

expectation is directly confirmed by the AT&T experiment (2), where (panel B of the figure) the $\nu = 1/2$ FQHE is observed at $d/\ell \sim 2.5$ as predicted (7) in a recent calculation.

The experimental situation is actually somewhat more complicated by the fact that each quantum well has a finite thickness λ that introduces a new length scale into the problem, reducing the intrawell interaction energy. The original theoretical work assumed (6) $\lambda \sim 0$, finite values of λ explain (7) the occurrence of the $\nu = 1/2$ FQHE at $d \sim 2.5 \ell$ rather than at $d \sim \ell$. Even though the observation of the $\nu = 1/2$ FQHE is quite similar in the two experiments (1, 2) a striking difference is that $d/\ell \sim 2.5$ in the Princeton results (1), and, 7 in the AT&T (2). It is noteworthy that the effective well thickness is also different [$(\lambda/\ell \sim 3$ in (1) and ~ 1 in (2)] in the two experiments, and, in the Princeton sample (1) there may be considerable quantum tunneling between the two layers, but not in that in the Bell sample (2). Larger values of λ/ℓ in (1) compared to those in (2) probably lead to the stabilization of $\nu = 1/2$ FQHE at larger values of d/ℓ . Thus, while the $\nu = 1/2$ FQHE in double-layer electron systems was theoretically anticipated (5–7) many details of the experimental results remain to be understood.

This stimulating observation of a clear-cut even-denominator FQHE, which was thought to be “impossible” at one time, should lead to considerable activity looking for other “unusual” fractions exhibiting FQHE. Among the possibilities that are likely to be experimentally explored in the near future are the search for other unusual states in double layers with unequal electron populations in individual wells, a detailed investigation of the interlayer tunneling effect on the new FQHE states, and a systematic investigation of the phase diagram of possible double-layer FQHE states as a function of magnetic field strength and orientation, layer separation, layer width, and interlayer tunneling rate. Observation of unusual states in three or more well structures is another exciting possibility.

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Conodonts: A Major Extinct Group Added to the Vertebrates

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After more than 130 years of the debate, definitive evidence has finally been discovered that allows the conodonts to be assigned to the vertebrates. The conodonts are a group of marine organisms that flourished for about 300 million years, ranging from Late Cambrian to Late Triassic. They are represented in the fossil record by tooth-like microfossils (conodont elements) usually from 0.2 to 2 mm in dimension, rarely as long as 14 mm. These elements are composed of calcium phosphate (carbonate fluorapatite) and are readily extracted from the host rock. They receive considerable attention in the paleontological literature (some 280 publications in 1991) because of their importance as biostratigraphic indicators in the correlation of sedimentary sequences. Conodont elements can reveal the

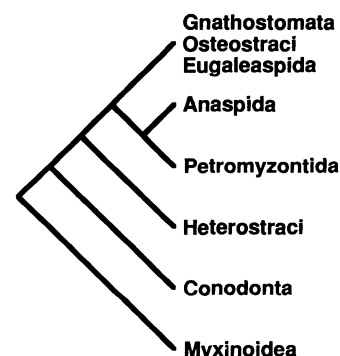
thermal history of sedimentary basins, because they undergo a proportional color change on heating due to their content of organic matter. In addition they retain a trace element and isotopic ratio signature that reflects the chemistry of the oceans in which they lived. Although conodont elements were first reported in 1856, the rest of the organism was completely unknown until specimens preserving traces of the soft tissues were described from the Lower Carboniferous of the Edinburgh district, Scotland, in 1983 (1). This discovery cast some light on the enigma of conodont affinities (they had previously been assigned to a range of invertebrate and vertebrate groups, and even plants) but a number of crucial questions remained unresolved.

