

BOOK REVIEW

The Great Fossil Enigma is still there!

When the book of Knell appeared in 2013 (Knell, 2013), it was just three years after I had participated to two critical papers to the theory that conodonts were vertebrates - what we called the 'conodont theory' (Turner et al., 2010; Blieck et al., 2011). I was not inclined to buy and read a book written by a British historian of science, working at the University of Leicester, UK, exactly where the conodont expert Richard 'Dick' Aldridge was also a professor, and head of a team of young British conodont workers settled in Leicester, Birmingham, and Bristol, that we called 'the British School' at origin of the 'conodont theory'. It was also because my British colleague Susan Turner, an active early vertebrate expert, and "most vociferous among the vertebrate paleontologists objecting to the conodont vertebrate" (Knell, 2013, p. 342), was largely offended by Knell's book. However, it appeared that, a few months earlier this year, while surfing on the Web, I found extracts from Knell's book, in particular the few pages where we ('a political confederation of opponents' as Knell defined us [Knell, 2013, p. 368]) were quickly and roughly cited [Knell, 2013, p. 334, 342, 352, 353]. This decided me to buy and read the book. At a first glance I must say that I was positively impressed. I learnt a lot on conodont history and on older and younger conodont workers. What particularly interested me is the 'US period' of development of conodont science when most influential results came from the USA in the 1930s to 1950s in various university centres, and was highly dependent upon utilitarian aspects of conodonts for prospecting oil throughout the country, in relation to the Black Shale problem at the Devonian-Carboniferous transition. This was followed by a 'German period' from the 1950s to 1970s, that developed around the University of Marburg, and partly Göttingen. Two fellows of latter period that are presented and analysed by Knell are Profs Willi Ziegler and Otto Walliser (Knell, 2013, fig. 6.1) that I have been lucky to meet in scientific meetings and in the field, and particularly in IGCP and SDS business meetings (O. Walliser was particularly supportive of IGCP Project 328 'Palaeozoic Vertebrate Biochronology and Global Marine/Non-Marine Correlation'). W. Ziegler was the 'pope of conodonts' during the 1960s - 1970s, and was SDS chairman when I met him for the first time at the International Devonian Congress in Calgary, Canada, in 1987.

I found chapter five of Knell's book ('Outlaws') highly interesting and astonishing. This chapter relies on parts of fossil organisms that received species names, but where the organisms themselves are unknown, in such a way that those named parts do not correspond (or seem not to correspond) to 'real' species or biological species. They received various qualifying words from palaeontologists such as 'form species' (and 'form genera'), and the concept of parataxon was proposed for them (see refs in [Knell, 2013]). This is the case for, e.g., sclerites of invertebrates, stem elements of crinoids, conodonts and ... isolated microremains of vertebrates that we generically call 'microvertebrates' or 'ichthyoliths' (Turner, 1988-2001), that is, teeth, scales, tesserae, spines, etc. Knell recalled the real fight between pro and contra among palaeontologists, and the opposition of the latter to a proposal made by the International Commission of Zoological Nomenclature to introduce the concept of parataxon, and its own nomenclature, in the Code (ICZN). Finally this failed. In that game, isolated conodonts were used as a case study. This is of course completed in Knell's book by several sections and chapters about natural fossil assemblages of conodonts found throughout the stratigraphic record from the Cambrian to the Triassic, and by the huge problem of how to name these assemblages, usually called 'conodont apparatuses'. More widely this problem relates to a more intellectual point, on whether or not these apparatuses

correspond to biological species, and further on, on how conodont palaeontologists imagine their preferred weird fossils (see 'Afterword' chapter 'The Progress of Tiny Things' for more philosophical ideas on this point).

One of the main questions asked by conodont workers (at least the ones being involved in what we now call 'palaeobiology' - not the 'utilitarian conodont workers' being acting for oil companies) was and still is whether or no conodonts were 'teeth', with the clue question of 'what is a tooth', morphologically and/or functionally. In this frame, I did not know that the German-speaking, early vertebrate expert Walter Gross (originally from Livonia, now in Latvia) had had such a strong influence on the conodont worker community through his few papers published in the 1950s (e.g., Gross, 1954; Gross, 1957). Conodonts were not fish teeth, Gross said. Together with another German, Wilbert Hass, Gross' works "cast a long shadow" during the 1960s on conodont studies concerning this point, after Knell's analysis (Knell, 2013, p. 123-124, 166, 363-364). And in fact Knell's book tells the story of the coming, disappearance, and coming back of this idea through conodont literature from the mid-19th Century up to the early 2010s. A truth must be resettled here. Contrary to what Knell says in his book (Knell, 2013, p. 11 and further on), when Pander described conodonts for the first time (Pander, 1856), he did not say that conodonts were certainly fishes. He certainly had doubts about this hypothesis (see translations by Hans-Peter Schultze in (Turner et al., 2010)).

