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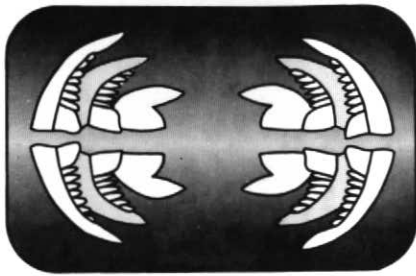
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Article abstract

In the last decade, accelerated studies of those exquisite microfossils, conodonts, have led to new advances in their taxonomy, ultrastructure, biostratigraphy, and paleoecology. There is now a clearer understanding of the arrangement of elements in the apparatus of the conodontophorid animal. Evidence also exists that the animal was largely nektobenthic rather than pelagic in habit. However, the beast is as mysterious as ever, reluctant to divulge its true affinity to a waiting world.



Conodonts: A Thing of the Past—and of the Future

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Summary

In the last decade, accelerated studies of those exquisite microfossils, conodonts, have led to new advances in their taxonomy, ultrastructure, biostratigraphy, and paleoecology. There is now a clearer understanding of the arrangement of elements in the apparatus of the conodontophorid animal. Evidence also exists that the animal was largely nektobenthic rather than pelagic in habit. However, the beast is as mysterious as ever, reluctant to divulge its true affinity to a waiting world.

Résumé

Durant la dernière décennie de nombreuses études effectuées sur les conodontes ont amené de nouveaux développements sur la taxonomie, l'ultrastructure, la biostratigraphie ainsi que la paléoécologie de ces microfossiles raffinés. Ainsi on possède maintenant une meilleure compréhension de l'agencement des organes dans l'appareil de l'an conodontophore. Certains faits tendent maintenant à démontrer que l'animal était en grande partie de moeurs nektobenthiques plutôt que pélagiques. La bête n'en demeure pas moins toujours aussi mystérieuse et répugne à révéler sa vraie identité à la face du monde.

Introduction

Enigmatic, microscopic, horn- and tooth-like, phosphatic, and, alas, extinct: such are conodonts, the apherodisiac of the Paleozoic and early Mesozoic. These elegant microfossils (Fig. 1) are the only known remains of a marine organism (conodontophorid) of unknown biologic affinities. Some (e.g., Tarlo, 1968) have modestly implied a position ancestral to the vertebrates. Their earliest occurrence is constantly being pushed back in time and now seems to lie in the late Precambrian. These leading lights of the Paleozoic were extinguished in the

Late Triassic. However, at least two specialists believe the conodontophorids are out there somewhere - perhaps nibbling at the recently found modern stromatoporoids. Regrettably, since Grant Agencies do not bless scouring of oceans in such a search, most conodontologists have been concerned with aspects of biostratigraphy, taxonomy, apparatus arrangement and paleoecology.

A Century of Conodonts

1856 was an eventful year in the history of mankind: William Logan was knighted by Queen Victoria and Christian Heinrich Pander (1794-1865) discovered conodonts. Born in Latvia, Pander (Fig. 2), a part-time farmer and scientist, conducted pioneer studies of Lower Paleozoic rocks near St. Petersburg (now Leningrad). "By using a method of finding the slightest traces of the smallest animals which were not discovered by previous investigators" he (1856) described the first conodonts in his monograph on (pre-Lapworthian) Silurian fish. Although his major task was to investigate the deposition, size and properties of coal beds, he recognized the potential value of conodonts. Considering the primitive optical equipment available and his recurring "eye sickness", his detailed descriptions and thin section examination of internal structure were a monumental achievement. Initially believing conodonts to be parts of fish, his thin section work warned "a full