The Scottish specimens which preserve the soft tissue morphology of conodonts revealed that the animal was elongate, laterally compressed, and somewhat eel-like

(1, 2). These examples, at least, represent a swimming carnivore. The elements form a bilaterally symmetrical feeding apparatus in the head, flanked by a pair of dark lozenge-shaped lobes that may represent the eyes. The trunk is divided into a series of V-shaped structures, traces of the muscle blocks that were separated by myosepta. Two parallel lines run the length of the trunk. Their nature is problematic, but comparison with observations on decaying specimens of the lancelet *Branchiostoma* supports their interpretation as the margins of the notochord rather than the gut. The tail region bears short, closely spaced fin rays. The evidence of the soft tissues indicates that the conodonts belonged among the primitive craniates (2). However, in the absence of evidence that the histology of the mineralized conodont elements had clear homologs among living craniates, this placement remained controversial. Vertebrate workers continued to regard conodonts as beyond their purview (3), and some authorities preferred to retain a separate phylum Conodonta for the group (4).

Now the taxonomic affinities of conodonts have been confirmed. Nomarski interference contrast microscopy and scanning electron microscopy of polished slices of conodont elements have revealed, for the first time, a number of tissue types characteristic of vertebrates (5). Conodont elements consist of a crown made up of centrifugally deposited lamellar tissue, overlying a less consistently preserved basal body. The new investigation shows that the growth pattern and arrangement of crystallites within the lamellae in the elements of many conodonts are typical of the structure of enamel in vertebrate teeth. Areas of opaque “white matter” that often occur in the crown include features histologically identical to the lacunae and canaliculi of cellular bone, and structures in the basal body are similar to globular calcified cartilage in various vertebrates. Dentine is absent.

The demonstration that the conodonts



Cladogram showing the likely position of the conodonts in early vertebrate phylogeny.

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are vertebrates will have little impact on the everyday work of the majority of conodontologists, whose immediate concern is the utility of these fossils in biostratigraphy rather than their biologic affinities. The new evidence prompts a reassessment, however, of the early phylogeny of the vertebrates and the position of the conodonts within it. The evidence of the soft tissues allowed two possible placements of the conodonts within the vertebrates, either (i) as a sister group of the Myxinoidea (hagfishes), based on the shared bilaterally operating feeding apparatus, or (ii) as a primitive sister group of the higher craniates (excluding the Myxinoidea) (2) (Fig. 7). This second possibility was based on the presumption that the tissue of conodont elements is acellular and homologous with the mineralized dermal tissue in heterostracans. What then is the phylogenetic significance of the discovery of cellular bone in conodonts some 40 million years older than the earliest previously known vertebrates?

Outside conodonts, cellular bone is essentially confined to the Eugaleaspida, Osteostraci, and Gnathostomata. Its occurrence in conodonts therefore might prompt their interpretation as a sister group of these more advanced vertebrates. The appearance of cellular bone so early in the history

of the vertebrates, however, supports the contention that it is more primitive than acellular bone. In that case the conodonts could still be regarded as a sister group of all other vertebrate taxa, apart from the myxinooids. It is not yet clear, however, why cells are incorporated into the elements of conodonts but not into the dermal armor of heterostracans.

The evidence for the early phylogeny of vertebrates is based largely on fossil material as mineralized tissues are lacking in living agnathans. The addition of the conodonts increases the number of well-established Cambro-Ordovician vertebrate genera by a factor of 30, from 5 to nearly 150 (6). The absence of dentine and presence of cellular bone in a highly adapted feeding apparatus in the earliest vertebrates leave current hypotheses of the early evolution of their skeletal tissues in some disarray. Dentine has generally been regarded as the primitive vertebrate hard tissue (7). The application of high resolution microscope methods to well-preserved material of a wide range of early vertebrate taxa is now necessary to unravel the details of their relationships. Current models of the growth of conodont elements also require reassessment. Further histological studies are needed on suitably preserved material of earlier Cambrian

paraconodonts, which some authors have argued to be ancestral to the true conodonts. If a relationship between true conodonts and these older taxa can be substantiated then the record of the vertebrates could be extended further back into the Cambrian, perhaps even predating the earliest chordate recognized so far, the soft-bodied *Pikaia* from the Middle Cambrian Burgess Shale. In any event the vertebrates can now be added to the list of major metazoan taxa that appeared during the Cambrian radiation.

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