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Beyond biostratigraphy: Conodont matters in evolving planetary scenarios

1. Conodonts beyond biostratigraphy

Conodont elements are mineralised skeletal remains of a soft-bodied, nektonic, extinct early chordate that inhabited ancient oceans for over 300 million years, from the latest Cambrian to the Triassic-Jurassic transition. Conodonts represent a unique biostratigraphic tool in this time frame thanks to their widespread occurrence in carbonate rocks and less frequent presence in marine shales and cherts. The recovery of isolated “tooth-like” elements of the conodont animal for over one century after the first report by Pander (1856) opened a long-lasting debate on the biological affinity of conodonts, that finally came to an end with the discovery of soft-part body impressions in the Carboniferous of Scotland (Briggs et al., 1983) and the Upper Ordovician of South Africa (Aldridge and Theron, 1993; Aldridge et al., 1995). It was possible to assign conodonts to chordates and place the elements, organised in an apparatus of generally 15 to 19 parts, in the mouth of the animal where it acted as a feeding structure.

Since their discovery, the usefulness of conodonts in biostratigraphic correlation has been well-tested even before any biological affinity was ever proposed. Later, conodonts have been essential to solve fundamental geological, environmental, evolutionary, and biological problems. It has become more and more evident that conodonts represent, for instance, fundamental geochemical archives tracing changes in the marine environment and climate, past geography, and biodiversity revolutions, as well as enhancing our understanding of the biology of these extinct organisms.

With this premise, a key objective of the Special Issue “Beyond biostratigraphy: Conodont matters in evolving planetary scenarios”, resulting in part from the homonymous Session held at the 5th International Conodont Symposium (ICOS 5) in Wuhan, China, in 2022, is to explore the role and significance of conodonts in modern geology. Based on the 16 selected papers, this Special Issue goes beyond biostratigraphy and explores conodont contribution to studies on biodiversity, evolution, geochemistry, paleoecology, paleogeography, and paleoclimatology.

2. Volume contents

The contributions have been arranged herein and grouped according to the above-mentioned topics.

Rueda and Albanesi compare the diversity of Floian (Lower Ordovician) conodonts from the Precordillera with that of the Cordillera Oriental, Argentina. Results and comparisons with other basins elsewhere suggest that the paleolatitudinal gradient is not a major factor controlling conodont diversity, which may be explained as resulting from a complex interaction of biological and physicochemical factors.

Valenzuela-Ríos and Liao discuss zone-by-zone changes in Lochkovian conodont biodiversity in the Pyrenees region and identify evolutionary phases within the Lochkovian. By qualitative and quantitative approaches, new indications on the conodont diversity dynamics in this region are provided. Comparative analysis of conodont records across various regions (Carnic Alps, Prague Synform, Central Nevada, and the Pyrenees) during the Lochkovian reveals significant differences in biodiversity, taxonomic composition, and zonal distribution.

Albanesi et al. analyse a large and mostly endemic conodont fauna from the Cordillera Oriental, NW Argentina. The lack of index species precludes a precise biostratigraphic assignment at a biozone level, but the overlapping ranges of selected species restrict the age range to the middle Darriwilian (Dw2, Middle Ordovician). The association indicates a shallow inner platform influenced by waves in mid-high latitudes along the Gondwanan margin. A narrow marine seaway along the suture zone connecting East and West Gondwana is proposed to explain the evolution of lineages of shallow cold-water conodont faunas from the Middle Ordovician onwards. The authors add a short *corrigendum* for this paper as a separate contribution.

Zhen et al. describe a conodont fauna of late Tremadocian to early Floian age (Early Ordovician) from South China, documenting the most primitive species of *Prioniodus*, one of the earliest conodont genera having a ramiform-pectiniform apparatus. Based on the review of nearly 200 species originally assigned to the genus, only six multielement species are confirmed, to document an evolutionary lineage starting from an adentate species. The biofacies distribution indicates that *Prioniodus* originated in deep-water slope settings and progressively spread into distal and then interior shelves. The origination of the ramiform-pectiniform apparatuses possibly reflects a major response of the conodont animals to occupy and adapt to the increasingly diversified environments in the shelf and slope settings.