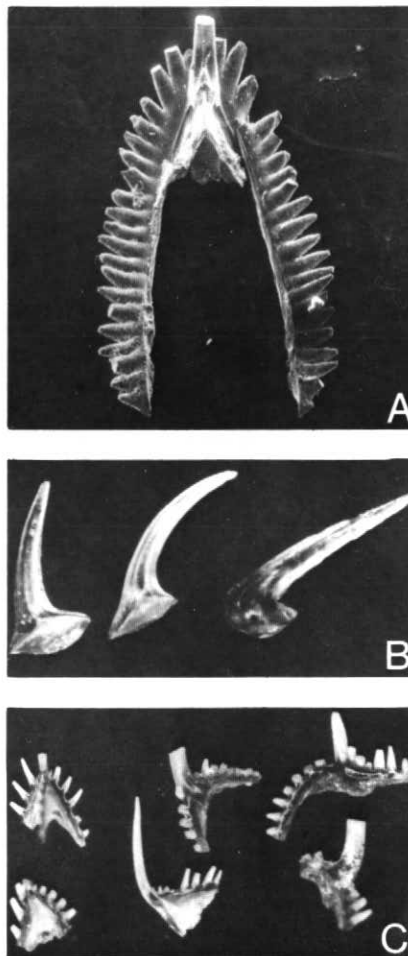


Figure 1
Conodonts. A: a trichonodelliform element (separate form species) X20. B: a multielement species (*Drepanoistodus suberectus* (Branson and Mehl)) comprised of three form species of simple cones—elements are all hyaline (no white matter in cusp) X50. C: a multielement species (*Oulodus serratus* (Stauffer)) bearing six form species of bar and blade type—all elements have white matter equally developed in their denticles and have a similar pattern of denticulation X40.



Figure 2
Christian Heinrich Pander, 1794-1865 (from Raikov, 1964).

conviction that these remains were really teeth of extinct fishes could be attained only if a similar structure could be proven in living fishes belonging to the same class."

The second major contribution to the study of conodonts was made by George Jennings Hinde (1839-1918), when, in 1879, he reported conodonts from some Ordovician and Devonian rocks of Canada and the United States. In Canada he collected from the Middle Ordovician (Chazy Group) near Grenville, Quebec and from the Upper Ordovician (Georgian Bay Formation) in Toronto. The publication of his paper sparked immediate controversy because he regarded different individual conodont elements as parts of the same animal. Previously, taxonomy had been based on form species, that is, each individual element was regarded as a practical, but artificial, species (Fig. 1A). His ideas were to lie dormant for nearly ninety years.

Relatively few publications concerning conodonts appeared in the first half of this century. Notable contributions were made by Drs. Branson and Mehl working in the United States, who published an extensive series of reports in 1933. European conodont research was rejuvenated about 1950, with the papers of Rhodes (1953) and Lindström (1955). Shortly afterwards, many workers developed extensive research programmes in the United States.

Thus it is really only in the last two decades that conodont studies have expanded. Three times as many reports on conodonts were published in the decade 1961-1971 as in the period 1856-1930 (Sweet and Bergström, 1971, p.1).

What's in a Name?

With the exception of Hinde (1879), conodont specialists followed Pander in describing faunas in terms of form taxa, with little consideration of how the elements were arranged within the conodont apparatus. Eventually three different types of study have led to grouping form taxa into what are believed to be natural, or multielement, taxa: assemblages, clusters, empirical associations.

Assemblages, or concentrated groupings, of conodonts (Fig. 3) were independently discovered from Carboniferous shales by Schmidt (1934; Germany) and Scott (1934; Montana). Several hundred are now known but still largely from the Carboniferous black shales. They represent odious coprolitic residues and also sites of death and burial of individual conodontophorids. In the latter case, the conodont elements commonly show an ordered bilateral symmetry of the apparatus with different forms occupying specific positions. The details and interpretations of these assemblages were well summarized by Rhodes (1962) and they still remain the best template for models of apparatuses.

Clusters have appeared unexpectedly in residues from dissolved carbonates. Several conodont elements are fused to each other and their arrangements discredit the possibility of diagenetic fusion, but favour a pathological merger within the conodontophorid tissue. Thus their size and relative position to each other provide unique information on growth and arrangement of the apparatus. The cause of this pathological deformity is open to speculation, Rexroad and Nicoll (1964) even conjured up tetanus poisoning.

With yields of up to several thousand conodonts per kilogram, many Panderers have amassed huge collections. From these, *empirical associations* of particular form species were noted. Such species tend to constantly co-occur with similar geographic, stratigraphic and ecologic limits, occur in rather constant ratios, and have similar size proportions,



Figure 3
A coprolitic(?) assemblage of conodonts; New Albany Shale, Mississippian; Berea, Kentucky (collected by Perry B. Wigley).

histological and preservational features (Fig. 1 B,C). The realization that multielement taxa could be established in this way occurred to several workers in the mid 1960s with the most notable study of nearly one quarter of a million Ordovician conodonts by Bergström and Sweet (1966), (see also Huddle *in* Lindström and Ziegler, 1972).

