated by *Baltoniodus* and *Amorphognathus* rather difficult) but later on the medial process in the **tr** element has been reduced and similar transformations took place in the **pl** elements (Fig. 9A).

It seems highly probable that *Complexodus* is an early representative of a still poorly known branch of the Pterospathodontidae, characterized by a similar morphology of the symmetry transition series. Late Ordovician *Birksfeldia* is probably a transitional form to several Silurian lineages of the family (see Uyeno & Barnes 1983) in which stellate **sp** elements are molarized either by developing a platform (*Astropentagnathus*) or icrions (*Distomodus*). In the latter genus a well developed platform occurs also in the symmetrical element (Over & Chatterton 1987).

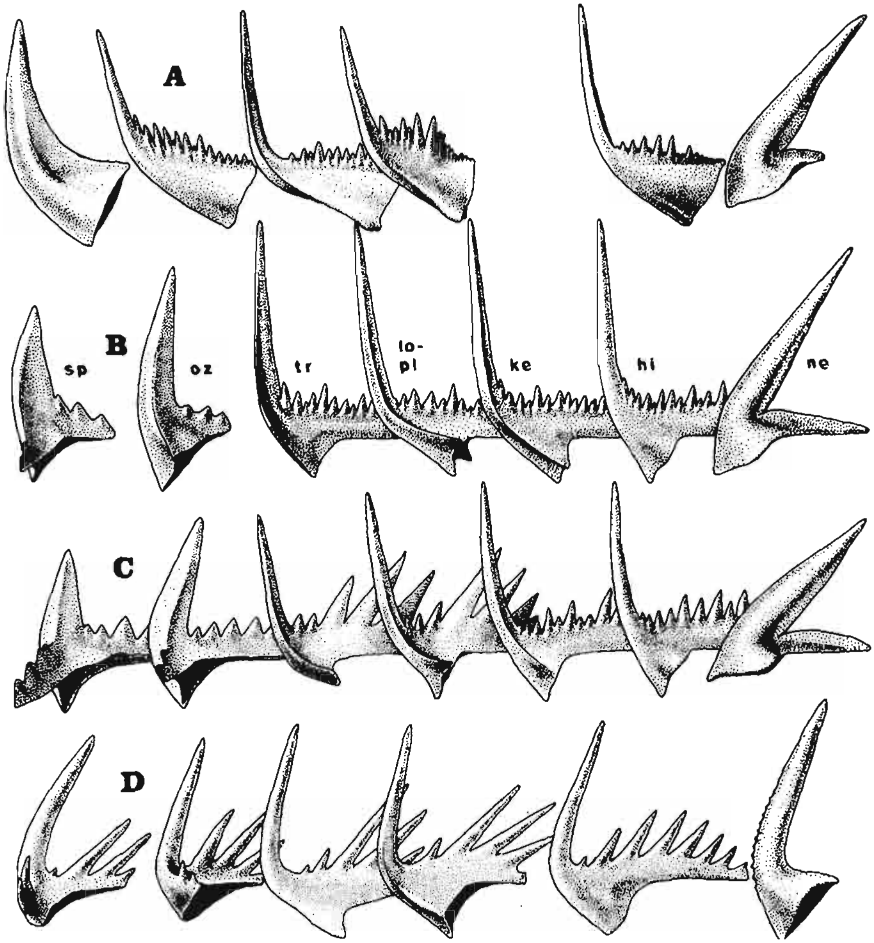

Fig. 8. Discrete element types in apparatuses of the Ansellidae and the Balognathidae. ❑A. *Ansella robusta* (Ethington & Clark 1981), Llanvirn (Volginian) of the Moyero River, Siberia. ❑B. *Phragmodus(?) crassulus* (Lindström 1955), Arenig (Latorpian) of the Baltic region (after Dzik 1984). ❑C. *P. polonicus* Dzik 1978, Llanvirn of the Holy Cross Mts (after Dzik 1990a). ❑D. *Acanthocordylodus(?) evenkiensis* (Moskalenko 1970), Llandeilo (Kirenian) of the Moyero River, Siberia. (A and D based on samples collected by Dr. T.A. Moskalenko, Novosibirsk.)

Within the Silurian lineage of *Pterospathodus* the **ne** element acquired an additional posterior process, becoming in this respect similar to Ordovician *Amorphognathus*, which is not directly related. This process became denticulated in Llandoverian *Pranognathus*. Männik & Aldridge (1989), discussing the composition of the apparatuses of *Pranognathus*, identified eight element types in it, introducing a third location for the platform complex. A relatively robust triramous element of this kind, not belonging to the platform series, occurs also in *Birksfeldia*. Possibly it represents the **pl** location, while the alleged second makelliform element in *Birksfeldia*

(McCracken *et al.* 1980), as well as the member of the symmetry transition series with short processes in *Pranognathus*, may belong to the **lo** location. If this interpretation is correct these pterospathodontids are the only conodonts that have morphologically discrete elements at all locations.

Secondarily coniform elements

In the Llanvirn of Thuringia and the Sudetes, as well as in the Llandeilo of the Armorican Massif and the earliest Caradoc of Wales an early species of *Icriodella* occurs that may help in understanding the origins of the Icriodontidae (Fig. 9B; Bergström 1983; Dzik 1990a). Despite a strange irregular denticulation it is somewhat similar in its apparatus structure to *Baltoniodus* except that it does not possess any tetraramous elements. Whether the lack of the fourth process in the homologue of the **pl** (and **lo**) elements is an effect of a secondary simplification (as in *Complexodus*) or is an ancestral feature remains unknown.The latter case would require derivation from another simple-cone ancestor than *Acodus*, which seems rather unlikely.

During the Caradoc the **sp** elements of *Icriodella* underwent a significant transformation, with its external ('posterior') process developing a fusiform molarized area (icrion) and the inner process starting its gradual reduction. At the same time the remaining elements of the apparatus became more and more simplified morphologically. In the Early Devonian *Pedavis* and *Latericriodus*, the elements of the symmetry transition series can still be easily homologized with respective locations in prioniodontid apparatuses (Serpagli 1983) but in the Late Devonian icriodontids there are only coniform elements present in all the locations except for the **sp** (Nicoll 1982).

In *Icriodus* (probably also in *Pelekysgnathus*) hundreds of small simple-cones co-occur in the apparatus with a single pair of molarized **sp** elements (Lange 1968; Nicoll 1982). The most reasonable interpretation of this phenomenon refers to a common feature of a weaker mineralization of denticle bases in the processes of ramiform elements (see Walliser 1964: Pl. 10: 1-6, 10-12). In some Middle Ordovician equatorial conodonts this resulted in development of several secondary 'simple-cones'. Among cold-water forms the balognathid *Sagittodontina* was proposed to have distal denticles of its ramiform elements attached to uncalcified processes (Dzik 1990a). Pathological specimens of Early Silurian *Carniodus* with basally connected units that usually occur separately (Walliser 1964: Fig. 4y) suggest that they too represent isolated parts of ramiform elements with weakly calcified bases. Growth increments visible in the basal cavity of *Coryssognathus* elements (van den Boogard 1990) show that initially isolated denticles have been unified later in histogeny.

Within the Icriodontidae the process of simplification not only expanded from the symmetry transition series to at least the **oz** elements in the

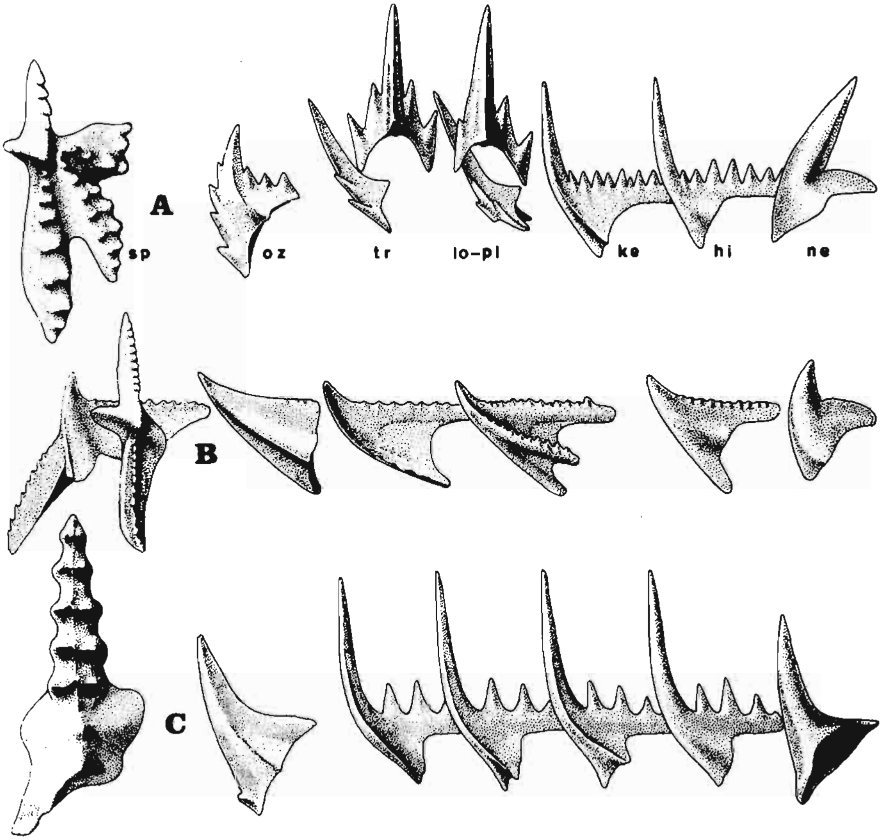

Fig. 9. Discrete element types in apparatuses of the Pterospathodontidae and the Icriodontidae. ☐A. *Complexodus pugionifer* (Drygant 1974), Llandeilo of the Holy Cross Mts (after Dzik 1990a). ☐B. *Icriodella praecox* Lindström, Racheboeuf & Henry 1974, Llandeilo of the European Variscan belt and earliest Caradoc of Wales (data compiled from Lindström *et al.* 1974, Bergström 1983 and Dzik 1990a). ☐C. *Latericriodus woschmidti* (Ziegler 1960), Gedinnian of Sardinia (after Serpagli 1983).

platform series, but also the **sp** elements lost their molarized icrion in *Pelekysgnathus*. This tendency was reversed again in some lineages and secondarily ramified **sp** elements developed in the latest Devonian icriodontids (Sandberg & Dreesen 1984). There are also examples of a molarization of **oz** elements that followed development of extremely complex icrions in the **sp** elements (Uyeno & Klapper 1980).

The most celebrated event of secondary simplification of apparatus elements is that preceding immediately the complete extinction of the conodonts in the latest Triassic. In the lineage of *Misikella* the **sp** elements became extremely small, with only a few denticles developing, evidently because of the minimum size of the denticle morphogenetic field typical for conodonts (see Dzik & Trammer 1980). Remaining elements preserve typically gondolellid morphologies but some extremely simplified, almost coniform elements tend to be associated with them in samples. Whether they represent another apparatus, as proposed by Fåhræus & Ryley (1989), remains not quite clear.

Evolutionary roots of the ozarkodinids

The oldest undoubtedly ozarkodinid apparatus yet known is that of early Arenig *Periodon*. The elements **pl** and **tr** in this apparatus are distinctly triramous, with all processes (or cristae) equally well developed. Among older conodonts with undenticulated cristae early representatives of the lineages of *Protoprioniodus* and *Histiodella* can be considered as potential ancestors of Periodon (see van Wamel 1974; McHargue 1982). The lineage of *Histiodella* is known to be derived from *Rossodus* (Fig. 10A), which in turn can be attached to *Utahconus*, one of the oldest known typical conodonts (Repetski & Ethington 1982). In the *Utahconus-Histiodella* lineage the medial process of the **tr** elements (and the analogous process in **pl** elements) is quite rudimentary, while in *Protoprioniodus* and its supposed close relative *Oistodus* (Fig. 10C) the medial crista and process are prominent. It remains unclear whether this is a primitive feature, then being suggestive of a relationships rather to early prioniodontids than to *Rossodus*, or a derived one. Bed-by-bed evolutionary studies in non-condensed Late Tremadoc to Early Arenig sections are thus of crucial importance to understanding the early phylogeny of the Ozarkodinida.

The evolutionary development of denticulation in early *Periodon* has been traced in the Arenig of Newfoundland (Stouge & Bagnoli 1988). Subsequently the lineage exhibits a tendency toward reduction of lateral processes in the **tr** element (and analogous processes in other members of the symmetry transition series) associated with an expansion in length of the medial process. This is exactly the same tendency that was somewhat later expressed in the balognathid lineage of *Phragmodus*. In effect, *Phragmodus* and *Periodon*, being ecological equivalents in different zoogeographic provinces, become so similar to each other that some authors classify them in the same family (Bergström *in* Clark *et al.* 1981).

A quite different (perhaps primitive) appearance of **tr**, **lo**, and **pl** elements is typical for *Microzarkodina*, probably the ancestor of all the remaining Ozarkodinida. This phylogenetic position of *Microzarkodina* is supported by the morphology of the oldest well dated species of *Plectodina* from the latest Arenig of Newfoundland (Stouge 1984; erroneously labelled *P. polonica in* Dzik 1983), which still had undenticulated, geniculate **ne** elements. Most species of *Plectodina* had this element denticulate, at least at the internal process. Such denticulation is known to occur at least from the Llandeilo, but possibly appeared as early as in the Middle Arenig (unless its co-occurence with Volkhovian conodonts in the Sudetes is not a turbiditic reworking; Dzik 1990a).