Chen et al., by the study of a conodont fauna in southwestern China assigned to the uppermost Ordovician *Amorphognathus ordovicicus* conodont Biozone, document a cool-water conodont biofacies (HDS biofacies) that supports the cold tongue model proposed to explain the contradiction between the paleogeographic reconstruction of the South China paleoplate, placed at paleoequatorial latitude during the Late Ordovician, and the paleontological, sedimentological, and the $\delta^{18}O_{conodont\text{-}apatite}$ data. In addition, the distribution of *Yaoxianognathus yaoxianensis*, a distinctive species of eastern Gondwana, confirms the close biogeographic ties among South China, North China, and Tarim.

The supercontinent of Gondwana occupied a paleogeographic position at high latitudes near the South Pole during the Devonian. The arrangement of continents, tectonic activity, climatic fluctuations, and

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the evolution of marine life played an important role in marine ecosystems during this period. Despite the occurrence of conodonts in high latitudes is rare, **Viccari et al.** recovered conodonts in the Upper Devonian (Frasnian/Famennian) of western Gondwana in anoxic black shale deposits associated with the maximum flooding surface of a distal shelf from the Barreirinha Formation of the Amazon Basin, and the Jandiatuba Formation of the Solimões Basin, northern Brazil. The low diversity fauna is characterised by well-preserved elements of *Mehlina gradata*, *Ozarkodina* sp. aff. *O. sannemanni*, *Cryptotaxis* sp., and *Polygnathus* sp. in the Amazon Basin, and *Cryptotaxis* sp., *Parapolygnathus* sp., *Pandorinellina* sp., and *Hibbardella* sp. in the Solimões Basin. The faunal association and the sedimentary succession suggest a marine input under cold water conditions in the Devonian sea of the Amazon region.

Wang et al. explore the intriguing theme of conodonts across the Permian-Triassic Boundary when many species survived the end-Permian mass extinction, and some became cosmopolitan in the earliest Triassic. The authors specifically focus on the family Ellisonidae, understudied due to the difficulties of reconstructing their multi-element apparatus. Material collected in South China is discussed and assigned to diverse species of the genus *Merrillina*. Their occurrence in various settings and latitudes indicates a cosmopolitan distribution of the genus *Merrillina* in surface-water habitats.

Kolar-Jurkovšek et al. analyse Triassic conodont faunas, including conodont clusters, from deep marine settings in Bosnia and Herzegovina. The association bears mono- and bi-platform types of *Pseudofurnishius* that contribute to getting to a precise age determination of the investigated strata. The recovery of a variety of morphotypes of *Budurovignathus* suggests the great potential for phylogenetic study of this genus before its extinction.

Plotitsyn and Zhuravlev discuss a phylogenetic model of the genus *Siphonodella* using over thirty species of siphonodellids of cosmopolitan and East European groups. A new phylomorphogeny of *Siphonodella* is proposed based on known mechanisms of morphological transformations of siphonodellid P1 elements during speciation processes, the presence of interspecies transitional forms, and data on ontogeny. The phylogeny of siphonodellids provides a basis for new phylogenetic zonal sequences based on the conodont phylogenetic-zone concept.

Ferretti et al. combine the use of optical and electron microscopy (including focused ion beam scanning electron microscopy), X-ray microdiffraction, and trace element (HFSE) analysis by mass spectrometry to test the affinity of the unusual conodont genus *Pseudooneotodus* and the enigmatic phosphatic plates of the genus *Eurytholia*. Differences between these fossil groups were observed and compared with data resulting from typical conodonts recovered from the same samples.

Zhuravlev, by the analysis of a conodont collection spanning from the Upper Devonian to the Mississippian, explores the potentiality of conodont elements as a geochemical archive, providing applications and limitations of the carbon isotope investigations in conodont research. The isotopic composition of carbon of conodont elements appears to mirror the conodont diet with only minor taphonomical and histological biases. In particular, variations in $\delta^{13}C_{con}$ are related to the C-isotope composition of the phytoplankton as the main part of conodont food, and, more generally, to perturbations acting in the pelagic ecosystems. Prominent excursions of the isotopic signal can be used as stratigraphic markers.