Before coming to the recent development of the 'conodont theory', Knell reviewed the wild beauties that imaginative palaeontologists invented for an idealized conodont animal. And I (re)discovered 'The Beast of Bear Gulch' which finally turned out to be a conodont eater (Knell, 2013, chapter 11), Lindström's barrel-like animals (Knell, 2013, fig. 12.2), Conway Morris' strange flat animal (Knell, 2013, fig. 12.3), as well as several attempts at reconstructing the way apparatuses worked, either as 'teeth' (Knell, 2013, fig. 12.4) or as water filters (Knell, 2013, fig. 12.5). As Knell said, "In the course of 120 years of study the conodont had generated 53 possibilities for what it might be" (Knell, 2013, p. 290)! It is in latter chapter 12 that the big confession is given: "Teeth are fundamentally more exciting than hidden supporting structures of unknown function." And again, during the 1980s episode of 'the' discovery of conodont animal, "of course, craniate affinities would be a more noble pedigree than mollusc affinities..." (Philippe Janvier, presented then as a devil advocate by Knell [Knell, 2013, p. 316]). Knell and Janvier should have said that it is more 'sexy' to be related to a vertebrate than to a 'worm'. But, what is a 'worm'? This word is as uninformative as the word 'fish', on a phylogenetic point of view. The conodont animal as revealed by Derek Briggs and collaborators IS a worm, with its long slender body, a head (with two eyes?), and a tail. But it is not a fish: it is a living being inhabiting an aquatic environment (supposedly always marine in the present case), but it does not have paired fins and scales.

Finally, the last two chapters of Knell's book (Knell, 2013, chapters 13 and 14) are devoted to Briggs et al.'s discovery of the conodont animal, its publication, and forced interpretation toward a more and more crownward vertebrate, that is, from a basal location in chordate phylogeny (as cephalochordate related), to a basal craniate-like (hagfish-like) location, and then to a 'stem gnathostome' (basal vertebrate) location. Those two chapters are a presentation of the last thirty years of conodont concept history from the original paper published in 1983 (Briggs et al., 1983) to Knell's book (Knell, 2013). They widely develop the wish of what we called the 'British School' (viz., R. Aldridge, the conodont expert of the original trio (Briggs et al., 1983), and his students, ironically self-named the 'Pommie Bastard Conodont Group' [(Knell, 2013, p. 342)] to make conodonts entering back again the

'club' of vertebrates (following Janvier's expression when he 'capitulated' [Janvier, 1995]). The first part of this story telling is based upon "an unpublished book-length account Dick Aldridge wrote of his scientific research, in part published..." (Knell, 2013, chapter 13, note 1).