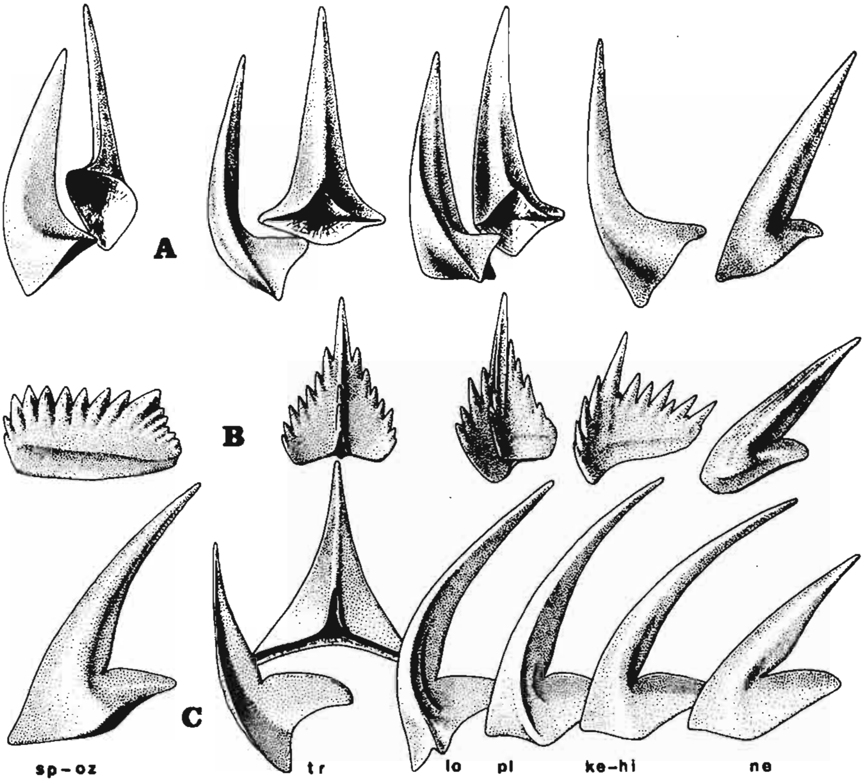

Fig. 10. Discrete element types in apparatuses of the Oistodontidae. ❑A. *Rossodus manitouensis* Repetski & Ethington 1983, Tremadoc (Gasconadian) of Colorado (after Repetski & Ethington 1983). ❑B. *Histiodella kristinae* Stouge 1984, Llanvirn of Newfoundland (after Stouge 1984). ❑C. *Oistodus lanceolatus* Pander 1856, Arenig of the Baltic region (after Dzik 1983).

The **oz** element in primitive *Plectodina* was triramous, with its anterior process being in the form of an undenticulated crista rather than a true process (Fig. 11A). The phylogenetic meaning of this feature remains unclear, possibly it developed secondarily at the anterior side of the base that is already strongly convex in *Microzarkodina*. In the Late Ordovician at least a few lineages developed from *Plectodina* in which the **oz** element was again biramous (Sweet 1979).

While the early evolution of *Plectodina* seems to have taken place in temperate climatic seas, *Erraticodon* itself represents an equatorial lineage. If the dating of the Sudetes population of *Plectodina* is correct than it precedes slightly the appearance of *Erraticodon*, known to occur already in the Late Arenig of Australia (Cooper 1981; Watson 1989). Despite its robust appearance and a prominent hyaline denticulation of elements, the apparatus of *Erraticodon* (Fig. 12A) is not unlike that of *Plectodina*, being even more similar to *Oulodus*, a Late Ordovician derivative of the *Plectodina* branch. Elements in the apparatus of *Erraticodon* supposed to be homologous with the **sp** location bear a rudimentary anterior process, similar to the **oz** elements in *Plectodina*. Again, the meaning of this discrepancy in the distribution of triramosity remains to be explained; definitely it makes the presently accepted homology somewhat uncertain.

The identification of discrete element types and their homologization by Sweet (1982) in robust apparatuses of ramiform elements of *Erismodus* and *Chirognathus* indicate their evolutionary proximity to *Erraticodon* (Fig. 12B, C). Possibly also *Archaeognathus*, with its unusually developed basal filling tissue (Bergström & Klapper 1983) and discontinuous crown tissue, confined only to the denticles, is a member of this group. The morphology of the *Archaeognathus* elements and its (still inadequately known) apparatus is of special interest because of its similarity to the jaws of hagfish (see Dzik 1986). Immunological studies on Recent *Myxine* documented biochemical affinities of its epithelium to the enamel tissue (Slavkin *et al.* 1983). This may be an expression of once functional but now quiescent genes (see Kollar & Fisher 1980). It cannot be thus excluded that, despite the purely organic composition of the *Myxine* teeth, its apparatus derived from an *Archaeognathus*-like ancestor. If any relationship of this kind occurs then the organic hagfish teeth might correspond to the basal filling tissue of the conodonts, the highly mineralized crown tissue being lost during evolution. Krejsa *et al.* (1990) comparing the 'white matter' of the conodont crown tissue with the tubular tissue of myxinid teeth apparently missed to notice the basic difference in ways of secretion of these tissues.

The oldest species of *Oulodus* (Fig. 11B) appeared in the North American Midcontinent in the Middle Caradoc without any obvious ancestor in the area (Sweet & Schönlaub 1975). It is most similar to *Plectodina* among species of the genus having undenticulated external processes of the symmetry transition series elements and blade-like **sp** elements. Later species have well denticulated external processes of the **hi** and **ne** elements. What is most important from the evolutionary point of view, close to the Ordovician-Silurian boundary the cusp of the **ne** element became slightly erect, while its inner process arched (McCracken & Barnes 1981). These transformations seem to mark the origin of an apparatus type that characterizes almost all post-Silurian conodonts.

Late Paleozoic successors of *Oulodus*

It is proposed here to consider the development of the 'neoprioniodiform' **ne** element shape in the *Oulodus* lineage as a convenient point of demarkation of the lower boundary of the Hibbardellidae. Beginning from the basal Silurian they are represented by the genus *Delotaxis*, which shows the same general organization of the apparatus as almost all other well known members of the Ozarkodinida (Sparling 1981). This is clearly evidenced also by clusters from the Frasnian Gogo Formation of Western

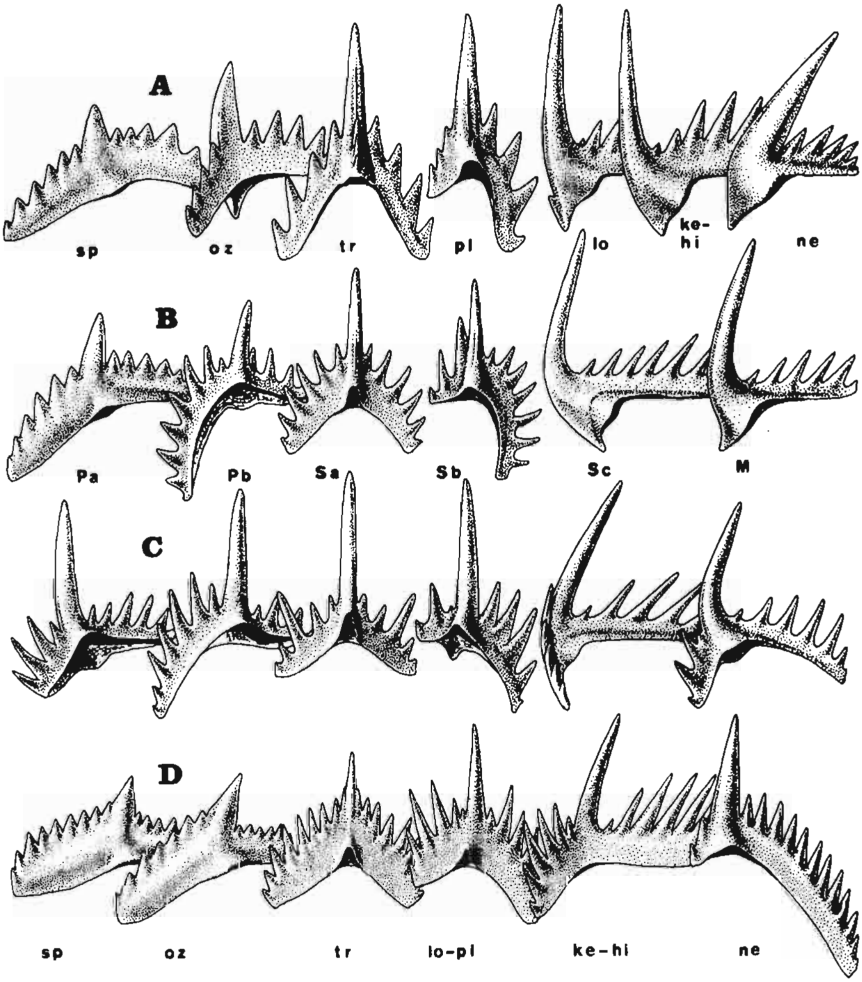

Fig. 11. Discrete element types in apparatuses of the Plectodinidae, Hibbardellidae, and Spathognathodontidae. ❑A. *Plectodina* aff. *flexa* (Rhodes 1953), Arenig (Volkhovian) of the Sudetes, Poland (after Dzik 1990a). ❑B. *Oulodus serratus* (Stauffer 1930), Caradoc (Kirkfieldian) of Iowa (after Sweet & Schönlaub 1975). ❑C. *Delotaxis(?) robusta* (Branson, Mehl, & Branson 1951), Ashgill of Kentucky (after Sweet & Schönlaub 1975). ❑D. *Ozarkodina hassi* (Pollock, Rexroad, & Nicoll 1970), Llandovery of the Anticosti Island (after McCracken *et al.* 1981).

Australia (Nicoll 1977). The main lineage of the hibbardellids continued into the Carboniferous with *Idioprioniodus*, also known from natural assemblages (e.g. Schmidt & Müller 1964), and distiguishable by the rather unusual shape of the **oz** elements, which superficially resemble rather **ne** elements of other conodonts (Baesemann 1973).

The diversification of the Hibbardellidae during the Devonian and Carboniferous resulted in development of several unusual and still superficially known kinds of apparatuses. Triramous elements of the symmetry transition series characterize *Kladognathus*, which in the Late Devonian is represented by species otherwise closely similar to *Delotaxis* but achieving rather aberrant appearance in the Carboniferous (Rexroad 1981; Horowitz & Rexroad 1982). In Late Carboniferous to Triassic *Ellisonia* all elements are secondarily simplified morphologically (von Bitter & Merrill 1983). Perhaps it gave rise to several other lineages of robust Early Triassic conodonts (Sweet *in* Clark 1981; Sweet 1988). Much less clear is the relationship of the Devonian group of *Erika* and *Apatognathus* characterized by highly derived morphologies of all elements (Murphy & Matti 1982; Nicoll 1980). Possibly they are rooted in some *Delotaxis* species having highly arched element processes (see Pickett 1980).

Chauff (1981) proposed a reconstruction of the apparatus of Early Carboniferous *Bactrognathus*, in which a stellate molarized **sp** element is associated with a symmetry transition series virtually identical with that of the hibbardellid *Idioprioniodus*. A test of this reconstruction by other data sets would be of great interest as it indirectly implies derivation of the Bactrognathidae from hibbardellid ancestors. An alternative possibility is to search for the ancestry of the group among Late Devonian *Branmehla*-like polygnathids (Chauff & Klapper 1978). The Bactrognathidae, represented by several aberrant kinds of apparatuses with stellate **sp** elements (like *Doliognathus* and *Scaliognathus*; Fig. 13B), became widely distributed close to the Tournaisian-Visean boundary, evidently in connection with a global transgression and climatic changes. Their origin remains unknown.

The *Ozarkodina* grade

No unequivocal record of *Ozarkodina* is known from the Ordovician. Most isolated elements once assigned to the genus are not associated with characteristic flattened **pl** and arched **ne** elements. *Yaoxianognathus* of Ashgill age, proposed by Nowlan & McCracken (1988) to be a connecting link between *Plectodina* and oldest Llandovery *Ozarkodina*, has the **ne** element of rather an aberrant shape (see also Savage 1990). Although, as in the post-Ordovician Ozarkodinida, denticles are oriented parallel to the cusp, the inner process is not arched at all. This highly characteristic arching is, nevertheless, well developed in Llandovery *Delotaxis* and seems to develop already in the Ashgill within the *Oulodus-Delotaxis* lineage (Fig. 11C). Thus, either successive species believed to represent this lineage developed independently from the true *Plectodina-Ozarkodina* lineage somewhere in the temperate climatic zone and migrated to the equatorial Midcontinent seas, or, which seems more likely to me, *Ozarkodina* developed from *Delotaxis*.

A good record of *Ozarkodina*, with samples rich enough to enable apparatus reconstruction, starts from the base of the Llandovery of regions located at that time close to the Equator. The oldest known species differ

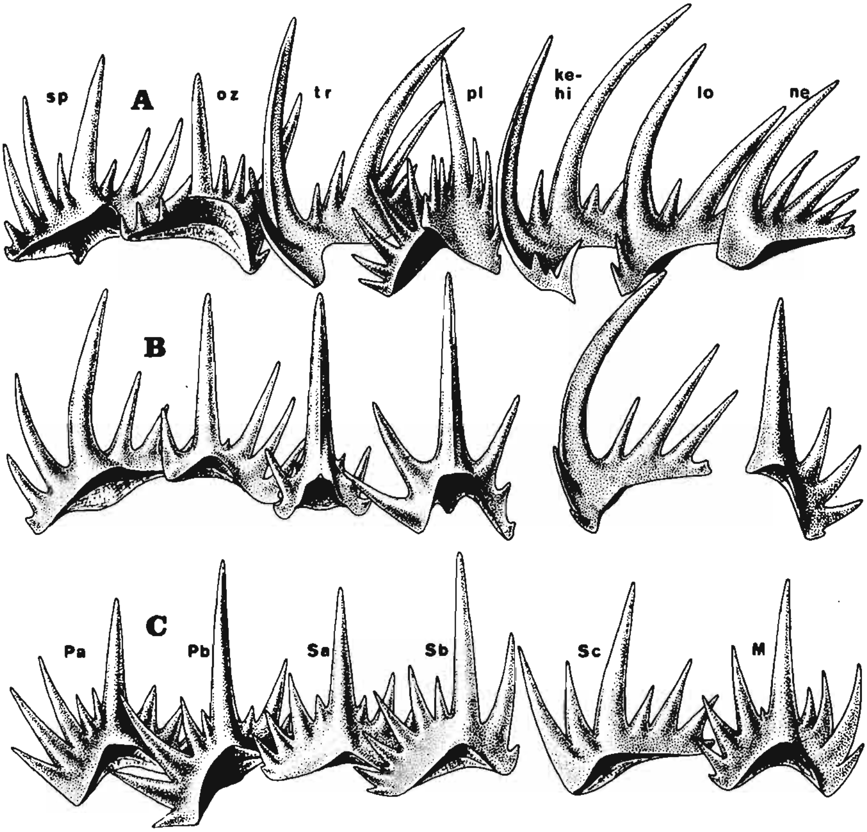

Fig. 12. Discrete element types in apparatuses of the Chirognathidae. ❑A. *Erraticodon balticus* Dzik 1978, Llanvirn of the Baltic region. ❑B. *Erismodus quadridactylus* (Stauffer 1935), Caradoc (Kirkfieldian) of South Dakota (after Sweet 1982). ❑C. *Chirognathus duodactylus* Branson & Mehl 1933, Kirkfieldian of South Dakota (after Sweet 1982).

from co-occurring hibbardellids only in the blade-like appearance of all elements of the apparatus (McCracken & Barnes 1982), which may be a feature indicating their origin in cooler-water faunas.