At about the same time, great excitement surged through the Panderers when William Melton discovered a number of remarkably preserved fossils, crudely resembling *Amphioxus*, but bearing conodonts within an internal "gut" (Fig. 4). Despite extensive search of tens of tons of hand-quarried material at the Mississippian locality in Montana only a limited number of specimens have been unearthed (Melton and Scott, 1973; Scott, 1973). While these investigators believe this new organism is the conodontophorid, other envious sceptics point to the possibility that it may simply have had a passion for conodontophorid casserole.

With these three lines of evidence for apparatus reassembly, it is now clear that most conodontophorids possessed about 10 - 20 conodont elements representing six for species (Fig. 1C). The simple cones (Fig. 1B), common in the Lower Paleozoic, were ordered into different apparatuses bearing one to four species, commonly with a distinct symmetry transition (Lindström, 1964, p. 79-90).

These variations in conodontophorid apparatus suggest subtle differences in function. It has seemed profitable to pursue study of conodont ultrastructure (Fig. 5A, B) to detect variations related to taxonomic hierarchy and function. Thus, the development of secondary white matter in the cusp and denticles

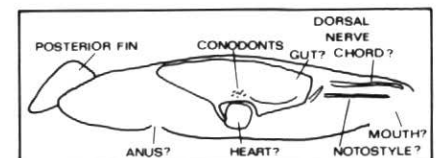


Figure 4
Reconstruction and interpretive morphology of the conodontochordate animal (*Lochriawellsi* Melton and Scott). Conodont elements are mostly found scattered throughout the gut and their arrangement does not entirely conform to assemblages on shale surfaces (after Melton and Scott, 1973, Figs. 6, 16).

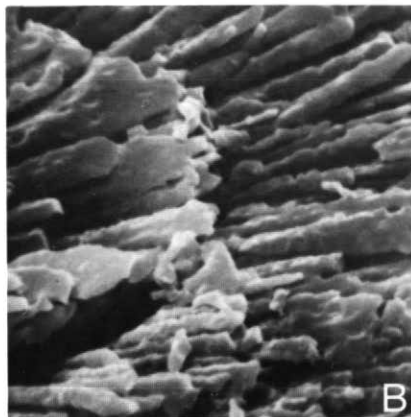
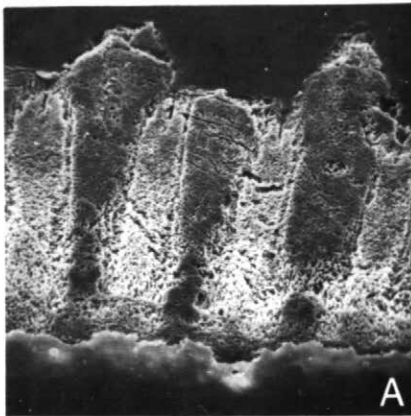


Figure 5

Conodont ultrastructure revealed by scanning electron microscope. A: view of denticulated process of a blade conodont (*Silurian ozarkodiniform* element of *Hindeodella confluens* Branson and Mehl *sensu* Jeppsson); specimen embedded in plastic, sectioned, and etched; note sharp distinction between white matter of the denticles and the intervening lamellar material, X300. B: lamellae of conodonts are constructed of rod-like apatite crystallites; those of two lamellae are illustrated from a similar blade conodont (*spathognathodiform* element of same taxon) X6000.

is possibly a method of limiting breakage to the entire element if they functioned as a masticating unit (Barnes, Sass, and Monroe, 1973). Alternatively, the narrow grooves and striae, now known to penetrate deep into the element of some cones, have been considered the site of muscle attachment with the muscles operating food-gathering lophophorate tentacles (Lindström, 1974). While these new techniques provide additional clues, the biologic affinities still remain obscure. Many of the earlier suggestions (Lindström, 1964, p. 117-130) invoked relationships to fish,

annelids, gastropods, algae, arthropods, and even considered conodonts as copulatory clasping structures of worms. It seems more likely that conodonts belonged within a taxonomically distinct group of organisms, perhaps of phylum or subphylum rank, and possibly a proto-vertebrate.

Panderers appear close to integrating information on ultrastructure, morphology, apparatus plan, and paleoecology to provide a paleozoological model for the various types of conodontophorids. However, before the icing must come the bread and butter of biostratigraphy.