It is during that process that a diversified group of opponents to the conovert theory expressed their opinions. This unorganized group (contrary to the military campaign of the 'British School' in Knell's interpretation [Knell, 2013, p. 367], supported by the British journal *Nature*) included both early vertebrate and conodont experts, both neontologists and palaeontologists, such as Pierre Bultynck, Carole Burrow, Anne Kemp, Godfrey Nowlan, Wolf-Ernst Reif, Carl Rexroad, Hans-Peter Schultze, Susan Turner, myself and others. Some of them, when seeing that their contra-arguments were not taken into account in the plethora of papers published by the 'British School', especially by *Nature*, decided to write a scientific, well-documented paper that appeared three years BEFORE the publication of Knell's book, but – again – was not cited and analysed (Turner et al., 2010). Contrary to what Knell said, we were not (and still are not) a "political confederation of opponents holding no single shared view other than a belief that the British School was wrong on certain key points" (Knell, 2013, p. 368), which is nothing else than a misleading and insulting proposal. (Subsidiarily it must be noted that the 'British School', after *Nature* editor Henry Gee suggestion, decided to "concentrate on convincing the broader and less politically organized biological community" (Knell, 2013, p. 342), a decision that led in their disappearance from early vertebrate meetings and their published thematic volumes.) Our opposition is based upon a thorough review of literature and a wide knowledge of what are conodonts and vertebrates, in order to come back to original definitions of what is a chordate, what is a craniate (in the case of cyclostome paraphyly), what is a vertebrate, what is a gnathostome..., how are conodont and early vertebrate mineralized tissues defined. The latter point was crucial long before the 'British School' study, as exposed in Knell's book (Knell, 2013, p. 123, 334; Gross, 1954). However, our paper was ignored. Only two meeting abstracts, one newsletter short article, and the short version of our paper were cited and 'politically' attacked (Knell, 2013, p. 342, 352, 353; Blicek et al., 2011), giving impression that our arguments were not scientifically based ("a manifesto for political change rather than a scientific argument", Knell said [Knell, 2013, p. 353]). Whether or not Knell's ignorance of our original paper (Turner et al., 2010) was deliberate, his insinuations are rough and injurious. As a historian of science, Knell should at least have interviewed the authors of the opposing view, but he did not; instead he libelled them with hearsay anecdotes from the British School members. Had he read and understood our paper, he would have seen that we based our phylogenetic analysis (a point that is not discussed in Knell's book) on the 'British School' one published in 2000 (Donoghue et al., 2000). The latter is, at least partly, the result of a discussion that I had with Aldridge's students Phil Donoghue and Mark Purnell during the 1998 European Conodont Symposium (ECOS) in Bologna, Italy. I was there because, inside the ECOS, a meeting of IGCP Project 421 'North-Gondwanan Mid-Palaeozoic bio-dynamics' was held, where Carole Burrow and I presented oral communications. During a reception in the ancient Natural History Museum of historical city of Bologna, Donoghue and Purnell asked how to proceed to eventually obtain acceptance of their conovert theory by the early vertebrate community (beyond a few already converted fellows such as Phil Janvier). I answered that the only way was to proceed with a phylogenetic analysis as had been the rule for the last 15 years among fish aficionados. Of course, Donoghue and Purnell having been trained as conodont workers were not phylogeneticists and did ignore what a cladistic analysis is. I suggested them to get in contact with their colleagues of the British Museum of Natural History in London. This resulted in the paper by Donoghue, Peter Forey and Dick Aldridge at the turn of the millennium (Donoghue et al., 2000), where conodonts (in fact what Janvier had called euconodonts to separate them from proto- and para-conodonts) came as sister-group to 'ostracoderms' + gnathostomes, in a more crownward situation than hagfish and

lampreys (cyclostomes), so inside what is usually called vertebrates. They had reached the 'British School' wish beyond the original suggestion of Briggs et al. (1983). Our own cladistic analysis, mostly driven by C. Burrow, H.-P. Schultze and S. Turner in our group of eight conodont and vertebrate experts, basically used Donoghue et al.'s characters/taxa matrix with the same cladistic software, and did arrive at a quite different result where conodonts are neither vertebrates, nor craniates, but just basal chordates. Having used the same outgroups as Donoghue et al. (i.e., cephalochordates and tunicates), our analysis could of course result only in a position within the chordates. Whether or not conodonts (euconodonts) are chordates is another question that can be answered only after a wider phylogenetic analysis including non-chordate invertebrates such as other deuterostomes (echinoderms *et alii*), and various 'worms' (hemichordates, chaetognaths, priapulians, annelids and many other) (Turner et al., 2010; Blicek et al., 2011).

So, for us, 'The Great Fossil Enigma' is not over. Conodont worms remain enigmatic. At least the re-opening of Pander's hypothesis that conodonts could eventually be vertebrates by our British colleagues did help both the conodont and early vertebrate communities of palaeontologists to think about the definition of their preferred fossils. It also helped Aldridge building a new, very active (and I would say scientifically aggressive) British conodont group where several young elements got positions in universities (Richard Fortey's personal communication at IGCP Project 410 'The Great Ordovician Biodiversification Event' meeting in Riverside, California, June 2001, where I gave a communication on Ordovician vertebrates and began by explaining what are not vertebrates, including conodonts, to Fortey's great surprise).

I will finish with the [hopefully] aftermath of the conovert theory. Our 2010 paper has not really been attacked or analysed in detail. Later, a paper by Murdock et al. (2013), including Phil Donoghue himself, arrived at the conclusion that, finally, what was homologized to vertebrate hard tissues among conodonts is not homologous to enamel, dentine... This was precisely one of the main points of our analysis where we had re-coded conodont mineralized tissues as non-vertebrate tissues (Turner et al., 2010). When you now go through recently published cladograms of vertebrates, conodonts have 'bizarrely' disappeared from some (Keating et al., 2015), or are out of the craniates (Janvier, 2015), suggesting that they are not considered as 'fish teeth' anymore and again. Would it be that Hans-Peter Schultze was right when he was telling us that, once a wrong idea is settled in scientific literature and textbooks, it needs at least 10 years to get rid of it. In the case of the conovert theory, firmly settled in Donoghue et al.'s paper (Donoghue et al., 2000), we needed ca. 15 years to reach that point. When and how will it come back? Will the 'Pander's box' be re-opened again?

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