Clusters of diverse geological ages (Pollock 1969; Nicoll 1985; Nicoll & Rexroad 1987)) indicate that there were seven pairs and a single medial element in the apparatus of the Spathognathodontidae, the **tr**, **lo**, and **pl** locations being occupied by biramous elements. The most persistent progressive evolutionary transformation that can be observed in apparatuses of Silurian *Ozarkodina* is the transformation of the **pl**-**lo** elements from their original shape of an asymmetrical 'trichonodella' to the appearance of a short 'hindeodella', i.e. a complete disappearance of a rudimentary third process and a linear elongation of the remaining processes in this element. In all the later Ozarkodinida the **pl** and **lo** elements resemble elements of the **ke**-**hi** locations not only morphologically but also in their processes being arranged parallel to each other. It is noteworthy that the reduction of quite another process in the apparatuses of *Periodon* or *Phragmodus* gave quite similar results. The difference is clearly visible only if **tr** elements of *Ozarkodina*, *Microzarkodina*, and *Periodon* are compared. If these totally different transformations resulted in the same final parallel arrangement of elements, some rotation of elements in the apparatus of the ancestor of *Ozarkodina* has to be accepted.

The transformation of the **lo-pl** elements did not affect the morphology of the **tr** element that has preserved its biramous shape until the Triassic, being represented in the Late Paleozoic by the lineage of *Hindeodus* (von Bitter & Merrill 1985). As early as in the Early Ordovician *Microzarkodina* (Stouge & Bagnoli 1991) morphologically distinct elements of **pl** and **lo** locations developed. Even if the difference is usually not apparent it persisted in the evolution of the branch (see Rexroad & Horowitz 1990: Pl. 1: 26-27). Rather early in the evolution of *Ozarkodina* a tendency to a molarization of the **sp** element appeared. This resulted in the origin of the lineage of *Kockelella* in the Wenlock (Barrick & Klapper 1976) and *Ancyrodelloides* in the Early Devonian (Murphy & Matti 1982), both having stellate elements with a wide platform. Nevertheless, the Spathognathodontidae generally continued to preserve a blade-like appearance of their **sp** elements, although in some cases a duplication of denticles took place (Murphy *et al.* 1981) and some shallow-water forms developed rather robust shapes in all elements (Klapper & Murphy 1980).

The polygnathid apparatuses

During the earliest Devonian in a lineage leading from *Ozarkodina* to *Pandorinellina* the **tr** element developed a long, denticulated medial process, while the **lo** and **pl** element experienced further elongation (Mashkova 1972). This well known evolutionary transition represents a convenient point of demarkation of the lower boundary of the Polygnathidae.

The apparatus of *Pandorinellina* is well known owing to excellently preserved natural assemblage from the Gedinnian of Tadjikistan (Fig. 3; Mashkova 1972) and equally complete clusters from the Late Devonian of Germany (Lange 1968). Several lineages of the polygnathid conodonts that preserved unmolarized, blade-like **sp** elements developed during the Devonian and continued into the Carboniferous (Norby & Rexroad 1985), Permian (Swift & Aldridge 1982; Wardlaw & Collison 1984) terminating probably in Anisian *Neospathodus*.

Lineages of the polygnathids with molarized, platform elements in the **sp** location were even more numerous. The most important branch of *Polygnathus* originated in the Early Devonian developing initially a lophodont icrion-like structure on the internal process of the **sp** element, somewhat later transformed into a platform-like structure (Klapper & Johnson 1975). Numerous Middle Devonian species of the genus have rather uniform apparatuses structure, with gently curved **lo** elements and

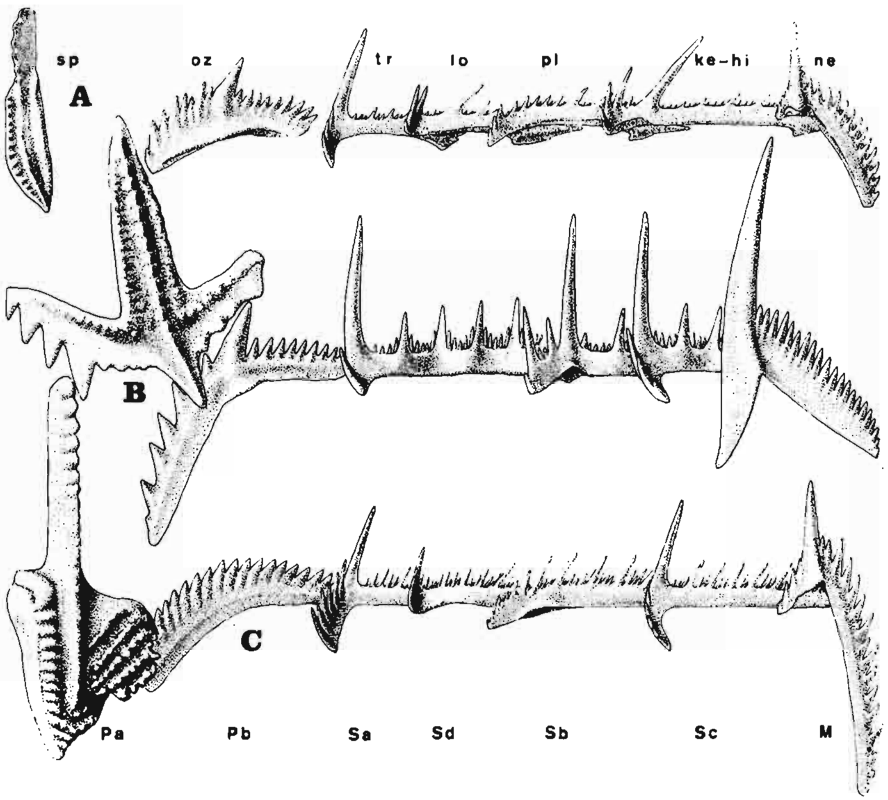

Fig. 13. Discrete element types in apparatuses of the Polygnathidae, Bactrognathidae, and Idiognathodontidae. ❑A. *Polygnathus xylus* Stauffer 1940, Frasnian of Western Australia (after Nicoll 1985). ❑B. *Scaliognathus anchoralis* Branson & Mehl 1941, Tournaisian of the Holy Cross Mts. ❑C. *Gnathodus bilineatus* (Roundy 1926), Visean of the Cracow area, Poland.

wide-arched **ne** elements (Sparling 1981), differing mostly in the morphology of the platform elements. Stellate **sp** elements developed in *Ancyrodella*, which belongs to this branch of the polygnathids. They developed by widening of the platform and only subsequent transformation of its tuberculation produced a process-like carina. All the Late Devonian and Early Carboniferous *Polygnathus*-like conodonts (including *Siphonodella*, which appears to be a typical polygnathid) share an angular shape of the **lo** elements with coeval unmolarized polygnathids (van dem Boogard 1983; Nicoll 1985). This suggests independent, 'iterative' origin of a platform in the **sp** elements. The elements **oz** preserved a generalized shape in many polygnathid lineages despite eleborate shapes of associated **sp** elements. Even if they were molarized, this was restricted to late stages of ontogeny.

Typical for the Carboniferous are derivatives of *Gnathodus*. Although classified in separate families they show almost the same apparatus structure as the polygnathids (Lane & Ziegler 1984). The only feature shared by them that is not known in the Polygnathidae is a process of the **ke-hi** elements, which is externally curved in the vertical plane, in association with an elongated inner process. This well exemplifies the basic difference in criteria of defining higher taxonomic units of the conodonts in the Early *versus* Late Paleozoic, being obviously an expression of gradual decrease in the morphologic (but not necessarily species) diversity of the group. Hundreds of well preserved natural assemblages of several species of the gnathodontids are known (e.g. Merrill & von Bitter 1977; von Bitter & Merrill 1985; Aldridge *et al.* 1987) but extremely fragile elements of the symmetry transition series are usually so badly fragmented that until recently (Lane & Ziegler 1984; Aldridge *et al.* 1987) their arrangement and homology have been poorly understood. Elements **sp** are usually molarized by development of robust denticulation at the margin of wide basal cone. In the lineage leading to *Sweetognathus* in the Late Carboniferous a characteristically tuberculated icrion developed (von Bitter & Merrill 1990) Its apparatus is known also from natural assemblages (Ritter & Baesemann 1991). During the Carboniferous the branch of the idiognathodontids was subject to intense speciation that resulted in appearance of many sympatric species (van den Boogard & Bless 1985) despite a virtually unchanged apparatus structure. The only element type that seems to differ deeply enough to enable distinction of the Gnathodontidae from Idiognathodontidae is the **lo**, being much elongated in *Gnathodus* while with a quite short internal process in the idiognathodontids (Grayson *et al.* 1990).

Axial symmetry in element pair

It was some surprise to early students of Carboniferous conodonts that some element types appeared to occur represented seemingly by only dextral specimens (Lane 1968). Despite this apparent lack of any counter-element there is a good evidence, provided by natural assemblages (von Bitter & Merrill 1985) that they undoubtedly occurred in pairs. The only anatomically well known conodont species posessed this peculiar kind of symmetry of its **sp** elements (Briggs *et al.* 1983). The usual mirror-image symmetry of elements was there replaced by axial symmetry.

Element morphologies so precisely duplicated could hardly originate randomly as an effect of evolutionary transformation of asymmetrical **sp** pairs of the kind identified in Ordovician conodonts by Bergström (1971, 1983). Perhaps this is rather a result of developmental mechanisms in the conodont histogeny that promoted repetition of units.

Axial symmetry is known to occur also in the ornamentation of the working surfaces of some crustacean mandibles (Dzik 1980) where its adaptive value, improving the grinding function, is self-evident. The oldest conodonts that show axial symmetry in ornamentation of the occlusal surface of the **sp** elements belong to Early Devonian *Eognathodus* (Lane

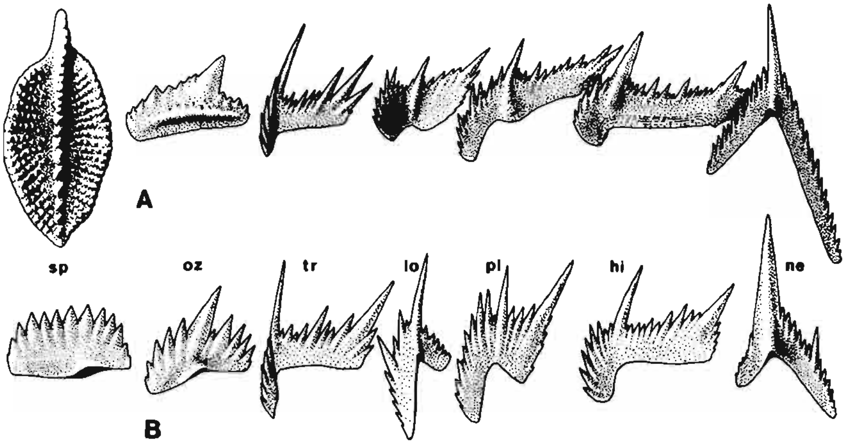

Fig. 14. Discrete element types in apparatuses of Devonian derivatives of *Ozarkodina* probably ancestral to the Palmatolepididae (A) and Gondolellidae (B). ❑A. *Mesotaxis* sp., Givetian-Frasnian boundary of the Holy Cross Mts. ❑B. *Pinacognathus*(?) sp., Famennian of the Holy Cross Mts.

1968, Murphy *et al.* 1981). The mirror-image symmetry can still be identified in the curvature of the whole elements. The analogy to the crustacean mandibles is thus apparent. More elaborated molar areas and more strict axial symmetry can be found in Late Devonian *Scaphignathus* and its derivative *Clydagnathus*, as well as in Carboniferous *Cavusgnathus*, *Taphrognathus*, and *Adetognathus*. Perhaps the most spectacular example of this kind of symmetry is provided by the **sp** pairs of *Mestognathus* (Beŭka 1982).

It remains unclear whether the initiation of the development of axial symmetry in the ozarkodinid conodonts was an unique event or took place several times. Too little is known about apparatuses of these conodonts (Baesemann 1973; von Bitter & Plint-Geberl 1982) to enable recontruction of their evolution.

The problem of the 'enantiognathus' element

Dinodus is perhaps the most ugly-looking Devonian and Early Carboniferous conodont. Only the elements of its symmetry transition series are matched together and elements of the platform complex remain to be identified. An intriguing feature of the oldest Middle Devonian representative of the lineage (Lindström & Ziegler 1965) is the presence of high-arched, laterally bent elements **lo-pl** associated with a three-ramous **tr** element. Such pattern is typical also for the apparatus of *Gondolella*, which appears in the Late Carboniferous without any clear relationship to older conodonts. In the gondolellids the **lo** elements are morphologically somewhat similar to elements of the **ne** location. In Anisian *Neogondolella* there is a continuous gradation between **pl** and **ne** elements while the **lo** elements, being spatially closest to the **pl** ones, are separated from them and other element types by a distinct morphologic hiatus (Dzik & Trammer 1980). Elements that are virtually homeomorphic to the **lo** elements in *Gondolella* are known from the Devonian ('lippertiform') but they presumably belong to some undescribed apparatuses of the Hibbardellidae, which are unlikely to have any relationships to *Gondolella*.