Please . . . No More Zones

A measure of an organism's fossilhood is surely the number of zones per unit time that can eventually be erected by ardent biostratigraphers. The successful initiation of conodonts came with the detailed zonal schemes for Devonian and Carboniferous strata in Europe, North America (several review papers in Sweet and Bergström, 1971), and Australia (Glenister and Klapper, 1966). In the latter study alone, 25 zones and subzones were recognized in the Upper Devonian. Conodontologists working elsewhere in the column have so far defined approximately 15 zones in the Ordovician (60 million years, cf. 15 graptolite zones), 11 zones in the Silurian (20 million years, cf. 23 graptolite zones) and 22 zones in the Triassic (45 million years, cf. 31 ammonoid zones). While many are assemblage zones and need greater refinement, even blushing graptolite, foram, and ammonoid specialists may admit it is not a bad start.

Rapid evolution together with ease of identification and abundant yields provide the essence of a fine zonal fossil. But what of the all important lateral distribution? The Treatise bible (Müller, 1962, p. W89) spread the good word: "Conodonts commonly are not confined to sedimentary facies, since the same species is found to occur in different lithologies (e.g., limestone, shale, sandstone). This fact is of great advantage in using conodonts for correlation. The independence of lithofacies suggests that the conodont animals were free swimming creatures. Because many species have a world-wide distribution, they may be

interpreted as having been pelagic". Surely therefore, these are ideal zonal fossils that did not suffer the same preservational or environmental biases as graptolites or forams.

Have Conodontophorids Hit Rock Bottom?

One of the most encouraging developments of paleontology in recent years has been the emergence of paleoecologic studies. These have attempted to make ancestral beasts come alive, at least in the minds of men. Concern for habits, habitats, food chains, enemies, and yes even intimate friends (Fossil Sex article in the last issue of *Geoscience Canada* - Hall, 1975; Jeppsson, 1972), has been expressed for most fossil groups.

The days of teaching that trilobites simply crawled over muddy substrates are over - now they burrowed, swam, and lived in surface waters as well. Similar widespread habit diversity exists in many other groups: those bizarre Cretaceous ammonites were seemingly benthic; graptolites were depth-stratified, with the dendroids largely sessile benthos. Studies of morphology are no longer esoteric exercises, they emerge as exciting interpretations of function.

As the initial flush of biostratigraphic success was fading, new data was forthcoming on lateral distribution of conodonts. Alas, they were not immune from provinciality, as well shown during the Ordovician when it appears nothing escaped regional differentiation (Barnes, Rexroad, and Miller, 1973; Sweet and Bergström, 1974). Further, the faunas within a province can be shown to suffer additional segregation. Marked faunal changes are recognized firstly at one location corresponding to fluctuating environments during transgressive or regressive phases and, secondly, in tracing a synchronous unit from shoreline to progressively offshore facies. These different faunas are predictable, and have been considered as communities (Barnes, Rexroad, and Miller, 1973; Barnes and Fåhræus, 1975).

Paleoecologic studies now become vital to properly understand the habit and distribution of the conodontophorids. Two contrasting models have been proposed to explain

these faunal variations (Fig. 6). Seddon and Sweet (1971) suggested that conodontophorids may have lived an active, pelagic, but depth-stratified, existence similar to modern chaetognaths (arrow-worms). Deep-water conodontophorids would thus not occur in shallow-water deposits but surface dwelling forms would settle, upon death, into deep-water environments. Not so, related the alternative model (Barnes, Rexroad, and Miller, 1973; Barnes and Fähræus, 1975): many shallow-water forms simply do not co-occur with deep-water forms and a lateral segregation is advocated. Such segregation would naturally imply that the conodontophorids were nektobenthic organisms rather than pelagic. That is, if they didn't hit rock bottom they lived just above it.

In their study, mentioned above, of the supposed conodont animal, Melton and Scott (1973, Fig. 16) illustrated a free-swimming, planktonic-feeding

organism. Ironically, their figure was printed upside down (by a subversive printer of the other school) thereby portraying the animal as nektobenthic.

The conodontophorids may have been small but they certainly demonstrated ecologic initiative. Like trilobites, they appear to have occupied a wide variety of niches. From a combined examination of conodont distribution and detailed morphology, it appears that not all conodontophorids were nektobenthic. The earliest conodontophorids and those later forms bearing simple cones lacking appreciable symmetry transition are all regarded as being pelagic in habit with wide distribution (Barnes and Fähræus, 1975).