Narkiewicz et al. apply the study of conodont biofacies at the Kačák Episode (KE) in the latest Eifelian. Comparison of the *Icriodus/Polygnathus* ratio as an indication of water depth and nearshore *vs.* offshore position with the oxygen isotope signal derived from the conodonts suggests caution when analyzing thermally altered conodonts. A conodont colour alteration index CAI 3 is proposed as a boundary value above which caution is necessary.

Girard et al. verify if the temperature-size rule (TSR: ectotherms mature at smaller adult body size in warmer conditions) may be applied to conodonts and to deep time in general. By the analysis of the size record of three conodont genera (*Palmatolepis*, *Ancyrodella*, and *Polygnathus*) in the Late Frasnian and the Famennian, related to oxygen isotope values as paleotemperature proxies, the rule was not validated as a general trend, possibly due to the interference of many other factors (demography and mortality patterns, temperature tolerance, size reduction due to stress). The only strong evidence of temperature as a possible driver of temporal variations was detected by *Palmatolepis* during the Kellwasser period, but with a reverse trend compared to the TSR model.

Assemat et al. analyse the shape diversification of conodont elements among conodont communities of the Late Famennian from the Montagne Noire Area (South France). The most robust platform P1 elements represent the most posterior dental elements of the apparatus, performing the ultimate stage of food processing before ingestion. Thus, the use of topographic indices characterizing the shape of these elements across various species of conodonts could be relevant to decipher the diversity of feeding behaviour among this group and to understand P1 element kinematics and feeding strategies among conodonts.

Malferrari et al. deal with the diagenetic imprinting on conodont bioapatite by measuring the Rare Earth Element (REE) and other High-Field-Strength Element (HFSE) in Late Ordovician conodonts from Sardinia and the Carnic Alps (Italy). The composition of euhedral crystals formed on the surface of conodont elements compared with that of crystal-free surfaces indicates a substantial contribution of diagenetic imprinting in all analysed material, although more evident on euhedral crystals that are significantly enriched in middle and, subordinately, in heavy REE compared to smooth surfaces.

Dias et al. discuss conodont variability across the different basins in the epicontinental sea located in modern-day South America during the Pennsylvanian. These basins contain a rich variety of marine (e.g., invertebrates, conodonts, foraminifers) and continental (plant pollen-spore assemblages) fossils. Recovered conodont associations provide a unique tool for biostratigraphic correlation and for identifying transgression episodes.

It took over one century, after the first discovery of conodonts in the mid-19th century, to finally assign conodonts to a precise group, namely the vertebrates. However, we are still far from having reached a global knowledge of this taxon as many fundamental arguments (e.g., ecology, trophic structure, paleobiogeography, evolution, extinction, etc.) are still waiting for an answer. There is no doubt that conodonts represent the best biostratigraphic markers, and the most used fossil group in the formal designation of chronostratigraphic boundaries in the Phanerozoic. Twenty-seven stage boundaries have been defined just with conodonts, from the uppermost Cambrian up to the Triassic/Jurassic transition, an unparalleled success compared to other taxa. Nevertheless, conodonts represent as well robust proxies for changes in paleoocean chemistry and paleoclimate for over 300 million years, and the potentiality of these microfossils as precise archives of the past has just started to be investigated. Of major interest is the use of conodonts as paleothermometers, used to resolve the thermal history of basins, likewise potentially mineralising hydrothermal events.

Our invitation to push conodont studies “beyond biostratigraphy” has resulted in this Special Issue with contributions spanning a wide and original spectrum of topics. Undoubtedly, many new perspectives will emerge in the future, giving us hope that conodont investigations, in continuous renaissance, are far from being extinct.

Our special thanks go to the organization of the 5th International Conodont Symposium (ICOS 5) in Wuhan, China, in 2022, for hosting the session in which some of these papers have been presented. Special acknowledgments are due to all Symposium participants and to the authors of the individual research papers for having accepted our invitation, for their hard work, and for their efforts in submitting their contributions. We are especially grateful to all the scientists who have reviewed the papers in this volume for their time and expertise.

Finally, just while completing the last steps of this long project, we were informed by the sudden passing of Prof. Enrico Serpagli, a pioneer in conodont studies, a starting point for many of us, and a true *Maestro* in science and life. “The end is where we start from” (T.S. Eliot, Little Gidding, 1942).

This volume is dedicated to the memory of Enrico Serpagli.

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