Dinodus, with its strange denticulation and ornamentation of the element surface, is too specialized to be seriously considered as an ancestor of the gondolellids. However, there is a species in the Famennian, possibly belonging to *Pinacognathus*, which may appear to be close to the common ancestor of *Dinodus* and *Gondolella* (Fig. 14B). Short processes of the **pl-lo** elements clearly show that it is more primitive than all the polygnathids. Despite a three-ramous appearance of the **tr** element the apparatus is quite close to those of the Spathognathodontidae. It may thus appear that the Gondolellidae share ancestry with the palmatolepidids in some Devonian *Ozarkodina*. In fact, the complete reduction of internal process of the **sp** elements, so typical for the gondolellids, is known to occur in the Devonian *Ozarkodina* (Nicoll 1985; see also Klapper & Lane 1985).

Despite some structural similarities to palmatolepidids the apparatus of *Gondolella* was basically different functionally from apparatuses of all other ozarkodinid conodonts. Both the element pairs of the platform complex had more or less reduced their internal ('posterior') processes. In this respect the gondolellids closely resemble members of the Icriodontidae and Ordovician *Scyphiodus*, but they developed a platform instead of an icrion at the remaining external process of the **sp** elements. The filtratory basket dit not undergo any reduction of the kind like *Icriodus* but, instead, a significant elaboration. The number of pairs of the 'hindeodellas' reached five (Ramovš 1977) instead of only two, **ke** and **hi** locations. The knowledge of the apparatuses of the Gondolellidae (Fig. 17) is based on many clusters described by Ramovš (1977) and Mietto (1982) and on natural assemblages of the Carboniferous (von Bitter 1976) and Triassic (Rieber 1981) age. During the Ladinian in some lineages a very prominent ornamentation developed on the **sp** elements, finally in *Pseudofurnishius* transformed into a structure of the appearance of an icrion (see Bandel & Waksmundzki 1986). Although in *Pseudofurnishius* a substitute of the internal process was developed, the whole platform continued to be located along the external process only, giving a false impression of a similarity to the oppositely located platforms in the Polygnathidae.

The youngest known Rhaetian conodonts completely lack any molarization of elements, an effect of reduction in adult size, and consequently resemble the appearance of early juveniles of their gondolellid ancestors (Gaździcki 1978; Swift 1989). It may be of some importance that the disappearance of conodonts both in the Ladinian of the Germanic basin and in the Rhaetian of Tethys was preceded by diminution in platform element sizes (Dzik & Trammer 1980).

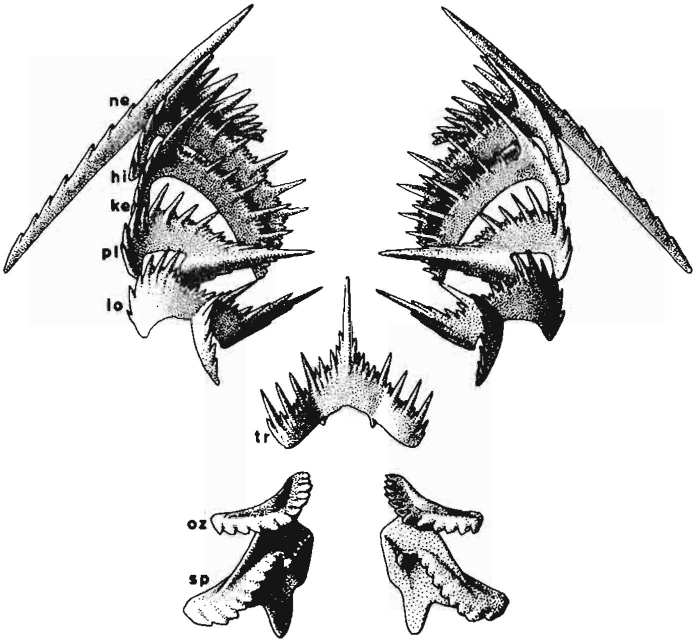

Fig. 15. Proposed spatial arrangement of elements in the apparatus of *Manticolepis subrecta* (Miller & Youngquist 1947) based on the cluster of Lange (1968), natural assemblages of Puchkov *et al.* (1981) and statistical studies on isolated elements by van den Boogard & Kuhry (1979); ventral view (see also Fig. 16A).

Apparatuses of top complexity

Although it is generally assumed that the palmatolepidids had their ancestry in some advanced polygnathids this is not supported by the structure of their apparatuses. In the latest Middle Devonian *Mesotaxis*, which seems to be the oldest member of the family, the **lo** and **pl** elements (still not bifurcated, biramous) are of the same shape as respective elements in *Ozarkodina* (see Fig. 14A). This clearly indicates the Spathognathodontidae as the ancestral group of the Palmatolepididae. The platform elements of *Palmatolepis* and *Polygnathus*, despite general similarity, developed independently. The only feature of the apparatus of *Mesotaxis* that makes it different from the spathognathodontids and similar to later palmatolepidids is the shape of the **ne** elements ('palmatodella'). Somewhat later in evolution also the **hi** elements attained their typical for the palmatolepidids appearance. This was soon followed by a bifurcation of the internal process of the **lo** element and subsequent bifurcation of lateral processes in the **tr** elements. This resulted in introduction of two types of 'scutula' elements, the asymmetrical and symmetrical ones (Fig. 15; Lange 1968; van den Boogard & Kuhry 1979). Another element type that was subject to profound modifications was the **oz**, which attained shapes unknown in other conodonts (Fig. 16). As a result an apparatus design was developed that seems to be the most sophisticated in the whole Conodonta with respect to diversity of the basic plans of the elements.

Particular lineages derived from *Manticolepis* differ profoundly from each other in organization of their apparatuses and it is without doubt that they deserve separation at the generic level. The family can be conveniently defined by the lack of any medial process in the **tr** element, a reclined cusp of the **ne** elements, and a tendency to develop triramosity of the **lo** elements. The evolution of the palmatolepidid **sp** elements has been extensively studied (Helms & Ziegler *in* Clarke *et al.* 1981) but the pattern of evolutionary transformations in the rest of the apparatus remains largely unknown. It is clear now that many species can be much more easily distinguished on the basis of the **ne** than **sp** elements (Klapper & Foster 1986). However, only a few of the most common species have their apparatuses fully reconstructed (Fig. 16; Lange 1968; van den Boogard & Kuhry 1979, Puchkov *et al.* 1981). Extremely unbalanced ratios of particular element types and the usual co-occurrence of several sympatric species hamper apparatus studies on this stratigraphically important group of conodonts.

Evolution of function of the apparatuses

There are reasons to believe that in the earliest conodonts the whole apparatus was exposed and worked in a way similar to grasping apparatuses of the Chaetognatha (Dzik & Drygant 1986). The apparatuses with the two posterior element pairs hidden in the throat and with the ventral end of the mouth opening armed with an unpaired element represent probably a later evolutionary invention. In the course of their phylogeny the elements, being originally coniform, developed denticulation of their processes and at least the posteriormost **sp** pair was molarized, having occlusal surfaces of the elements ornamented with robust ribs and tubercles. Obviously, particular parts of the apparatus performed different functions (e.g. Nicoll 1985; Nicoll & Rexroad 1987). Some elements worked probably as tools for grasping, others for fragmentation of food. In evolutionarily advanced apparatuses the **ne** element pair was an analogue of the incisors in the mammalian jaws and arthropod mandibles, while the platform complex corresponded functionally to molars. The filtratory basket of the symmetry transition series may be functionally compared with elaborated combs of the lacinia mobilis in mandibular apparatus of some crustaceans (Dzik 1980).

In accordance with this model of the apparatus, the molarization proceeded polarly in the course of evolution, being introduced first in the

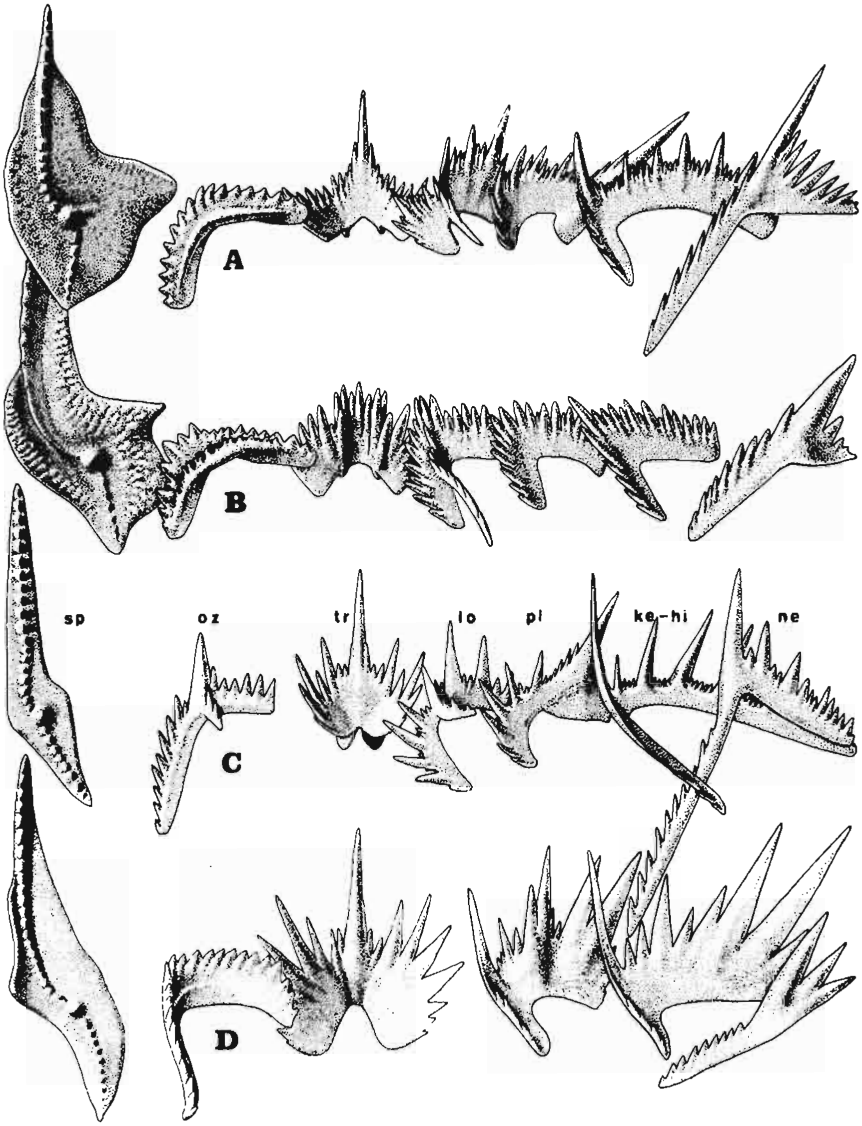

Fig. 16. Discrete element types in apparatuses of the Palmatolepididae. ❑A. *Manticolepis subrecta* (Miller & Youngquist 1947), Frasnian of Germany (after van den Boogard & Kuhry 1979). ❑B. *Palmatolepis rugosa* Branson & Mehl 1934, Famennian of the Holy Cross Mts. ❑C. *Tripodellus gracilis* (Branson & Mehl 1934), Famennian of the Holy Cross Mts. ❑D. *Panderolepis falcata* (Helms 1959), Famennian of the Holy Cross Mts.

sp pair, usually reaching soon the subsequent **oz** pair ('ambalodus' element of the Balognathidae, 'nothognathella' of the Polygnathidae) and in some rare cases (Pterospathodontidae, *Steptotaxis*) expanded also to other locations. The molarized surfaces developed either by a lateral expansion of ridges at the base of denticles (platform) or as a lateral widening of denticle tips (icrion). Frequently the effects of the molarization are strenghtened by a ramification of processes. Paths of modification of the elements of the platform complex were sometimes so complex that without knowledge of the real course of evolution, derived from stratigraphically dense sampling (stratophenetics), it seems virtually impossible to say in which way particular 'grinding' surfaces developed (*Hadrognathus*, *Pseudofurnishius* or *Mestognathus* are good examples). The molarized area was usually located along the internal ('posterior') process of the **sp** element. Also ramification of elements was generally directed inward of the mouth. This seems reasonable as in a scissor-like action the inner processes pressed at food pieces with a stronger force. The external process of the **sp** element is almost always blade-like, with sharp denticles. The incisor-molar model is thus applicable not only to the distribution of the elements along the apparatus but also to its dorso-ventral dimension.

Rather unexpectedly, in some advanced conodonts the external, instead of internal, process of the **sp** elements is molarized. A platform developed along this process in *Gondolella*, while in *Pygodus* in this part of the element additional rows of tubercles developed at margins of gaping bases. In an attempt to explain this peculiar reversal of the common trend one may recall the supposed mechanical consequences of the enclosure of the posterior part of the apparatus within the throat. The ventral muscular cover of the throat could possibly transform into an adductor apparatus supplementing and finally replacing the original scissor-like action of dorsally located buccal muscle mass. With the development of the ventral adductor muscles the elements started to move parallel to each other, so that no longer was the inner end preferred for molarization. Moreover, simple contraction of the ventral adductors, being more efficient mechanically, promoted ventral migration of the molarized area.