Models are designed to be tested and modified and those above should receive critical examination at the Conodont Paleocology Symposium at the GAC-MAC-NC GSA Annual Meeting in May, 1975. Pandorers will be discussing not only

conodontophorid habit, but also whether ultrastructure, micromorphology, and apparatus type may reflect different dietary modes. Perhaps, from consideration of faunal associations, Pandorers will ponder what pernicious predator persecuted their problematic protovertebrates.

Have Conodonts Failed Us?

Have we come full circle: starting with an ideal pelagic zone fossil only to find its grovelling near the bottom like so many of the other beasts of the time? Are those myriad zones valid? Is it all worth it: each year dissolving tons of limestones while the discarded acetic waste flows to the oceans to prevent further carbonate precipitation?

Certainly, the zonations are empirically valid. The biostratigraphic value of conodonts rivals or surpasses most other fossil groups: the application of biostratigraphic data must, however, be tempered with the new paleoecologic data. Shrewd paleontologists must put this to a variety of additional uses. Successions of conodont communities can be used to detect subtle marine oscillations not revealed in the lithostratigraphic record. The effects of the Late Ordovician Saharan glaciation with the consequent sea level drop should be recognizable from conodont community studies of the low latitude carbonates that are widespread in Canada. Such communities can define specific microfacies and be of value in determining certain host-rock environments in base-metal exploration. On a larger scale, the varying responses of such communities to climatic change or plate divergence-convergence can be used to advantage because of the abundance and relative ubiquity of conodonts (Barnes and Fähræus, 1975).

With such recent rapid advances in multielement taxonomy, ultrastructure, refined biostratigraphy, enigmatic conodontophorid (?) impressions, and paleoecology we can look both back with hindsight and forward to pandering future conodont workers with intriguing problems

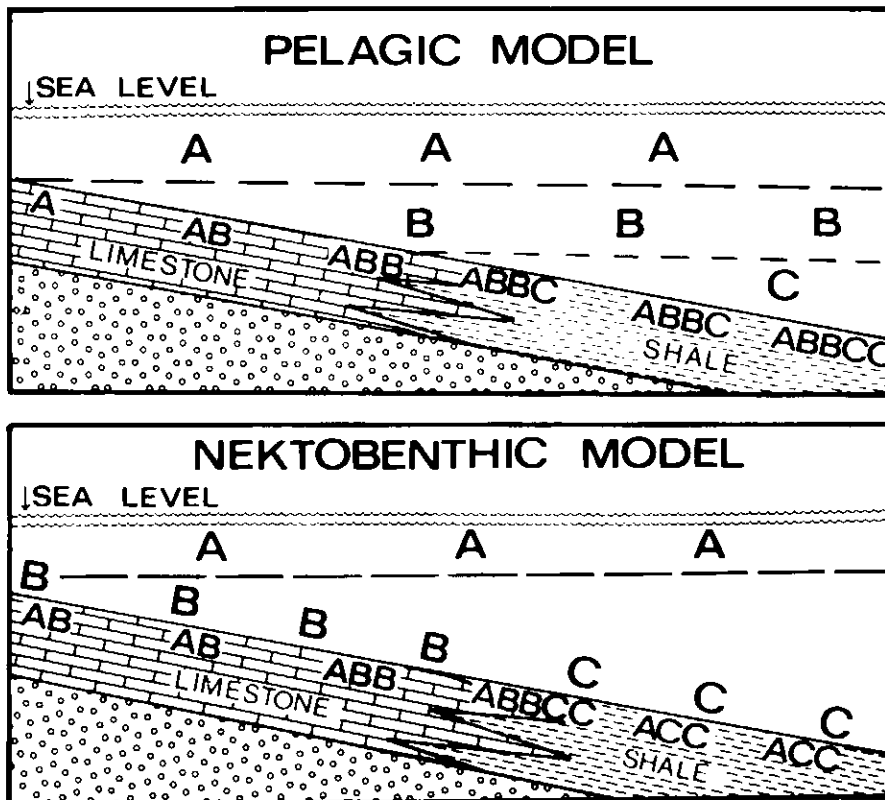


Figure 6

Two highly simplified models of conodontophorid habit: A, B, and C representing different groups of genera, with a simple two-component facies change, and the resulting generic associations in the substrate. The pelagic model portrays a depth-stratification for the

conodontophorids which produces progressively more diverse faunas in deeper water. The nektobenthic model shows a widespread pelagic group (A) but stresses that most conodontophorids are laterally segregated (with some overlap) into progressively offshore communities.

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