Taxonomic importance of the apparatuses

According to the view prevailing among neontologists, classification should refer exclusively to morphologic criteria. It is equally widely assumed than a good classification is that one which adequately expresses the true evolutionary relationships of classified organisms. The history of development of the conodont research shows that there is an unbridgeable contradiction between these two claims. Paradoxically, our understanding of the phylogeny of conodonts is quite advanced although no generally accepted classification of the group has yet been established. The phylogeny and classification of the conodonts are thus obviously quite different

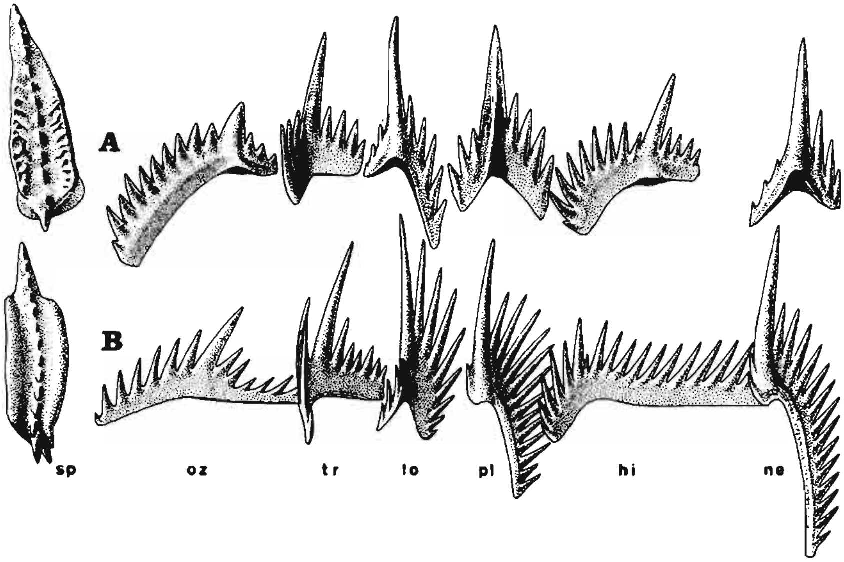

Fig. 17. Discrete element types in apparatuses of the Gondolellidae. ❑A. *Gondolella sublanceolata* Gunnell 1933, Virgillian of Iowa (after von Bitter, 1976). ❑B. *Epigondolella truempyi* (Hirsch 1971), Ladinian of Sardinia (after Bagnoli *et al.* 1985).

things. One may say that while classification is a measure of a blood relationship, a phylogenetic tree shows the network of ancestor-descendant relationships among taxa of different age.

The present knowledge of the phylogeny of conodonts is hard to imagine without stratigraphically dense sampling. The methodology of processing empirical data obtained in this way is based on the rule of supremacy of the time and space order in distribution of data. The objective time-and-space coordinates of particular samples form in fact the background from which any analysis of the distribution of morphologies has to be performed. Any hypothesis of the ancestor-descendant relationship postulates a transfer of the genetic information along the lineage represented by successive samples. When ranges of morphologic variability in stratigraphically and geographically neighbouring samples overlap significantly, suggesting a genetic proximity of the populations represented by them, one may consider the hypothesis corroborated by the empirical evidence. A conclusive evidence of the (ancestor-descendant) relationship can be provided thus only by a documented continuity of evolutionary transformations along densely sampled sections. In such a case nothing else remains than to accept the relationship even if the end-members of the studied lineage are quite morphologically dissimilar to each other.

Owing to such phylogenetic methodology it is well known now that almost every morphologic type of elements developed independently many times in the evolution of the Conodonta. One may thus conclude that a shape of any single element, without reference to associated parts of the apparatus, cannot be used as a trustworthy guide to identification of relationships. Moreover, the information that can be extracted from the morphology of any apparatus is not just a sum of information about particular elements. It is more, as long as much supplementary information concerns a spatial organization of the apparatus and patterns of morphologic relationships between particular element types. Therefore studies on the evolution of particular isolated element types (without regard to other parts of the apparatus) can not substitute for apparatus studies. The change of interest from separate elements to apparatus reconstructions seems to reflect an unavoidable methodologic evolution of our branch of science. Now, after almost thirty years of apparatus studies, it can be safely stated that there is no objective reason to continue the 'form taxonomy' approach in any conodont group or period of geologic time.

Classification of conodonts

Although it is quite doubtful whether it is possible to establish uniform morphologic criteria of ranking of particular taxonomic units, there is some need for consistency in this respect, at least regarding related groups. Accordingly, the differentiation of elements into discrete series *versus* smooth gradation of shapes in a grasping apparatus allows us to subdivide the class into orders. The more or less sudden appearance of a particular Baupläne of element types that subsequently became quite conservative may serve to diagnose families. These criteria cannot be used in the same way for conodonts of different geological age. While in the Ordovician there was a tremendous diversity of apparatus patterns and element morphologies, during the Late Paleozoic the conodonts were very monotonous in this respect. Perhaps in the course of evolution some kind of stabilization and canalization of the expression of the genome occurred, resulting in a decrease of intrapopulation variability and consequently shorter morphologic distances between sympatric species. A strict application of the same criteria for the Ordovician and later conodonts would thus result in an unnecessary exaggeration of the otherwise well established fact that this was the period of the most intense diversification of the group (Fig. 18). On the other hand, use of such features as the depth of the basal cavity or the shape of the platform in the **sp** elements as the only character for distinguishing families is somewhat questionable even in the Late Paleozoic.

There is no generally accepted classification scheme of the conodonts. The *Treatise* (Clark *et al.* 1981) classification was harshly criticized by Fåhræus (1984), but his proposals are not free of discrepancies with respect to well established phylogenetic relationships of several genera. Sweet's (1988) improved version of the *Treatise* system, with several new and useful high-rank taxa added, is the closest one to that accepted for the present purposes. Modifications concern mostly simple-cones, with new

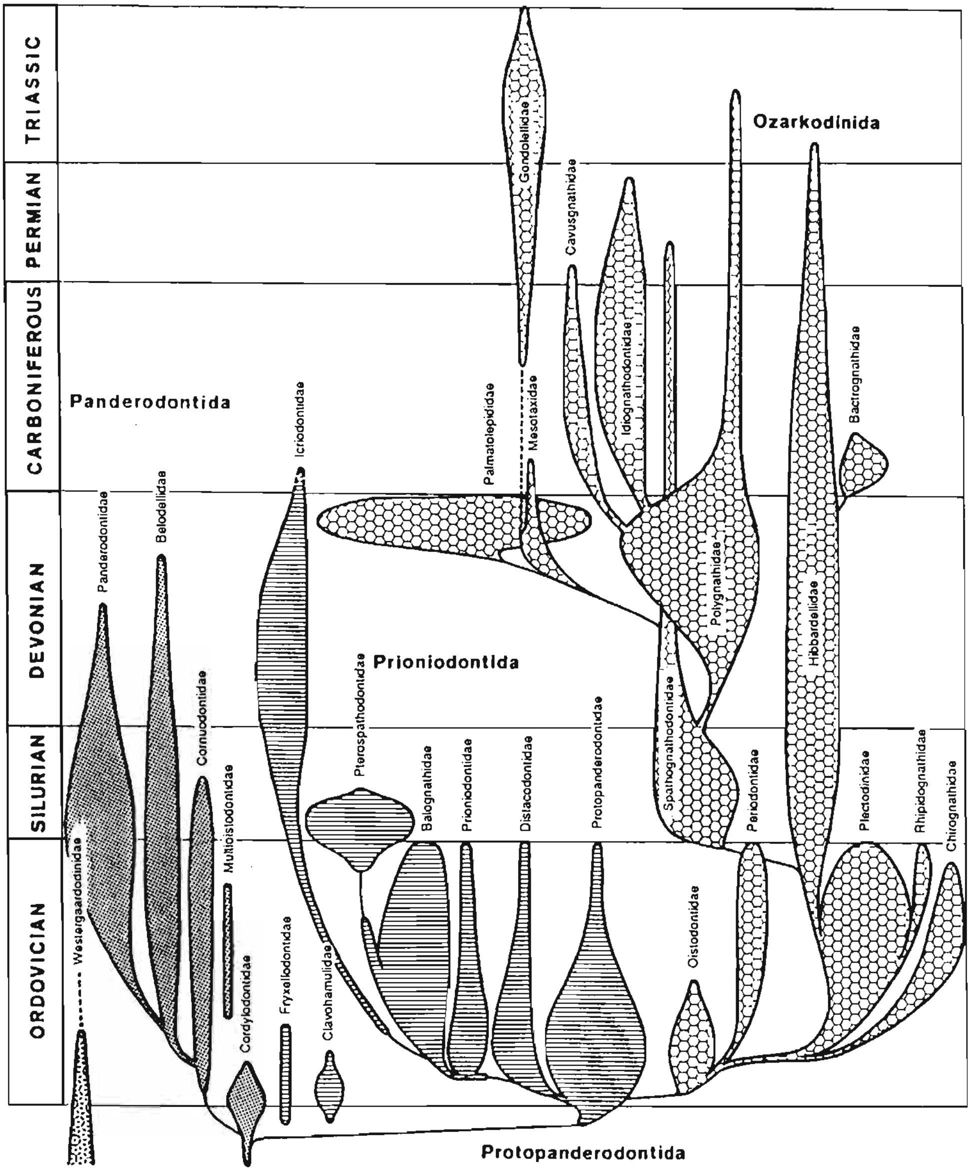

Fig. 18. Phylogenetic relationships and stratigraphic distribution of higher taxa discussed in the text.

data on their apparatuses and evolution used, and somewhat differently interpreted relationships of the major groups of the ozarkodinid conodonts.

Class Conodonta Pander 1856

Order Westergaardodinida Lindström 1970

Elements initially growing uniformly from all sides, later in histogeny their tips were exposed.

Family **Furnishinidae** Müller & Nogami 1971
Furnishina Müller 1959, *Prooneotodus* Müller & Nogami 1971, *Problematoconites* Müller 1959

Family **Westergaardodinidae** Müller 1959
Westergaardodina Müller 1959

Order Panderodontida Sweet 1988 (incl. Belodellida Sweet 1988)

Medial element in the apparatus missing(?).

Superfamily **Cordylodontacea** Lindström 1970
Radial microstructure of the crown tissue.

Family **Proconodontidae** Lindström 1970
Coniform elements.
Proconodontus Miller 1969

Family **Cordylodontidae** Lindström 1970
Denticulated elements (geniculate in oldest forms).
Cordylodus Pander 1856, *Eoconodontus* Miller 1980, *Iapetognathus* Landing 1983, *Cambroistodus* Miller 1980, ?*Paracordylodus* Lindström 1971

Family **Fryxellodontidae** Miller 1981
Elements with tubercle rows radiating from the cusp tip.
Fryxellodontus Miller 1969, ?*Pseudooneotodus* Drygant 1972

Incertae familiae: *Loxodus* Furnish 1938, *Cristodus* Repetski 1982, *Coleodus* Branson & Mehl 1933, *Leptochirognathus* Branson & Mehl 1943, *Thrincodus* Bauer 1987

Superfamily **Panderodontacea** Lindström 1970
Crystallites oriented parallel to the cusp.

Family **Strachanognathidae** Bergström 1982 (=Cornuodontidae Stouge 1984)
Simple coniform elements with deep basal cavities.
Cornuodus Fåhræus 1966, *Dapsilodus* Cooper 1976, *Scabbardella* Orchard 1980, *Decoriconus* Cooper 1975, *Besselodus* Aldridge 1982, *Strachanognathus* Rhodes 1955

Family **Belodellidae** Khodalevich & Chernich 1973
Prominently cristate coniform elements with deep basal cavities.
Belodella Ethington 1959, *Walliserodus* Serpagli 1967, *Scalpellodus* Dzik 1976, *Drepanodistacodus* Moskalenko 1977, *Dvorakia* Klapper & Barrick 1983

Family **Panderodontidae** Lindström 1970
Panderodont furrow present.
Panderodus Ethington 1959, *Taoqupognathus* An 1985, *Belodina* Ethington 1959, *Culumbodina* Moskalenko 1973, *Plegagnathus* Ethington & Furnish 1959, *Pseudobelodina* Sweet 1979, *Parabelodina* Sweet 1979, *Neopanderodus* Ziegler & Lindström 1971

Order Protopanderodontida Sweet 1988

Coniform symmetrical medial element separates the 'platform' series of coniform elements from the rest of the apparatus.

Family **Protopanderodontidae** Lindström 1970
Simple coniform elements with relatively shallow basal cavities.
Protopanderodus Lindström 1971, *Semiacontiodus* Miller 1969, *Staufferella* Sweet, Thompson & Satterfield 1975, *Parapanderodus* Stouge 1984, *Drepanodus* Pander 1856, *Teridontus* Miller 1980, *Ulrichodina* Furnish 1938, *Scandodus* Lindström 1955, *Oneotodus* Lindström 1955, *Scolopodus* Pander 1856

Family ?**Clavohamulidae** Lindström 1970
Robust tuberculated elements.
Clavohamulus Furnish 1938, *Hirsutodontus* Miller 1969, *Hispidodontus* Nicoll & Shergold 1991, *Serratognathus* Lee 1970

Family **Distacodontidae** Bassler 1925
Geniculate anteriormost elements.
Drepanoistodus Lindström 1971, *Paroistodus* Lindström 1971

Order Prioniodontida Dzik 1976

Originally elements of the platform series triramous, **ke** and **hi** locations distinct morphologically.

Superfamily **Prioniodontacea** Bassler 1925

Tetraramous **lo-pl** elements.

Family **Prioniodontidae** Bassler 1925

Elements of approximately uniform size.

Prioniodus Pander 1856, *Oepikodus* Lindström 1955, *Acodus* Pander 1856, *Tripodus* Bradshaw 1969, *Eoneoprioniodus* Mound 1965, *Baltoniodus* Lindström 1971, *Phragmodus* Branson & Mehl 1933, *Paraprioniodus* Ethington & Clark 1981, *Acanthocordylodus* Moskalenko 1973

Family **Balognathidae** Hass 1959 (incl. Cyrtoniodontidae *sensu* Sweet 1988)

Larger, platform-bearing elements of the platform complex.

Lenodus Sergeeva 1963, *Rhodesognathus* Bergström & Sweet 1966, *Amorphognathus* Branson & Mehl 1933, *Eoplacognathus* Hamar 1966, *Cahabagnathus* Bergström 1983, *Polyplacognathus* Stauffer 1935, *Sagittodontina* Knüpfer 1967 (= *Noixodontus* McCracken & Barnes 1982), *Promissum* Kovacs-Endrody 1986, ?*Polonodus* Dzik 1976

Family ?**Ansellidae** Fåhræus & Hunter 1985

Geniculate **ne** element associated with *Belodella*-like rest of the apparatus.

Ansella Fåhræus & Hunter 1985, ?*Tokognathus* Nieper 1969

Family **Pygodontidae** Bergström 1981

Reduced inner process in **sp** elements that bears a few radial rows of tubercles.

Pygodus Lamont & Lindström 1957, ?*Nericodus* Lindström 1955

Superfamily **Icriodontacea** Müller & Müller 1957

Triramous **lo-pl** elements.

Family **Pterospathodontidae** Cooper 1977

All the element pairs in the apparatus morphologically distinct from each other.

Pterospathodus Walliser 1964 (?=*Aulacognathus* Mostler 1967, *Astropentagnathus* Mostler 1967, *Pranognathus* Männik & Aldridge 1989), *Complexodus* Dzik 1976, *Carniodus* Walliser 1964, *Birksfeldia* Orchard 1980 (= *Gamachignathus* McCracken, Nowlan & Barnes 1980), *Apsidognathus* Walliser 1964, *Astrolecignathus* Over & Chatterton 1987, ?*Distomodus* Branson & Branson 1947, *Coryssognathus* Link & Druce 1972

Family **Icriodontidae** Müller & Müller 1957

Elements, except for the **sp**, more or less reduced.

Icriodus Branson & Mehl 1938, *Icriodella* Rhodes 1953, *Pedavis* Klapper & Philip 1971, *Latericriodus* Müller 1962, *Pelekysgnathus* Thomas 1949, *Antognathus* Lipnyagov 1978, *Steptotaxis* Uyeno & Klapper 1980, *Mitrellataxis* Chauff & Price 1980, ?*Dollymae* Hass 1959

Order Ozarkodinida Dzik 1976

Originally biramous elements of the platform series.

Suborder Plectodinina new

Proclined cusp of **ne** elements.

Superfamily **Oistodontacea** Lindström 1970

Geniculate **ne** element; triramous **lo-pl** elements.

Family **Oistodontidae** Lindström 1970

Undenticulated (rarely serrated) external processes of all elements.

Oistodus Pander 1856, *Utahconus* Miller 1980, *Rossodus* Repetski & Ethington 1983, *Histiodella* Harris 1962, *Protoprioniodus* McTavish 1973, *Fahraeusodus* Stouge & Bagnoli 1988, ?*Juanognathus* Serpagli 1974

Family **Periodontidae** Lindström 1970

Except for **ne** all elements sharply denticulated.

Periodon Hadding 1913, ?*Hamarodus* Viira 1974

Incertae familiae: *Bergstroemognathus* Serpagli 1974, *Appalachignathus* Bergström, Carnes, Ethington, Votaw & Wigley 1974, *Ruetterodus* Serpagli 1974.

Superfamily **Chirognathacea** Branson & Mehl 1944

Biramous **lo-pl** elements.

Family **Plectodinidae** Sweet 1988

Plectodina Stauffer 1935, *Microzarkodina* Lindström 1971, *Yaoxianognathus* An 1985, *Aphelognathus* Branson, Mehl, & Branson 1951, *Bryantodina* Stauffer 1935, *Scyphiodus* Stauffer 1935, *Oulodus* Branson & Mehl 1933

Family **Rhipidognathidae** Lindström 1970

Rhipidognathus Branson, Mehl, & Branson 1951, *Tasmanognathus* Burrett 1979

Family **Chirognathidae** Branson & Mehl 1944

Chirognathus Branson & Mehl 1933, *Erismodus* Branson & Mehl 1933, *Erraticodon* Dzik 1978, *Archaeognathus* Cullison 1938, *Stereoconus* Branson & Mehl 1933, *Mixoconus* Sweet 1955, ?*Scapulidens* Ethington, Droste, & Rexroad 1986, ?*Lumidens* Ethington, Droste, & Rexroad 1986, ?*Oistodella* Bradshaw 1969, ?*Spinodus* Dzik 1976

Family ?**Multioistodontidae** Harris 1964

Multioistodus Cullison 1938, *Multicornus* Moskalenko 1970

Suborder Ozarkodinina Dzik 1976 (=Prioniodinina Sweet 1988)

Erect cusp and arched process of **ne** elements.

Superfamily **Hibbardellacea** Müller 1956

Robust denticulation.

Family **Hibbardellidae** Müller 1956

Hibbardella Bassler 1925, *Delotaxis* Klapper & Philip 1971, *Idioprioniodus* Gunnell 1933, *Apatognathus* Branson & Mehl 1934, *Kladognathus* Rexroad 1958, *Erica* Murphy & Matti 1982, *Cryptotaxis* Klapper & Philip 1971, *Prioniodina* Bassler 1925, ?*Ellisonia* Müller 1956

Family **Bactrognathidae** Lindström 1970

Elements **ne** with short, robustly denticulated process.

Bactrognathus Branson & Mehl 1941, ?*Doliognathus* Branson & Mehl 1941, ?*Scaliognathus* Branson & Mehl 1941, ?*Staurognathus* Branson & Mehl 1941, ?*Lochriea* Scott 1942, ?*Cudotaxis* Chauff 1981

Superfamily **Polygnathacea** Bassler 1925

Compressed denticles.

Family **Spathognathodontidae** Hass 1959 (= Anchignathodontidae Clark 1972, Kockelellidae Klapper 1981)

Biramous **tr** element.

Ozarkodina Branson & Mehl 1933, *Kockelella* Walliser 1957, *Polygnathoides* Branson & Mehl 1933, *Amydrotaxis* Klapper & Murphy 1980, *Hindeodus* Rexroad & Furnish 1964, *Falcodus* Huddle, 1934, *Aethotaxis* Baesemann 1973, ?*Pachycladina* Staesche 1964, ?*Furnishius* Clark 1959, ?*Hadrodontina* Staesche 1964

Family **Polygnathidae** Bassler 1925

Triramous **tr** element.

Polygnathus Hinde 1879, *Pandorinellina* Müller & Müller 1957, *Eognathodus* Philip 1965, *Ancyrodelloides* Bischoff & Sannemann 1958, *Ancyrodella* Ulrich & Bassler 1926, *Pseudopolygnathus* Branson & Mehl 1934, *Bispathodus* Müller 1962, *Branmehla* Hass 1959, *Mehlina* Youngquist 1945, *Skeletognathus* Sandberg, Ziegler & Bultynck 1989, *Siphonodella* Branson & Mehl 1944, *Hemilistrona* Chauff & Dombrowski 1977, *Merrilina* Kozur & Mock 1974, *Stepanovites* Kozur 1975.

Family **Cavusgnathidae** Austin & Rhodes 1981 (incl. Mestognathidae Austin & Rhodes 1981)

Axial symmetry of **sp** elements with platform developed only on one side.

Cavusgnathus Harris & Hollingsworth 1933, *Mestognathus* Bischoff 1957, *Adetognathus* Lane 1967, *Clydagnathus* Rhodes, Austin & Druce 1969, *Patrognathus* Rhodes, Austin, & Druce 1969, *Scaphignathus* Helms 1959, *Rhachistognathus* Dunn 1966

Family **Idiognathodontidae** Harris & Hollingsworth 1933

Arched external process of **ke-hi** elements.

Idiognathodus Gunnell 1931, *Idiognathoides* Harris & Hollingsworth 1933, *Neognatho-*

dus Dunn 1970, *Protognathodus* Ziegler 1969, *Streptognathodus* Stauffer & Plummer 1932

Family **Sweetognathidae** Ritter 1986

Apparatus like idiognathodontids, tendency to develop pustulose ornamentation and icrion in **sp** elements.

Sweetognathus Clark 1972, *Vogelgnathus* Norby & Rexroad 1986, *Diplognathodus* Kozur & Merrill 1975, *Neostreptognathodus* Clark 1972

Family **Gnathodontidae** Sweet 1988

Gnathodus Pander 1856

Superfamily **Palmatolepidacea** Sweet 1988

Elements **ne** with straight, denticulated processes.

Family **Mesotaxidae** new

Ozarkodina-like elements of the symmetry transition series but triramous **tr** elements.

Mesotaxis Klapper & Philip 1971, ?*Dinodus* Cooper 1939, ?*Pinacognathus* Branson & Mehl 1944., ?*Ancyrognathus* Branson & Mehl 1934, ?*Polylophodonta* Branson & Mehl 1934.

Family **Palmatolepididae** Sweet 1988

Triramous **lo** element, biramous **tr** with bifurcating processes.

Palmatolepis Ulrich & Bassler 1926, *Conditolepis* Boogard & Kuhry 1979, *Panderolepis* Helms 1963, *Manticolepis* Müller 1956, *Tripodellus* Sannemann 1955

Superfamily **Gondolellacea** Lindström 1970

Family **Gondolellidae** Lindström 1970

Reduced inner processes of the platform series elements, highly arched **lo**, triramous **tr** element, more than two pairs of **hi**-like elements in advanced forms.

Gondolella Stauffer & Plummer 1932, *Epigondolella* Mosher 1968, *Neogondolella* Bender & Stoppel 1965, *Pseudofurnishius* van den Boogard 1966, *Misikella* Kozur & Mock 1974, ?*Axiothea* Fåhræus & Ryley 1989

Acknowledgements

The final version of the manuscript of this paper has been edited during my Alexander von Humboldt scholarship at the University of Tübingen. The paper owes much to critical comments of Gilbert Klapper (The University of Iowa) who also improved its language.

References

Aldridge, R.J. 1982. A fused cluster of coniform conodont elements from the Late Ordovician of Washington Land, Western North Greenland. *Palaeontology* **25**, 425-430.

Aldridge, R.J., Briggs, D.E.G., Clarkson, E.N.K., & Smith, M.P. 1986. The affinities of conodonts - new evidence from the Carboniferous of Edinburgh, Scotland. *Lethaia* **19**, 279-291.

Aldridge, R.J., Smith, M.P., Norby, R.D., & Briggs, D.E.G. 1987. The architecture and function of Carboniferous polygnathacean conodont apparatuses. In: Aldridge, R.J. (ed.) *Palaeobiology of Conodonts* 63-75. British Micropalaeontological Society Series.

Andres, D. 1981. Beziehungen zwischen kambrischen Conodonten und Euconodonten. *Berliner geowissentschafliche Abhandlungen (A)* **32**, 19-31.

Andres, D. 1988. Strukturen, Apparate und Phylogenie primitiver Conodonten. *Palaeontographica* **200A**, 105-152.

Baesemann, J.F. 1973. Missourian (Upper Pennsylvanian) conodonts of northeastern Kansas. *Journal of Paleontology* **47**, 689-710.

Bagnoli, G., Perri, M.C., & Gandin, A. 1984. Ladinian conodont apparatuses from northwestern Sardinia, Italy. *Bolletino della Societa Paleontologica Italiana* **23**, 311-323.

Bandel, K. & Waksmundzki, B. 1985. Triassic conodonts from Jordan. *Acta Geologica Polonica* **35**, 289-304.

Barnes, C.R., Kennedy, D.J., McCracken, A.D., Nowlan, G.S., & Tarrant, G.A. 1979. The structure and evolution of Ordovician conodont apparatuses. *Lethaia* **12**, 125-151.

Barrick, J.E. 1977. Multielement simple-cone conodonts from the Clarita Formation (Silurian), Arbuckle Mountains, Oklahoma. *Geologica et Palaeontologica* **11**, 47-68.

Barrick, J.E. & Klapper, G. 1976. Multielement Silurian (late Llandoverian-Wenlockian) conodonts of the Clarita Formation, Arbuckle Mountains, Oklahoma, and phylogeny of *Kockelella. Geologica et Palaeontologica* **10**, 59-100.

Bełka, Z. 1983. Evolution of the Lower Carboniferous conodont genus *Mestognathus. Acta Geologica Polonica* **33**, 73-84.

Bengtson, S. 1976. The structure of some Middle Cambrian conodonts, and the early evolution of conodont structure and function. *Lethaia* **9**, 115-206.

Bengtson, S. 1983. The early history of the Conodonta. *Fossils and Strata* **15**, 5-19.

Bergström, S.M. 1971. Conodont biostratigraphy of the Middle and Upper Ordovician of Europe and eastern North America. *Geological Society of America, Memoir* **127**, 83-161.

Bergström, S.M. 1983. Biogeography, evolutionary relationships, and biostratigraphic significance of Ordovician platform conodonts. *Fossils and Strata* **15**, 35-58.

Bergström, S.M. & Sweet, W.C. 1966. Conodonts from the Lexington Limestone (Middle Ordovician) of Kentucky and its lateral equivalents in Ohio and Indiana. *Bulletins of American Paleontology* **50**, 271-441.

Bitter, P.H. von 1976. The apparatus of *Gondolella sublanceolata* Gunnell (Conodontophorida, Upper Pennsylvanian) and its relationship to *Illinella typica* Rhodes. *Life Sciences Contribution, Royal Ontario Museum* **109**, 1-44.

Bitter, P.H. von & Merrill, G.K. 1983. Late Palaeozoic species of *Ellisonia* (Conodontophorida): Evolution and palaeoecological significance. *Life Sciences Contribution, Royal Ontario Museum* **136**, 1-56.

Bitter, P.H. von & Merrill, G.K. 1985. *Hindeodus, Diplognathodus* and *Ellisonia* revisited - an identity crisis in Permian conodonts. *Geologica et Palaeontologica* **19**, 81-96.

Bitter, P.H. von & Merrill, G.K. 1990. Effects of variation on the speciation and phylogeny of *Diplognathodus. Courier Forschungsinstitut Senckenberg* **118**, 105-129.

Bitter, P.H. von & Plint-Geberl, H.A. 1982. Conodont biostratigraphy of the Codroy Group (Late Carboniferous), southern Newfoundland, Canada. *Canadian Journal of the Earth Sciences* **19**, 193-221.

Boogard, M. van den 1983. Conodont faunas from Portugal and southwestern Spain. Part 7. A Frasnian conodont fauna near the Estacao de Cabrela (Portugal). *Scripta Geologica* **69**, 1-17.

Boogard, M. van den 1989. Isolated tubercles of some Palaeoscolecida. *Scripta Geologica* **90**, 1-12.

Boogard, M. van den 1990. A Ludlow conodont fauna from Irian Jaya (Indonesia). *Scripta Geologica* **92**, 1-27.

Boogard, M. van den & Bless, M.J.M. 1985. Some conodont faunas from the Aegiranum marine band. *Proceedings Koninklijke Nederlandsche Akademie van Wetenschappen (B)* **88**, 133-154.

Boogard, M. van den & Kuhry, M.J.M. 1979. Statistical reconstruction of the *Palmatolepis* apparatus (Late Devonian conodontophorids) at the generic, subgeneric, and specific level. *Scripta Geologica* **49**, 1-57.

Briggs, D.E.G., Clarkson, E.N.K., & Aldridge, R.J. 1983. The conodont animal. *Lethaia* **16**, 1-14.

Carls, P. 1977. Could conodonts be lost and replaced? *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* **155**, 18-64.

Chauff, K.M. 1981. Multielement conodont species from the Osagean (Lower Carboniferous) in Midcontinent North America and Texas. *Palaeontographica* **175A**, 140-169.

Chauff, K.M. & Klapper, G. 1978. New conodont *Apatella* (Late Devonian) possible homeomorph *Bactrognathus* (Early Carboniferous, Osagean Series) and homeomorphy in conodonts. *Geologica et Palaeontologica* **12**, 151-164.

Clark, D.L., Sweet, W.C., Bergström, S.M., Klapper, G., Austin, R.L., Rhodes, F.H.T., Müller, K.J., Ziegler, W., Lindström, M., Miller, J.F., & Harris, A.G. 1981. Conodonta. In: R.A. Robison (ed.) *Treatise on Invertebrate Paleontology. Part W. Miscellanea. Supplement 2*, 202 pp. Geological Society of America and The University of Kansas, Boulder, Colorado, and Lawrence, Kansas.

Cooper, B.J. 1975. Multielement conodonts from the Brassfield Limestone (Silurian) of southern Ohio. *Journal of Paleontology* **49**, 984-1008.

Cooper, B.J. 1976. Multielement conodonts from the St.-Clair Limestone (Silurian) of southern Illinois. *Journal of Paleontology* **50**, 205-217.

Collinson, C., Avcin, M.J., Norby, R.D., & Merrill, G.K. 1972. Pennsylvanian conodont assemblages from La Salle County, northern Illinois. *Illinois State Geological Survey Guidebook* **10**, 1-37.

Cooper, B.J. 1981. Early Ordovician conodonts from the Horn Valley siltstone, central Australia. *Palaeontology* **24**, 147-183.

Dzik, J. 1976. Remarks on the evolution of Ordovician conodonts. *Acta Palaeontologica Polonica* **21**, 395-455.

Dzik, J. 1980. Isolated mandibles of early Paleozoic phyllocarid Crustacea. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* **1980**, 87-106.

Dzik, J. 1983. Relationships between Ordovician Baltic and North American Midcontinent conodont faunas. *Fossils and Strata* **15**, 59-85.

Dzik, J. 1986. Chordate affinities of the conodonts. In: M.H. Nitecki & A. Hoffman (eds) *Problematic Fossil Taxa*, 240-254. Oxford University Press, New York.

Dzik, J. 1990a. Conodont evolution in high latitudes of the Ordovician. *Courier Forschungsinstitut Senckenberg* **117**, 1-28.

Dzik, J. 1990b. The concept of chronospecies in ammonites. - In: Pallini, G. *et al.* (eds) *Atti del secondo convegno internazionale Fossili, Evoluzione, Ambiente, Pergola 25-30 ottobre 1987*, 273-289. Pergola.

Dzik, J. & Drygant, D. 1986. The apparatus of panderodontid conodonts. *Lethaia* **19**, 133-141.

Dzik, J. & Trammer, J. 1980. Gradual evolution of conodontophorids in the Polish Triassic. *Acta Palaeontologica Polonica* **25**, 55-89.

Fåhræus, L. 1984. A critical look at the Treatise family-group classification of Conodonta: an exercise of ecclecticism. *Lethaia* **17**, 293-305.

Fåhræus, L. & Hunter, D.R. 1985. Simple-cone conodont taxa from the Cobbs Arm Limestone (Middle Ordovician), New World Island, Newfoundland. *Canadian Journal of Earth Sciences* **22**, 1171-1182.

Fåhræus, L.E. & Ryley, C.C. 1989. Multielement species of *Misikella* Kozur and Mock, 1974 and *Axiothea*, n. gen. (Conodonta) from the Mamonia Complex (Upper Triassic), Cyprus. *Canadian Journal of Earth Sciences* **26**, 1255-1263.

Gaździcki, A. 1978. Conodonts of the genus *Misikella* Kozur & Mock, 1974 from the Rhaetian of the Tatra Mts. (West Carpathians). *Acta Palaeontologica Polonica* **23**, 341-350.

Graves, R.W. & Ellison, S.P. jr. 1941. Ordovician conodonts of the Marathon Basin, Texas. *University of Missouri School of Mines and Metallurgy, Bulletin (Technical Series)* **14**, 1-26.

Grayson, R.C.jr, Merrill, G.K., & Lambert, L.L. 1990. Carboniferous gnathodontid conodont apparatuses: evidence of a dual origin for Pennsylvanian taxa. *Courier Forschungsinstitut Senckenberg* **118**, 353-396.

Gross, W. 1954. Zur Conodonten-Frage. *Senckenbergiana Lethaea* **35**, 73-85.

Hinde, G.J. 1879. On conodonts from the Chazy and Cincinnati group of the Cambro-Silurian, and from the Hamilton and Genesee-shale divisions of the Devonian in Canada and the United States. *Quarterly Journal of the Geological Society London* **35**, 351-369.

Hinz, I., Kraft, P., Mergl, M., & Müller, K.J. 1990. The problematic *Hadimopanella, Kaimenella, Milaculum* and *Utahphospha* identified as sclerites of Palaeoscolecida. *Lethaia* **23**, 217-221.

Horowitz, A.S. & Rexroad, C.B. 1982. An evaluation of statistical reconstructions of multielement conodont taxa from Middle Chesterian rocks (Carboniferous) of southern Indiana. *Journal of Paleontology* **56**, 959-969.

Huckriede, R. 1958. Die Conodonten der mediterranen Trias und ihr stratigraphischer Wert. *Paläontologische Zeitschrift* **32**, 141-175.

Huddle, J.W. 1972. Historical introduction to the problem of conodont taxonomy. *Geologica et Palaeontologica (SB)* **1**, 3-16.

Jeppson, L. 1969. Notes on some Upper Silurian multielement conodonts. *Geologiska Föreningens i Stockholm Förhandlingar* **92**, 12-24.

Jeppson, L. 1971. Element arrangement in conodont apparatuses of *Hindeodella* type and in similar forms. *Lethaia* **4**, 101-123.

Jeppson, L. 1974. Aspects of Late Silurian conodonts. *Fossils and Strata* **6**, 1-54.

Jeppson, L. 1979. Conodont element function. *Lethaia* **12**, 153-171.

Jeppson, L. 1986. A possible mechanism in convergent evolution. *Paleobiology* **12**, 80-88.

Ji, Z. & Barnes, C.R. 1990. Apparatus reconstructions of Lower Ordovician conodonts from the Midcontinent province. *Courier Forschungsinstitut Senckenberg* **118**, 333-351.

Klapper, G. & Barrick, J.E. 1983. Middle Devonian (Eifelian) conodonts from the Spillville Formation in northern Iowa and southern Minnesota. *Journal of Paleontology* **57**, 1212-1243.

Klapper, G. & Bergström, S.M. 1984. The enigmatic Middle Ordovician fossil *Archaeognathus* and its relationship to conodonts and vertebrates. *Journal of Paleontology* **58**, 949-976.

Klapper, G. & Foster, C.T. jr. 1986. Quantification of outlines in Frasnian (Upper Devonian) platform conodonts. *Canadian Journal of Earth Sciences* **23**, 1214-1222.

Klapper, G. & Lane, H.R. 1985. Upper Devonian (Frasnian) conodonts of the *Polygnathus* biofacies, N.W.T., Canada. *Journal of Paleontology* **59**, 904-951.

Klapper, G. & Murphy, M.A. 1980. Conodont zonal species from the delta and pesavis zones (Lower Devonian) in central Nevada. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* **1980**, 490-504.

Klapper, G. & Johnson, D.B. 1975. Sequence in conodont genus *Polygnathus* in Lower Devonian at Lone Mountain, Nevada. *Geologica et Palaeontologica* **9**, 65-85.

Klapper, G. & Philip, G.M. 1971. Devonian conodont apparatuses and their vicarious skeletal elements. *Lethaia* **4**, 429-452.

Klapper, G. & Philip, G.M. 1972. Familial classification of reconstructed Devonian conodont apparatuses. *Geologica et Palaeontologica (SB)* **1**, 97-105.

Kohut, J.J. 1969. Determination, statistical analysis, and interpretation of recurrent conodont groups in Middle and Upper Ordovician strata of the Cincinnati region (Ohio, Kentucky, and Indiana). *Journal of Paleontology* **43**, 392-412.

Kollar, E.J. & Fisher, C. 1980. Tooth induction in chick epithelium: expression of quiescent genes for enamel synthesis. *Science* **207**, 993-995.

Kraft, P. & Mergl, M. 1989. Worm-like fossils (Palaeoscolecida; ?Chaetognatha) from the Lower Ordovician of Bohemia. *Sborník geologických věd, Paleontologie* **30**, 9-36.

Krejsa, R.J., Bringas, P.jr., & Slavkin, H.C. 1990. The cyclostome model: an interpretation of conodont element structure and function based on cyclostome tooth morphology, function, and life history. *Courier Forschungsinstitut Senckenberg* **118**, 473-492.

Lane, H.R. Symmetry in conodont element-pairs. *Journal of Paleontology* **42**, 1258-1263.

Lane, H.R. & Ziegler, W. 1984. Proposal of *Gnathodus bilineatus* (Roundy, 1926) as type species of the genus *Gnathodus* Pander, 1956 (Conodonta). *Senckenbergiana Lethaea* **65**, 257-283.

Lange, F.-G. 1968. Conodonten-Gruppenfunde aus Kalken des tieferen Oberdevon. *Geologica et Palaeontologica* **2**, 37-57.

Lindström, M. 1964. *Conodonts.* 196 pp. Elsevier, Amsterdam.

Lindström, M. 1971. Lower Ordovician conodonts of Europe. *Geological Society of America, Memoir* **127**, 21-61.

Lindström, M. 1973. On the affinities of conodonts. *Geological Society of America, Special Paper* **141**, 85-102.

Lindström, M. 1974. The conodont apparatus as a food-gathering mechanism. *Palaeontology* **17**, 729-744.

Lindström, M. & Ziegler, W. 1966. Ein Conodonten-taxon aus vier morphologisch verschiedenen Typen (Grenze Mittel/Oberdevon, Rheinisches Schiefergebirge). *Fortschrifte der Geologie Rheinland und Westfalen* **9**, 209-218.

Löfgren, A. 1978. Arenigian and Llanvirnian conodonts from Jämtland, northern Sweden. *Fossils and Strata* **13**, 1-129.

Löfgren, A. 1978. Non-platform elements of the Ordovician conodont genus *Polonodus*. *Paläontologische Zeitschrift* **64**, 245-259.

Männik, P. & Aldridge, R.J. 1989. Evolution, taxonomy and relationships of the Silurian conodont *Pterospathodus*. *Palaeontology* **32**, 893-906.

Mashkova, T.V. 1972. *Ozarkodina steinhornensis* (Ziegler) apparatus, its conodonts and biozone. *Geologica et Palaeontologica (SB)* **1**, 81-90.

McCracken, A.D. 1989. *Protopanderodus* (Conodontata) from the Ordovician Road River Group, northern Yukon Territory, and the evolution of the genus. *Geological Survey of Canada, Bulletin* **388**, 1-39.

McCracken, A.D. & Barnes, C.R. 1981. Conodont biostratigraphy and paleoecology of the Ellis Bay Formation, Anticosti Island, Quebec, with special reference to Late Ordovician - Early Silurian chronostratigraphy and the systemic boundary. *Geological Survey of Canada, Bulletin* **329**, 51-134.

McCracken, A.D., Nowlan, G.S. & Barnes, C.R. 1980. *Gamachignathus*, a new multielement conodont genus from the latest Ordovician, Anticosti Island, Quebec. *Geological Survey of Canada, Paper* **80-1C**, 103-112.

McGoff, H.J. & Briggs, D.E.G. 1988. The hydrodynamics of conodont elements - experimental results and implications. *Courier Forschungsinstitut Senckenberg* **102**, 248.

McHargue, T.R. 1982. Ontogeny, phylogeny, and apparatus reconstruction of the conodont genus *Histiodella*, Joins Fm., Arbuckle Mountains, Oklahoma. *Journal of Paleontology* **56**, 6, 1410-1433.

McTavish, R.A. 1973. Prioniodontacean conodonts from the Emanuel Formation (Lower Ordovician) of western Australia. *Geologica et Palaeontologica* **7**, 27-58.

Merrill, G.K. & Bitter, P.H. von 1977. Apparatus of the Pennsylvanian conodont genus *Neognathodus*. *Life Sciences Contributions, Royal Ontario Museum* **112**, 1-22.

Mietto, P. 1982. A Ladinian conodont-cluster of *Metapolygnathus mungoensis* (Diebel) from Trento area (N.E.Italy). *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* **1982**, 600-606.

Miller, J.F. 1980. Taxonomic revisions of some Upper Cambrian and Lower Ordovician conodonts, with comments on their evolution. *University of Kansas Paleontological Contributions, Paper* **99**, 1-44.

Moskalenko, T.A. 1972. Ordovician conodonts of the Siberian Platform and their bearing on multielement taxonomy. *Geologica et Palaeontologica (SB)* **1**, 47-56.

Müller, K.J. & Nogami, Y. 1971. Über den Feinbau der Conodonten. *Memoirs of the Faculty of Sciences of the Kyoto University, Series of Geology and Mineralogy* **38**, 1-88.

Murphy, M.A. & Matti, J.C. 1982. Lower Devonian conodonts (hesperius-kindlei zones), central Nevada. *University of California Publications in Geological Sciences* **123**, 1-82.

Murphy, M.A., Matti, J.C., & Walliser, O.H. 1981. Biostratigraphy and evolution of the *Ozarkodina remscheidensis - Eognathodus sulcatus* lineage (Lower Devonian) in Germany and central Nevada. *Journal of Paleontology* **55**, 747-772.

Nicoll, R.S. 1977. Conodont apparatuses in an Upper Devonian paleoniscid fish from the Canning Basin, Western Australia. *BMR Journal of Australian Geology and Geophysics* **2**, 217-228.

Nicoll, R.S. 1980. The multielement genus *Apatognathus* from the Late Devonian of the Canning Basin, western Australia. *Alcheringa* **5**, 133-152.

Nicoll, R.S. 1982. Multielement composition of the conodont *Icriodus expansus* Branson & Mehl from the Upper Devonian of the Canning Basin, western Australia. *BMR Journal of Australian Geology and Geophysics* **7**, 197-213.

Nicoll, R.S. 1985. Multielement composition of the conodont species *Polygnathus xylus xylus* Stauffer, 1940 and *Ozarkodina brevis* (Bischoff & Ziegler, 1957) from the Upper Devonian of the Canning Basin, western Australia. *BMR Journal of Australian Geology and Geophysics* **9**, 133-147.

Nicoll, R.S. 1987. Form and function of the Pa element in the conodont animal. In: R.A. Aldridge (ed.) *Palaeobiology of Conodonts*. 77-90. British Micropalaeontological Society Series.

Nicoll, R.S. 1990. The genus *Cordylodus* and latest Cambrian-earliest Ordovician conodont biostratigraphy. *BMR Journal of Australian Geology and Geophysics* **11**, 529-558.

Nicoll, R.S. & Rexroad, C.B. 1987. Re-examination of Silurian conodont clusters from northern Indiana. In: R.A. Aldridge (ed.) *Palaeobiology of Conodonts*. 49-61. British Micropalaeontological Society Series.

Nicoll, R.S. & Shergold, J.H. 1991. Revised Late Cambrian (pre-Payntonian–Datsonian) conodont biostratigraphy at Black Mountain, Georgina Basin, western Queensland, Australia. *BMR Journal of Australia Geology and Geophysics* **12**, 93-118.

Nowlan, G.S. 1979. Fused clusters of the conodont genus *Belodina* Ethington from the Thumb Mountain Formation (Ordovician), Ellesmere Island, District of Franklin. *Geological Survey of Canada Paper* **79-1A**, 213-219.

Nowlan, G.S., McCracken, A,D., & Chatterton, B.D.E. 1988. Conodonts from Ordovician-Silurian boundary strata, Whittaker Formation, Mackenzie Mountains, Northwestern territories. *Geological Survey of Canada Bulletin* **373**, 1-99.

Over, D.J. & Chatterton, B.D.E. 1987. Silurian conodonts from the southern Mackenzie Mountains, Northwest Territory, Canada. *Geologica et Palaeontologica* **21**, 1-49.

Pander, C.H. 1856. *Monographie der fossilen Fische des silurischen Systems der russisch-baltischen Gouverments*. 91 pp. Akademie der Wissenschaften, St. Petersburg.

Philip, G.M. & McDonald, L. 1975. A provisional phylogeny for some reconstructed Late Devonian polygnathid conodont apparatuses. *Alcheringa* **1**, 97-107.

Pickett, J. 1980. Conodont assemblages from the Cobar Supergroup (Early Devonian), New South Wales. *Alcheringa* **4**, 67-88.

Pollock, C.A. 1969. Fused Silurian conodont clusters from Indiana. *Journal of Paleontology* **43**, 929-935.

Puchkov, V.N., Klapper, G. & Mashkova, T.V. 1981. Natural assemblages of *Palmatolepis* from the Upper Devonian of the northern Urals. *Acta Palaeontologica Polonica* **26**, 281-298.

Priddle, J. 1974. The function of conodonts. *Geological Magazine* **111**, 255-257.

Ramovš, A. 1977. Skelettapparat von *Pseudofurnishius murcianus* (Conodontophorida) in der Mitteltrias Sloveniens (NW Jugoslawien). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* **153**, 361-399.

Ramovš, A. 1978. Mitteltriassische Conodonten-clusters in Slovenien, NW Jugoslawien. *Paläontologische Zeitschrift* **52**, 129-137.

Repetski, J.E. 1982. Conodonts from El Paso Group (Lower Ordovician) of westernmost Texas and southern New Mexico. *New Mexico Bureau of Mines and Mineral Resources, Memoir* **40**, 1-121.

Repetski, J.E. & Ethington, R.L. 1983. *Rossodus manitouensis* (Conodonta), a new Early Ordovician index fossil. *Journal of Paleontology* **57**, 289-301.

Rexroad, C.B. 1981. Conodonts from the Vienna Limestone Member of the Branchville Formation (Chesterian) in southern Indiana. *Geological Survey Indiana Occasional Paper* **34**, 1-16.

Rexroad, C.B. & Horowitz, A.S. 1990. Conodont paleoecology and multielement associations of the Beaver Bend Limestone (Chesterian) of Indiana. *Courier Forschungsinstitut Senckenberg* **118**, 493-537.

Rexroad, C.B. & Nicoll, R.S. 1964. A Silurian conodont with tetanus? *Journal of Paleontology* **38**, 771-773.

Rhodes, F.H.T. 1952. A classification of Pennsylvanian conodont assemblages. *Journal of Paleontology* **26**, 886-901.

Rhodes, F.H.T. 1954. The zoological affinities of the conodonts. *Biological Reviews* **29**, 419-452.

Rieber, H. 1980. Ein Conodonten-cluster aus der Grenzbitumenzone (Mittlere Trias) des Monte San Giorgio (Kt. Tessin/Schweiz). *Annalen des Naturhistorisches Museum Wien* **83**, 265-274.

Rohon, J.V. & Zittel, K.A. von 1887. Ueber Conodonten. *Bayerische Akademie der Wissenschaften, Sitzungsberichte (Mathematisch-Naturwissenschaftliche Klasse)* **16**, 108-136.

Ritter, S.M. & Baesemaun, J.F. 1991. Early Permian conodont assemblages from the Wolfcamp Shale, Midland Basin, West Texas. *Journal of Paleontology* **65**, 670-677.

Sandberg, C.A. & Dreesen, R. 1984. Late Devonian icriodontid biofacies models and alternate shallow water conodonts. *Geological Society of America Special Paper* **196**, 143-178.

Savage, N.M. 1990. Conodonts of Caradocian (Late Ordovician) age from the Cliefden Caves Limestone, Southeastern Australia. *Journal of Paleontology* **64**, 821-831.

Scott, H.W. 1935. The zoological relationships of the conodonts. *Journal of Paleontology* **8**, 448-455.

Schmidt, H. 1934. Conodonten-Funde in ursprunglichen Zusammenhang. *Paläontologische Zeitschrift* **16**, 76-85.

Schmidt, H. & Müller, K.J. 1964. Weitere Funde von Conodonten-Gruppen aus dem oberen Karbon des Sauerlandes. *Paläontologische Zeitschrift* **38**, 105-135.

Serpagli, E. 1983. The conodont apparatus of *Icriodus woschmidti woschmidti* Ziegler. *Fossils and Strata* **15**, 155-161.

Slavkin, H.C., Graham, E., Zeichner-David, M., & Hindemann, W. 1983. Enamel-like antigens in hagfish: possible evolutionary significance. -*Evolution* **37**, 404-412.

Smith, H.P. 1990. The Conodonta - palaeobiology and evolutionary history of a major Palaeozoic chordate group. *Geological Magazine* **127**, 365-369.

Smith, M.P., Briggs, D.E.G., & Aldridge, R.J. 1987. A conodont animal from the Lower Silurian of Wisconsin, USA, and the apparatus architecture of panderodontid conodonts. In: Aldridge, R.J. (ed.) *Palaeobiology of Conodonts*. 91-104. British Micropalaeontological Society Series.

Sparling, D.R. 1981. Middle Devonian conodont apparatuses with seven types of elements. *Journal of Paleontology* **55**, 295-316.

Stouge, S.S. 1984. Conodonts of the Middle Ordovician Table Head Formation, western Newfoundland. *Fossils and Strata* **16**, 1-145.

Stouge, S. & Bagnoli, G. 1988. Early Ordovician conodonts from Cow Head Peninsula, western Newfoundland. *Palaeontographica Italica* **75**, 89-179.

Stouge, S. & Bagnoli, G. 1991. Lower Ordovician (Volkhovian–Kundan) conodonts from Hagudden, northern Öland, Sweden. *Palaeontographia Italica* **77** (1990), 1-54.

Sweet, W.C. 1979. Late Ordovician conodonts and biostratigraphy of the western Midcontinent province. *Brigham Young University Geology Studies* **26**, 45-74.

Sweet, W.C. 1982. Conodonts from the Winnipeg Formation (Middle Ordovician) of the northern Black Hills, South Dakota. *Journal of Paleontology* **56**, 1029-1049.

Sweet, W.C. 1988. *The Conodonta. Morphology, Taxonomy, Paleoecology and Evolutionary History of a Long-Extinct Animal Phylum.* 212 pp. Clarendon Press, Oxford.

Sweet, W.C. & Bergström, S.M. 1962. Conodonts from the Pratt Ferry Formation (Middle Ordovician) of Alabama. *Journal of Paleontology* **36**, 1214-1252.

Sweet, W.C. & Schönlaub, H.P. 1975. Conodonts of the genus *Oulodus* Branson & Mehl, 1933. *Geologica et Palaeontologica* **9**, 41-59.

Swift, A. 1989. First record of conodonts from the Late Triassic of Britain. *Palaeontology* **32**, 325-334.

Swift, A. & Aldridge, K.J. 1982. Conodonts from Upper Permian strata of Nottinghamshire and North Yorkshire. *Palaeontology* **25**, 845-856.

Szaniawski, H. 1971. New species of Upper Cambrian conodonts from Poland. *Acta Palaeontologica Polonica* **16**, 401-414.

Szaniawski, H. 1982. Chaetognath grasping spines recognized among Cambrian protoconodonts. *Journal of Paleontology* **56**, 806-810.

Theron, J.N., Rickards, R.B., & Aldridge, R.J. 1990. Bedding plane assemblages of *Promissum pulchrum*, a new giant Ashgill conodont from the Table Mountain Group, South Africa. *Palaeontology* **33**, 577-594.

Uyeno, T.T. 1990. Biostratigraphy and conodont faunas of Upper Ordovician through Middle Devonian rocks, eastern Arctic Archipelago. *Geological Survey of Canada Bulletin* **401**, 1-211.

Uyeno, T.T. & Barnes, C.R. 1983. Conodonts of the Jupiter and Chicotte Formations (Lower Silurian), Anticosti Island, Quebec. *Geological Survey of Canada, Bulletin* **355**, 1-30.

Uyeno, T.T. & Klapper, G. 1980. Summary of conodont biostratigraphy of the Blue Fiord and Bird Fiord formations (Lower-Middle Devonian) at the type and adjacent areas, Southwestern Ellesmere Island, Canadian Arctic Archipelago. *Geological Survey of Canada, Current Research Part C, Paper* **80-1C**, 81-93.

Walliser, O.H. 1964. Conodonten des Silurs. *Abhandlungen der Hessischen Landesamtes Bodenforschung* **41**, 1-106.

Van Wamel, W.A. 1974. Conodont biostratigraphy of the Upper Cambrian and Lower Ordovician of north-western Öland, south-eastern Sweden. *Utrecht Micropalaeontological Bulletin* **10**, 1-125.

Wardlaw, B.R. & Collison, J.W. 1984. Conodont paleoecology of the Permian Phosphoria Formation and related rocks of Wyoming and adjacent areas. *Geological Society of America Special Paper* **196**, 263-281.

Watson, S.T. 1988. Ordovician conodonts from the Canning Basin (W. Australia). *Palaeontographica* **203A**, 91-147.

Webers, G.F. 1966. The Middle and Upper Ordovician conodont faunas of Minnesota. *Minnesota Geological Survey Special Publication Series* **4**, 1-123.

Ziegler, W. (ed.) 1981. *Catalogue of Conodonts. Vol.* **4**. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart.

Streszczenie

Pokrój ciała z asymetryczną płetwą grzbietową i V-kształtnymi myomerami tudzież sposób sekrecji fosforanowych elementów aparatu gębowego wskazują na przynależność konodontów do strunowców. Na podstawie wytrawionych z wapieni zespołów zlepionych elementów (clusters) i naturalnych agregatów na powierzchni łupku (natural assemblages) możliwe jest odtworzenie przestrzennego rozmieszczenia elementów aparatu. U najpierwotniejszych konodontów (typu *Panderodus*) aparat składał się z siedmiu par elementów tworzących aparat chwytny analogiczny do właściwego dzisiejszym szczecioszczękim (Chaetognatha). Dwie pary elementów w przodzie aparatu (**ne**, **hi**) wyróżniały się kształtem, a rozmiary elementów zmniejszały się ku tyłowi aparatu. Już wśród konodontów o prostych elementach (typu *Protopanderodus*) nastąpiło dalsze zróżnicowanie elementów aż do wyodrębnienia trzech serii przejść morfologicznych. Powstał aparat analogiczny funkcjonalnie do żuwaczek skorupiaków, z częścią siekaczową w przodzie, grzebykowatą pośrodku i żującą w głębi. Tuż za skrajnym elementem (**ne**) z ostrym, masywnym wierzchołkiem następowała seria 4 par (**hi**, **ke**, **pl**, **lo**) delikatnych elementów połączonych pośrodku symetrycznym nieparzystym elementem (**tr**); tworzyły one rozwarty ku przodowi kosz filtracyjny. W pewnym oddaleniu od kosza filtracyjnego, zapewne wewnątrz gardzieli, znajdowały się dwie pary masywnych elementów serii platformowej (**oz**, **sp**), być może służących do rozgniatania pokarmu. W skrajnych przypadkach każda z par elementów była odmienna morfologicznie a w serii platformowej prawe i lewe elementy różniły się kształtem. Przynajmniej część ordowickich Balognathidae miała trzy pary elementów serii platformowej a u triasowych Gondolellidae powiększona była liczba par elementów kosza filtracyjnego.

Do identyfikacji elementów aparatu używa się różnorakich systemów terminologicznych, których omówieniu towarzyszy propozycja ujednolicenia w oparciu o mający pierwszeństwo schemat Jeppsona (z uzupełnieniami von Bittera). Przy opisach elementów winno się respektować fizjologiczną orientację elementów w aparacie zamiast konwencji Pandera, wprowadzonej w wyniku błędnej interpretacji elementów aparatów konodontowych jako rybich ząbków.

Artykuł zawiera ilustrowany przegląd poszczególnych typów aparatów i zmodyfikowany system klasyfikacji konodontów, zgodny z nową interpretacją filogenezy.